Introduction to the issues impacting mangroves in the Costa Alegre of Mexico

The coastal wetlands of Mexico comprise a major part (1,567,300 ha) of the terrestrial-water interface of Mexico. Exhibiting a broad range of primary and secondary production depending on the type of wetland and its hydrologic characteristics, coastal wetlands can be rich in biological diversity compared with other ecosystems. Mangrove ecosystems, in particular, are known to be important rearing grounds for marine fishes and provide important habitat for migratory and endemic birds species, reptiles, and small mammals. On the Costa Alegre of the Mexican Pacific, mangroves are the dominant coastal wetland and are home to the largest populations of American crocodiles in Mexico. Our previous investigations of the red and white dominated ecosystems in Tanacatita bay demonstrate these mangroves are important habitat for these species as evidenced by our bird and crocodile counts determined from past research.

Similar to other mangrove ecosystems worldwide, anthropogenic influences that are either direct (i.e habitat modification) or indirect (i.e. changes to hydrological exchange, climate change) are altering the biology and function of these ecosystems. During the last few years, the Great Basin Institute and colleagues have collected critical information that described the unique aspects (ie. biological composition) and the disturbances (i.e habitat encroachment and human use) to one of the mangroves in the bay, La Manzanilla. La Manzanilla, is proximate to the city and structurally different than the second mangrove, Tenacatita which has permanent surface water connections between the mangrove and the ocean. In the past year, the city of La Manzanilla has initiated a program that would input wastewater discharge into La Manzanilla mangrove. Wastewater contains higher concentrations of nutrients (nitrogen and phosphorus) which can alter ecosystem structure and species composition particular in systems that do not flush regularly like La Manzanilla mangrove. Development around Tenacatita mangrove however is less compared with La Manzanilla with only recent encroachment in this area due to increased tourism. Overall, we believe the anthroprogenic influences although significant are still in the early stages of impacts. Thus, this a critical period for 1) determining baseline conditions prior to major alterations and 2) predicting ecosystem alterations and developing a natural resource management plan for the lower watershed.

Objectives of our program

With the assistance of students from the Universities of South Florida and Nevada-Reno we hope to characterize basic ecological interactions within each mangrove. Furthermore, the goal is to determine the potential impact from the rapid development in the area on the mangrove and provide the local community with information they need to develop a more sustainable resource management plan for this area. Thus, the objectives are to determine the ecosystem dynamics (physical, chemical, and biological) that result in the ecological production in the mangrove. We will also focus on understanding the cultural importance of the mangroves to determine conservation approaches need to interface protection of these mangroves with local beliefs. Specifically, the goals over a three year period are to

- Characterize the cultural importance of the mangrove to the local community and the perception of how wastewater treatment additions will influence the mangrove ecosystems,
- Quantify the hydrologic and chemical linkages for each mangrove,
- Measure historical changes in the mangrove distribution and
- Evaluate mangrove plant structure and identify contemporary vegetative composition and below ground soil and nutrient dynamics,
- Quantify the primary (aquatic and terrestrial plants) and secondary (aquatic invertebrate) production as they may pertain to fisheries and crocodile production,
- Determine fish composition and ecological characteristics (population growth rates, condition factors, etc) for species in each mangrove
- Determine ecological relationships for each species by determining the food web structure for each mangrove as they pertain to fisheries and crocodiles, and
- Determine a preliminary assessment if crocodiles are sedentary and isolated populations

These objectives will allow for a broader understanding of the function and importance of these mangroves to broader environment as well as the local community. An interface of science used to improve public understanding of these mangroves will be critical to the overall success of the conservation focus of this project.

Module information for students

The following chapters describe the rationale and methods utilized in this conservation project. This is a grass, roots project and these packets were created by students in the previous year to lay the foundation for future research in this area. Please note that some of the modules are better developed than others. The instructors' hope is that each module is refined and developed as information for each section is generated over time. Please feel free to provide constructive, written comments to further develop this material. While the crocodile and bird module will be developed on the Jan 08 trip, this packet contains information on the following modules
- Hydrology
- Water Quality
- Vegetation
- Fisheries
- Birding

Additionally, there are a few select papers that provide background on previous research in mangroves. These papers are not exhaustive of the mangrove literature and we encourage you over Winter break to read papers related to mangrove ecosystems.

HYDROLOGY MODULE

ABSTRACT

Our objectives are (a) to provide physical and chemical hydrological information to facilitate an understanding of the controls on ecosystem structure and function, particularly species composition and primary productivity and (b) to develop a numerical model of surface water and groundwater flow to better understand current conditions and to generate hypotheses regarding potential future conditions under a variety of potential land-use and climate-change scenarios. To do so, we must first quantify the water sources and hydrodynamics using natural geochemical tracers and physical measurements of surface water and groundwater levels. Participants in this module will install and maintain equipment, collect and process surface water and groundwater samples, and collect surface water and groundwater level data in selected locations in the basin, the mangrove, and near-shore marine environment.

BACKGROUND AND LITERATURE REVIEW

General Overview

In recent years, there has been a dramatic rise in tourism along Mexico's central pacific coast, the Costa Alegre. As a result, many small communities along this coastline have begun to experience the ecological and economic impacts that accompany "being discovered" by the international tourism industry. One such community, La Manzanilla, is a small fishing community in the state of Jalisco. La Manzanilla, along with other communities on the Tenacatita Bay, is experiencing rapid conversion from an agricultural based economy to an economy based on commerce, real estate, tourism, and the service industry. The development accompanying this economic conversion has increased the pressures on the natural resources of the area, both marine and terrestrial. Terrestrial and aquatic species, including the American Crocodile (*Crocodylus acutus*) and the Boat-Billed Heron (*Cochlearius cochlearius*), are being affected by habitat encroachment and the biology of the local mangrove ecosystem is being altered by these anthropogenic changes.

Mangroves are the dominant coastal wetland on the Costa Alegre and are home to the largest populations of American Crocodiles in Mexico. Mangrove ecosystems are an intertidal plant community dominated by salt and flood tolerant trees and shrubs. They are widely valued for their ecological uniqueness and linkages to estuarine food webs in subtropical and tropical coastal regions (Twilley and Chen, 1998; Primavera, 1998); providing important rearing grounds for marine fishes and habitat for migratory and endemic bird species, reptiles, and small mammals. The mangroves and the habitat provided by the mangroves at La Manzanilla are being degraded by the direct (i.e., habitat modification) and indirect (i.e., altered hydrology, climate change) impacts of development.

Previously, information was collected that described the unique aspects (i.e., biological composition) and the disturbances (i.e., habitat encroachment and human use) to the mangroves at La Manzanilla and efforts were started to raise the awareness of the local community and tourists to the ecological and economic importance of the mangroves. Although the anthropogenic influences on the La Manzanilla mangroves are significant, the impacts are still in the early stages. Thus, this is a critical period for determining baseline conditions prior to

major alterations, predicting ecosystem alterations, and developing a natural resource management plan for the lower watershed.

In order to obtain a more thorough and accurate understanding of the ecological conditions and processes occurring in the mangrove ecosystems at La Manzanilla, five research modules have been developed for further study; hydrology, vegetation, water quality, fisheries, and GIS. From the data generated through studying these modules, more objective and concise information will be given to the local community and community leaders about the major threats to the biodiversity of the mangroves and the impact on the quality of life of residents in La Manzanilla. This data may also be used to help develop strategies for the sustainable and responsible use of the natural resources of the area.

Mangrove Hydrology

The flux of water into and out of mangroves controls the physical and chemical hydrological characteristics of mangroves and facilitates the exchange of mass, energy, and organisms between mangroves and the surrounding hydrological landscape (Twilley and Chen, 1998). Water sources can vary, with the relative contributions of direct precipitation, surface water runoff, groundwater discharge, and seawater intrusions varying depending on climate, geology, and the proximity to the coast (Drexler and De Carlo, 2002; Barlow, 2004).

Seawater intrusion may occur even in the absence of surface intrusions (Figure 1). Seawater piles up on shore faces due to high tides, waves, and wind. When it does so, seawater can be driven into the shore face and ultimately into the surface water and/or groundwater of coastal ecosystems (Cable et al., 1996; Barlow, 2004).
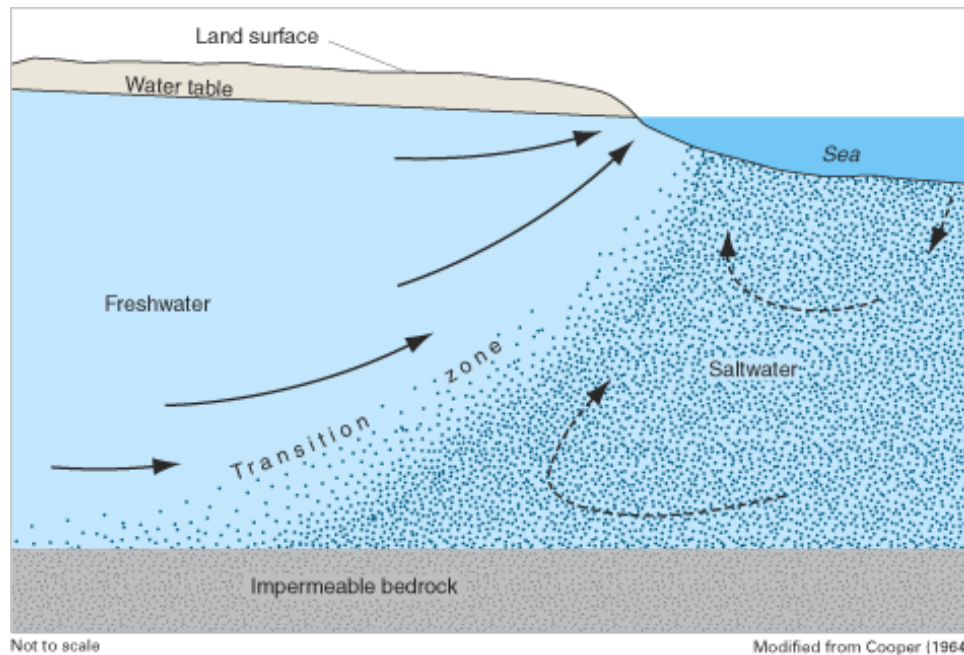

Figure 1. Mixing of seawater and groundwater due to tidal-, wave-, and/or wind-forced pumping (Barlow, 2004).

Water sources may vary in importance both intra- and inter-annually. Groundwater discharge can be slow but steady, while direct precipitation, surface water runoff, and seawater

intrusion can be either slow and steady or fast and episodic. The tropical and subtropical regions in which mangroves occur typically experience wet and dry seasons, so precipitation, surface water runoff, and groundwater typically are seasonal (Twilley and Chen, 1998). Seawater intrusion may also be seasonal, though driven instead by tidal cycles and storm surges (Barlow, 2004).

The salinity and specific solute concentrations vary as functions of water sources. The salinity of direct precipitation is typically ~0.01 ppt; the salinity of surface water runoff and groundwater discharge typically range from ~0.1-0.6 ppt; and the salinity of seawater is ~32 ppt. Therefore, the degree of seawater intrusion strongly controls the salinity of surface water and groundwater. Direct precipitation has almost no solutes, surface water runoff and groundwater discharge are enriched in solutes commonly found in soils and rocks such as silica and nitrate, and seawater is enriched in all common solutes that are not typically used by marine biota. Therefore, the relative contributions of the various water sources strongly control the specific solute concentrations. However, water evaporates while solutes remain in solution, so salinity and specific solute concentrations also may be strongly controlled by the rate at which water flows through the mangrove and the rate at which water evaporates while in the mangrove.

Classification of Mangrove Ecosystems

Mangroves can be grouped into functional types based on landscape position, water source, and hydrodynamics (Lugo and Snedaker, 1974; Clintròn et al., 1985; Woodroffe, 1992; Dawes, 1998). Depending upon these conditions, mangroves are either river dominated, tide dominated, or interior, though these conditions are continuous rather than discreet so mixed mangroves also are possible (Figure 2).
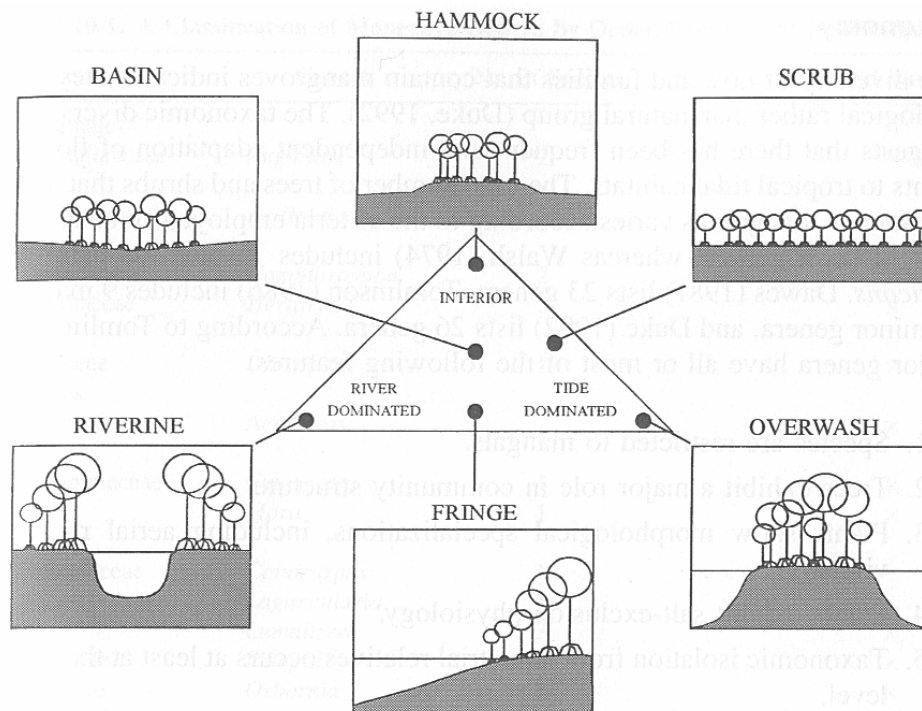

Figure 2. Mangrove classification diagram (Dawes, 1998).

River-dominated mangroves are located along rivers. River-dominated mangroves are dominated by freshwater inflows from direct precipitation, surface water runoff, and groundwater discharge, though seawater inflows do occur and maintain salinities that favor the establishment and maintenance of mangrove species. Tide-dominated mangroves are located on shorelines and small islands partially or completely submerged at high tides. Tide-dominated mangroves are dominated by tidal inundations, and may have little to no freshwater inflows due to precipitation, surface water runoff, or groundwater discharge. Interior mangroves are located in basins, the shoreward extent of which may be delineated by a beach ridge. Interior mangroves can be dominated by any one or combination of the water sources. In all mangroves, water levels and fluxes are at least in part controlled by tidal variations which can be propagated throughout he surface water and groundwater flow systems (Ataie-Ashtiani et al., 2001). The La Manzanilla mangrove is likely an interior mangrove.

Objectives

Our objectives are (a) to provide physical and chemical hydrological information to facilitate an understanding of the controls on ecosystem structure and function, particularly species composition and primary productivity and (b) to develop a numerical model of surface water and groundwater flow to better understand current conditions and to generate hypotheses regarding potential future conditions under a variety of potential land-use and climate-change scenarios. Developing a numerical model begins with an overview of the environment. The climate and geology, as well and the land use, that control water inflow and outflow must first be characterized. Then, the water sources and hydrodynamics must be carefully quantified to provide data that can be used for both the calibration and validation of the numerical model.

We will quantify the water sources primarily through the use of natural geochemical tracers. Salinity, specific solute concentrations, and isotopic compositions can be used to determine the source and evolution of surface water and groundwater in mangroves. To do so, water samples from the mangrove and from each of the possible end-members (i.e., direct precipitation, surface water runoff, groundwater discharge, and seawater) must be collected and analyzed for solute concentrations and isotopic compositions.

Some solutes are excellent naturally-occurring tracers that can be used to infer the relative contribution of the various end-members. For example, silica concentrations are typically high in surface water runoff and groundwater discharge because there is a great deal of silica in soils and rocks, but are typically low in seawater because silica is rapidly uptaken by organisms such as diatoms that use silica to make their exoskeletons. Similarly, chloride is typically low in surface water runoff and groundwater discharge because there is little chloride in most soils and rocks, but are typically high in seawater because it does not readily precipitate out of solution and it has therefore evapoconcentrated in the oceans over the course of geological time. Therefore, silica and chloride, as well as other solutes, can be used to infer the relative contributions of the various water sources to the surface water and groundwater in a given mangrove (Drexler and De Carlo, 2002).

We will quantify the hydrodynamics by making physical measurements of surface water and groundwater levels at selected locations throughout the watershed, the mangrove, and the ocean. Surface water levels will be measured at stage gages, and groundwater levels will be measured in water supply wells located throughout the basin and in piezometers located in the

mangrove. We will make instantaneous measurements while in the field, but we will rely more so on continuous measurements that will be logged by instruments deployed in our absence.

This information will then be used to facilitate an understanding of the controls on ecosystem structure and function and to develop a numerical model of surface water and groundwater flow. The former is critical to the understanding of current conditions; the latter is critical to the understanding of potential future conditions. Substantial changes in water sources and hydrodynamics may be reflected in substantial changes in ecosystem structure and function. Anthropogenic impacts already appear to have altered water sources and hydrodynamics. Groundwater pumping in surrounding aquifers can reduce freshwater inflows to aquatic ecosystems (Barlow, 2004; Rains et al., 2004), and wastewater discharges can substantially alter both the quantity and quality of the water in aquatic ecosystems (Barlow, 2004). In La Manzanilla, resident and transient populations have increased in recent years, so groundwater pumping and wastewater discharges also have increased in recent years. However, the degree of alteration and the ecological consequences to the La Manzanilla mangrove remain unclear. The connection between current and potential future conditions, the physical and chemical hydrology, and the associated ecological structure and function is at the heart of this research effort.

Suggested Additional Reading

Additional information can be found by reading Barlow (2004), Drexler and De Carlo (2002), and Twilley and Chen (1998). All are attached to this document in Appendix C.

METHODS

One-Time Activities

Rain Gage

A rain gage is on site and ready to be installed at the La Manzanilla Water Master's residence. The installation should be self-explanatory. However, care must be taken to ensure that the rain gage is installed in a location where rainfall will not be intercepted or otherwise influenced by vegetation and/or structures.

Stage Gages

The stage gages are partially assembled with the stage plates attached to the wood stage-plate supports, holes pre-drilled in the wood stage-plate supports so the wood stage-plate supports can be u-bolted to the standpipes. There also are eye-bolts attached on the front where the water level loggers will be attached. There are two sets of stage gages. They should be installed in locations that are easy to access, but also are somewhat hidden to discourage theft and/or vandalism. The two locations should be in the vicinity of T1B and T2B. Most importantly, the stage gages should be installed where water is to be expected. Two stage gages can be installed at each location to account for high and low water levels (Figure 3). A 0-3 m gage should be installed at the low level, and a 3-6m gage should be installed at the high level.

- Pound steel pipe in using hammer until secure in ground.
- Leave just enough pipe above ground to u-bolt wood stage-plate support.
- U-bolt wood stage-plate support to pipe.
- Repeat with second gage, trying to align the top of the lower stage gage to the bottom of the upper stage gage.
- Attach an S-hook to a water level logger, then attach the water level logger to an eye-bolt on the stage gage. Attach the water level logger to the eye-bolt that will ensure that the water level logger will remain under water until the next sample period but will not be too deep to retrieve during the next sample period.
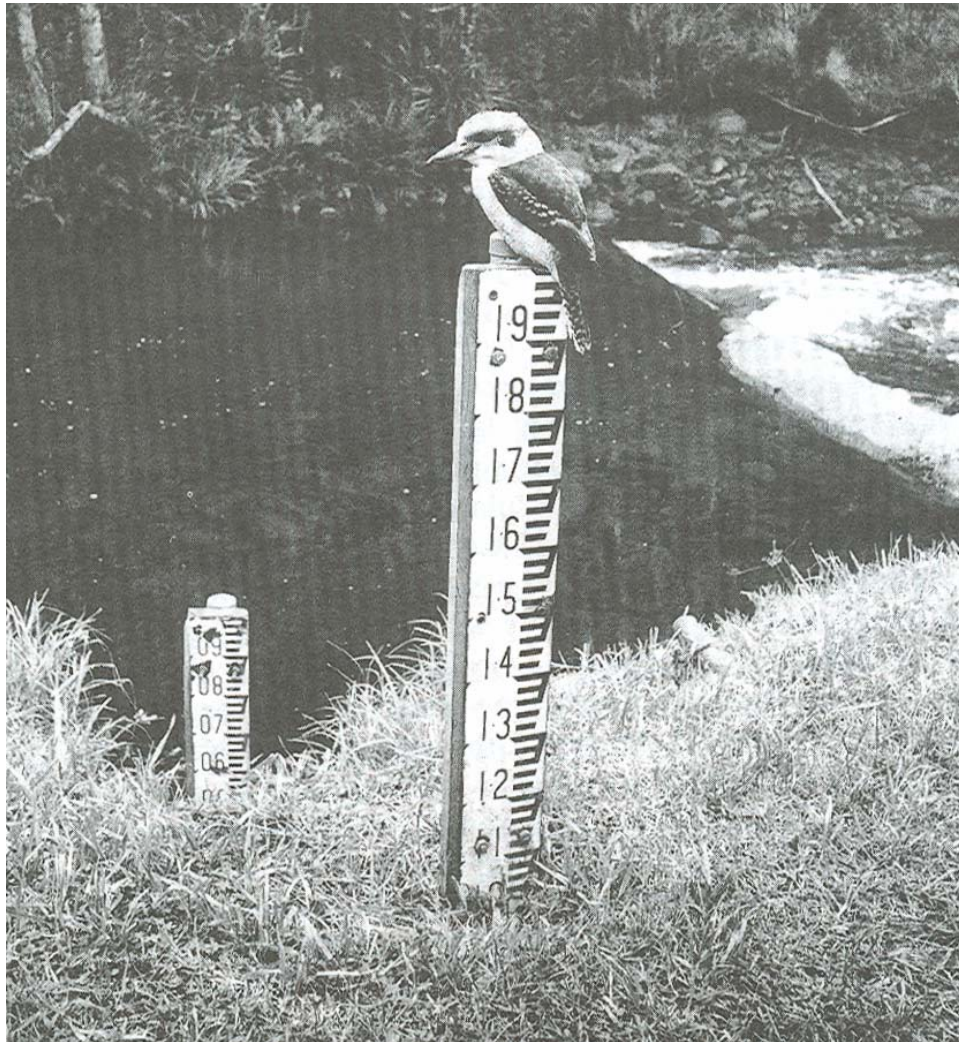- Take GPS coordinates if possible and give detailed instructions on getting to the site.

Figure 3. Series of stage gages for measuring water level over a range of elevations (Gordon et al. 1992).

Piezometers

Two piezometers have been fully assembled. Four more piezometers should be assembled from the materials either available on site or purchased from local vendors.

- Attach endcaps to screens with glue.
- Attach screens to standpipes with couplings and glue.
- Drill one small hole near top of each standpipe to allow ventilation. This is essential, because the otherwise the air above the water will be under positive pressures when the water rises and negative pressures when the water falls. In both cases, the water levels will not be the same as in the surrounding formation.
- Attach a cap to the top of each standpipe. The cap should be loose and not glued because it will need to be removed when readings are taken and samples are collected.
- Measure the total inside length of each piezometer.
- Measure a length of nylon string that will allow a water level logger to hang inside the piezometer approximately 5 cm from the bottom with extra length to be used to attach the water level logger to the top of the piezometer as explained, below.
- Attach the nylon string to the water level logger and feed the top end of the nylon string through the ventilation hole at the top of the piezometer.
- Attach the top end of the nylon string to a metal washer. The metal washer must be larger than the ventilation hole. Alternatively, a loop could be tied in the top end of the nylon string and the loop could be passed over the top of the piezometer. Either way, the total length of the nylon string in the piezometer cannot change each time the water level logger is retrieved or the data cannot be used.

The 6 piezometers will be installed in 6 locations: T1A, T1C, T1D, T2A, T2C, and T3A (Appendix A). UTM coordinates for the entry points to these locations are provided on the data sheets (Appendix B). From these entry points, blue flagging leads into the mangroves and blue and pink flagging together mark the piezometer installation locations. Piezometer should be installed as described below and in Figure 4.

- Using the auger, auger a hole down to approximately 1.5 m or until you get as far below the water table as possible, whichever is less. Be careful not to allow hole to collapse in on itself. (The hole will collapse soon after you go below the water table.)
- Insert piezometer into the hole with the screen side down.
- Make sure that the piezometer is perfectly vertical.
- Fill hole with coarse beach sand up to a level above the top of the screen. As you're pouring the sand in, use a stick to poke at the sand to pack it tightly around the screen.
- Backfill the rest of the hole with material excavated from the hole with the auger.
- Make a solid and unmistakable mark on one side of the lip of the piezometer with a Sharpie pen. This will be the mark from which all water level measurements will be made.
- The piezometer should stick up out of the hole but be sturdy. Make sure it is capped, but not too firmly.

Continued Monitoring

All continued monitoring should be completed using the data sheets (Appendix B). Not all fields will be filled during all visits. The frequency of sampling is included as part of the descriptions, below.
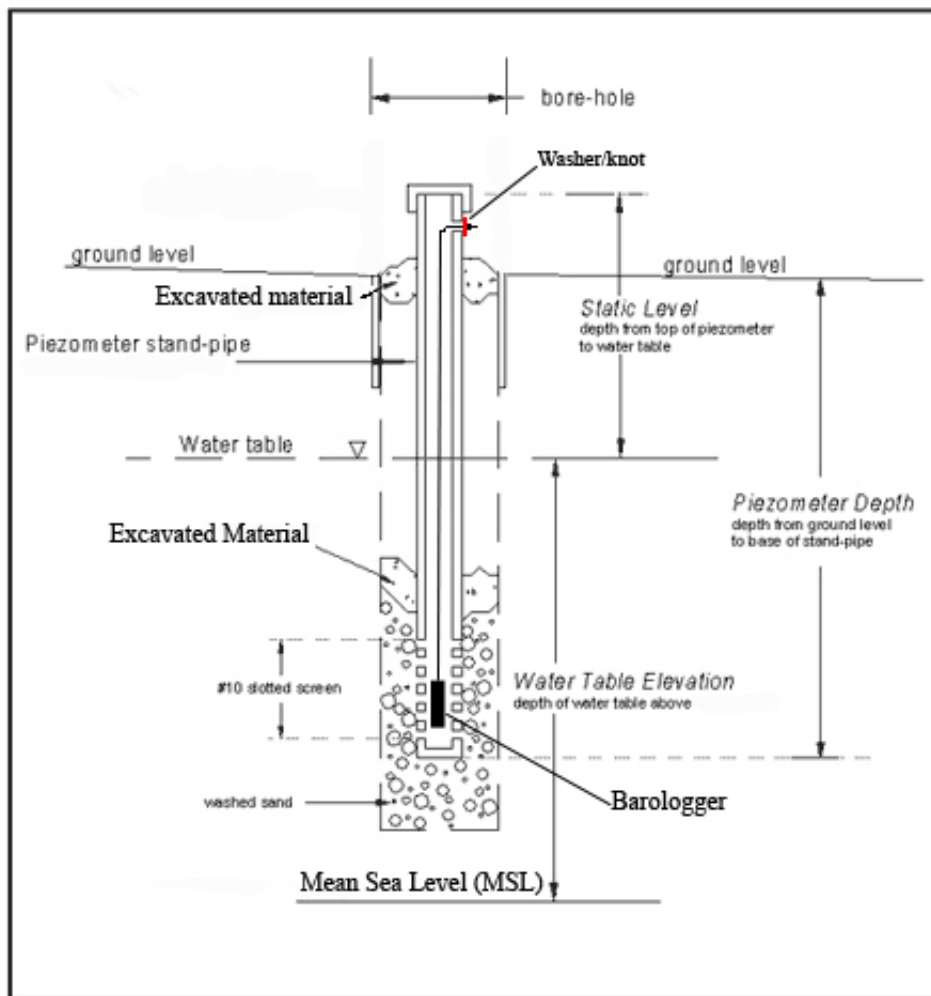
Figure 4. Diagram of properly installed piezometer.

Rain Gage

The rain gage should be measured once during each field visit if possible. The rain gage will be installed at the La Manzanilla Water Master's residence. The Water Master will be making regular measurements, so you may simply need to totalize and record the data he has recorded. However, you might also need to make the measurements yourself. In this case, you must do the following.

- Read the rainfall in mm on inner tube. This number really is in mm even though it looks like it is in cm, because the catchment funnel is 10x larger than the inner tube and 10x 1 mm is 1 cm.
- Record the rainfall.
- Carefully pull off the catchment funnel and remove inner measuring tube.
- Dump out this water, unless you are also collecting a sample for geochemical analyses. (See below.)
- Replace inner tube and catchment funnel.

8

If more than 25.4 mm of rain has fallen since the last measurement, then the additional rainfall will spill out of the inner tube and into the outer cylinder. In this case, you must do the following.

- Read, record, and discard or sample the rainfall as above.
- Refill the inner tube with water from the outer cylinder.
- Repeat until all of the rainfall has been read, recorded, and discarded or sampled.

Stage Gages

The stage gages should be monitored at least once during each field visit if possible. The stage gages will be monitored continuously with water level loggers, but the instantaneous measurements are necessary to ensure that the water level loggers are accurately measuring water levels and are properly calibrated to the datum. The stage gages are installed in two locations: T1B and T2B (Appendix A). UTM coordinates for the stage gages are provided on the data sheets (Appendix B).

- Once near stage gage, find water level on stage gage. You may do this with binoculars if the stage gage is visible from a distance.
- Record water level on data sheet.
- Remove the water level logger from the stage gage and download the data to a laptop. (See below for downloading directions.)
- When replacing the water level logger, be sure to hang it from one of the eye-bolts that is slightly below the water level now and is likely to remain at least slightly below the water level up until the next field visit. This will ensure that data are continuously collected and that subsequent field monitoring personnel do not need to reach excessively deep into the water.

Piezometers

The piezometers should be monitored at least once during each field visit if possible. The piezometers will be monitored continuously with water level loggers, but the instantaneous measurements are necessary to ensure that the water level loggers are accurately measuring water levels and are properly calibrated to the datum. The piezometers are installed in 6 locations: T1A, T1C, T1D, T2A, T2C, and T3A (Appendix A). UTM coordinates for the entry points to these locations are provided on the data sheets (Appendix B). From these entry points, blue flagging leads into the mangroves and blue and pink flagging together mark the piezometer installation locations.

- Turn on the water level sounder.
- Use the test button to test the volume of the water level sounder. (The water level sounder beeps when the tip comes into contact with water. Make sure that it is loud enough to hear.)
- Remove the top cap.
- Slowly reel end of water lever sounder down into the well until it beeps.

- The depth to the water level is recorded at the solid and unmistakable mark on one side of the lip of the piezometer that has been made with a Sharpie pen.
- Record the depth to water level.
- Remove the water level logger from the piezometer and download the data to a laptop. (See below for downloading directions.)
- Replace the water level logger in the piezometer, making sure that the length of the line down the piezometer is exactly as it was before.
- Replace the top cap.
- At site T3A, also remove the barometric pressure logger from where it hangs on the props roots of the red mangrove and download the data to a laptop. (See below for downloading directions.)

Geochemical Sampling

Full geochemical sampling for laboratory analyses will be conducted by one of the PIs twice annually, once in the wet season and once in the dry season. However, basic field geochemical sampling, i.e., temperature, conductivity, salinity, and pH, should conducted during each field visit if possible. There are 30 permanent sampling locations. UTM coordinates for the entry points to these locations are provided on the data sheets (Appendix B). From these entry points, blue flagging leads into the mangroves and blue and pink flagging together mark the piezometer installation locations. Additional sampling locations should be added opportunistically. For example, basic field geochemical sampling should e conducted when surface water is flowing in streams.

- If sampling surface water, then collect some sample into a wide-mouthed bottle or bucket.
- If sampling deep surface water at sites T1B and T2B with the peristaltic pump, then lower one end of the sample tubing to the desired depth in the water column. If sampling groundwater, then lower one end of the sample tubing into the piezometer until it is near but not touching the bottom of the piezometer. In either case, proceed as described below.
- Attach the alligator clips on the pump to the small gel-cell battery. (The battery should be charged periodically!)
- One end of the tubing on the peristaltic pump sucks, the other end of the tubing on the peristaltic pump pushes. Turn on the pump and put your finger over each end of tubing on the peristaltic pump to figure out which end sucks and which end pushes.
- Attach the upper end of sample tubing to the end of the tubing on the peristaltic pump that sucks.
- Turn on the peristaltic pump. The pumping rate can be adjusted with the dial. A low to moderate flow rate should suffice.
- Collect the sample into a wide-mouth bottle or bucket.
- Use the provided meters to measure temperature, conductivity, salinity, and pH. (The meters should be calibrated periodically!)
- Record data on data sheet. (Note the units!)
- If collecting a sample at an additional sampling location, then measure and record the GPS coordinates. (Make sure you note the coordinate system!)

Downloading Data from the Water Level and Barometric Pressure Loggers

The water level and barometric pressure loggers can be downloaded in the field or at the beach camp. If they are downloaded at the beach camp, then it is absolutely essential that you note the serial number on the housing to make sure they can be returned to the same locations from which they were taken.

- Connect the USB Cable/Shuttle (Figure 5) to the laptop.
- Remove the plastic cap from the loggers to expose the optical connections. If the loggers are downloaded at the beach camp, then leave the plastic caps connected to the nylon strings in the piezometers so they will hang at the same depth when they are returned. This is less important for the other loggers because the lengths of the S-hooks on the water level loggers at the stage gages will not change and the precise level at which the barometric pressure logger hangs is irrelevant except inasmuch as it must remain above water.
- Place the logger with the connections facing downwards into the receptor on the USB Cable/Shuttle. Spin until the fit is loose but secure.
- On the laptop, launch Solinst Levelogger 3.0 software by clicking on Start > Programs > Solinst > Levelogger > Levelogger 3.0.
- In the "Levelogger Settings" Tab, click on the option "Retrieve Settings From Levelogger."
- At this point the software should connect to the logger. If this does not happen, and instead you get an error message, then there are a few things to troubleshoot. Try to (a) re-seat the logger in the receptor on the USB Cable/Shuttle or (b) re-set your Com port. If it the latter, then first try Com port 4 (COM4), which is listed at the top center of the software window, and then continue to cycle though all other com port options. Eventually, the software should connect to the logger.
- Go to the "Data Control" Tab, click on the downward arrow says "Download Data from Levelogger", and click "All Data."
- The software will then download and graph the data. Save the data by clicking the "Save as" button at the top left corner of the software window.
- For a naming scheme, use the location name followed by the date. For example, "T1A_05-20-07.xls"
- Export the data by clicking on the button next to the "Save as" button called "Export Data." Choose to export the data as an Excel file.
- Close the program, disconnect the equipment, and replace the logger.

INTERDISCIPLINARY INTERSECTIONS

Hydrological processes directly or indirectly control the structure and function of mangroves systems. Water level and salinity play roles in seedling survivorship (Cardona-Olarte et al., 2006), primary productivity (Yates et al., 2002; Arreola-Lizárraga et al., 2004; Suarez and Medina, 2005, 2006), and nutrient concentrations and related nutrient limitations (Boyer 2006). Furthermore, ongoing studies indicate that spatial variations in porewater salinities correlate with

spatial variations in species composition, primary productivity, nutrient cycling, and microbial composition in south Florida.
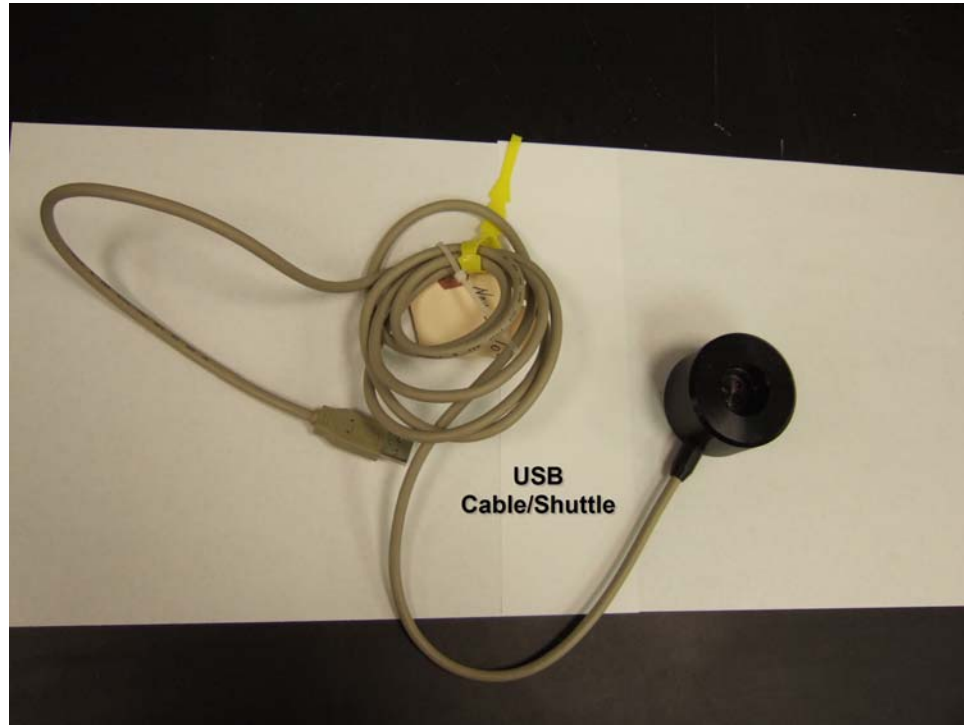

Figure 5. USB Cable/Shuttle.

Conversely, some mangrove plant species may exert some control over local porewater salinities. Red, black, and white mangroves exclude salts at the root zone, and black and white mangrove extrude salts from specialized glands (Dawes 1998). These salts may accumulate locally and in some cases may maintain porewater salinities that are higher than seawater salinities. As porewater salinities increase, the species responsible for the salt accumulations ultimately may be out competed by more salt-tolerant species.

Hydrological controls are particularly important for plants, because plants are sessile and therefore unable to move around the landscape except as free-floating propagules prior to rooting. Therefore, the linkages between physical and chemical hydrology and species composition and primary productivity are particularly important. It is for this reason that the hydrology and vegetation modules share monitoring stations. Primary productivity, in turn, is the basic building block of food webs which play a role in controlling invertebrate and vertebrate species distributions.

The mangrove is hydrologically connected to the larger surrounding hydrological landscape. Surface water flows into and out of the mangrove during the wet season, and groundwater may flow into and out of the mangrove throughout the year. However, groundwater pumping increases in the dry season when aquifer levels are likely at their lowest to support transient residents and tourists in La Manzanilla and at the Hotel Tamarindo. Increased groundwater pumping almost certainly reduces groundwater discharge from the aquifer to the mangrove, at least during the dry season. Therefore, mangrove hydrology, and the associated structure and function of the mangrove, are integrally linked to water use throughout the basin.

Increased groundwater pumping may also reverse flows and cause groundwater recharge from the mangrove to the aquifer during the dry season. There is some evidence of saltwater intrusion into the aquifer, with dry-season salinities of the wells closest to the mangrove ~2 ppt and dry-season salinities of the other wells and mountain springs ~0.5 ppt. Our work, though focused on the mangrove, may also benefit the local communities by helping them understand the safe yield of the aquifer and the potential consequences of exceeding the safe yield of the aquifer.

APPLICATIONS AND ANALYSIS

The hydrology module will proceed in three stages. In the first stage, the wet- and dry-season sources and hydrodynamics of the surface water and groundwater in the mangrove will be quantified. In the second stage, linkages between the physical and chemical hydrology and the species composition and primary productivity, water quality and food web dynamics, and fisheries will be explored. In the third and final stage, a numerical model will be developed and used to generate hypotheses about the likely physical and chemical hydrological consequences of various water use and climate change scenarios. Results will be used to inform the community of the potential impacts of excessive and unregulated water use to the integrity of both the mangrove and the aquifer on which the community relies.

INSTRUMENTATION

Materials List

Rain Gage Installation
- rain gage in box (all parts should be in box)
- drill and drill bits
- screwdriver

Stage Gage Installation
- stage gages (4) with wood stage-plate support attached
- steel pipe (4)
- u-rings (8)
- hammer or post driver (to hammer in standpipe)
- wrenches
- water level loggers (2)
- S-hooks (2)
- GPS unit

Piezometer Installation
- piezometers, including caps (6)
- auger
- tape measure
- beach sand (bucketful or so for each site)
- sticks (to pack sand)
- water level loggers (6)

- nylon string
- metal washer (6)
- GPS unit

Rain Gage Monitoring
- data sheets

Stage Gage Monitoring
- data sheets
- binoculars
- laptop
- USB Cable/Shuttle
- Solinst Levelogger 3.0 software

Piezometer Monitoring
- data sheets
- water level sounder
- laptop
- USB Cable/Shuttle
- Solinst Levelogger 3.0 software

Geochemical Sampling
- data sheets
- wide-mouthed bottle or bucket
- sample tubing
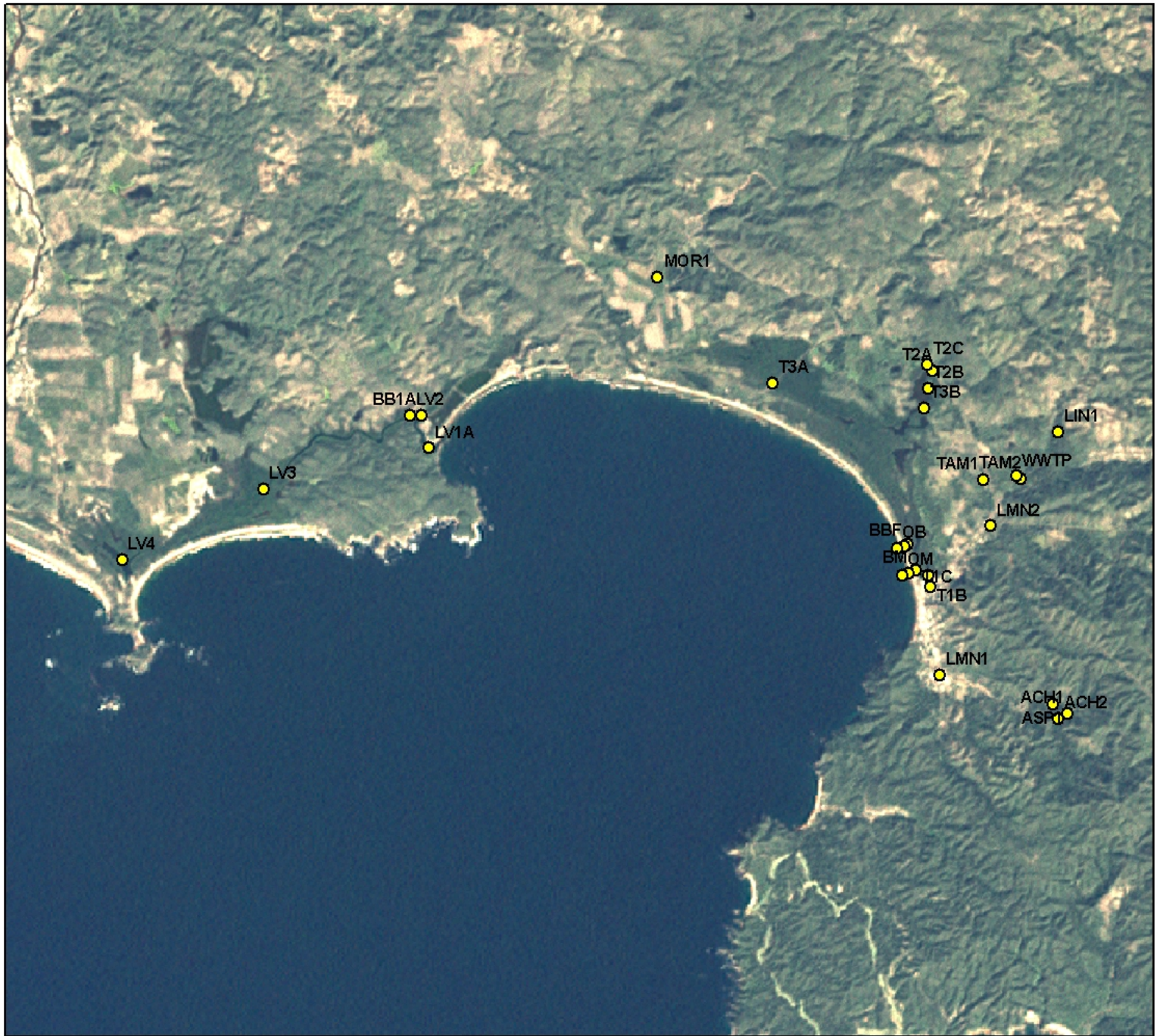- peristaltic pump
- battery
- field geochemistry meters

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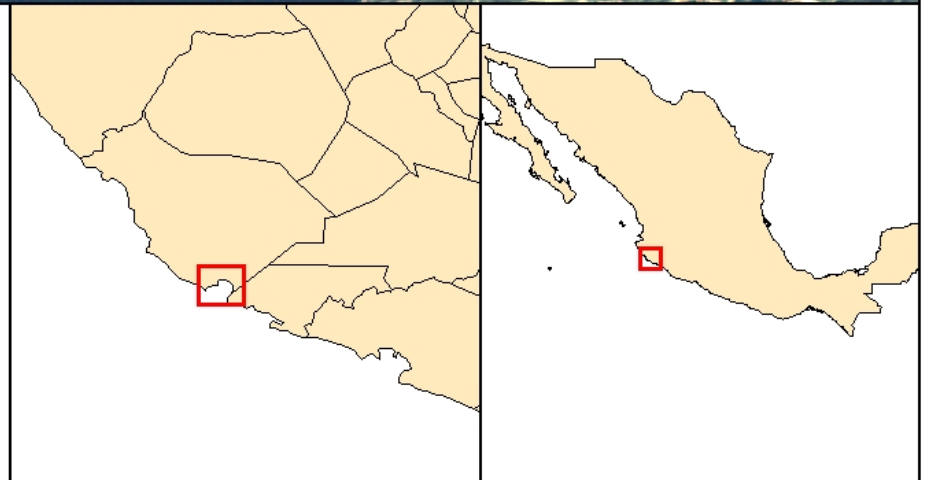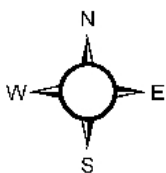
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APPENDIX A

Sample Locations January 2007

MOR1

T2A T2C
T2B
T3B

T3A

LIN1

BB1A LV2
LV1A

TAM1 TAM2 WWTP

LV3

LMN2

LV4

BBF QB
BMOM
DIC
T1B

LMN1

ACH1 ACH2
ASP1

0   1,000   2,000   4,000 Meters

N
W   E
S

Sample Locations January 2007

T3A

T2C
T2A

T2B

T3B

LIN1

WWTP
TAM1
TAM2

LMN2

OB T1D
BBW BBF

T1C
OM T1A
BM

T1B

LMN1

ASP1

0   250   500   1,000 Meters

N
W   E
S
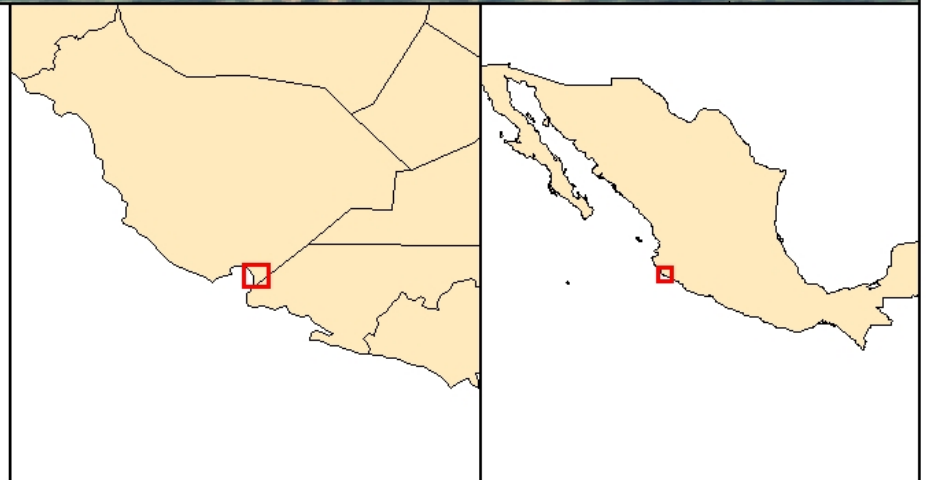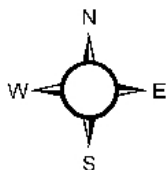
APPENDIX B

Physical Hydrology - Instantaneous Measurments

Team_____   Date_____

e-mail_____

Rain Gauge

Rain Total (mm)

Stage Gauge

Location	Time	Height (m)	Height of Stage Gauge above MSL (m)	Elevation (m) *
T1B				
T2B				

* Elevation = Height + Height of Stage Gauge above MSL

MSL = Mean Sea Level

Piezometers

Location	Time	Depth to Surface water (m) *	Depth to Groundwater (m) *	Height to top of well from MSL (m)	Elevation of Surface water**	Elevation of Groundwater ***
T1A						
T1C						
T1D						
T2A						
T2C						
T3A						
BB						

* These two are measured from the top of the well casing to the depth of either the surface water or groundwater

** Elevation of Surface water = Height to top of well - Depth to Surface water

*** Elevation of Groundwater = Height to top of well - Depth to Groundwater

MSL = Mean Sea Level

Physical Hydrology - Continuous Measurements

Team_____   Date_____

e-mail_____

Stage Gauge Barologgers

Location	Time	Filename	Depth to Barologger *	Notes **
T1B				
T2B				

* Depth to Barologger from where it is anchored

Submerged Barologgers

Location	Time	Filename	Depth to Barologger *	Notes **
T1A				
T1C				
T1D				
T2A				
T2C				
T3A				
BB				

* Depth to Barologger from the top of the casing

Open Air Barologger

Location	Time	Filename	Notes **
T3A			

Temperature Loggers (Tidbit)

Location	Time	Filename	Depth to Logger *	Notes **
SW-1				

* Depth to Temperature Logger from where it is anchored if applicable

** Any useful site specific information, i.e. problems downloading data, changes to logger location, etc.

Hydrology Module Data Sheet.xls

Chemical Hydrology

Team_____   Date_____

e-mail_____

Location	Time	pH	Conductivity (µS/cm)	Temperature (°C)	Salinity (ppt)	Notes
Rainfall						
T1AS						
T1AG						
T1BS						
T1BD						
T1CS						
T1CG						
T1DS						
T1DG						
T2AS						
T2AG						
T2BS						
T2BD						
T2CS						
T2CG						
T3AS						
T3AG						
T3BS						
T3BD						
BBW						
BBF						
BM						
OM						
OB						
LMN1						
LMN2						

Hydrology Module Data Sheet.xls

TAM1						
TAM2						
MOR1						
ASP1						

Hydrology Module Data Sheet.xls

Chemical Hydrology - Additional Sample Locations

Team_____   Date_____

e-mail_____

Additional Sample Locations *

Location	Time	pH	Conductivity (µS/cm)	Temperature (°C)	Salinity (ppt)	Notes/UTM coordinates

* Opportunistic or interesting samples

GPS Coordinates of Sample Locations

Hydrology*	WQ*	Zone**	E**	N**	Notes
Rainfall	-	13	na	na	Rain gage at La Manzanilla Water Master's residence
T1AS	M3	13	522349	2132500	Surface water
T1AG	M3	13	522349	2132500	Groundwater
T1BS	M2	13	522371	2132367	Near surface
T1BD	M2	13	522371	2132367	0.5m below surface
T1CS	M1	13	522202	2132561	Surface water
T1CG	M1	13	522202	2132561	Groundwater
T1DS	M4	13	522112	2132858	Surface water
T1DG	M4	13	522112	2132858	Groundwater
T2AS	M9	13	522393	2134848	Surface water
T2AG	M9	13	522393	2134848	Groundwater
T2BS	M8	13	522341	2134641	Near surface
T2BD	M8	13	522341	2134641	0.5m below surface
T2CS	M7	13	522337	2134916	Surface water
T2CG	M7	13	522337	2134916	Groundwater
T3AS	M11	13	520566	2134707	Surface water
T3AG	M11	13	520566	2134707	Groundwater
T3BS	M6	13	522299	2134415	Near surface
T3BD	M6	13	522299	2134415	0.5m below surface
BBW	-	13	522077	2132841	Groundwater from large well in beach camp
BBF	-	13	522066	2132839	Water from the bathroom faucett in beach camp
BM	-	13	522115	2132524	Groundwater from hole that must be augered in beach near but above current tide line at the mouth of the mangrove
OM	-	13	522042	2132507	Ocean water from just offshore at the mouth of the mangrove
OB	-	13	521983	2132811	Ocean water from just offshore at the beach camp
LMN1	-	13	522473	2131360	La Manzanilla Well No. 1
LMN2	-	13	523063	2133068	La Manzanilla Well No. 2
TAM1	-	13	522971	2133595	Tamarindo Well No. 1
TAM2	-	13	523408	2133606	Tamarindo Well No. 2
MOR1	-	13	519246	2135918	Morgan Well No. 1
ASP1	-	13	523765	2131027	Spring in Aguacatillo drainage (just upstream of this UTM on river right)

* Different site names for the two different groups, but for the same location
** UTM (NAD83)

APPENDIX C

Source water partitioning as a means of characterizing hydrologic function in mangroves

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Abstract

Mangrove ecosystems rely on seawater, rain-derived flow, and groundwater for hydrologic sustenance, flushing, and inflow of nutrients and sediments. The relative contribution of these source waters and their variability through time and space can provide key information concerning the hydrologic function of ecosystems. We used hydrologic tracers to partition source waters and trace their movements in the Enipoas stream, a river-dominated mangrove ecosystem on the island of Pohnpei, Federated States of Micronesia (FSM) and in the Yela watershed, an interior mangrove ecosystem on the island of Kosrae, FSM. The Enipoas site was characterized as a salt wedge estuary whose source water contributions alternated between predominantly seawater and rain-derived flow, depending on the tide. The source waters in the interior Yela site were also predominantly seawater and rain-derived flow, however the relative contribution of each was much more stable. The mean groundwater contribution was 5% (SD = 5.5) for the Enipoas site and 20% (SD = 11.0) for the Yela site. Although a small contributor to flow, groundwater was a steady source of freshwater for both systems. Hydrologic linkages between mangroves and adjacent ecosystems were demonstrated by the temporal and spatial distribution of source waters. The 0.8 km Enipoas estuary, with its highly dynamic bi-directional flows, transported source waters along a hydrologic continuum comprised of coral reef, mangroves, and palm forest. In the interior mangroves of the Yela watershed, the presence of rain-derived flow and groundwater demonstrated a hydraulic connection between the mangroves and an upstream freshwater swamp. Interior mangroves with such linkages avoid stresses such as desiccation and heightened salinity, and thus are more productive than those with little or no freshwater flows.

Introduction

The importance of freshwater flow to the sustenance and productivity of mangroves has been demonstrated in a variety of climatic and geographical settings (Macnae 1968; Walsh 1974; Semeniuk 1983; Diop et al. 1997; Alongi 1998; Mazda et al. 1990a; Medeiros and Kjerfve 1993). Recent work on mangrove hydrodynamics has illustrated that groundwater in addition to surficial flow and precipitation can be an important source of freshwater in mangrove ecosystems

(Wolanski and Gardiner 1981; Ovalle et al. 1990; Mazda et al. 1990a, 1990b; Wolanski 1992; Wolanski et al. 1992; Kitheka 1998). For example, Kitheka (1998) found that groundwater flow was the major freshwater component sustaining dense mangroves in the Mida basin, Kenya. In Missionary Bay, northern Australia, Wolanski (1992) noted the importance of crab burrows as a conduit for groundwater flow, a process found to be more prevalent in sites in Japan (Mazda et al. 1990a) and Brazil (Ovalle et al. 1990). In undisturbed sites, mangrove hydrology is largely

determined by climate and hydrogeomorphic setting. Site hydrogeology may also be important, especially in areas dependent on groundwater flow. While climate largely determines regional characteristics, hydrogeomorphic setting together with hydrogeology determine local-scale hydrologic processes. Hydrogeomorphic setting has long been used to classify different types of mangrove ecosystems (e.g., Thom (1982, 1984), Semeniuk (1985), Woodroffe (1992)). In this paper, we will use the classification system employed by Woodroffe (1992), in which he described three broad functional types of mangroves: river-dominated (estuarine), tide-dominated, and interior.

Source water contributions clearly differ among the three functional types of mangroves. River-dominated or estuarine systems are supported by freshwater and seawater, with the relative contribution of each determined by local precipitation, groundwater flow rates, and site hydrodynamics. Tide-dominated systems are supported primarily by tidal inundation, yet most receive some freshwater inputs. Interior or basin systems, which are largely removed from the direct influence of rivers and tides, are supported by rain and occasional tidal inundation as well as overland flow, interflow, and/or groundwater. Because mangrove functional types often grade into each other (especially in large systems), there may be great spatial variability in the relative contributions of source waters. In addition, anthropogenic impacts to mangroves such as roads, dams, and water diversion may alter hydrological processes, and, in turn, source water contributions.

Little attention has been devoted to differentiating source waters that sustain mangrove ecosystems, despite the strong heritage of hydrogeomorphic comparisons in the literature (e.g., Lugo and Snedaker (1974), Thom (1982), Semeniuk (1985), Woodroffe (1992)). This is surprising because once source waters are identified, their chemical signatures can be used to trace their movements through time and space. This information can then be used to characterize the hydrologic regime of a system, thus providing a powerful approach for determining functional differences among mangrove types or between mangroves and adjacent ecosystems.

The goal of this study was to determine the relative contribution of source waters and their spatial and temporal variability in two types of mangrove-dominated ecosystems: an interior mangrove ecosystem and adjacent freshwater swamp on the island of

Kosrae and a river-dominated system on the island of Pohnpei, Federated States of Micronesia. These sites each contain extensive stands of a particular hydrogeomorphic type of mangrove, are situated in well-defined watersheds, receive multiple source waters, and have no seasonality in climate (Merlin et al. 1993; Mink 1986). Because of the remote location of the study sites, sampling was infrequent, and, therefore, variability could not be constrained on an inter-annual basis. We conducted source water partitioning using the conservative tracer Cl to determine the seawater contribution to flow and the quasi-conservative tracer Si to distinguish groundwater from rain-derived flow (i.e., river flow, overland flow, and interflow). Although Si may be taken up by biota such as benthic diatoms, it has recently been shown to be useful as a hydrologic tracer for groundwater in coastal systems with elevated silicate levels and near conservative mixing with respect to salinity (Herrera-Silveira 1995; Herrera-Silveira and Ramirez-Ramirez 1998). Both of these conditions were demonstrated in the Enipoas estuary by Muckenhaupt (1992), hence the rationale for using this approach here.

Study sites

Kosrae (5°19′ N, 163° E) originated as an alkalic-basalt oceanic volcano formed between 1.2 and 2.5 million years ago as part of the East Caroline Island chain (Mink 1986). Pohnpei (6° 54′N, 158° 14′E), the largest island of this chain, was formed between 3 and 8.4 million years ago and is also an alkalic-basalt volcano (Keating et al. 1984). Kosrae is 112 km^2 and contains approximately 1562 ha of mangroves on its narrow coastal fringe (Whitesell et al. 1986). Pohnpei is larger at 355 km^2 and contains approximately 5680 ha of mangroves (MacLean et al. 1986). *Rhizophora apiculata* Bl., *R. mucronata* Lamk. and *Bruguiera gymnorrhiza* (L.) Lamk. are the dominant species of mangroves in the sites studied. Average air temperature on the islands is approximately 27.4 °C (Mueller-Dombois and Fosberg 1998). Annual precipitation is between 4000–6000 mm and is evenly distributed throughout the year (Muckenhaupt 1992; Merlin et al. 1993). Tides are mixed semi-diurnal. Mean tidal amplitude is 0.98 m for Kosrae and 0.76 m for Pohnpei (Nautical Software, Inc. 1997).

The Yela watershed, a 659 ha area on the northwestern side of Kosrae, contains a largely intact mangrove swamp (105 ha) situated adjacent to a
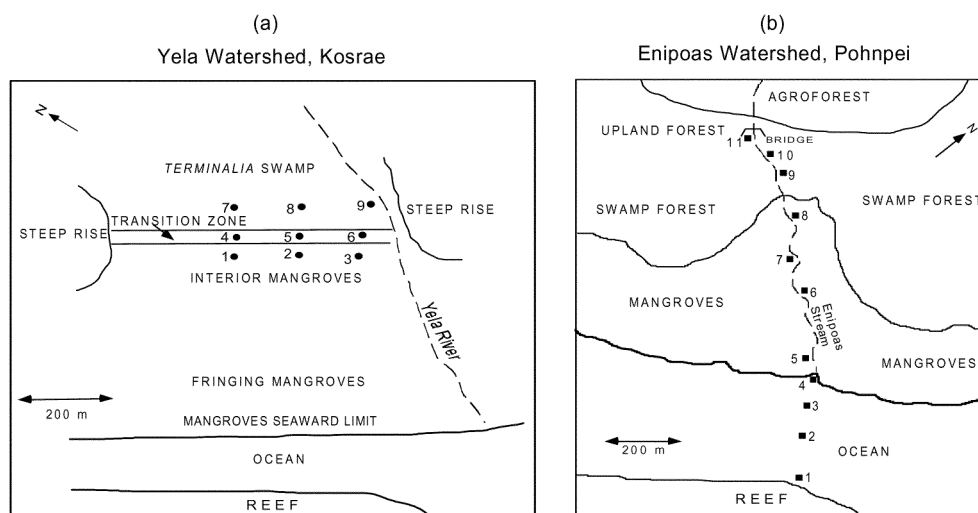
Figure 1. Study sites on (a) Kosrae and (b) Pohnpei. Solid circles represent piezometer clusters and solid squares represent stream sampling stations.

freshwater swamp (77.3 ha) dominated by *Terminalia carolinensis* Kaneh., a tree endemic to the eastern Caroline Islands. Between these two wetlands lies a narrow transition zone dominated by the trees *Hibiscus tiliaceus* L. and *Barringtonia racemosa* L. Spreng. Samples were collected along an area of the wetland complex comprising the downstream edge of the freshwater *Terminalia* swamp, the transition zone, and the upstream edge or interior of the mangrove swamp (Figure 1a).

The Enipoas stream, a small mangrove-dominated estuary located on the southeastern coast of Pohnpei, is the main drainage (0.77 km) for a 2.2 km^2 watershed (Muckenhaupt 1992). Sampling was conducted at 11 stations, which lie along a transect running from the edge of a fringing reef to a small bridge situated 370 m from the coast (Figure 1b). Stations 5–8 encompass the mangrove-dominated portion of the stream. The area around station 9 represents the transition between mangroves and an upland swamp forest containing species such as *Cocos nucifera* L. and *Hibiscus tiliaceus* L. Inland from station 10 is a palm forest containing the species *Metroxylon amicarum* (Wendl.) Becc. and *Nypa fruticans* Wurmb.

Methods

On Kosrae, we collected water samples in March, June, and September 1998 and January 1999. Samples were collected from a previously installed, piezometer

network (see Drexler and Ewel (2001)), a rain gauge, the Yela River, a spring in the Yela valley, inside the fringing reef, and the open ocean. In addition, water samples were collected from four nearby drinking water wells drilled into the saprolite-alluvium zone of the coastal plain (Mink 1986). These drinking water wells have a 15 cm diameter galvanized steel casing, are screened, and range in depth from 9 to 23 m.

Samples were collected during spring tides (high and low) and neap tides using acid-washed polyethylene bottles. All piezometers were evacuated immediately before sampling. For the March samples, all piezometers were sampled on each sampling day. For the rest of the study, water sampling was conducted along the following transects on alternate days: (1) piezometer clusters 3, 6, and 9 and (2) piezometer clusters 2, 5, and 8. Sampling apparatus having any contact with samples was acid-washed before use. A battery-operated peristaltic pump (Geotech Series II, Geotech Environmental Equipment, Inc., Denver, CO, USA) was used to collect samples from piezometers. An in-line 0.45 μm filter (dispos-a-filter, Geotech Environmental Equipment, Inc., Denver, CO, USA) was used to filter samples during collection. Filtered samples were placed in clean 60 ml polyethylene bottles and stored in a cooler until they were refrigerated at the end of the day.

On Pohnpei, we collected water samples in July and October 1998 and January 1999 from a rain gauge, a 15 m deep drinking water well (constructed similarly to those on Kosrae) situated within 1 km

from the Enipoas stream, a spring within the Enipoas valley, and along the transect. Samples were collected during spring tides (high and low) and neap tides using acid-washed 60 ml polypropylene syringes (Becton-Dickinson & Co., Franklin Lakes, NJ, USA). For each station in the transect, one sample was collected near the bottom of the channel and another was collected 15 cm below the water surface. The syringe was rinsed three times with sample before the sample was taken. Samples were filtered with 0.2 μm cellulose acetate syringe filters (Syrfil, Corning Inc., Corning, NY, USA) and placed in clean 60 ml polyethylene bottles and stored in a cooler until they were refrigerated at the end of the day.

All samples were carefully packed in a cooler and shipped by air to the University of Hawaii and kept refrigerated at 7 °C until analysis. Dissolved Na and Si (elemental form) were determined by inductively coupled plasma-optical emission spectroscopy (ICP/OES) using a high resolution model PS1 echelle grating spectrometer (Leeman Labs, Hudson, NH, USA). Analytical procedures followed methods previously described by De Carlo (1992). Detection limits were 2 μg/L for Na to 7 μg/L for Si.

Concentrations of Cl were determined using a Dionex (Sunnyvale, CA, USA) model DX 300 gradient elution ion chromatograph calibrated with standards prepared by serial dilution of IAPSO standard seawater. The detection limit for Cl was 0.01 mg/l.

End member concentrations of Si and Cl that were used to partition source waters were determined as follows. For both solutes, low end member estimates were essentially set to zero, based on the concentration of Si and Cl in rain water. For Cl, the concentration in pure seawater was used as the high end member concentration (HEMC) because this measurement is very stable globally and has long been used as a tracer (Aston 1983). Determining the HEMC for Si was more complex, because it depends to a great extent on local bedrock geochemistry (Stumm and Morgan 1981). In order to best constrain the Si HEMC, we collected literature values for Si concentrations in deep groundwater from the Hawaiian Islands (the closest similar islands for which data were available), analyzed water samples from drinking water wells and springs on both Pohnpei and Kosrae to determine the equilibrium concentration of Si in groundwater, and conducted a rock-water interaction experiment to estimate the hypothetical ceiling concentration of Si in Kosraean groundwater. In the experiment, replicate 100 g por-

tions of greater than 2 mm, crushed Kosraean (volcanic) quarry rocks from 6–12 m deep were placed in 2-liter plastic bottles with 1000 g of reverse osmosis, deionized water (RODW). Bottles were capped, sealed with parafilm, and placed on a Rotatox tumbler (syncrogear module) in a room kept at 22 °C. A blank experiment was also run consisting of RODW with no addition of rock. Ten ml aliquots were taken from the bottles with an Oxford pipettor at selected time intervals and pressure-filtered through a 0.2 μm cartridge filter using a syringe. The tumbler was run continuously until the end of the experiment 6284 hours later. Samples were analyzed in duplicate for Si as described above. All reported experimental concentrations for Si were blank subtracted.

We calculated the relative contribution of groundwater and seawater in each water sample by dividing its concentration of Cl and Si by the respective end member concentration for each solute:

$$G_s = (Si_s)/(Si_{em}) \tag{1}$$

and

$$S_s = (Cl_s)/(Cl_{em}) \tag{2}$$

where for each water sample (s), G_s = relative (%) contribution of groundwater, S_s = the relative (%) contribution of seawater, Si_s is the concentration of Si, and Cl_s is the concentration of Cl. Cl_{em} and Si_{em} are the HEMCs of Cl and Si, respectively. Next we estimated the relative contribution of rain-derived flow (R_s) for each water sample as the residual:

$$R_s = 100 - (G_s + S_s) \tag{3}$$

For the purposes of this paper, we differentiate the term groundwater from rain-derived flow, which does not recharge into the aquifer (Freeze and Cherry 1979).

Results

The relationship between Na vs. Cl in the Enipoas estuary consisted of a highly conservative dilution curve with rain and seawater as end members. Sodium concentrations ranged from 0.104 mmol/L to 477 mmol/L (median = 394) and Cl concentrations ranged from 0.143 mmol/L to 583 mmol/L (median = 443). The greatest change in Na-Cl signatures occurred between high and low tide. During high tide, most samples had Na and Cl concentrations above 400 and 475 mmol/L, respectively, except for some

samples from the upland swamp forest that were much fresher. During low tide and neap tide, the range of Na and Cl concentrations was much greater than during high tide. The largest spread of values was in the mangroves during low tide when Na and Cl concentrations ranged from less than 25 mmol/L in the freshwater swamp to 350 mmol/L in the mangroves.

On Kosrae, the relationship between Na vs. Cl also consisted of a highly conservative dilution curve with rain and seawater as end members. Na concentrations in the Yela site ranged from 0.02 to 474 mmol/L (median = 43.5) and Cl ranged from 0.09 to 586 mmol/L (median = 59.5). Concentrations of Na and Cl within the Yela watershed generally decreased along the upstream gradient from the mangrove swamp through the transition zone and to the freshwater swamp. This was evident during high tide, low tide, and neap tide. Some piezometers, however, had Na-Cl signatures consistently fresher than their locations would suggest. For example, the 1.83 m piezometer in cluster 1 had Na and Cl concentrations less than 10 mmol/L even though the well was situated within the mangroves.

Si concentrations ranged from below the detection limit (0.4–0.7 μmol/L) to 223 μmol/L in the Enipoas estuary on Pohnpei (median = 34 μmol/L) and from near the detection limit to 771 μmol/L in the Yela watershed on Kosrae (median = 232 μmol/L). Overall, lower Si concentrations were observed in the Enipoas estuary because no groundwater samples, except for the spring and drinking water well, were collected there. The mixing diagrams of Si vs. Cl suggest a small net uptake of Si within both systems, yet there is also a clear mixing curve along the Si axis with groundwater and rain serving as end members (Figure 2). In the Yela site, the 1.0 m piezometer in cluster 9 (in the freshwater swamp) and the 1.83 m piezometer in cluster 1 show close affinity to the rain end member (Figure 2b).

The three approaches for estimating Si HEMC's resulted in a range of values. In the first approach we used groundwater quality data collected between the 1970's and 1990's on Oahu and Kauai, the Hawaiian islands closest in age to Kosrae and Pohnpei (Mueller-Dombois and Fosberg 1998). Deep groundwater on these islands had an average Si concentration of 935 μmol/L (United States Geological Survey, 2001). For the second approach we measured Si concentrations in drinking water wells and springs on Kosrae and Pohnpei. All the drinking water wells and

the spring on Pohnpei were found to be highly diluted by rain-derived flow and, therefore, could not be used to determine the Si HEMC. The spring sample from Kosrae had an average Si concentration of 762 μmol/L. This value was significantly lower than the Hawaiian estimate, strongly suggesting lack of equilibrium with bedrock. The results from the third approach, the water-rock interaction experiment, showed that deep quarry rocks had greater Si concentrations through time than shallow quarry rocks. For both types of rock, the release of Si reached an asymptote at approximately 1500 hours. The average Si concentration of deep quarry rocks after the asymptote was reached was approximately 1150 μmol/L. This is a maximum value as the experimental design led to mechanical weathering of the samples in addition to chemical exchange of Si. We chose this hypothetical ceiling concentration as the experimental HEMC.

For the purpose of an error analysis, source water contributions were calculated using all three Si HEMCs during low tide (when groundwater contributions were greatest) for select piezometers on Kosrae (Figure 3). Groundwater contributions estimated using the hypothetical ceiling concentration of 1150 umol/L were 18% less than those using the Hawaiian HEMC estimate of 935 umol/L. Groundwater contributions estimated using the 1150 umol/L HEMC were 35% less than those calculated with the Kosraean HEMC of 762 umol/L. Differences in the HEMC of groundwater also affected estimates for the contribution of rain-derived flow due to the use of equation (3). The contributions of rain-derived flow were from 0.03 -14 % (mean = 8%) greater for the 1150 umol/L HEMC than the 935 umol/L HEMC. This difference grew to between 7–30% (mean = 18%) between the 1150 and 762 umol/L HEMCs. The true HEMC of Si is most likely between 935–1150 umol/L. In order not to inflate the groundwater contribution, we used the 1150 umol/L ceiling Si HEMC, causing estimates of groundwater contributions to be conservative and rainwater estimates to be somewhat greater than their true value.

Seawater and rain-derived flow were the main hydrologic components in the Enipoas estuary (Figure 4). During high tide, in all but three samples from the upland swamp, seawater represented over 83% of flow (Figure 4). Rain-derived flow was much more important during neap tide and low tide. During neap tide, over 70% of the flow above the mouth of the estuary consisted of rain-derived flow (not shown).
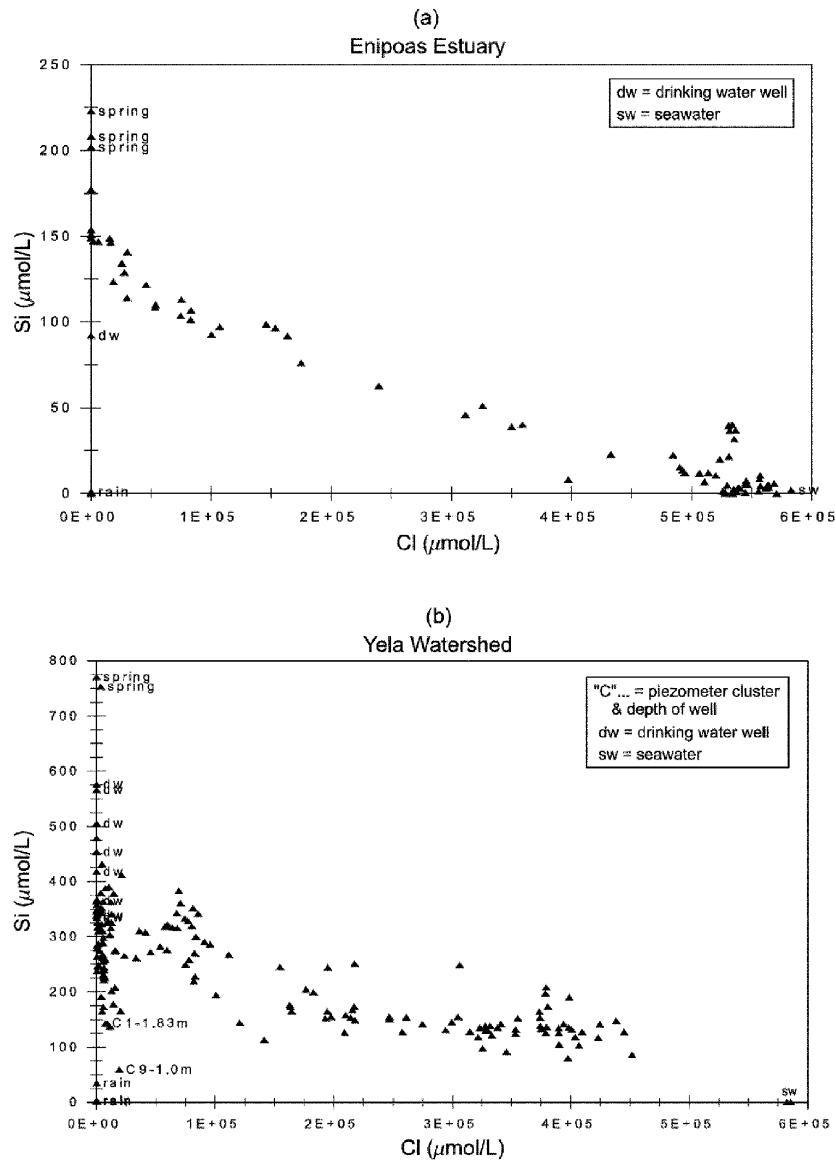
Figure 2. Mixing diagrams of Si vs. Cl in water samples from (a) the Enipoas estuary and (b) the Yela watershed. Samples are represented by triangles except for end members and a few well samples labeled separately.

During low tide the same was true for surface samples, but many bottom samples also contained significant contributions from seawater (Figure 4). The mean groundwater contribution for the entire site during all times in the tidal cycle was approximately 5% (SD = 5.5). During low tide the groundwater contribution ranged from 0–10% in the mangroves (stations 5–8) to 7–13% in the palm forest (stations 9–11) (Figure 4).

Seawater and rain-derived flow also comprised the chief source waters in the Yela site (Figure 4). The mean groundwater contribution during all times in the tidal cycle was approximately 20% (SD = 11.0). The maximum groundwater contribution reached or exceeded 30% during low, neap, and high tide. There were no major changes apparent in source water contributions during different times in the tidal cycle. The emergence of rain-derived flow in the mangroves was evident during high, low, and neap tide in the 1.83 m piezometer of cluster 1. Throughout the tidal cycle, the most changeable sampling points were the Yela River and the 0.5 m wells in the mangroves and
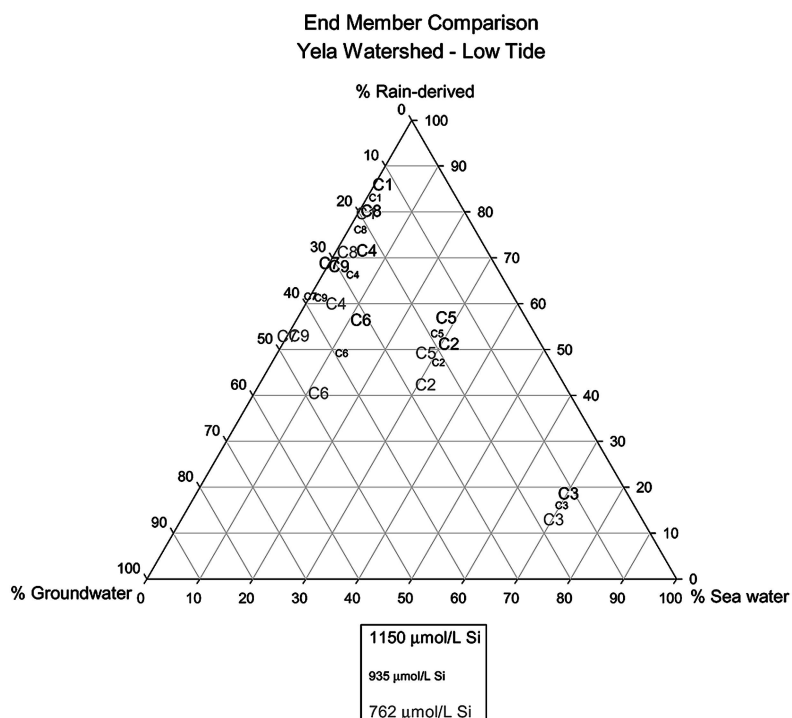
End Member Comparison
Yela Watershed - Low Tide

Figure 3. Ternary diagram comparing source water contributions estimated using the three different Si HEMCs. The 1150 umol/L estimate is the hypothetical ceiling estimate from the rock-water interaction study; the 935 umol/L estimate is the average Si concentration of Hawaiian groundwater; and the 762 umol/L estimate is the average Si concentration of the groundwater spring in the Yela watershed, Kosrae. All samples shown were collected during low tide when groundwater contributions were greatest. "C" refers to the piezometer cluster from which each sample was taken.

transition zone (not shown). In the transition zone and the freshwater swamp, localized conditions strongly affected the relative contributions of source waters. For example, during low tide the 1 m well in piezometer cluster 9 was strongly influenced by rain-derived flow near the banks of the Yela River (Figure 4).

Discussion

The overall hydrologic regimes of both the interior Yela mangroves and the Enipoas estuary can be categorized as "pulsed" (Odum et al. 1995). However, the amplitude of pulses (tidal fluctuations) in the Enipoas estuary was greater than those in the interior Yela site because of differences in relative source water contributions. On average, the Yela site received a mean groundwater input four times higher than the Enipoas estuary. However, both systems were largely sustained by a combination of seawater and rain-derived flow. Source water contributions in the Enipoas estuary were highly variable through the

tidal cycle, while those of the Yela site were much more consistent (Figure 4). At the Yela site, the only highly variable sampling points were the Yela River and the shallow piezometers in the mangroves and transition zone. Such variability was the result of tidal fluctuations in the case of the Yela River and a combination of tidal fluctuations and pulses of rain-derived flow in the shallow groundwater piezometers.

The Enipoas estuary functioned as a salt wedge estuary, with bottom samples at each station usually containing considerably more seawater than surface samples of the same station (Figure 4). During high tide, the salt wedge migrated upstream just short of the upland swamp forest. The estuary alternated between seawater domination during high tide and rain-derived flow domination during low tide and neap tide. The far upstream stations exhibited the freshest signatures, indicating that runoff from upstream ecosystems was the chief source of freshwater flow. Because of the relatively short length of the estuary, dramatic changes in source water contributions occurred throughout most of the transect measured.
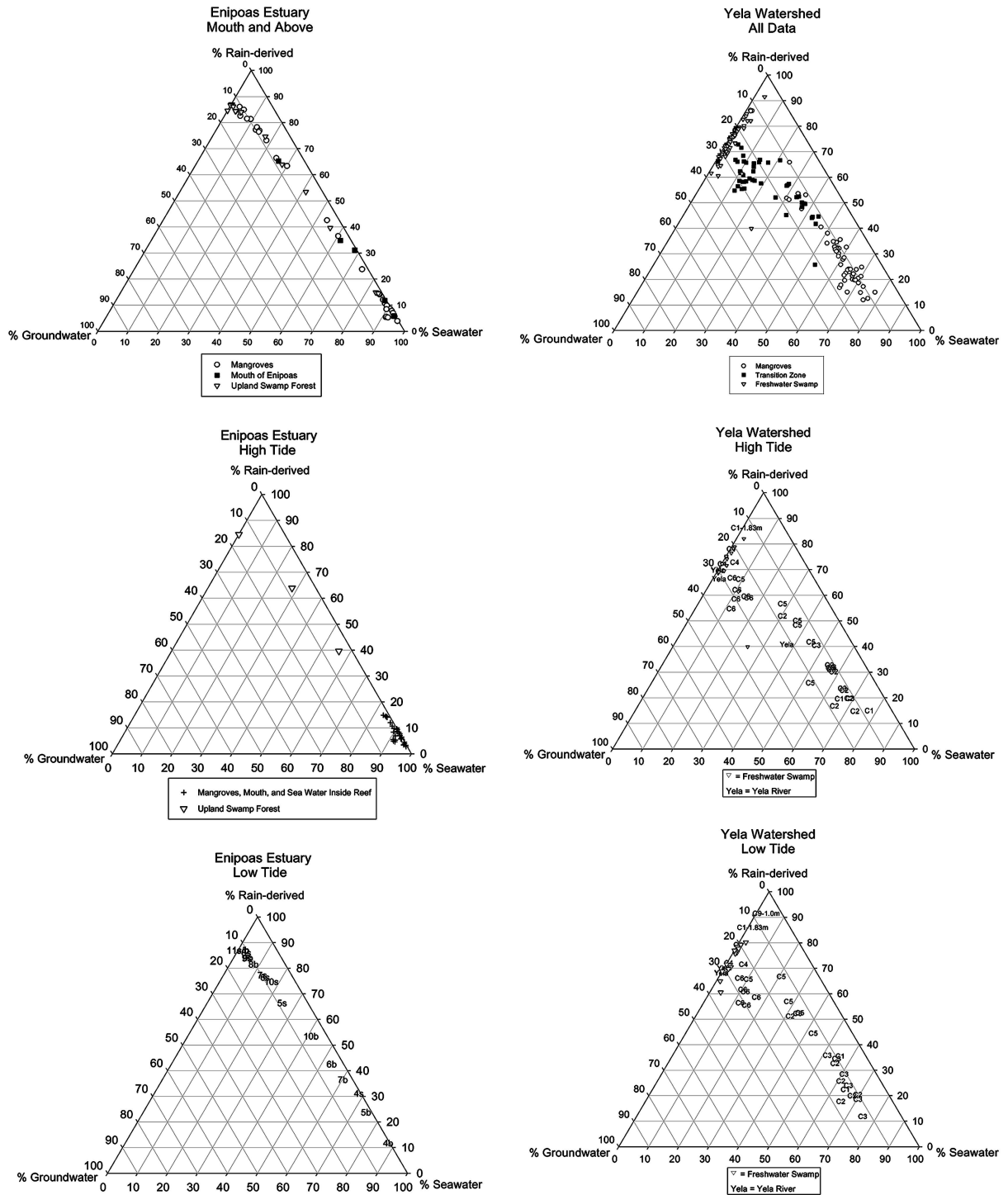
Figure 4. Ternary plots showing the relative contributions of seawater, groundwater, and rain-derived flow in the Enipoas estuary and Yela site. For Enipoas estuary plots, numbers refer to sampling stations and "s" and "b" refer to surface and bottom samples, respectively. For Yela watershed plots, "C" followed by a number refers to a particular piezometer cluster in the sampling network.

Groundwater discharge was a small yet consistent component of flow, with the highest contribution (13%) in the upstream palm forest (Figure 4).

At the Yela site, source water contributions in the mangroves differed from those in the adjacent freshwater swamp, indicating a difference in the hydrologic regimes. The mangroves, though interior, were subject to consistent influence from the tides (Figure 4). Even during low tide, seawater was the dominant source water (Figure 4). In the freshwater swamp, which is only 60 cm higher topographically than the mangroves (Drexler and Ewel 2001), the influence of the tides was apparent from occasional spikes in concentrations of Na and Cl in surface piezometers (not shown). The seawater contribution in the freshwater swamp reached a maximum of approximately 20% during high tide, indicating less frequent and/or less intense inundation than the mangroves. Rain-derived flow accounted for over 60% of flow in the freshwater swamp at all times. Groundwater contributions generally ranged from 10–20% in the mangroves and 20–40% in the freshwater swamp (Figure 4). This range did not change considerably during high or neap tide, suggesting strongly that groundwater was a consistent contributor to the system. These differences in source water contributions between the freshwater swamp and mangrove occurred over a distance of only 50 m.

The predominance of rain-derived flow and seawater in the interior Yela mangroves and the Enipoas estuary indicates their strong linkages to coastal *as well as* upstream ecosystems. A particularly clear indicator of an upstream linkage in the interior Yela mangroves was the 1.83 m piezometer in cluster 1, whose source waters consisted of approximately 85% rain-derived flow and 15% groundwater (Figure 4). Previous hydrogeological investigations at the Yela site demonstrated the hydraulic connectivity between the mangroves and freshwater swamp and the sensitivity of this linkage to drought (Drexler and Ewel 2001). Such hydrologic linkages between mangroves and upstream ecosystems have been documented in other mangrove ecosystems as well. Studying estuarine mangroves in arid hinterlands of Australia, Semeniuk (1983) concluded that low porewater salinities were likely the result of groundwater seepage and the reason for the existence of mangroves far upstream. Cintron et al. (1978), studying mangroves in arid environments of Puerto Rico, found that the site with the tallest mangroves was largely isolated from seawater by a sand dune and was sustained by

percolating freshwater from upstream. Mazda et al. (1990b), working in a mangrove-dominated lagoon in Japan, demonstrated subsurface flow dynamics across a shore bank that occasionally closed off the lagoon from the open sea. During such times, groundwater seeping from upstream into the mangroves was shown to reduce anoxia and promote benthic algal productivity. These examples indicate that groundwater flow may permit mangroves to inhabit areas otherwise unsuitable for growth, increase productivity in mangrove systems, and play an important role in different functional types of mangroves. Our study, in particular, demonstrates that interior or basin sites, which have long been assumed to be less productive due to desiccation stress, waterlogging, and/or reduced conditions (Woodroffe 1992), may be immune from these negative impacts if sustained at least partially by groundwater flow. As a case in point, Ewel et al. (1998), studying a larger area within the Yela watershed of Kosrae, found that when diameters and heights of mangrove trees were compared between river-dominated, tide-dominated, and interior (basin) sites, interior trees were the tallest and of greatest girth.

This study shows that hydrograph separation techniques represent a useful tool for improved understanding of mangrove hydrology. Here we applied such techniques to partition the source water contributions as well as determine the hydrologic linkages between mangroves and adjacent ecosystems. These techniques can also be applied to problems involving water residence time, storm water flow dynamics, groundwater flow rates, and ages of source waters (Hooper and Shoemaker 1986; Kennedy et al. 1986; Wels et al. 1991; Mazor and Nativ 1992). Of particular interest would be using such approaches to quantify fluxes of ecologically relevant materials (e.g., nutrients, detritus, and sediment) within and between mangroves and adjacent ecosystems in order to better understand processes of nutrient cycling.

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Characterisation of the hydrology of an estuarine wetland

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Abstract

The intertidal zone of estuarine wetlands is characterised by a transition from a saline marine environment to a freshwater environment with increasing distance from tidal streams. An experimental site has been established in an area of mangrove and salt marsh wetland in the Hunter River estuary, Australia, to characterise and provide data for a model of intertidal zone hydrology. The experimental site is designed to monitor water fluxes at a small scale (36 m). A weather station and groundwater monitoring wells have been installed and hydraulic head and tidal levels are monitored over a 10-week period along a short one-dimensional transect covering the transition between the tidal and freshwater systems. Soil properties have been determined in the laboratory and the field. A two-dimensional finite element model of the site was developed using SEEP/W to analyse saturated and unsaturated pore water movement. Modification of the water retention function to model crab hole macropores was found necessary to reproduce the observed aquifer response. Groundwater response to tidal fluctuations was observed to be almost uniform beyond the intertidal zone, due to the presence of highly permeable subsurface sediments below the less permeable surface sediments. Over the 36 m transect, tidal forcing was found to generate incoming fluxes in the order of 0.22 m^3/day per metre width of creek bank during dry periods, partially balanced by evaporative fluxes of about 0.13 m^3/day per metre width. During heavy rainfall periods, rainfall fluxes were about 0.61 m^3/day per metre width, dominating the water balance. Evapotranspiration rates were greater for the salt marsh dominated intertidal zone than the non-tidal zone. Hypersalinity and salt encrustation observed show that evapotranspiration fluxes are very important during non-rainfall periods and are believed to significantly influence salt concentration both in the surface soil matrix and the underlying aquifer. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Wetlands; Salt marshes; Tidal flats; Water balance; Unsaturated zone; Hunter Valley

1. Introduction

Estuarine wetlands are characterised by complex interactions between vegetation type, surface water fluxes and porewater movement. The hydrology of tidal wetlands is very sensitive spatially to small changes in topography and associated tidal regime. In addition to tidal fluxes, several other factors play an important role in the hydrology of wetlands. These include vegetation, rainfall, seasonal variations in evapotranspiration, extreme tidal or flood events, and variations in regional groundwater flow.

Mitsch and Gosselink (1993, p. 68) have noted that ''*hydrology is probably the single most important determinant of the establishment and maintenance of specific types of wetland*'' (their italics). In particular, hydrology is a key determinant in species distribution, in wetland productivity (biomass produced per unit time), and nutrient cycling and availability.

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To be able to understand the ecology of these environments it is crucial to understand the hydrology. The reverse is also true, with ecology being critical to determining the hydrological balance. Because of the intimate relationship between estuarine wetland ecology and hydrology, knowledge of wetland hydrology is critical if we are to predict and manage change in wetland environments. These include both long-term gradual changes such as climate change and projected sea-level rise, and sudden changes resulting from human interference e.g. hydraulic modification of tidal flow.

The bulk of research on salt marsh hydrology has concentrated on the *Spartina alterniflora* dominated mid and high latitude salt marshes of the Northern Hemisphere, which typically occupy the entire intertidal zone. Groundwater and porewater fluxes have been found to be important factors affecting wetland productivity, through their influence on accumulation and removal of chloride, nutrients and toxins, hyper-salinisation, sediment oxidation potential, pH and soil moisture content (Chalmers, 1982; Howes et al., 1986; Nuttle and Harvey, 1988). Studies of porewater flow in salt marsh sediments have focused on solute

fluxes (e.g. Yelverton and Hackney, 1986; Howes and Goehringer, 1994; Nuttle and Harvey, 1995), creek bank drainage following tidal inundation (e.g. Nuttle and Harvey, 1988; Harvey et al., 1987), porewater transport mechanisms (e.g. Harvey and Nuttle, 1995; Harvey et al., 1995), and regional groundwater discharge (e.g. Nuttle and Harvey, 1995).

In the Hunter Region of Australia, salt marsh is often found in the upper intertidal zone in conjunction with mangroves, which dominate the lower intertidal zone. To date research in Australian tidal wetlands has tended to concentrate on mangal or mangrove communities and has largely neglected the adjacent salt marsh zone. Consequently, little is known about the similarities and differences in hydrology between Australian and Northern Hemisphere salt marsh environments.

This paper presents the results of a field investigation of the hydrogeology at a site at Tomago South in the Hunter River estuary, Newcastle, Australia (Fig. 1). Measurements of water table response to tidal forcing from salt marsh creeks have generally found a rapid decline in water table movement with increasing distance from the creek,
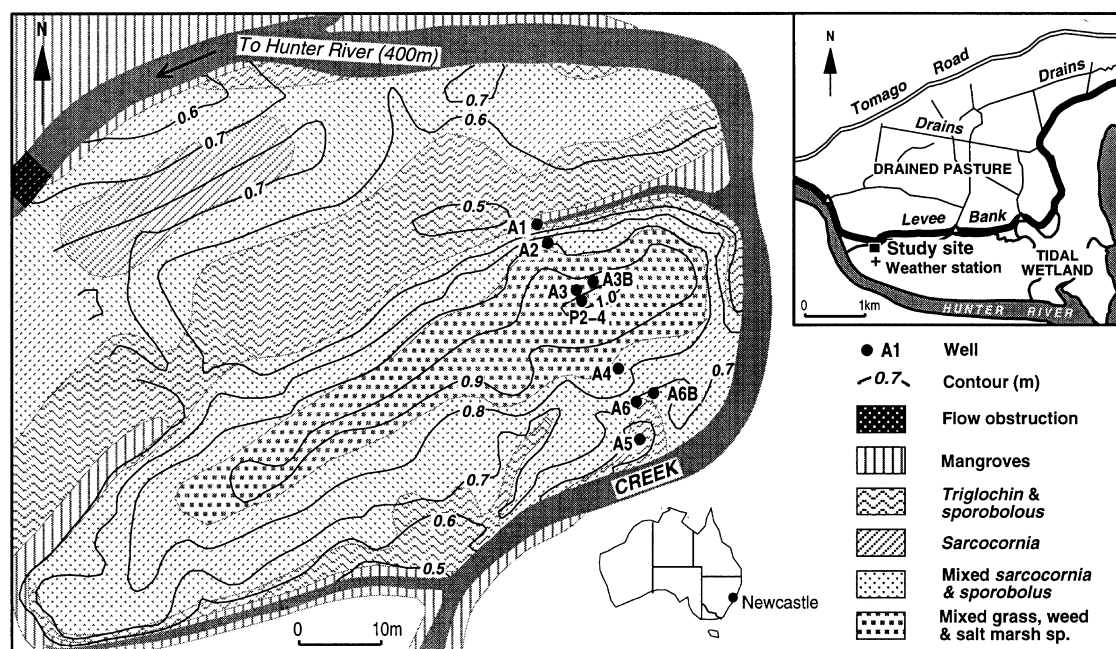

Fig. 1. Contour and vegetation map of study site with well locations; map of Tomago South rehabilitation site, Hunter River, Newcastle (inset).

with vertical movement becoming negligible within 5 to 10 m (Howes and Goehringer, 1994; Nuttle and Harvey, 1988). In this study, the groundwater response to tidal inundation extends over a greater distance because of the characteristics of the underlying sand aquifer and the location of the study site in relation to the creek. In contrast to previous studies, groundwater response beyond the normal intertidal zone has been observed to remain almost uniform with increasing distance from the creek. To understand the soil water and salt balance beyond the immediate creek bank zone it is therefore necessary to be able to predict water table response to tidal forcing as well as to rainfall and evapotranspiration.

In this study measurements of hydraulic head, climate, and soil and aquifer properties were made, aquifer response to tidal forcing is analysed and temporal and spatial scale issues relating to groundwater in a wetland are discussed. A finite element model was developed in order to further understand the relative contribution of tidal forcing, evapotranspiration and rainfall to saturated and unsaturated flow.

2. Site description

The Tomago South wetlands are located in an inter-barrier depression overlying an Inner Barrier sand unit (Thom et al., 1992). The aquifer flowing through the sand unit, known as the Tomago Sandbeds, is an important groundwater resource for the area. During the past 3000 years mud flats have developed on top of the sand unit so that the surface soils comprise estuarine muds upon which the tidal wetlands of the area have established (Thom et al., 1992). Located at the edge of this estuarine mud unit in the floodplain of the Hunter River, the study site has a surface layer of only 0.5 to 1.0 m of muds overlying the Inner Barrier sand unit which is estimated from regional bore hole data to be approximately 20 m thick (Woolley et al., 1995). The stratigraphy of the study site is shown in Fig. 2.

Salt marsh and mangrove wetlands in the Hunter River estuary have suffered varying degrees of disturbance since European settlement in the early 1800s. Wetlands at Tomago South have been largely reclaimed for agriculture through the excavation of
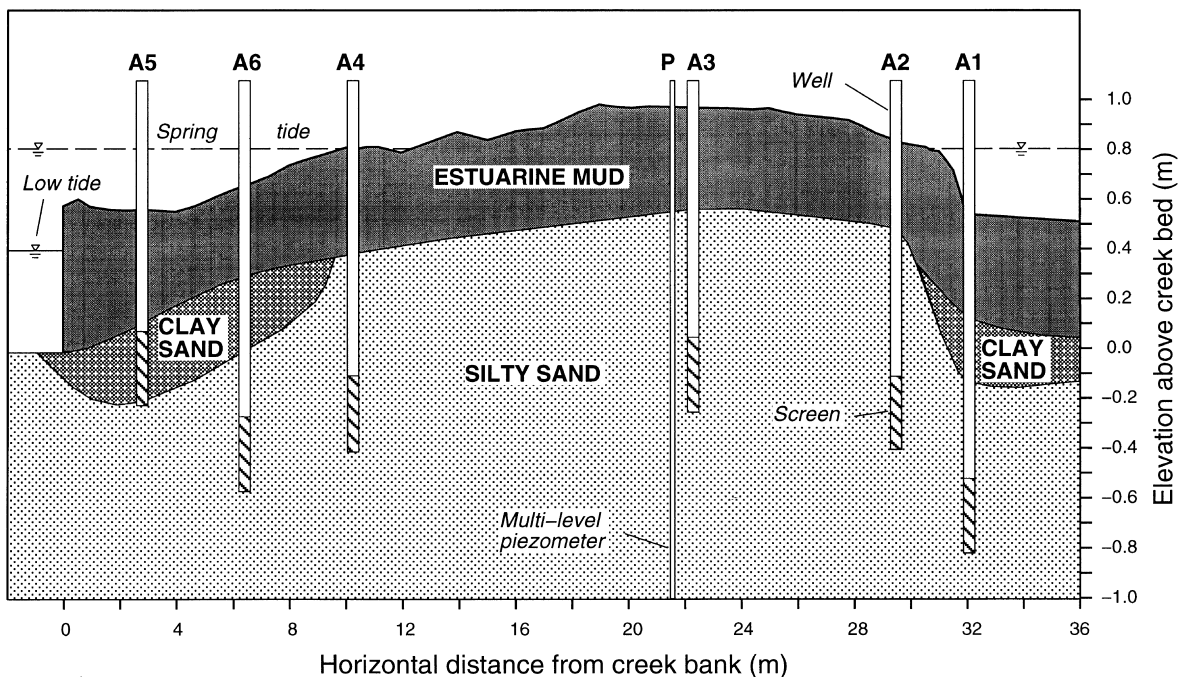

Fig. 2. Stratigraphic cross-section and well locations at the study site.

a series of drains and construction of a levee bank with one-way floodgates. A portion of the original wetland, fringing the Hunter River, has been allowed to remain tidal but has also been modified by past grazing, mangrove clearance and drain construction. Approximately half of the area is managed by the NSW National Parks and Wildlife Service and the remainder is part of an industrial buffer zone owned and managed by the Tomago Aluminium Company. Under the auspices of the Kooragang Wetland Rehabilitation Project, the entire area of approximately 11 km^2 has been identified for wetland restoration and rehabilitation, with emphasis on habitat creation for migratory water birds and fisheries, combined with recreational and educational opportunities.

The study site is located approximately 500 m from the Hunter River (Fig. 1, inset) which experiences semidiurnal and mixed tidal fluctuations with a normal maximum range of about 2 m. Tidal range at the study site is attenuated significantly and is not sinusoidal, due primarily to a flow obstruction in the tidal creek. Only tides above 0.37 m Australian Height Datum (AHD) exceed the blockage and are transmitted to the site, which is therefore often subject to only a single tidal peak each day. Maximum elevation at the site is 0.65 m above the minimum tidal level and the normal tidal range is approximately 0.5 m. Such a degree of tidal attenuation appears to be typical of the salt marsh areas at Tomago.

Storm surges in the Hunter River have been observed to have a significant effect on tidal fluctuations resulting in tidal levels considerably exceeding normal king tide levels. Historical reports of major flood events indicate inundation of the entire floodplain area at Tomago occurs at approximately 50-year intervals with local flooding occurring at 10-year intervals (PWD, 1994).

Vegetation at the site includes salt marsh species *Sporobolus virginicus*, *Sarcocornia quinqueflora*, *Triglochin striata* and *Suaeda australis* and mangrove species *Aegiceras corniculatum* and *Avicennia marina*. Salt tolerant grass and weed species are found at the fringe of the intertidal zone. Salt marsh and mangrove species distribution corresponds broadly with degree of tidal inundation (Fig. 1) with mangroves adjacent to waterways.

Animal burrows, particularly crab holes, are a dominant feature of soils in the intertidal zone.

These have been found to dramatically increase surface infiltration rates in other mangrove and salt marsh areas (Clarke and Hannon, 1967; Harvey and Nuttle, 1995), increase accumulation of porewater solutes in the soil matrix (Harvey et al., 1995) and form a significant pathway for tidal flow (Ridd, 1996; Wolanski et al., 1992).

3. Data collection

Groundwater behaviour at the site is controlled by a combination of periodic tidal and evapotranspiration fluctuations, irregular rainfall events and possibly regional groundwater flow.

In order to characterise groundwater response to short term tidal and climatic forcing, a series of wells was installed at the site at locations shown in Figs. 1 and 2. Six small 56 or 70 mm diameter wells (A1–A6) were placed to depths ranging from 0.8 to 1.4 m from the surface along a one-dimensional transect from the creek across the highest part of the site to a shallow tidal depression, a nested set of 22 mm wells (P2–P4) was installed at 2, 3 and 4 m depths adjacent to well A3, and two 22 mm wells (A3B, A6B) were placed perpendicular to the 1D transect at 3 m distance from, and at similar depths to, A3 and A6, respectively. Wells were screened over the bottom 30 cm and located in the more permeable sand layers in order to ensure a rapid borehole response to changing groundwater conditions. The vertical location of the wells is shown in Fig. 2.

An automatic climate station was placed approximately 300 m from the study site. The station measured rainfall, temperature and humidity, wind speed and direction and incoming short wave solar radiation data averaged on an hourly basis. Potential evaporation was calculated using the Penman combination equation (Maidment, 1993, p. 4.16). Measurements of energy balance components made using eddy correlation apparatus during August, September and October 1997 enabled the actual evapotranspiration of three vegetation types at the study site to be estimated. Daily pan evaporation and rainfall values from Williamtown Airport Meteorological Office (AMO), approximately 10 km to the north-east, were also acquired for comparison and for a longer-term record.

Continuous monitoring of head levels in the wells A1, A3 to A6 was carried out in a maximum of three wells at any one time over two periods from 16/1/97 to 4/3/97 and 11/3/97 to 1/4/97. Measurements were taken at 15 min intervals using pressure transducers powered by rechargeable batteries and recorded with a variety of dataloggers. During these periods water level in the creek adjacent to the site was also monitored. Electronic measurements were calibrated using manual data collected at intervals of 3 days to 1 week with standard errors in the order of 1 to 3 mm calculated.

Hydraulic conductivity was estimated using a variety of methods. Slug tests were performed in four of the six large wells. Measurements of infiltration and hydraulic conductivity of surface sediments were made in the field using double ring infiltrometers and a Guelph permeameter. In the laboratory, falling head tests were performed on samples from the same locations, bulk density and moisture content were determined gravimetrically, particle size analysis was undertaken using the hydrometer method, organic matter content was determined by ignition at 450°C and porosity was estimated based on the assumption that organic matter density is 0.224 g/cm^3 and mineral density is 2.65 g/cm^3 (Maidment, 1993, Eq. 5.1.1 and p. 5.35).

4. Results and discussion

4.1. Soil properties

The basal sediments are medium grained silty sands with clay lenses and thin layers of shell, and the surface sediments are highly organic fine silt sands or ''estuarine mud''. Due to capillary rise in the fine mud layer and regular tidal inundation, the surface moisture content remains at or near saturation in the lower intertidal zone. Above the lower intertidal zone the water table is further from the surface, therefore, the surface moisture content is more variable and is influenced by the action of rainfall and evapotranspiration.

Hydraulic conductivity determined from slug test results ranged from 0.54 to 26.7 m/day, and averaged 16 m/day for the silty sand and 0.7 m/day for the clay sand layer underlying the muds in the low marsh. Results from Guelph permeameter, falling head and double ring infiltrometer tests at seven locations were in good agreement and are summarised in Table 1. Based on these results, surface hydraulic conductivity was estimated to be approximately 0.01 m/day for the estuarine mud matrix and 1 m/day for non-tidal topsoils. The presence of crab holes and smaller macropores appears to increase the overall surface infiltration rate to a range of 0.1 to 1 m/day, which is 1 to 2 orders of magnitude larger than the matrix hydraulic conductivity. Individual crab hole infiltration rates average 11 m/day. Ponded areas in the lower intertidal zone have virtually no measurable infiltration.

Particle size analysis revealed that the surface sediments are predominantly silty sands with clay content ranging from 6 to 12%. The bulk density of these sediments ranged from 0.63 to 1.35 g/cm^3, organic matter comprised 8 to 22% and porosity varied from 0.45 to 0.7. Sediment properties are summarised in Table 1.

Frequent tidal and soil moisture content fluctuations would be expected to induce a shrink–swell response of 10 to 20 mm in the highly porous surface muds, particularly in the less frequently inundated zones (Fityus and Welbourne, 1996).

Table 1
Soil property results for the four major sediment zones

Material location	Sat hydraulic activity (m/day)	Initial infiltration (m/day)	Porosity	Clay content (%)	Organic matter (%)	Bulk density (g/cm^3)
Subsurface sands	0.5–27[a]	–	0.45	–	–	–
Lower intertidal zone	0.01–0.06[b]	0–1.7	0.5–0.7	6–9	8–22	0.68–1.24
Upper intertidal zone	0.01–0.17[b]	0.17–0.28	0.45–0.61	6–8	8–14	0.9–1.35
Non-tidal zone	0.7–3.4[b]	4.5	0.71	12	19	0.63

[a] Before slug tests. [b] Guelph permeameter and falling head tests.

The concentration of crab holes in the intertidal zone is approximately $38/m^2$ (1% of surface area) with diameters of 2–75 mm (mean diameter 17 mm). Each of these crab holes is likely to have multiple exits and they extend in depth from the surface to the lowest tidal levels of the water table. A small rim containing excavated material is commonly found encircling the entrance to each crab hole. Infiltration measurements at the study site have shown infiltration rates as high as 1 m/day for a single crab hole located in a low permeability (0.01 m/day) soil matrix. Crab hole and other macropore flow is a major contributor to rainwater and tidal infiltration while matrix flow dominates the process of water table drainage and evapotranspiration.

The salinity of the groundwater at the site increases with depth, and has been measured to be up to 50 ppt or 1.5 times that of seawater at a depth of 4 m.

4.2. Water table response to tidal forcing

As can be seen in the typical examples of the hydraulic head data given in Fig. 3, hydraulic head measurements showed a large rapid response to tidal fluctuations across the entire site.

In Fig. 3, the ground surface is inundated by high tides at locations A4 and A6, whereas the ground surface at A3 is not. The hydraulic heads measured in piezometers A4 and A6 are different from the surface water level as the piezometer is screened in the deeper sand layer and not at the surface. The measured heads are similar in all piezometers. These observations suggest that during tidal inundation there is little hydraulic response through the low permeability mud to surface flooding, and that most of the observed head change is due to tidally induced lateral flow of water in the underlying high permeability sand layer.

Vertical head gradients measured using the nested wells P2 to P4 (10^{-3} to 10^{-2}) were up to an order of
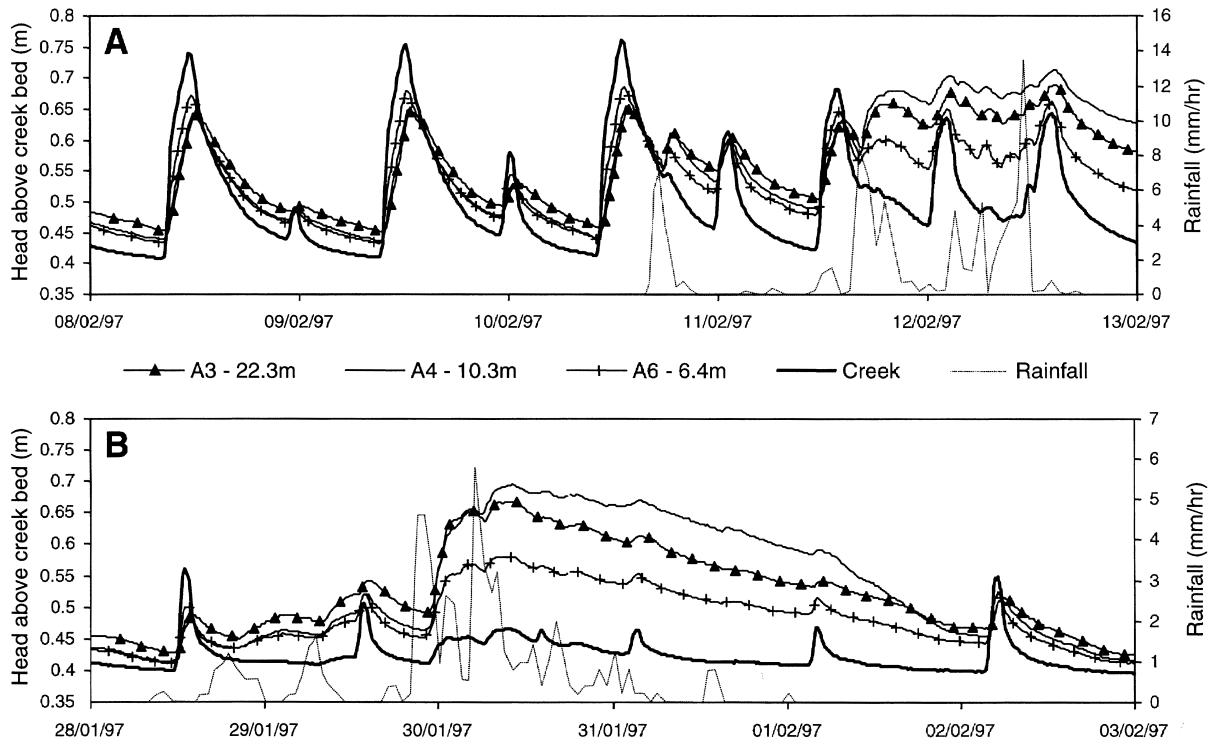

Fig. 3. Typical hydraulic head response to (A) spring tide forcing (8/2/97 to 10/2/97); tidal forcing and rainfall (10/2/97 to 12/2/97); and (B) neap tide forcing and rainfall (28/1/97 to 2/2/97). The legend shows the distance of each piezometer from the creek.

magnitude greater than horizontal gradients around A3 with maximum gradients occurring in a short time period following the tidal peak. This implies that vertical flow in the top 4 m of the sediment is significant at the site. Because of these vertical gradients, water table location differs slightly from measured head. Horizontal gradients perpendicular to the transect, from A3 to A3B and A6 to A6B, were commonly less (10^{-3}) than horizontal gradients along the transect and perpendicular to the creek (10^{-3} to 10^{-2}), suggesting that the wetland system may be adequately represented by a two-dimensional vertical transect of the field site.

4.3. Rainfall

In the 6 months prior to the study period, the study site at Tomago South experienced typical climatic conditions. Pan evaporation and rainfall measurements from Williamtown AMO were similar to long-term averages. During the period modelled in January and February 1997, Tomago South experienced two significant storm events of 64 and 111 mm in 72 h. February rainfall recorded at Williamtown was 34 mm higher than the average of 152 mm.

Significant rainfall events induced a similarly large response in the groundwater, but both the peak and decay of the rainfall response lag behind the rainfall. This is due to the low conductivity of surface sediments, which limit the rate of infiltration and drainage. Comparison of Periods A and B (Fig. 3) indicate that during the neap tide period the rainfall response is slower. This can be explained by the relatively low initial soil moisture content expected in the absence of significant tidal groundwater fluxes.

The groundwater response to rainfall was observed to be significant across the whole site with similar lag time and drainage rates in both tidally inundated and non-tidal zones. Very small rainfall events of about 4–5 mm are sufficient to produce a groundwater response. The maximum hydraulic head observed for two separate major rainfall events was similar indicating a possible maximum soil storage capacity at the point where the rate of sub-surface drainage to the creek equals the infiltration rate of the soil. Initial rainfall in the order of 10 to 20 mm (over the first 2 to 4 h) is required to produce this response.

4.4. Evapotranspiration

For the study period, the Penman potential evaporation calculated using on-site weather station data from a fixed reference location averaged 3.8 mm/day with a maximum of 7.4 mm/day. During the same period, pan evaporation rates of up to 11.2 mm/day and with an average of 5.6 mm/day were observed at Williamtown AMO. Average monthly rainfall and pan evaporation at Williamtown AMO for the 49 and 22 years of record are given in Fig. 4.

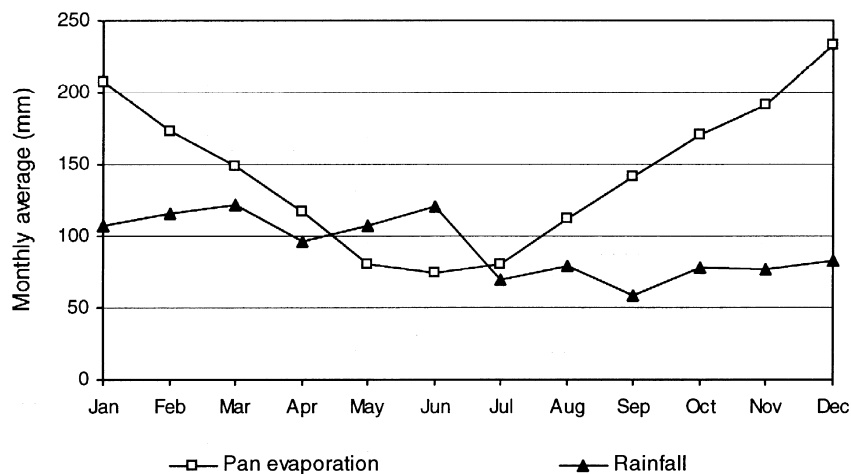Actual evapotranspiration (AET) was determined at three sites, with different dominant vegetation

Fig. 4. Average monthly rainfall and pan evaporation, Williamtown AMO.

types during the spring of 1997, using eddy correlation measurements. Actual evapotranspiration was compared with Penman potential evaporation and Penman-Monteith potential evapotranspiration (PET) at the fixed reference location. AET/Penman open water evaporation ratios were averaged from four daily measurements for each salt marsh community and three for the kikuyu pasture, with values of 0.6 ($\pm$0.1), 0.72 ($\pm$0.03) and 0.85 ($\pm$0.13) for kikuyu, *Sporobolus virginicus* and *Sarcocornia quinqueflora* dominated sites respectively (standard deviations of measurements shown in brackets). Corresponding AET/PET ratios were 0.87 ($\pm$0.04), 1.01 ($\pm$0.13) and 1.05 ($\pm$0.08). The higher evapotranspiration corresponds to vegetation found in the intertidal zone, where soil-water saturation values are higher.

The limited data available suggest that on an average yearly basis, rainfall at Williamtown and evapotranspiration at Tomago South are similar, with rainfall exceeding evapotranspiration in the winter months, and evapotranspiration exceeding rainfall in the summer months. Therefore, after allowing for rainfall loss due to surface runoff, it is likely that evapotranspiration exceeds rainfall infiltration most of the time. The extra water lost to evapotranspiration is supplied by tidal flooding and soil water movement from the tidal creeks to the soil surface.

Evapotranspiration is an important factor in the soil moisture and salt balance of tidal wetlands and in some studies has been found to be a dominant factor in groundwater fluctuations (Harvey and Nuttle, 1995;

Dacey and Howes, 1984; Hemond and Fifield, 1982). Inspection of the well data from the study site to date, however, provides no indication of underlying water table sensitivity to evaporative forcing. Given that tidally driven head fluctuations in the order of 100 to 250 mm occur daily in the groundwater table, it seems reasonable that an evaporative response in the order of 5 to 10 mm/day would be undetectable in head measurements.

4.5. Analytical solution for groundwater response to tidal forcing

Several analytical methods have been developed to analyse the response of an aquifer to periodic forcing. Such solutions may be used to determine the properties of tidally influenced aquifers (e.g. Millham and Howes, 1995). Townley (1995) recast Williams' (1982) solution for periodic flow in a homogeneous one-dimensional unconfined aquifer bounded on one side by sinusoidally varying tides, in terms of complex variables as follows:

$$h(x, t) = H_s + \text{Re} \left[\frac{H_p \cosh(bx/l)(\cos(\omega t) + i \sin(\omega t))}{\cosh(b)} \right]$$

(1)

where $h(x,t)$ is the head at time t and distance x from the tidal fluctuation, H_s is the steady component of head, H_p is the periodic component of head or the tidal amplitude, $b^2 = 2\pi i(L^2 S/TP)$ where L is the length of the aquifer, S is the specific yield, T is the
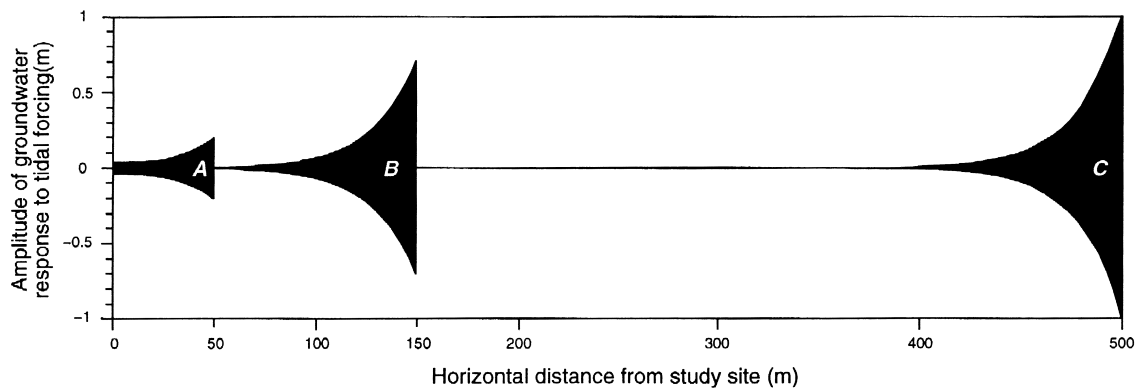

Fig. 5. Analytical solution for groundwater response with $H_s = 20$, $S = 0.35$, $T = 1000$, $P = 0.5$ to (A) 0.4 m tidal forcing adjacent to the study site ($H_p = 0.2$, $L = 50$); (B) 1.4 m tidal forcing downstream of the creek obstruction 150 m from the study site ($H_p = 0.7$, $L = 150$); and (C) 2 m tidal forcing at the Hunter River 500 m from the study site ($H_p = 1.0$, $L = 500$).

aquifer transmissivity, P is the tidal period and the angular frequency of fluctuations, $\omega = 2\pi/P$.

Townley's analytical solution can be used to estimate the response of groundwater at the Tomago site to various scales of tidal influence. Specifically it can be used to determine whether groundwater behaviour at the study site is due to the 0.4 m tidal range in the adjacent creek, the 1.4 m tides in the creek 100 m downstream or the 2 m tides in the Hunter River 500 m away.

Fig. 5 shows Townley's analytical solution evaluated for these three scales of tidal forcing in an idealised homogeneous, one-dimensional aquifer, using hydraulic parameters estimated for our site. The results show clearly that the larger tidal forcing in the river is not transmitted over the long distance to the field site, while the smaller tidal fluctuations observed in the adjacent creek are. Therefore, the local groundwater movement is dominated by tidal forcing directly adjacent to the site. These results are consistent with observed head data from the study site, suggesting that the Townley solution

broadly represents the behaviour of the groundwater in the sand unit at the study site.

The scale of the study site is small in comparison with the range of scales encountered at the Tomago South wetlands, where distance between tidal waterways varies from approximately 40 m as seen at the study site, up to 300 m. Tides vary from small attenuated fluctuations such as those encountered at the study site to the full 2 m range of the Hunter River. Most of the wetland is close enough to a tidal creek or channel to experience tidal forcing of groundwater.

5. Two-dimensional finite element analysis

Conditions at the study site are far more complex than the simple assumptions required for Townley's solution. The Townley model predicts a diminishing tidal response with distance from the tidal forcing, even at the small scales of the field site. Such a field response has been observed by Howes and Goehringer (1994) and Nuttle and Harvey (1988). Several factors
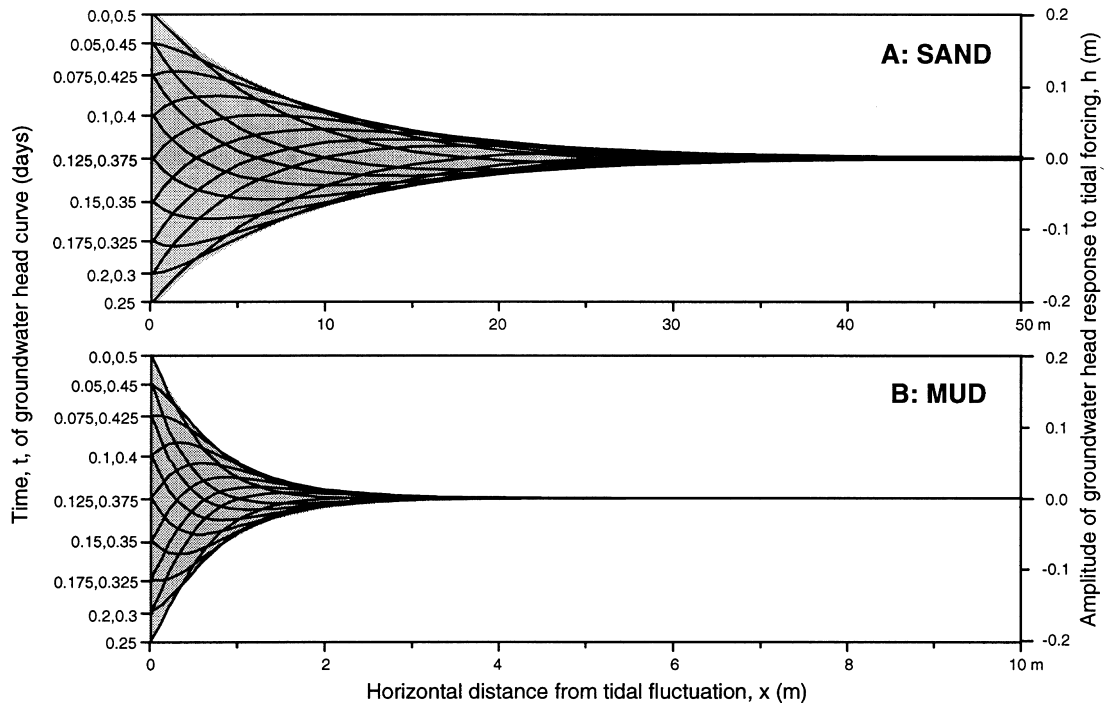

Fig. 6. SEEP/W and Townley solutions ($H_s = 6$, $H_p = 0.2$, $P = 0.5$) for (A) sand ($S = 0.35$, $T = 1000$, $K_s = 26$ m/d, $\Theta_s = 0.45$) and (B) mud ($S = 0.1$, $T = 0.35$, $K_s = 0.05$ m/d, $\Theta_s = 0.7$). Grey shading represents the amplitude of the Townley solution at any distance and lines represent the SEEP/W solution at specific times.

distinguish our study site from the idealised situation described by Townley and in some instances from the other sites. These include the presence of over-bank flow, observed three-dimensional ground water flows, aquifer heterogeneity, and non-sinusoidal tidal behaviour. SEEP/W, a commercial two-dimensional finite element model was used to model the site (GEO-SLOPE, 1994). A two-dimensional model was used rather than a three-dimensional model because the observed fluxes in the third dimension are smaller than those in the modelled dimensions.

SEEP/W is based on a mass balance statement and Darcy's Law applied to both saturated and unsaturated flow (GEO-SLOPE, 1994). The governing differential equation used by SEEP/W is:

$$\frac{\partial}{\partial x}\left(K_x \frac{\partial H}{\partial x}\right) + \frac{\partial}{\partial z}\left(K_z \frac{\partial H}{\partial z}\right) Q = \frac{\partial \theta}{\partial t} \tag{2}$$

where H is total head, K_x and K_z are hydraulic conductivity in the x and z directions respectively, Q is the applied boundary flux, θ is the volumetric water content and t is time.

No examples of SEEP/W being used to model a tidally forced aquifer were found, so confidence in the ability of SEEP/W to model a sinusoidally varying tidal head boundary was gained by successful replication of Townley's analytical solutions for a 0.4 m tidal range in sand and mud. This comparison is valid despite the linearisation assumption in the solution of Townley because the head changes are small compared to the aquifer thickness. Consequently, the linearised solution of Townley is close to the solution of the fully non-linear phreatic aquifer equations. A comparison of the results from the SEEP/W model and the Townley analysis is given in Fig. 6.

Not only is the amplitude of groundwater response to tidal forcing modelled accurately by SEEP/W, as seen in Fig. 6, the shape of the tidal wave at any specific stage of the tidal cycle is also comparable (not shown in Fig. 6).

To model saturated and unsaturated flow at the study site, the finite element mesh shown in Fig. 7 was constructed. The full mesh extends down to an elevation of −20 m. Element layers and material types were based on the site stratigraphy shown in Fig. 2.

5.1. Soil water retention and conductivity curves

Application of SEEP/W to model unsaturated flow requires detailed functions of hydraulic conductivity and volumetric moisture content versus pore pressure to define the behaviour of each material. Saturated conductivity and saturated moisture content (using porosity) were based on the values in Table 1. Saturated moisture content was fixed at 0.45, 0.7, 0.6 and 0.7 for the silty sand, estuarine mud, clayey sand and surface layer, respectively. Initial saturated hydraulic conductivity values were 26, 0.06, 1 and 0.04 m/day for the silty sand, estuarine mud, clayey sand and surface layer, respectively; these values were modified to 20, 0.15, 2 and 0.043 m/day during calibration. The forms of the functions were not measured for the materials at the site. Functions were selected for each material type from Appendix A.5 of the SEEP/W manual (GEO-SLOPE, 1994) then modified during calibration to those shown in Fig. 8. By calibrating
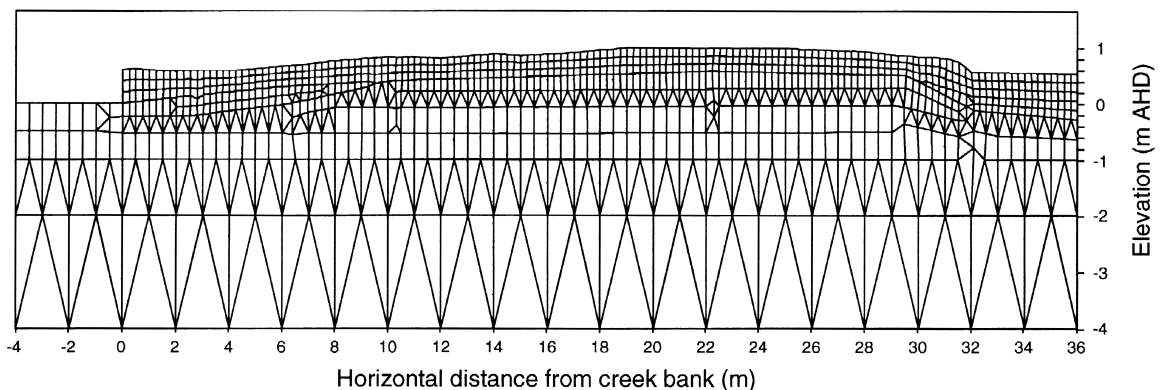

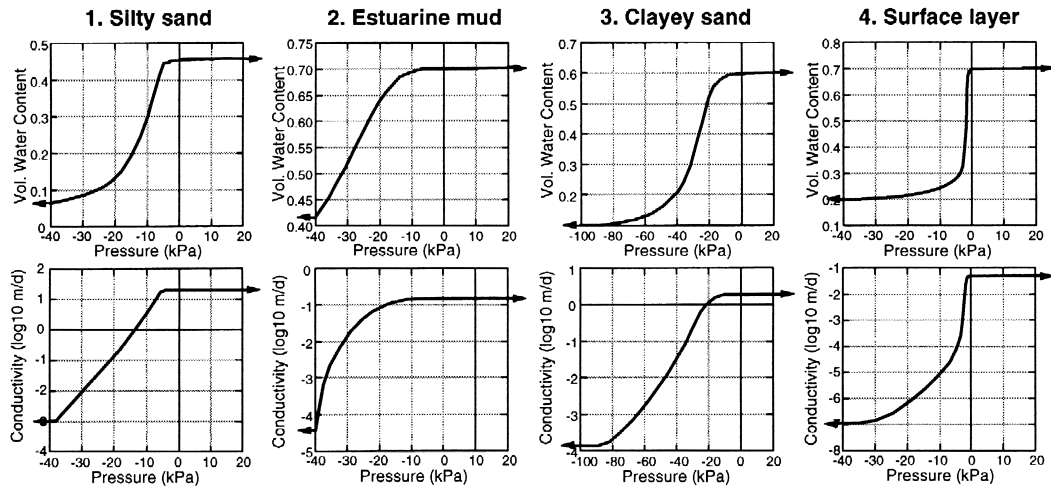Fig. 7. SEEP/W mesh for the top 5 m of the study site (grid goes to 20 m).

Fig. 8. Volumetric water content and hydraulic conductivity versus pore pressure for the four material types used in the SEEP/W model.

these functions and the 2D model to measured hydraulic head for a variety of different scenarios, an operational model was created that would apply to any plausible values of recharge, tidal flux and evapotranspiration within the ranges of calibration.

During the calibration process it became apparent that the water table response to tidal forcing is determined largely by the hydraulic conductivity of the sand and mud units. The response to rainfall was found to be determined primarily by near-surface characteristics. Calibration of the model for both rainfall and tidal forcing demanded conflicting material characteristics for the mud layer. To produce the observed rapid response to tidal inundation, a high air entry pressure of −15 kPa was set for the estuarine mud in Fig. 8, so the mud remains saturated and the conductivity does not decrease rapidly when the water table drops. In contrast, to produce the slow water table decline observed after a rainfall event, a surface layer was constructed with a low air entry pressure to ensure a rapid decrease of conductivity with saturation. The material type of the top layer of elements in Fig. 7 is given the hydraulic functions of the surface layer.

At the study site, a significant component of both surface infiltration and subsurface transport is believed to occur in macropores rather than through the sediment matrix. Use of Darcy's Law and relative hydraulic conductivity functions is not generally considered appropriate in modelling macropore flow

(J. Long, personal communication). However, considerable research has been completed on measuring soil water retention and hydraulic conductivity curves in soils where two or multi-domain macropore flow is observed (Jarvis and Messing, 1995; Timlin et al., 1994; Harvey, 1993). Large macropores, such as the crab holes found at the study site, have been observed to drain at matric potentials of less than 0.1 kPa (Beven and Germann, 1982). When the soil is nearly saturated, macropores dominate the flow and the conductivity is high, however, when the pressure drops slightly, the macropores de-saturate and the conductivity rapidly drops to that of the soil matrix.

In order to better reflect the behaviour of macropores in the near surface region of the estuarine mud, a surface layer was created as described above. The upper soil layer at the site is characterised by a high concentration of crab holes in the intertidal zone and by loose highly organic topsoils above the intertidal zone. This contrasts with the relatively undisturbed estuarine mud matrix beneath. The air entry pressure is low (−1 to −3 kPa) and the slope of the moisture content function of this surface layer is very steep, which is consistent with curves for macropore soils reported in the literature.

The soils were modelled to be anisotropic, with anisotropy ratios (K_z:K_x) equal to 0.25, 0.5, 1, 1.5 in the silty sand, estuarine mud, clayey sand and surface layer, respectively, where K_x is taken from the conductivity function. The higher anisotropy value

employed in the surface layer reflects the influence of the macropores, while the lower values in the silty sand and estuarine mud reflect horizontal stratification in the deposit. The model was quite sensitive to variations in anisotropy and saturated hydraulic conductivity of all layers except the clayey sand unit.

In addition, retention and conductivity functions vary with changes in the pore water salt concentration. Bresler (1981) showed that solute composition (Na:Ca ratio) and concentration affect the unsaturated hydraulic conductivity and water retention of clayey soils. Hydraulic conductivity increases and the slope of the water retention function becomes steeper with increasing solute concentration in soils with a high Na:Ca ratio. The implications of this on the near surface water and solute balance at the study site may be significant, making it a topic for further investigation outside the scope of this paper.

5.2. Boundary functions

Three types of boundary conditions were applied in the model at various nodes and times (Fig. 9).

Tidal head (m) was applied at all surface nodes of lower elevation than the maximum tidal height as a varying head boundary function. When the head specified is less than the elevation of the node the boundary condition is set to $Q = 0$.

Rainfall was applied as a flux (m/day) to the surface layer of nodes above the zone influenced by tidal inundation. Once the surface is saturated, this boundary condition approximates infiltration by setting the head boundary condition so that the head equals node elevation. At such times, the applied rainfall flux exceeds the saturated hydraulic conductivity. This is equivalent to infiltration excess or surface ponding.

Potential evaporation was applied as a nodal flux (m^3/day) equally to the top three layers of nodes in the mesh (approximately 0 mm, 130 mm and 260 mm below the surface) in order to approximate the actual vertical distribution of moisture extraction through evapotranspiration. During periods of tidal inundation and rainfall, the surface evaporation is taken from the surface ponding store rather than the soil matrix so as not to affect soil moisture.
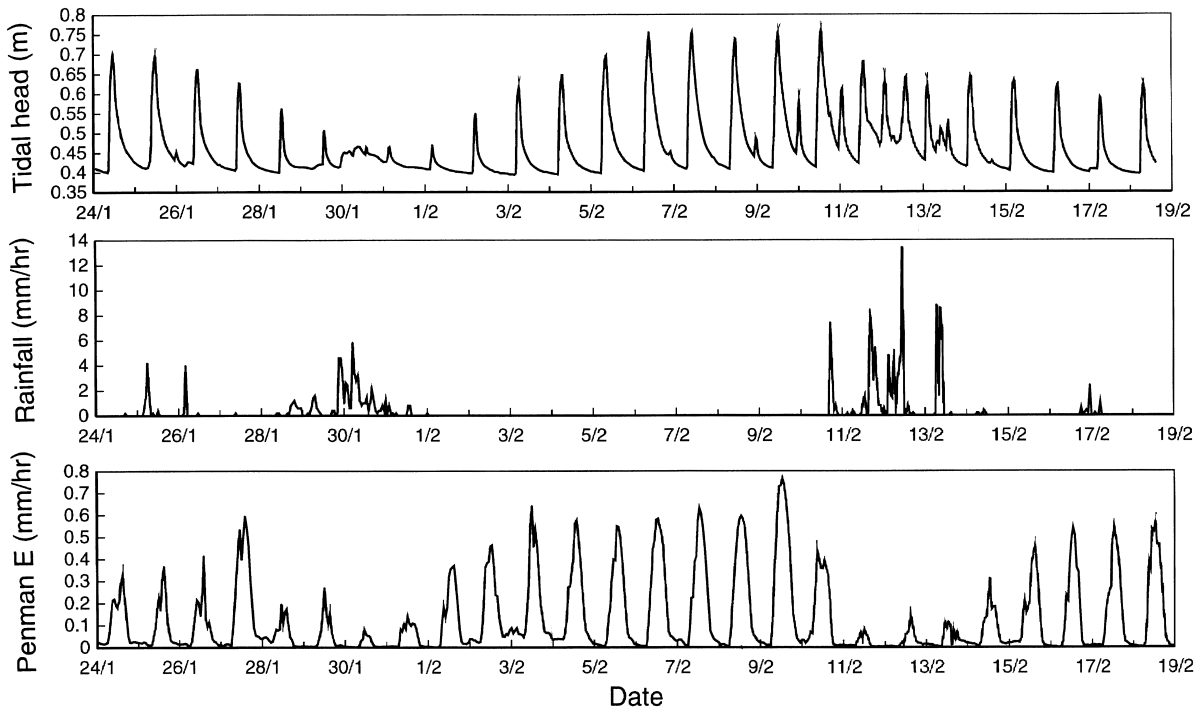

Fig. 9. Boundary condition input data.

The SEEP/W software does not allow two boundary conditions to be applied to the same node, nor does it allow for automatic exchange of boundary conditions. However, rainfall, tidal inundation and evapotranspiration occur simultaneously at surface nodes. Therefore, when conflicting boundary requirements occur, the dominant process at that time is given priority, in the order tidal inundation, rainfall, evaporation. The tidal boundary condition was applied to the highest node inundated during each period for the whole of the period.

Due to limitations in the number of time steps allowed in SEEP/W, the model was run in nine sections. The boundary conditions applied at each node were changed at the beginning of each section and at the commencement or end of a rainfall period (more frequent altering of boundary conditions does not significantly alter results). The final time step of the previous section was used as the initial condition for the following section. The length of time step was varied from 15 min to 2 h. The shorter intervals were used for periods where more rapid change was expected, e.g. the onset of rainfall and during the rapid rise and fall of the tide.

SEEP/W is not capable of modelling the evapotranspiration process directly; however, a modifier function may be applied to scale potential evaporation data according to the pore pressure at each node. An evaporation modifier based broadly on the stress index principle (i.e. modifier $= SI = (\theta - \theta_{\text{wilting point}})/(\theta_{\text{field capacity}} - \theta_{\text{wilting point}}))$ was used in the model. The potential evaporation for each time step is multiplied by the modifier value calculated from the matrix pressure at that node to calculate the evaporative boundary flux in the model. The modifier decreases the magnitude of the evaporation boundary flux as the matrix pressure, and correspondingly the soil moisture available for evaporation, decreases at any evaporation node. In the absence of actual wilting point and field capacity data for the study site, the modifier was developed using estimates within normal ranges then adjusted during calibration to remove the sharp decreases in water table during low tide.

5.3. Model results

The SEEP/W model was calibrated for the two data sets in Fig. 3: first, a 2-day rainfall event during neap
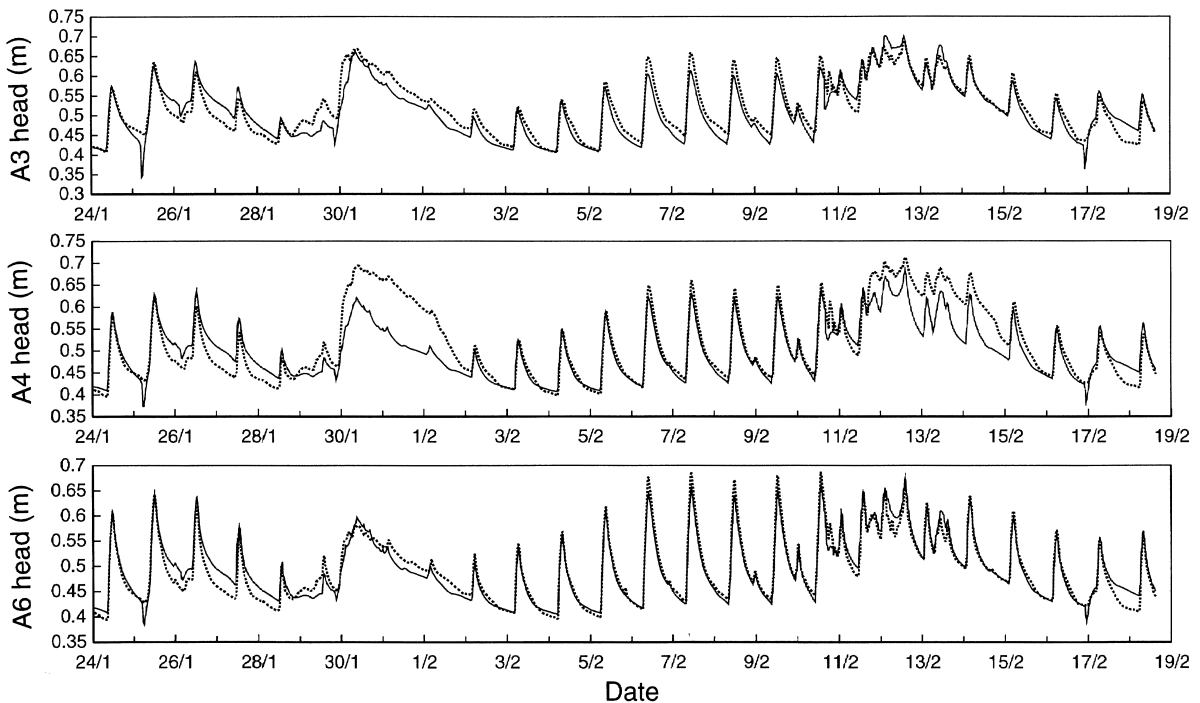

Fig. 10. Comparison of model results and observations (dashes represent observations, solid line is SEEP/W output).
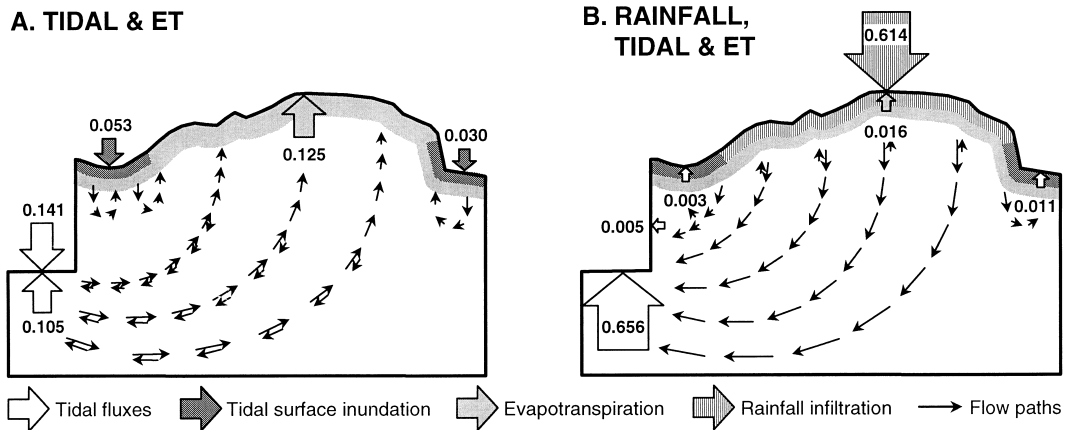
Fig. 11. Hydrologic budget and generalised flow paths for (A) tidal and evaporative forcing 7:00 9/2/97 to 10:00 10/2/97; and (B) rainfall, tidal and evaporative forcing 21:30 11/2/97 to 16:30 12/2/97. Flux units are m^3/day per metre width of creek bank.

tides; second, a spring tide period with significant evapotranspiration followed by a rainfall event during the end of the spring tide period. Model parameters for each soil type were determined by the relative balance of fit between wet and dry periods. The model was then applied to a continuous period of 26 days, as shown in Fig. 10.

The average deviation of model heads from observed heads was in the order of 5 mm for A3, 15 mm for A4 and 2 mm for A6. Maximum deviations of up to 61 mm occurred when extreme drops in head were predicted by the model at the commencement of rainfall, e.g. on 25/1/97 and 17/2/97. A4 shows a significant ''under prediction'' for high rainfall periods from 30/1/97 to 2/2/97 and 12/2/97 to 15/2/97 which is believed to be an artefact of the field data due to disturbance during bore hole installation. SEEP/W underpredicts the peak tidal response during the dry period from 6/2/97 to 10/2/97.

Model results are highly sensitive to variations in saturated hydraulic conductivity, anisotropy ratio, retention and conductivity function slope in the surface layer and estuarine mud units. Predictions of tidal forcing are much less sensitive to these variations than are predictions of rainfall. Reviewing and changing the surface boundary condition between tidal and rainfall and evaporation more frequently (e.g. between each time step in the model run) was not found to significantly alter head response.

5.4. Relative magnitude of porewater flows

Boundary fluxes for ''representative'' tidal and rainfall periods were compiled from SEEP/W output (Fig. 11). The fluxes presented in the Figure are the total flux in a given direction over 1 day, summed over the length of the boundary to which they are applied. Initial and final times with similar observed hydraulic heads were chosen for each figure to facilitate direct comparison.

Peak modelled saturated specific discharge is indicative of the maximum zone of groundwater movement. For the tidal period (A), peak specific discharge was in the order of 0.38 m/day below the creek bed and 0 to 0.1 m/day in the centre of the site. Specific discharge for the rainfall period (B) peaked at around 0.43 m/day below the creek bed, and was generally in the range 0 to 0.1 m/day in the centre of the site, decreasing to around 0.05 in the unsaturated zone. Flow paths through the sand unit to and from the creek are dominant during both periods. The tidal period is characterised by a strong cyclic response to tidal fluctuations in both the sand and mud units, with an equally significant evaporation loss. Surface tidal inundation provides a smaller but substantial contribution to the water balance. The rainfall period is completely dominated by subsurface drainage of infiltrated rainfall, which is only slowed, not reversed, during high tides. The maximum rainfall fluxes occur

during a neap tide period when there is a minimum initial storage and maximum hydraulic gradient for recharge.

The fluxes above can be examined and used to explain the high salt concentrations in the piezometers, which were observed to be at concentrations up to 1.5 times that of seawater. Water salinity in estuarine surface water at the site has been observed to range from 6 to 35 ppt, so concentration of salts through evapotranspiration must be occurring. Indeed salt encrustation is often observed at the site. These concentrations can be explained by the climate data, which suggest that annual average evapotranspiration exceeds rainfall infiltration. Furthermore, the zone of tidal infiltration into the soil matrix is small, as seen from the above fluxes (a peak flux of 0.38 m/day was observed to occur at the creek edge), so that mixing of soil water with estuarine water is minimal. Ultimately it is the balance between the concentrating of salts due to evapotranspiration and the diluting effect due to rainfall and tidal mixing that gives the final soil salt concentration.

6. Conclusion

This study has found that at the Tomago South site, in contrast to previous studies at other sites (Howes and Goehringer, 1994; Nuttle and Harvey, 1988), tidal forcing is a dominant mechanism of porewater movement in the saturated and intertidal zones, with the largest fluxes due to subsurface drainage to the creek. Major rainfall events are observed to have a highly significant but short-term effect on water table levels due to rapid drainage through the underlying sand aquifer. Evapotranspiration was estimated to be very important during dry periods and is anticipated to be highly significant in determining the salt balance in the soil matrix.

The range of influence of tidal forcing extends far beyond the zone of surface inundation and it was not possible to observe a significant attenuation in groundwater response over the small scale studied. Analytical methods have enabled us to estimate the decay of the tidal response for a variety of scenarios encountered at Tomago. From these results, we can conclude that tidal fluctuations will influence the water table throughout a large part of the Tomago

South wetlands, due to the density of the tidal drainage network.

Finite element modelling of the site has provided insight into the path of water movement and the partitioning of rainfall and tidal effects within the sediments. Future work will couple a two-dimensional solute transport model with the flow model.

The anticipated application of this research at the Tomago site is in predicting groundwater and surface water balance response to alterations in the tidal and surface water regimes arising from proposed wetland restoration works.

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A water budget and hydrology model of a basin mangrove forest in Rookery Bay, Florida

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Abstract.　　Water budgets of two basin mangrove forests in Rookery Bay were determined by measuring during a 2-year period the inputs of precipitation and tides, together with losses through seepage, runoff and evapotranspiration. Precipitation inputs to the forest floor were 75.1% from throughfall and 19% from stemflow for a total of 1097 mm year^{-1}, or 91% of annual rainfall. Runoff was estimated at 896 mm year^{-1}, or nearly 77% of the combined input of throughfall and stemflow. Loss from evapotranspiration was linear with saturation deficit of the atmosphere and was 967 mm year^{-1} (0.7–4.5 mm day^{-1}). Loss from horizontal flow of groundwater in shallow mangrove soils was ~285 mm year^{-1}. Frequency of tidal inundation was seasonal, ranging from <5 tides month^{-1} in February to 30 tides month^{-1} in September. Tides recharged soil saturation deficits, the cumulative tidal input being 12 276 mm year^{-1} and efflux being 11 767 mm year^{-1}. The relative significance of tides and rainfall deficits (rainfall – evapotranspiration) on the seasonal patterns of soil saturation (water levels) and soil salinity were simulated with a finite-difference hydrology model (HYMAN). Model simulations demonstrate that soil salinity at higher elevations in the intertidal zone, where tidal inundation frequency is reduced, is more sensitive to changes in rainfall deficit.

Extra keywords: evapotranspiration, soil salinity, intertidal wetlands, simulation modeling

Introduction

Hydrology is probably the single most important determinant of ecological processes in wetlands (Gosselink and Turner 1978). The apparent influence of physical forcings, such as river discharge, rainfall, evapotranspiration and tides, on the structure and function of wetlands has led to the development of different typologies of wetlands. The functions of wetlands are also classified not only by the nature of water flow, but also the geomorphology of the landscape (Brinson 1993). These typologies are based on the general premise that the structure and function of wetlands are constrained by the gradients in hydrodynamic energy that control the quantity and quality of water. However, these analyses are limited by fundamental information on the hydrology of different types of wetlands, particularly infrequently flooded tidal ecosystems. Although description of the hydrology of coastal ecosystems has improved, there is still a need to identify the mechanisms by which hydrology controls the ecological processes of coastal wetlands.

Coastal geomorphology and geophysical processes have been recognized as important environmental constraints on the establishment, maintenance and function of mangrove ecosystems (Thom 1982; Woodroffe 1983; Lugo *et al.* 1988, 1990; Twilley 1988; Kjerfve 1990; Twilley 1997). Thom (1982) developed the idea that the geomorphic and geophysical characteristics of the coastal zone are important to the structure of mangrove forests, while microtopography controls more local hydrologic factors that influence mangrove ecology (Twilley 1988; Twilley *et al.* 1996). Lugo and Snedaker (1974) qualitatively classified mangrove forests in south Florida into six major types depending largely on local patterns of hydrology. The distinction between the structure and function of riverine, fringe and basin forests has been related to the variation in water turnover among these three types of mangroves. The basin forest is located inland of fringe mangroves in the upper intertidal zone forming a paludal basin (Davis 1940, 1943; Provost 1973; Lugo and Snedaker 1974). Hydrology of the upper intertidal zone above regular tidal inundation is complex because of the seasonal nature of infrequent tides, rainfall, and evapotranspiration (Provost 1973). Although basin forested wetlands may cover most of the total intertidal zone in some regions of south Florida, their ecology is least understood among mangrove types because of the complex nature of their hydrology.

The water budget for a wetland provides an initial framework for understanding and interpreting all other wetland functions (Kadlec *et al.* 1988). Tide frequency and duration are commonly used to explain the distribution of biota in mangrove ecosystems (MacNae 1968; Rabinowitz 1978; citations in Por and Dor 1984). Differences in the productivity (Twilley *et al.* 1986) and detritus export (Twilley 1985) of basin forests compared with regularly flooded fringe

and riverine mangroves have been related to reduced tidal activity in the upper intertidal zone. In addition, salinity of mangrove soils with less frequent tidal inundation, along with other potential stressors such as hydrogen sulfide, may vary depending on the balance of water, affecting the zonation and growth of these forests (Nickerson and Thibodeaux 1985; Carlson and Yarbro 1988; McKee *et al.* 1988). It is evident that the ecology of basin mangroves may be linked to the complex hydrology of the upper intertidal zone.

There are few quantitative water budgets for mangroves, which limits our understanding of how hydrology controls ecological processes of mangrove ecosystems. Some studies use residuals of geophysical models at the mouth of tidal creeks to infer the influence of mangroves on the flux of water, salt, nutrients and pollutants in coastal waters (Ridd *et al.* 1980; Wolanski and Ridd 1986; Wattayakorn *et al.* 1990; Wolanski *et al.* 1990). The use of mangroves as a forcing on such hydrodynamic models, while giving insight into the geophysical processes of exchange in the coastal margin, do not give much resolution to the hydrologic parameters within mangrove wetlands. There have been several studies of specific hydrologic parameters of mangroves; most of these are associated with the unique ecophysiology of forested halophytes but lack the comprehensive analysis of a water budget of the mangrove ecosystem (e.g. Naidoo 1985).

Hydrology models have been helpful in verifying many of the linkages in marsh production and factors that control pore water chemistry (Howes *et al.* 1981; Hemond and Fifield 1982; King *et al.* 1982; Dacey and Howes 1984). These models have made important contributions to understanding complex feedback effects of rooted vegetation on hydrology that in turn control plant production (Howes *et al.* 1986). Such complex interactions have not been simulated in mangrove wetlands. The first objective of this paper is to summarize a water budget of data collected during a two-year period, 1978–79, in two basin mangrove forests in south Florida to determine parameters that control water levels and salinity in the upper intertidal zone. A general set of equations can be used to describe the major processes associated with the exchange of water and salt between mangroves and coastal waters as follows:

$$\mathrm{d}L/\mathrm{d}t = R_\mathrm{t} + R_\mathrm{s} + S_\mathrm{i} - S_\mathrm{p} - E_\mathrm{T} - S_\mathrm{o} + T_\mathrm{i} - T_\mathrm{o}; \qquad (1)$$

$$\mathrm{d}(SL)/\mathrm{d}t = (T_\mathrm{i} \times S_\mathrm{t}) - (T_\mathrm{o} \times S_\mathrm{s}) - (S_\mathrm{p} \times S_\mathrm{w}) - (S_\mathrm{o} \times S_\mathrm{s}); \qquad (2)$$

where L is water level (above mean sea level, cm); R_t is throughfall (cm day^{-1}); R_s is stemflow (cm day^{-1}); S_i is surface inflow (cm day^{-1}); S_p is seepage (cm day^{-1}); E_T is evapotranspiration (cm day^{-1}); S_o is surface outflow (cm day^{-1}); T_i is water input by flood tide (cm day^{-1}); T_o is water output by ebb tide (cm day^{-1}); and t is time (day); S is the concentration of salt (g kg^{-1}); S_t is the salinity of bay waters at slack flood tide (g kg^{-1}); S_w is the salinity of pore water (g kg^{-1}); and S_s is the salinity of surface water (g kg^{-1}). These

parameters were used to develop a hydrology model, HYMAN, for basin mangroves and simulations of this model were used to test the sensitivity of soil salinity to changes in precipitation and evaporation. Results of model simulations on the temporal and spatial resolution of water levels and soil salinity were used to calibrate the hydrology model.

Site description

Rookery Bay National Estuarine Research Reserve is in south-western Florida near Naples (25°62′N,80°25′W) (Fig. 1). Rookery Bay is part of a larger subtropical lagoon system with a barrier island isolating the estuary from the Gulf of Mexico. The lagoon is dominated by tidal and wind energies and minor river flow resulting in mesohaline salinities. Mean salinities at three bay stations were 30.8 to 33 g kg^{-1} in 1971, and 29.3 to 33.1 g kg^{-1} in 1972 (Yokel 1975). Extreme ranges for these stations were from 16.1 to 37.7 g kg^{-1} and 17.3 to 36.1 g kg^{-1} for the two years. Minimum values were always recorded during September during peak river discharge. The average air temperature for this area is 23.6°C, and water temperatures range from 13.3 to 34.7°C. Precipitation is 1346 mm, 69–65% of which occurs from June to August. The major source of fresh water to the bay is from Henderson Creek with an average annual discharge rate of only 0.68 m^3 s^{-1} (11-year average, USGS). The bay is a shallow, non-stratified, mesohaline estuary with an average depth of 0.91 m and volume of 3.83 × 10^6 m^3. Tides are semidiurnal with unequal amplitude and the annual mean tide range is 0.55 m, resulting in a tidal prism of 4.312 × 10^6 m^3. Since this estuary is so shallow, the tidal prism represents 112% of the mean volume. From determinations of 'new water' into Rookery Bay during each tidal exchange, Yokel (1975) estimated a residence time of about 3.2 days.

Mangroves are the major habitat of the intertidal area of Rookery Bay and they cover 1453.8 ha (52.7%) of the total area. Two sites were chosen in the Rookery Bay estuary to study hydrology within basin mangrove wetlands, referred to as Forests 1 and 2. Both forests are exposed to infrequent inundation occurring when tidal amplitude reaches the height of a berm, which separates fringe and basin mangroves. Rookery Bay Forest 1 (RBF1) was located in the south-east corner of the bay (Fig. 1). This study site is approximately 1.5 ha and consists of a mixed vegetation zone just inland of the fringe mangrove system and a pure stand of *Avicennia germinans* inland of the mixed associes. Rookery Bay Forest 2 (RBF2) is located in the north-central area of the estuary, adjacent to Hidden River, which is a tidal creek that drains the northern wetlands of Rookery Bay (Fig. 1). This study site had an area of about 3 ha and was a nearly pure stand of *Avicennia*. The general characteristics of forest structure are summarized in Table 1. The biomass of mangroves in RBF1 ranges from 55 to 72 Mg ha^{-1} (Twilley *et al.* 1992).
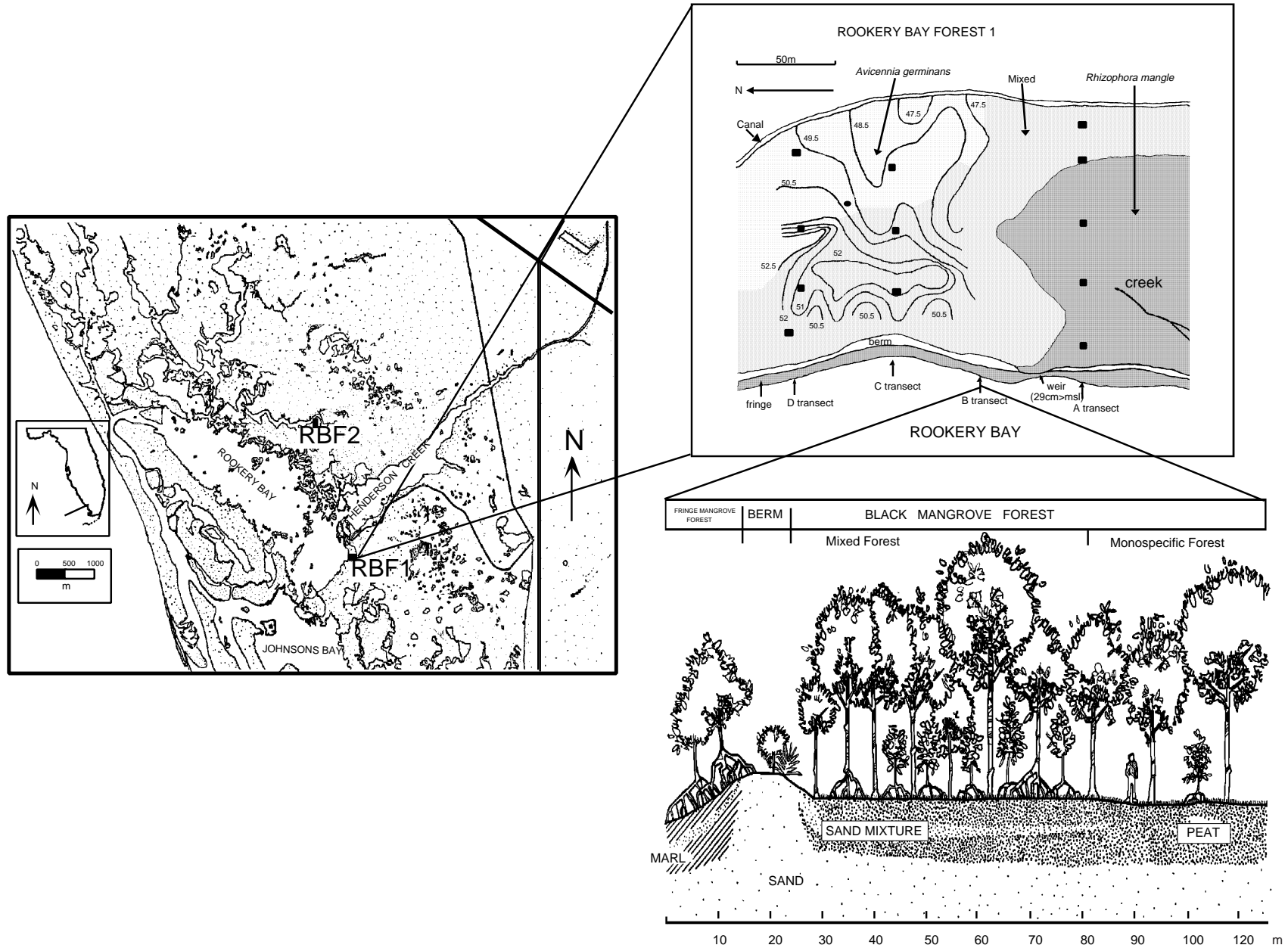
Fig. 1. Map of basin mangrove forest in Rookery Bay used to develop hydrology budget and model. Contour lines represent elevations in cm > mean sea level (msl). (■) salinity wells; (●) water level recorder ~65 m inland between transects C and D. Cross section describes mangrove forest structure along the B transect perpendicular to the shore.

Table 1.   Forest structure and complexity indices for the three veget-ation transects in the basin mangrove forests at Rookery Bay

Complexity Index (CI) is a quantitative description of the structural com-ponents of a forest. CI = (Height (m) × No. species × Basal area (m²/0.1 ha) × Density (no./0.1ha))/1000

	Rookery Bay Forest 1 Mixed	Rookery Bay Forest 1 Monospecifc	Rookery Bay Forest 2 Monospecific
Height (m)	10.7	8.3	9.3
No. species	3	2	2
Basal Area (m²/0.1 ha)	2.31	1.56	1.05
Density (no./0.1 ha)	448	308	428
Complexity Index	33.2	8.0	8.4

The topography of the forest floor was determined in RBF1 and 2 by measuring water depth at a grid of 60 and 200 stations, respectively, during slack ebb tide when no water level changes were observed (based on continuous water level records). Surface water during the survey represents a level plane that at one station was surveyed to a bench mark to determine its height relative to mean sea level (msl). The topography of RBF2 was bowl shaped with a centre low of 45 cm > msl. The elevations increased to greater than 50 cm > msl along the outer edges (particularly the western edge) of the study site, but most this forest was between 48 and 49 cm > msl. Contour lines at RBF1 did not show a concentric low point within the forest, but the elevation decreased from the berm inland (Fig. 1). Survey lines along a transect in RBF1 perpendicular to shore describes the topographic relationship between the bay, berm and basin mangrove forest floor (Fig. 1). Fringe mangroves inhabited the bayward edge of the berm and were dominated by *Rhizophora*. Along this transect the berm reached a peak height of 0.61 m > msl. The inland edge of the berm subsided to between 0.45 and 0.50 m >msl, which was the area inhabited by the basin mangrove forest. The berm prevented the semidaily tides that occurred in the fringe mangrove zone from reaching the interior basin mangrove forest.

Rookery Bay is at the junction of two contrasting physio-graphic regions of south-west Florida. The region from Marco Island to Fort Myers has been characterized as poorly drained coastal wetlands with limited runoff from the interior. The uplands of this sandhill region have relatively high elevations consisting of sandy soils and dunes of Pleistocene origin that are well drained. The coastal region south of Cape Romano in the Ten Thousand Island area to Cape Sable of the Everglades National Park is characterized by very small relief (2 cm km⁻¹), a broad, well developed marsh–mangrove complex, deep peat deposits, and extensive freshwater runoff from the interior. Mangrove soils of Rookery Bay reflect the accumulation of organic matter over the past 4000 years in response to rise in sea level (Scholl 1964; Scholl and Stuiver 1967; Coultas 1978). The soils of the intertidal area colonized by mangroves are Histosols classified as Typic Sulfihemists.

These peat layers range from 0.45 to 2.0 m deep, have an organic content of 24% dry mass to depth of 0.2 m, have a porosity of 82%, and usually overlay a sand layer of variable thickness (Coultas 1978; Twilley 1982). The deposition rate at RBF1 was estimated at 1.5 mm year⁻¹ based on ²¹⁰Pb measurements (Lynch *et al.* 1989).

Methods for water budget

Precipitation

Rainfall data were provided by the Rookery Bay Marine Research Station from a collector located in a clear area about 0.35 km from RBF1 and 1.52 km from RBF2. The interception of rainfall by the forest canopy at each site was determined by measuring throughfall and stemflow. Ten throughfall collectors, constructed by attaching plastic funnels (13.5-cm diameter) to the top of 3.9-L plastic cartons, were placed in both RBF1 and 2. Stemflow was measured from six trees (*Avicennia*) in each forest, representing size classes ranging from 8 to 10 cm dbh (diameter at 1.5 m height). A polyurethane collar placed around the trunk of each tree diverted stemflow into 78-L collectors (Likens and Eaton 1970). Measurements of volume were made at two-week intervals for each tree for 9 months at both sites. Missing stemflow values were determined from correlation between rainfall and stem volume of individual trees.

Water level records

Steven type F-1 water level recorders were used to measure water level fluctuations within RBF1 and 2. A water level station in RBF1 was established at a site 65 m inland from the berm (Fig. 1). At slack flood tide, the height of the water above ground level within both forests was correlated with the height of water in Rookery Bay >msl at Shell Point. Tidal records for Rookery Bay at Shell Point were collected by the Rookery Bay Marine Research Station from 1972 to 1980. These continuous records were used to predict tidal water fluctuations in both basin mangrove forests.

Evapotranspiration

Evapotranspiration was measured in RBF1 and 2 by comparing night and day changes in groundwater levels (Carter *et al.* 1973; Zoltek *et al.* 1979; Heimburg 1984). Water level changes during the night were assumed to be due to hydrostatic pressures, whereas daytime changes were also influenced by evapotranspiration. To determine the change in water level due only to evapotranspiration, the night-time slopes of water levels recorded before and after a given day were extrapolated to noontime of that day (Fig. 2). The distance between these two depths at noon represented a decrease in water level from evapotranspiration (ΔD_n). This method assumes a negligible night-time evapotranspiration rate. Lugo *et al.* (1975) did not observe any transpiration from the surface of either *Rhizophora* or *Avicennia* leaves in RBF1 at night.

The amount of evapotranspiration represented by this change in water level was determined as follows:

$$[ET] = \Delta D_n \times Sy; \qquad (3)$$

where ΔD_n is the change in water level depth below the surface of the forest floor (cm) at noon, and S_y is the specific yield of the soil. Only water level recordings that were not influenced by rains or tides could be used for this analysis.

Specific yield is the relative volume of water that is hydrostatically free and can be drained by gravity from a soil. One method of determining specific yield is by noting the rise in groundwater level in response to an inflow of water, e.g. rainfall (Todd 1959). Specific yield would be the ratio of the input (R) to the change in water level (dD). Specific yield may vary with depth of soils, particularly mineral soils, because of capillary action of water near the surface of the soil (Zoltek *et al.* 1979). This study used an
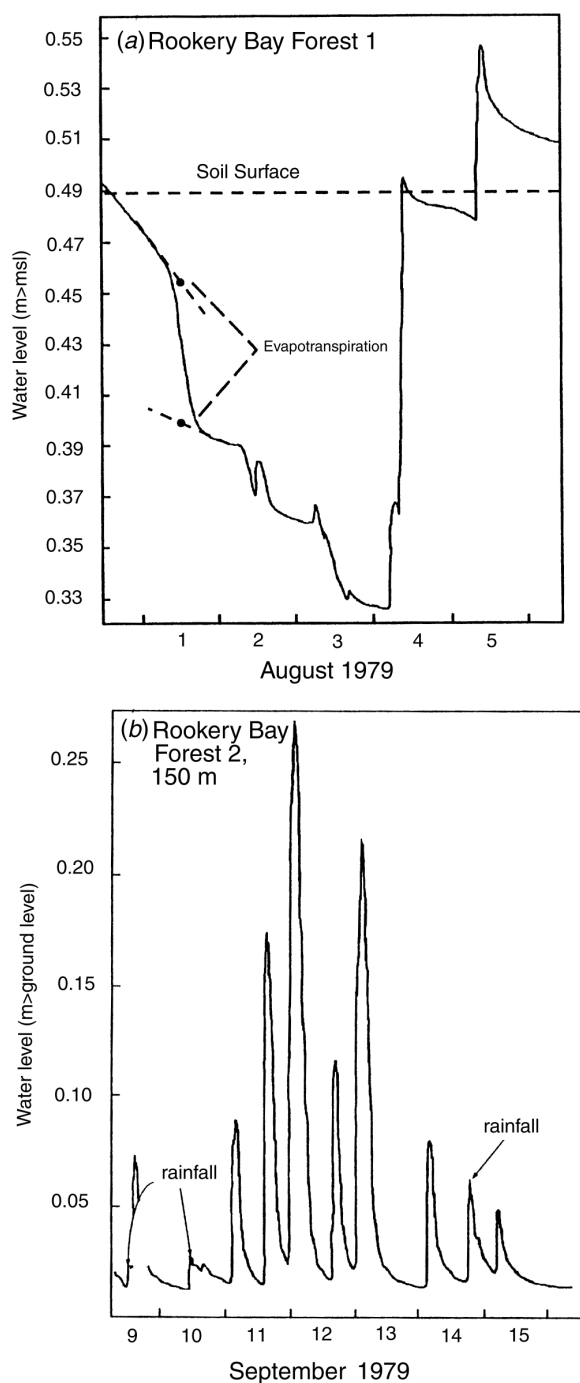
Fig. 2. Water level records at 65 m inland of the berm in a basin mangrove forest. *(a)* Rookery Bay Forest 1: difference in water levels extrapolated to noon on 1 August 1979 represents technique used to estimate evapo-transpiration. *(b)* Rookery Bay Forest 2: changes in water level due to tidal inundation except for specific responses associated with rainfall.

average specific yield for the top 40 cm of soil as used by Carter *et al.* (1973) and Burns (1978) for the soils in the south Florida cypress stands. Only four measurements of specific yield could be accurately determined in this study since periods when groundwater fluctuations were rainfall specific (with no tidal influence) were uncommon. A mean value of 0.065 based on these four measurements in RBF1 was used in this water budget.

If water levels within the forest were above the ground level or if changes in water height were influenced by tides, evapotranspiration could not be determined by the method described. Therefore a linear regression was developed that would predict evapotranspiration on the basis of the saturation deficit of air. Saturation deficit was determined by using the mean temperature and relative humidity (at 1300 hours) data in climat-ological records for Fort Myers (Anon. 1979). The saturation deficits were determined by the equation:

$$S_D = e_s(1 - [RH]); \qquad (4)$$

where S_D is the saturation deficit (in millibars), e_s is the saturation vapour pressure (in millibars), and RH is the relative humidity (percent/100). Daily saturation vapour pressure was obtained from Smithsonian Meteorological Tables (1951) and compared with five estimates of evapotranspiration representing seasonal differences. Monthly evapotranspiration values for the entire study period were determined from this regressive equation and the climatological data for Fort Myers.

We also used the Penman (1948) estimate of evapotranspiration, which combines energy balance and aerodynamic theory, to derive a relationship between evapotranspiration and meteorologic variables (Chow 1964; Fleming 1975). This estimate is best suited for estimating water loss from a free water surface or for a crop constantly supplied with water, but has been shown to be one of the most accurate estimates of evapotranspiration in wetlands (Kadlec *et al.* 1988), including mangroves (Blasco 1984). An empirical estimate of evapotranspiration was also determined from the Thornthwaite equation (Chow 1964; Mitsch and Gosselink 1993 p. 97), which uses easily measured meteorological variables. These empirical estimates were compared with the field estimates of evapotranspiration in the basin mangrove forest of this study.

Seepage

When water level was below ground level and not influenced by tides or rainfall events, the equation for the water compartment of mangrove peat is:

$$dW/dt = R_C - ([ET] + S_p); \qquad (5)$$

where W is the water level of soil, R_C is the input from uplands (recharge), and S_p is seepage of groundwater from soil to the estuary. When upland inflow was negligible, as during the dry season, then seepage was equal to the total change in water depth minus evapotranspiration. Total change in water depth was determined from shallow groundwater level records by noting midnight water depth before and after a given day. Change in water depth due to evapotranspiration was subtracted from this total change to determine seepage flow.

Salinity

Groundwater wells made of 2.54 cm diameter pipe were placed at depths of 0.5 m, 1.0 m and 2.0 m along transects in RBF1 and 2 (Fig. 1). At monthly intervals the water in these wells was evacuated, and 24 h later the wells were sampled and salinity determined with an American Optic refractometer.

Statistics

Significance was recognized at the $P<0.05$ level in simple *t*-tests.

Results of water budget

Soil salinity

Groundwater salinity at all the mangrove sites exhibited very little seasonal change, especially in the wells of 0.5 m depth (Fig. 3). Most of the few seasonal changes that were observed occurred in the 1.0 m or 2.0 m wells. The most

Rookery Bay Forest 1 – Transect D   Rookery Bay Forest 1 – Transect A   Rookery Bay Forest
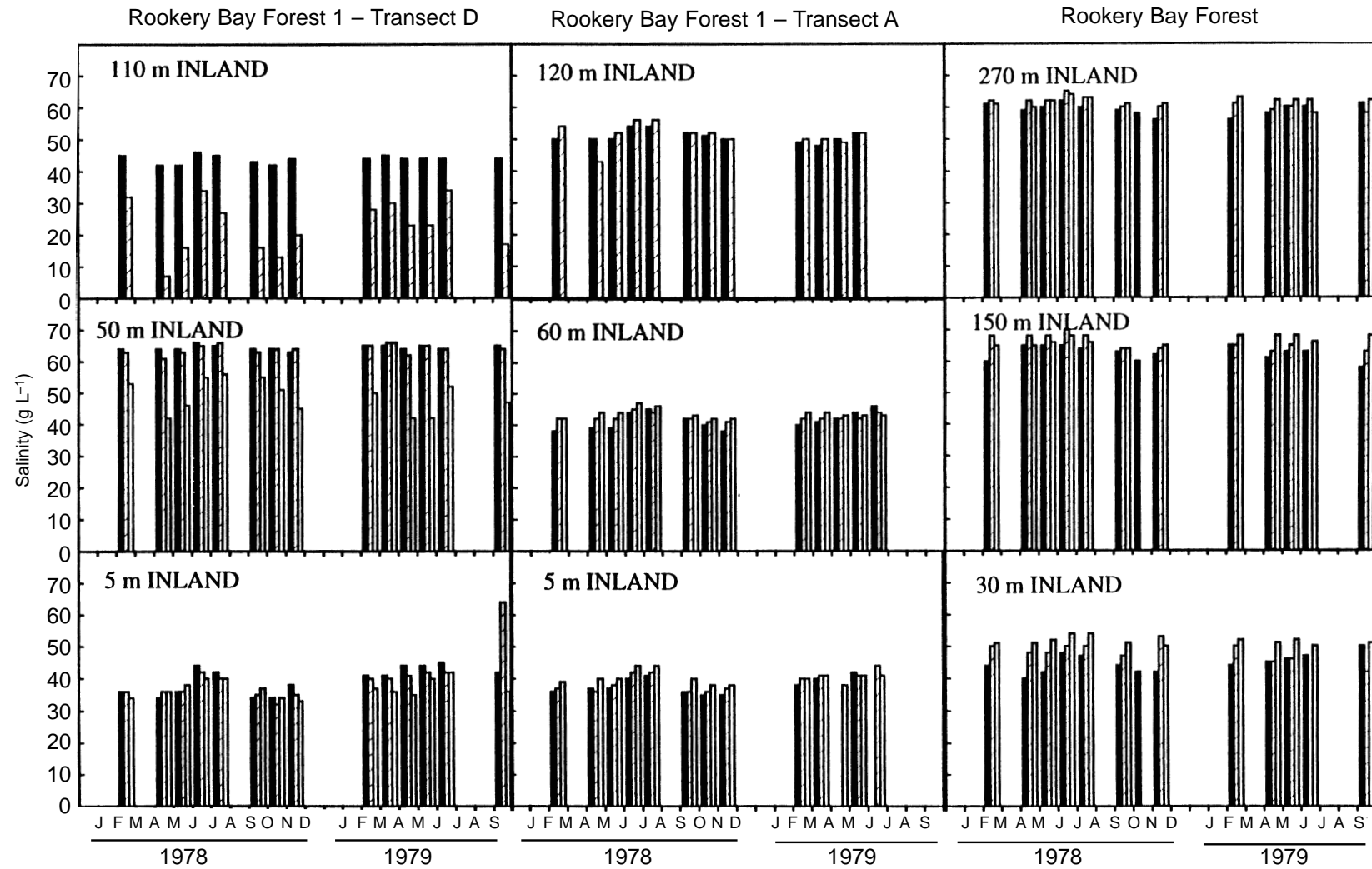

Fig. 3.   Salinity of groundwater at three depths in wells located along transects D and A in Rookery Bay Forest 1, and the centre transect in Rookery Bay Forest 2.

noticeable exception was a 1.0 m well at a site 110 m inland along the D transect in RBF1 (Fig. 3). Soil salinities in this well were highest (35 g kg^{-1}) during June of 1978 and 1979, and also peaked in February–March of both years. Low values occurred from April to May and September to October. But throughout that study period soil water salinity from the 0.5 m well along the D transect was consistent at 48 g kg^{-1}. At the site 50 m inland along the same transect, both the 0.5 and 1.0 m wells had consistently similar salinities, whereas salinity in the 2.0 m well exhibited temporal differences. The seasonal pattern of high and low salinity readings in this 2.0 m well at 50 m inland of the D transect was similar to the pattern observed in the 1.0 m well at 110 m inland; but the absolute values were much higher in the well closer to the bay. There were no seasonal changes in groundwater salinities in RBF2 (Fig. 3).

Precipitation

Annual throughfall based on funnel collectors in RBF1 was 907 mm, or 75.1% of annual rainfall. Throughfall in RBF2 was lower at 877 mm year^{-1} or 62.7% of annual precipitation. The annual amount of stemflow (R_s, m^3 year^{-1}) for the 12 trees measured in RBF1 and RBF2 was proportional to tree diameter (dbh) ($R_s = 0.061 \times$ [dbh] $+ 0.302$). Annual stemflow was converted to unit area by using information of tree density (5 x 10 m quadrats) and the equation above. Stemflow based on 20 quadrats in each forest (mean ± s.e.) was 228 ± 11 mm year^{-1} for RBF1 and 181 ± 14 mm year^{-1} for RBF2. This was 19% and 15% of the annual rainfall during 1979, respectively. The total annual precipitation input to the forest floor was 1135 mm in RBF1 and 1058 mm in RBF2, giving an average of 1097 mm year^{-1} (Fig. 4).

Runoff

Infiltration of rainfall from stemflow and throughfall was considered negligible when soil was saturated. Runoff coefficients were determined by comparing the volume of precipitation entering the forest floor during specific rainfall events to the volume of runoff measured from hydrographs within the forest, which averaged about 90% (Fig. 2). The percentage of each month during 1979 that the forest floor at RBF1 was submersed was calculated from water level records and reported in Twilley (1985). During February, submergence occurred during only about 25% of the month, whereas there was standing water on the forest floor throughout the month of September. The forest floor was submersed for 66% of 1979 (241 days). Each rainfall event was evaluated as to its occurrence relative to a saturated forest floor; if it occurred when the forest floor was submersed, then it was considered potential runoff. The monthly runoff potential was corrected for precipitation actually reaching the forest floor in the respective sites and multiplied by the runoff coefficient (90%). Runoff was higher in August and September and lower in October and March (Table 2). Runoff
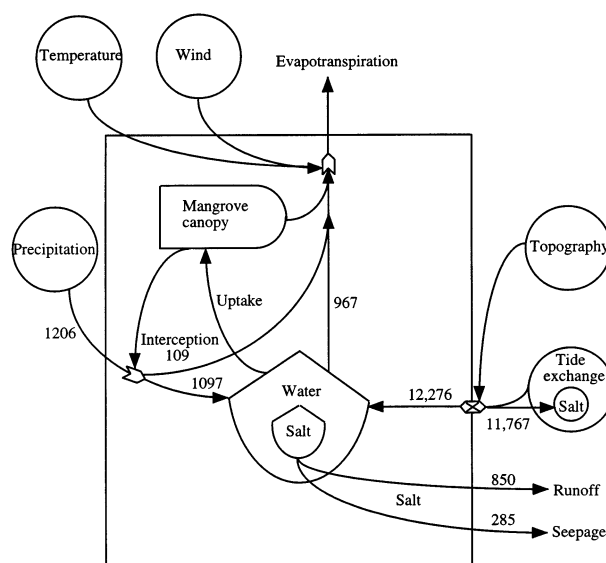
Fig. 4. Conceptual model of hydrology in a basin mangrove forest based on average values for Rookery Bay Forest 1 and 2 (mm year^{-1}). Symbols are from Odum (1983).

was 879 mm in RBF1 and 821 mm in RBF2, giving an average of 850 mm year^{-1} (Fig. 4). These values represented 73% and 68% of annual precipitation, respectively.

Evapotranspiration and seepage

Evapotranspiration exhibited a linear relationship with saturation deficits in the atmosphere: $[ET] = 0.41 \times S_D - 3.24$, $r^2 = 0.77$). By using this regression equation and the climatological data at Fort Myers to predict saturation deficits, daily evapotranspiration rates (mm day^{-1}) were

Table 2. Rainfall runoff calculations (mm) for basin mangrove forests at Rookery Bay Forests 1 and 2

Month	Rainfall (mm)	Potential runoff (mm)	Runoff (mm) RBF1	Runoff (mm) RBF2
January	79	79	67	63
February	61	61	52	48
March	16	16	14	13
April	105	46	39	36
May	112	85	72	67
June	110	66	56	52
July	101	85	72	67
August	208	208	176	165
September	268	268	227	212
October	22	0	0	0
November	25	25	21	20
December	98	98	83	78
Annual	1205	1037	879	821
Percentage of total rainfall	100.0	86.0	72.9	68.1
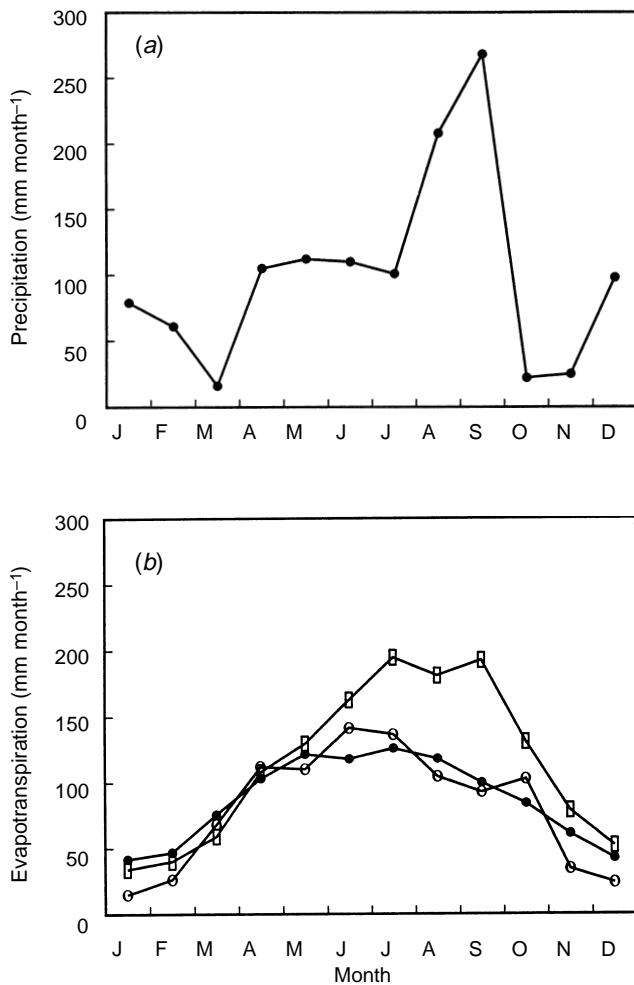
Fig. 5. Annual pattern of *(a)* precipitation and *(b)* evapotranspiration in Rookery Bay Forest 1. In (b): ○, field estimates; ●, from the Penman equation; ▫, from the Thornthwaite equation.

determined for a basin mangrove forest for each month of 1979 (Fig. 5). The annual loss of water by evapotranspiration in RBF1 was estimated at 967 mm. During August the estimated evapotranspiration rates for RBF1 and RBF2 were the same, at 3.90 mm day^{-1}. Low evapotranspiration rates occurred during the cooler months from November to March, and peak rates occurred during June and July (Fig. 5). Rainfall exceeded evapotranspiration from December to March when evapotranspiration was low and rainfall moderate. Rainfall also exceeded the actual field measurement of evapotranspiration during late summer when both rates were high, but the large pulse of rainfall was greater (Fig 5). Rainfall deficits occurred during October and November. Reference to the field measurements showed that the Thornthwaite equation overestimated evapotranspiration for every month except March. Although evapotranspiration predicted by the Penman equation is higher than actual field measurements during cooler months

(November–February), the energy-based estimate is more suitable for predicting evapotranspiration in mangroves than is Thornthwaite equation.

There were 16 dates with tidal records that could be used for determination of seepage based on night-time changes in water level. The mean seepage rate (± s.e.) was 0.78 mm ± 0.12 mm day^{-1}, or 285 mm year^{-1} (Fig. 4). These rates ranged from a high of 1.43 mm day^{-1} in August 1979 to 0.07 mm day^{-1} in March 1978.

Tides

Tidal curves in RBF1 and RBF2 were slightly asymmetrical as a result of the bowl-shaped topography of basin mangrove forests (Fig. 2). Tidal waters did not flood the forest until they reached a threshold level equal to the lowest elevation of the berm surrounding the forest. There was a sharp rise during flood tide, followed by a similar decrease during the first 4 h of ebb tide (Fig.2). Nearly 80% of the water was exported during this initial period of ebb tide but the remaining 20% was exported at a much slower rate. Fluctuations in water level due to rainfall were distinct and depended on the intensity of the storm (Fig. 2).

There was a significant linear relationship between the water levels at slack flood tide at the bay station (m>msl) with water levels within RBF1 and RBF2 (m>ground level)
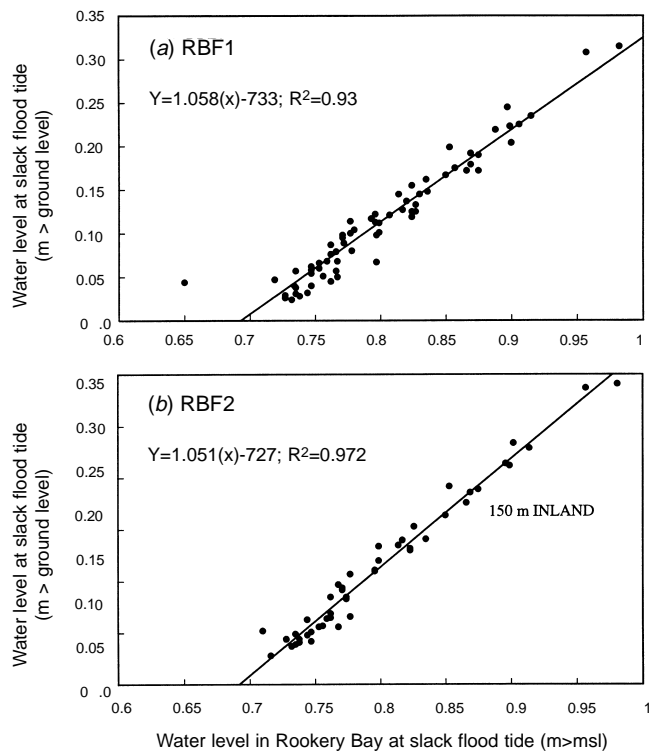

Fig. 6. Relationship between the water height above mean sea level (msl) in Rookery Bay and above ground level at two sites in a basin mangrove forest at slack flood tide: *(a)* RBF1; *(b)* RBF2.

(Fig 6a and 6b, respectively). From Fig. 6 and the continuous tidal recordings at Station 2 in Rookery Bay, the numbers of tides in RBF1 and RBF2 were calculated for each month of 1979. The seasonal pattern was exactly the same for both forests, and the annual number of tides was 158 for RBF1 and 152 for RBF2. Continuous tidal records existed back to 1973, and from these the mean number of tides for each month was predicted (Fig. 7). Monthly variations were minor, with coefficients of variation less than 25%. The peak number of tides within basin mangroves was 30 tides month^{-1} during September, compared with fewer than 8 tides month^{-1} from January to April. The number of tides during the three-month period from August through October was nearly 50% of the annual total.
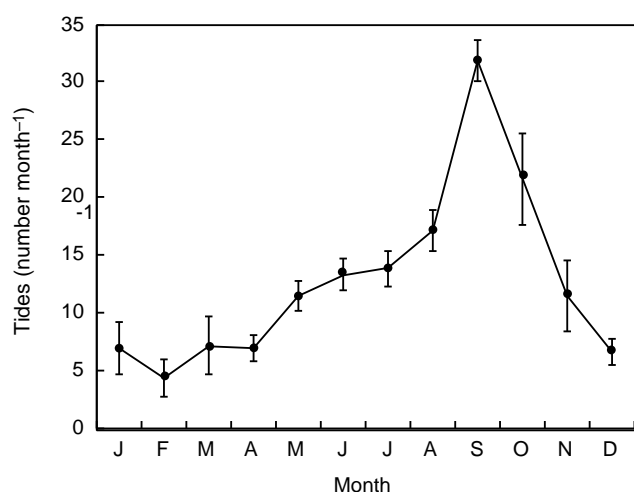

Fig. 7. The monthly number of tides in the basin mangrove forest at Rookery Bay. Values (mean and s.d.) based on 7 years of tidal data from Rookery Bay and on the model in Fig. 6a.

The cumulative input and export (in mm) of tides actually measured in RBF1 and 2 show that the total input of water during flood tide was greater than the export volume for each month except for April and July in RBF1 (Table 3). The bowl-shaped topography of basin forests resulted in a surface water depth of ~40 mm at bank-full storage. If surface water depth was below this level at the initiation of a tide, then the export volume was less than the import volume. The tides measured represented 46.4% and 37.3% of the total tidal amplitude predicted for RBF1 and 2, respectively, based on the correlations in Fig 6. Based on these percentages, the annual flux of water in and out of RBF1 was 12 090 mm and 11 546 mm. Annual flux was greater at RBF2, at 12 461 mm and 11 987 mm for flood and ebb tides. The result was a net annual input of tidal water of 544 mm for RBF1 and 474 mm for RBF2. Average tidal input of water was 12 276 mm year^{-1} and export was 11 767 mm year^{-1} for an average net input of 509 mm year^{-1} (Fig. 4).

Table 3.   Change in mean water depth (mm) during each tidal stage for those tides measured in Rookery Bay Forest 1 and 2

Month	Rookery Bay Forest 1			Rookery Bay Forest 2		
	In	Out	Net	In	Out	Net
January	163	154	9			
February	553	533	20			
March	112	95	17	44	43	1
April	450	455	–5	264	250	14
May	249	246	3	301	261	40
June	501	493	8	722	671	51
July	415	427	–12	501	457	44
August	890	824	66	437	422	15
September	1429	1355	74	2181	2194	–13
October	601	576	5	220	197	3
November	131	118	13	22	18	4
December	89	73	16			
Annual	5583	5349	234	4692	4513	179

Fig. 2 illustrates the significance of a tide in recharging water deficits in the soil of a basin mangrove forest. Within a 3-day period during August 1979 the water level in RBF1 decreased from ground level to 16 cm below ground level because of water losses from evapotranspiration and seepage. On 3 August, minimal recharge from two high tides occurred. The flood tide of 4 August recharged the water deficits within the peat, and by 5 August the surface water within this basin forest was 2 cm deep. The increase in water level on 4 August from a depth of 0.33 m > msl to bank full stage represented a water volume of 0.8 cm using a specific yield of 0.065.

Mass balance

Although tides are infrequent in the upper intertidal zone for nine months of a year, they are still the dominant source of water in this basin mangrove (92% of total inputs). Inputs totalled 13 373 mm and exports 13 915 mm, resulting in a deficit of 542 mm or 4% of the inputs (Fig. 4). Settlemyeare and Gardner (1977), Boon (1980) and Ward (1981) all agree that the error associated with water budgets for intertidal creeks is about 7% of the total influx. This deficit of the water budget of 542 mm could represent subsurface flow from uplands adjacent to the basin forests. However, decreases in soil water salinity at depths of 50 cm during periods of high rainfall did not occur, suggesting that subsurface inputs to shallow mangrove sediments from upland sources are minor. Thus, no significant groundwater connections among the soil of basin forests and adjacent upland ecosystems in Rookery Bay could be discerned in this study.

Model design and parameters

The HYMAN model establishes an algorithm to calculate the daily water level, salt content and salinity as the combined effects of tidal exchange, rainfall, runoff,

evapotranspiration and seepage. The basin mangrove forest at RBF1 was separated into three zones to calibrate and verify the hydrology model. The zones were 0–50, 50–100 and 100–150 m from the point in the berm where tide waters inundate the forest (Fig. 1). Three forcing functions, precipitation (Fig. 5a), tidal flood frequency (Figs 6a and 7), and evapotranspiration (Fig. 5b) were used as inputs to the model based on actual field data for all three zones. The net input of precipitation to the forest floor is calculated by precipitation and corrected for interception based on throughfall and stemflow results of the water budget described above (91%). Another input file includes the salinity of bay waters each month that inundate the forest with tides (Twilley 1982). HYMAN is used to simulate water and salt movement in a vertical layer of sediment of unit area extending from ground surface to 0 msl (depth of 50 cm) in each of the three zones. In addition, a surface water level of 2 cm was used as depth at bank full stage. Thus the depth of water at bank full stage (BF) is 52 cm.

The main program of the model includes four alternative functions that depend on whether water level within the forest is above or below ground level; and whether a flood tide occurs that day. These four alternatives determine the correct equations to account for surface water and calculations of salinity. A daily integration begins with evaluation of water level (whether > or < ground level) and whether a tide will occur; this determines which alternative to perform. The prediction of tidal frequency in these basin mangroves is not simply a relationship between intertidal topography and tidal height in the estuary or bay; but is also a function of tidal duration, which depends on distance from shore. The distance from shore is not a perpendicular transect, but is the distance from the point on the shore where the tide enters the paludal basin (Fig. 1). Twilley (1985) used a weir to measure organic carbon flux between the basin forest and bay at this point of tide entry to RBF1. We used an equation that accounted for both the elevation at this point of tidal entry and distance inland within the basin forest. This relationship was determined from direct measures of tidal frequency at different places in a basin forest (Fig. 6b). A threshold tidal height (T_h, m > msl) was calculated for three different zones of the basin mangroves to determine which tides in the bay inundated the forest:

$$(T_h) = 0.61 + (0.708Z); \qquad (6)$$

where Z is the distance from point of tidal entry into the forest (km). From this relationship, T_h was 0.61 m for the 0–50 m zone, 0.65 m for the 50–100 m zone and 0.69 m for the >100 m zone of the basin forests. This establishes the T_i in Eqn 1, while T_o is determined by subtracting BF from T_i.

Initial water level, bank-full stage of surface water, and specific yields for surface (0.90) and ground (0.065) water control the amount of water that occurs per unit area of

mangrove after accounting for the daily water flux events. To evaluate the terms in this mass balance equation, we must know the volume of water moving at specific time intervals. Although this may seen obvious, most climatological data are available only on a daily basis. Therefore the time step for the simulation is daily while the model allows for updating water level and salinity after each hydrologic event. The relative timing of a tide and precipitation occurs in time steps of less than a day, whereas surface flow, evapotranspiration and seepage are integrated daily. In the model we programmed the sequence of events as tide, precipitation, surface flow, evapotranspiration and seepage. Thus, once the initial water level and salinity are included, the model calculates changes in each by accounting for the influence of a tide (T_i) and amount of salt input ($T_i S_t$) as described in Eqns 1 and 2. This water level and salinity are then modified by the effects of net precipitation; followed by the loss of water and salt due to runoff. If water levels are >BF, then height decreases by T_o plus amount of net precipitation. If water levels are <BF, then the amount of water required to reach BF remains in the forest and the remainder becomes runoff. Once runoff has been accounted for, water levels and salinity are calculated. Finally, these water levels and salinities are changed according to the effects of E_T and S_p (Eqns 1 and 2) as input functions and a constant (0.078 cm day^{-1}), respectively. At this point the water level and salinity after these final two events are used as initial conditions for the next day and the sequence of events is repeated to modify water levels and salinity in each zone. Simulations of the hydrology model were developed with both STELLA II 2.2.2 on a Macintosh microcomputer and in C language using a SUN workstation. We found little difference in the output of the two programs; the results of HYMAN presented in this paper are based on simulations with C.

Simulation results

Simulations of daily water levels by HYMAN show the seasonal variability that occurs in these infrequently flooded basin mangroves (Fig. 8). Water levels are lower than soil surface for longer durations in the late winter and spring (February to May), whereas the forest floor was submersed for most of the fall (September to December). Reduced frequency in tidal inundation and lower precipitation inputs, along with increasing evapotranspiration, result in drier soil conditions from February to April. We imposed a boundary condition of msl as the minimum level of groundwater in the model. In the more inland sites (50–100 and >100 m inland), there were 10–15 day periods from 90 to 121 julian days during which this boundary condition was imposed (Fig. 8). It was assumed that subsurface recharge from tides would maintain this boundary condition, based on field groundwater records and results from other mangrove studies (Mazda et al. 1990a).
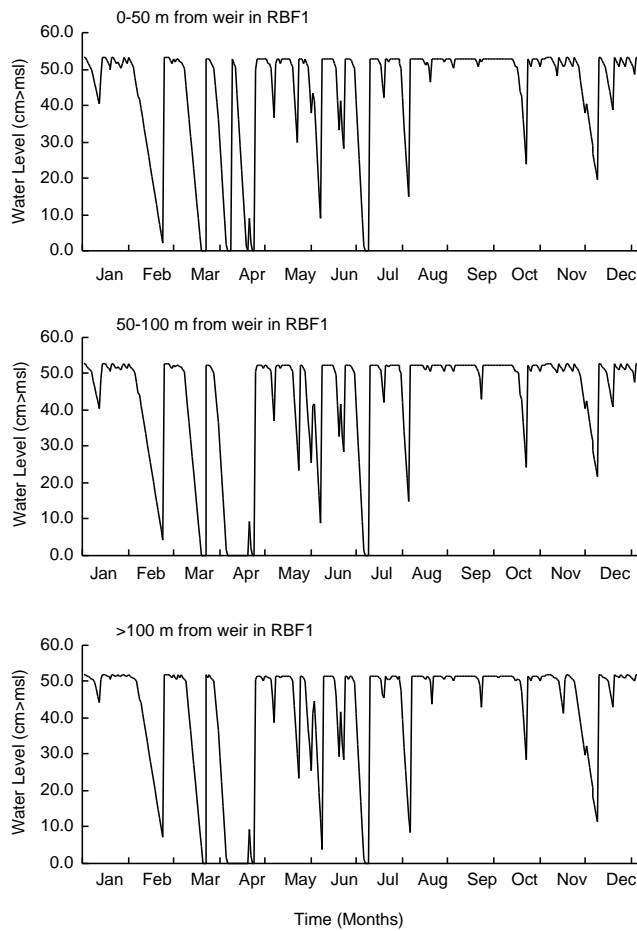
Fig. 8. Changes in water level in Rookery Bay Forest 1 based on simulation of the HYMAN model.

zone at different times of the year for both forests. There was a slight seasonal variability of salinity in pore water, with higher values from July to August. Salinity of pore waters increased with distance from the bay at both sites (Fig. 9). Pore-water salinities are higher at RBF2 than at RBF1 in the three zones, particularly in the 50–100 m zone, and the model accurately accounts for these site variations. This is due to the different topography of sites and the salinity of the inflowing water, since precipitation and evapotranspiration are similar for both sites.
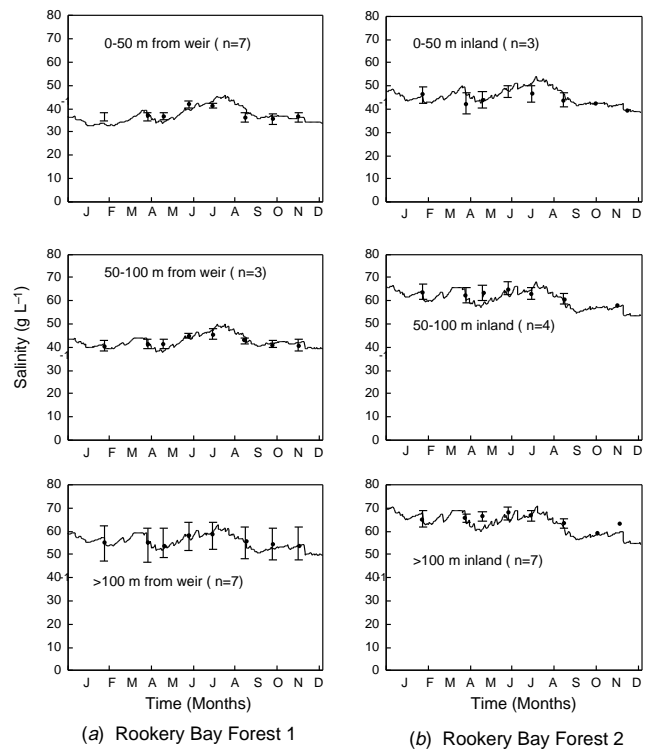
Fig. 9. Sensitivity test for tide frequency in *(a)* Rookery Bay Forest 1 and *(b)* Rookery Bay Forest 2. Model output is compared with field measurement (mean and s.d.) of salinity from groundwater wells.

There are intermittent periods of wet and dry conditions in the forest due to less frequent spring tides from May to July. On the Gulf coast of Florida, there is a seasonal rise in mean sea level in May and a peak in September (Provost 1973). The amplitude of tides in this region is less than 1 m, yet slight seasonal changes in sea level are very important in determining the frequency of tidal inundation of basin mangroves. The seasonal nature of increased tidal frequency coincides with higher precipitation in September to produce almost continuously flooded mangroves from mid August to mid October (215 to 280 julian days). Similar observations have been made on inland forests on the south-east coast of Florida (Carlson and Yarbro 1988).

Salt is a conservative tracer that can be used to evaluate the performance of our hydrology model. Comparisons of model output to empirical data show that the model is able to estimate both the spatial and seasonal pattern of pore-water salinity in the three zones of RBF1 and RBF2 (Fig. 9). Pore-water salinity values from the model fall within the standard deviation of measured values for each respective

Discussion

The low seepage rates from this study indicate that horizontal flow in soils is minimal in this mangrove wetland. In a study by Lugo *et al.* (1980), cores of saturated mangrove soils were sampled with polyvinylchloride tubes (5.08 cm diameter) at different depths and connected to a permeameter. The permeability of mangrove soils in the basin forest at RBF1 averaged 0.01 mm s^{-1}, characteristic of wetland soils with high organic content (Mitsch and Gosselink 1993, p. 72), such as those found in this basin forest. The average hydraulic gradient for any given day using a reference point 75 m inland and mean low water of the two tides was 5.1×10^{-3} (Lugo *et al.* 1980). Using Darcy's equation for groundwater flow (Chow 1964), and

average permeability and hydraulic head estimates above, the annual seepage rate would be 1587 mm, much higher than the 285 mm year^{-1} based on measures of night-time groundwater levels.

Mangroves with adjacent sandy soils have significant flow of groundwater with permeability coefficients reaching 8.4 mm s^{-1} (Mazda *et al.* 1990*a*). Given the high permeability of sands, it was evident that groundwater flow in this mangrove area was important to the water properties of the Bashita–Minato lagoon (Mazda *et al.* 1990*b*). But no measures of seepage were made directly in the mangrove forest adjacent to the lagoon. The lagoon and tidal creek are linked by the lateral flux of groundwater through porous sand, but it is not clear whether such large fluxes of water actually occur within the forested wetland. Organic-rich mangrove soils such as in the basin mangroves in this study, with small hydraulic head due to minor tidal amplitude, have negligible lateral movement of water. In this study, lateral flow in shallow depths of mangrove soil accounted for only 2% of the cumulative vertical annual inputs of water to the forest (Fig. 4). Studies of coastal marsh ecosystems have also demonstrated that groundwater movements in marsh soils are primarily influenced near the soil surface (0–20 cm) by capillary action controlled by evapotranspiration (Riedeberg 1975; Nestler 1977; Dacey and Howes 1984; Howes *et al.* 1986). Although the influence of shallow groundwater flux from basin mangroves in south-western Florida is minor, seepage of groundwater at greater soil depths than those simulated in HYMAN may be significant to the physical and chemical properties of adjacent bay waters.

Total evapotranspiration for a basin mangrove forest averaged 2.68 mm day^{-1} (977 mm year^{-1}) based on direct measures of groundwater, which was 80.2% of annual precipitation. This value is similar to a transpiration rate of 2.53 mm day^{-1} (924 mm year^{-1}) for *Avicennia* in RBF1 derived from gas-exchange methods (Lugo *et al.* 1975). Those authors also measured the evapotranspiration rate of *Rhizophora* and found a higher rate of 4.19 mm day^{-1} (1531 mm year^{-1}), which has been associated with the exclusion of salt at the root surface in this species. Higher rates of evapotranspiration have been measured in a mangrove lagoon in Japan at 7.1 mm day^{-1} (Mazda *et al.* 1990*a*) and in mangroves along Coral Creek in Australia at 30 mm day^{-1} (Wolanski *et al.* 1980). The latter estimate is based on a hydrodynamic model that used a mass-balance calculation of salt flux in a tidal creek to estimate the amount of fresh water that had to be transpired by mangroves to account for the salinity inversion observed in the tidal creek. Ridd *et al.* (1990) estimated from model results that evaporation in a mangrove tidal creek was lower, at 1.5 to 8 mm day^{-1}. Assumptions of salt export from mangroves and model estimates of exchange coefficients in a tidal creek along the Wenlock River were used to calculate an evapotranspiration

rate of 2 mm day^{-1} for mangroves (Wolanski and Ridd 1986), which is within the range of values in our study.

Mangroves transpire fresh water, causing a tendency for salt to accumulate in pore waters, and this controls the seasonal nature of salt concentrations in the pore water (Carlson and Yarbro 1988; Passioura *et al.* 1992). The relative small fluctuation of pore-water salinity through a year indicates that there are mechanisms that control the salt balance in mangrove wetlands. Rainfall runoff, tidal export and seepage are the salt-exporting mechanisms in the model. From February to April, pore-water salinity has a slight increase, which is related to lower tidal inundation and precipitation when evapotranspiration is low. Higher evapotranspiration increases pore water salinity from May to August, yet the coincident increase in tidal frequency and rainfall from July to October maintains steady soil salinity during periods of peak evapotranspiration. More frequent tidal inundation from August to October keeps forest soils saturated, and this increases the runoff coefficient of basin mangroves during the summer and helps export salt to the bay. Only 18% of the net rainfall inputs to the forest were lost by evapotranspiration; the remainder of the evapotranspiration demand was provided by tides. Consequently, tidal efflux of water was 509 mm less than tidal influx. The consumption of tidal water by evapotranspiration represented only 4.1% of the total tidal input. Increased soil saturation by tides and rainfall, combined with the lower salinity of the bay waters, enhances the export of salt and this results in a decrease in pore-water salinity in September.

Understanding the relative influence of tides and precipitation on the hydrology of the upper intertidal zone is important to understanding the ecological properties of coastal wetlands. de Leeuw *et al.* (1991) proposed that rainfall deficit (rainfall – evapotranspiration) controlled seasonal and interannual patterns of pore-water salinity in higher elevations of the intertidal zone. Pore-water salinity is controlled by tidal frequency and duration below mean high water, whereas salinities in areas of wetland with elevation above this datum are determined by the relative rates of precipitation and evapotranspiration. The rainfall deficit was demonstrated to be correlated to soil salinity in higher salt marshes and to control the interannual variation in salt marsh production (de Leeuw *et al.* 1990). Field measurements of soil salinity in high and low marsh sites showed that seasonal variation in salinity of tidal waters entering the marsh was an important factor in soil salinity in lower (<MHW) salt marsh sites. In the upper marsh, rainfall deficit was important to the seasonal changes in soil salinity. Thus, climate changes resulting in variation in rainfall deficit may only influence intertidal vegetation above the MHW sections of the intertidal zone.

We tested the relative influence of rainfall deficit on soil salinities along elevational gradient in the intertidal zone of

basin mangroves in Rookery Bay using the hydrology model. The sensitivity of three basin mangrove zones to input or loss of fresh water was analysed by increasing and decreasing precipitation and evapotranspiration. Impact of climate change on mangroves may be caused by increasing temperature and changing precipitation. These two processes influence the input of fresh water in mangrove ecosystems, and this may control the dynamics of salinity in pore water. Simulations of changes in rainfall deficit were established for each zone by either decreasing precipitation or increasing evapotranspiration by 10% and 20%. The results of the simulations are shown relative to pore-water salinities of normal conditions discussed above (Fig. 10). For each of the changes in precipitation and evapo-transpiration, changes in salinity were similar between the 0–50 and 50–100 m zones, but higher in the >100 m zone of the forest. Salinity increased by an average of 2.3g kg^{-1} and 4.9g kg^{-1} in the 0–50 and 50–100 m zones by decreasing rainfall by 10% and 20%, respectively (Fig. 10). Similar changes in pore-water salinity in these two zones were observed by increasing evapotranspiration. Pore-water salinity increased by 4.2 and 7.2 g kg^{-1} in the >100 m zone by decreasing precipitation by 10% and 20%, respectively. Changes in pore-water salinity of 4–7 g kg^{-1} occur in the zone of normally higher salinities, approaching values that are stressful to mangrove production (Cintron et al. 1978; Naidoo 1987). Thus, interannual changes in precipitation in the upper intertidal zone of mangroves should influence the productivity and zonation of mangroves in the upper elevations of intertidal zone of lagoons.

This hydrology model gives insight into the geophysical mechanisms that influence the coupling of basin mangroves in microtidal environments to fringe mangroves in more macrotidal systems. The hydrodynamics of trapping material in mangroves has been the focus of studies on estuarine and lagoon systems with 3 m tidal amplitude in north-eastern Australia (Wolanski et al. 1990). The topography and hydro-logy of these systems is depicted as having a flat surface with a gradual increase in elevation (Wattayakorn et al. 1990). These models use symmetrical tides to transport material from mangroves to coastal waters. The present study describes the hydrodynamics of basin mangroves in the upper intertidal zone of lagoons. In these types of mangroves, paludal basins surrounded by a berm causes tides to be asymmetrical. Similar to the hydrodynamic models of Australian mangroves, the basin forest in our study is not flooded until the latter portion of a flood tide. Therefore, duration of tide in the forest is less than half of the duration of semi-tide. In addition, water depths in the mangrove forest are much less than height of water in the bay during the slack flood tide of an inundation. In Rookery Bay, the average water depth in the mangrove forest is 10 cm per tide, while height of water in the bay is about 150 cm.
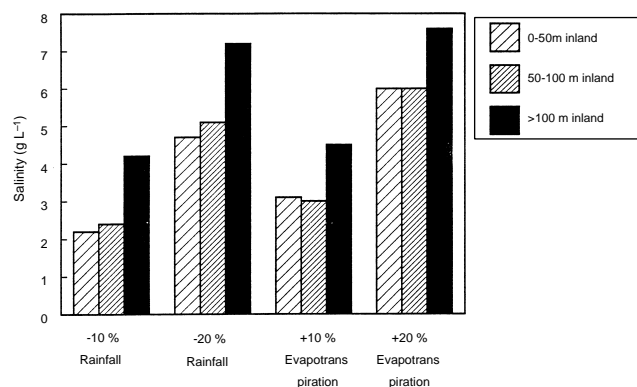
Fig. 10. Sensitivity test for effect of rainfall (10% and 20% decrease) and evapotranspiration (10% and 20% increase) on salinity of pore water in three zones of RBF1. Salinities are relative to normal conditions.

The asymmetrical nature of tidal exchange and the residual flow of water during ebb tide from inland forest caused by the presence of a berm just inland of the fringe may influence the trapping of materials in basin mangroves (Twilley 1985; Woodroffe 1985a, 1985b).

There are several limitations to the generality of the present hydrology model that need to be overcome before simulations can be applied to mangroves in other types of environmental settings. HYMAN uses a daily time step to follow hydrologic events, and the sequence of these events during a given day is arbitrary. Timing of events may influence the chemical characteristics of wetland soils and nutrient cycling (Twilley 1982; Mazda et al. 1990b). However, simulations only provide monthly average concentrations, thus limiting the utility of the hydrology model. A more mechanistic approach is needed to estimate seepage using soil parameters such as soil type, hydraulic gradient, and bioturbation factor (e.g. crab holes and root density). This is particularly important in coastal systems with more sandy soils and regional slope. Estimates of regional evapotranspiration rates need to be related to specific type and structure of the mangrove canopy. Indicators of canopy structure such as leaf area index, or basal area could be incorporated as biological modifiers of the energy-based Penman models to generalize rates of evapotranspiration. Finally, tidal harmonic analyses are needed to predict tidal inundation frequency of inland forests for different regions of the coast.

This hydrology model is also site specific for soil parameters, climate and evapotranspiration for mangroves in lagoons of south-western Florida. Simulations demonstrated that the ecological properties of mangroves in the upper intertidal zone of lagoons in this region are sensitive to changes in rainfall deficit. Yet these simulations are for mangroves in the upper intertidal zone of lagoons where the transition with uplands has minor freshwater input. Satellite images of mangroves in this region of south-western Florida

show the common occurrence of salinas as the ecotone between mangroves and upland vegetation. From Cape Romano to Cape Sable, particularly in the sloughs of the Everglades, overland sheetflow is an important component of the hydrology of the upper intertidal zone. Vegetation zonation in these ecotones is very different and the hydrology of the upper intertidal zone of these regions will have to include this parameter. The present version of HYMAN has been shown to be an accurate description of the hydrology of basin mangroves in lagoons with little upland input of fresh water, which is characteristic of south-western Florida and throughout the Caribbean. The site-specific nature of this hydrology model and its implications to the ecology of mangroves demonstrates the utility of a hydrogeomorphic classification of wetlands to describe the diverse properties of these coastal ecosystems (e.g. Thom 1982; Brinson 1993; Twilley 1995, 1997) .

Acknowledgments

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WATER QUALITY AND LOWER FOOD WEB MODULE

ABSTRACT

Aquatic systems along the coast of Mexico are experiencing intense environmental pressure due to an increase in anthropogenic activities such as urbanization and overfishing. Different water quality parameters, such as secchi depth, nutrient composition and limitations, pH, and abundance and distribution of phytoplankton may be used to detect change in aquatic environments over time. Bioassay experiments determine limiting nutrients in the mangroves and further, to infer how changes in nutrient compositions will affect the system. Zooplankton and shrimp serve as important trophic linkages between sestonic particulate organic matter and secondary consumers. Observed fluctuations in community and species indexes of these organisms may be useful in monitoring changes in water quality, ecosystem function, and contaminant load. This module provides background information and methods used in aquatic environments to detect changes to aquatic ecosystems. When possible, specific information is provided for coastal mangrove ecosystem. Preliminary information collected in January 2007 from two central Pacific coastline mangroves is also presented.

INTRODUCTION

Coastal zones are currently experiencing increased environmental pressure as a result of many different forms of anthropogenic exploitation such as over-fishing, increased pollution, and habitat loss due to development. In many parts of Mexico, this pressure is seen as increased tourism has lead to the construction of many hotels and luxury homes along the coastline, putting many aquatic systems at risk. How a system responds to such anthropogenic stress varies and the responses of certain systems, such as mangroves, have not been well documented. Using various water quality measurements, it is possible to quantify change in a system due to natural and anthropogenic stresses. Such measurements often include nutrient composition, secchi depth, pH, phytoplankton growth, and zooplankton/ macroinvertebrate abundance and composition. The goal of this project is to establish baseline water quality characteristics in La Manzanilla and La Vena mangroves. Additionally, this project will potentially establish major sources, sinks, and fluxes of nitrogen and phosphorous in the mangroves. This information will be used to determine future potential impacts of sewage discharge, increased tourism, and alterations in land cover to the functioning of La Manzanilla and La Vena mangroves.

WATER QUALITY AND BIOASSAYS
 Ecosystems contain particular nutrient compositions unique to that system, and in order to maintain the health of that system, those nutrient compositions must be maintained. The addition of nutrients, particularly nitrogen (N) and phosphorous (P), into a body of water often leads to the rapid eutrophication and often deterioration of that water body (Tappin, 2002). Because mangrove are located on the edge of terrestrial and marine systems, they receive a unique mix of water from a variety of sources including terrestrial and marine overland flow, terrestrial and marine groundwater flow, and anthropogenic sources, such as sewage discharge and atmospheric inputs (Tappin, 2002). Understanding the sources and fluxes of nutrients in a system is important in determining potential nutrient sources as well.
 When a system becomes overloaded with nutrients, the common result is modified ecosystem structure and/or deteriorated ecosystem function. It has been shown that river and estuary nutrient concentrations are directly correlated to the watershed in which they are located

(Balls, 1994). Developed areas where agriculture is high and freshwater inputs are low, nitrates and phosphates become more abundant. Likewise, in areas where other anthropogenic sources are prevalent, such as industry, sewage discharge, or deforestation there are concentrations of N and P (Dauer et al., 2000; Balls, 1994; Feller et al., 2003; Tappin, 2002). In relatively pristine mangroves, the main source of nitrogen and phosphorous is riverine transport of naturally eroded and weathered substrate. Where soils are nutrient poor and agriculture is not significant, water sources to mangroves will be depleted of N or P (Balls, 1994).

One consequence of altering nutrient composition is a change in primary productivity within that system and, consequently, water clarity and quality. Visibility of surface water, which is determined by the transmission of light through that water, can be distorted by the amount of phytoplankton, bacterioplankton, dissolved organic matter, detritus, sediments, and the water itself (Erlandsson and Stigebrandt, 2006). Different techniques may be applied to determine water clarity, but the most frequently used is the Secchi disc. It does not determine the amount of material suspended in the water column, but rather provides an accurate estimate of short- and long-term changes of suspended material in that system (Erlandsson and Stigebrandt, 2006). These changes can later be correlated to other changes in system, such as nutrient composition.

Measuring primary production allows researchers to understand nutrient limitations in a system as well. As nutrient composition plays a role in primary production and phytoplankton abundance, change in phytoplankton growth over time may be determined to further quantify the effect of nutrient composition in a system. Light availability, temperature, predation, sinking, and distribution through water movement also determine phytoplankton abundance and distribution, but nutrients are often the most easily measured and quantified (Lane and Goldman, 1984). In many aquatic systems, nitrogen and phosphorous are two essential elements that often limit primary production. Knowing which nutrient is limiting in a system helps determine what will happen in that system when it experiences a large nutrient pulse.

Many temperate coastal systems have been shown to be nitrogen limited while their upstream freshwater reaches are P limited (Boyer, 2006; Vitousek and Howarth, 1991). Other tropical and subtropical mangrove systems have been shown to be P limited, such as the southern Everglades which are strongly P-limited (Boto and Wellington, 1983; Davis and Childers, 2007; Feller et al. 1999; Feller et al., 2003; Valiela and Teal, 1979). In addition, some mangrove forests show that nutrient availability that is not homogeneous, instead shifting from N to P limitation across small environmental gradients (Boto and Wellington, 1983). Like many estuaries, mangroves are unique as they are influenced by marine, freshwater, and groundwater sources consequently having distinct nutrient compositions. Many mangroves receive constant marine water inputs; however La Manzanilla mangrove is often disconnected from the ocean. It is important to determine nutrient limitations in La Manzanilla in order to understand how the system will respond to excess nutrient additions from anthropogenic sources, such as sewage discharge. Prior to disturbance it is crtical to characterize the baseline conditions (nutrient conditions) that drive biological composition and production. Previous data collected in January 2007 is presented for reference (Table 1).

Bioassays are a common technique to determine limitation or chemical toxicity and a number of methods have been developed to do so. One common method is the addition of nutrients to water samples containing phytoplankton or natural algae populations and later measure change in biomass over time (Lane and Goldman, 1984). Using this simple, effective technique, this study is will be able to determine nutrient limitations throughout La Manzanilla and La Vena mangroves. In addition, it will allow further examination of the influences of different natural (i.e. water source influence, drought, flooding, connectivity to the ocean, etc) and anthropogenic (i.e. sewage discharge, construction, etc) processes influencing these limiting elements.

ZOOPLANKTON

Zooplankton collected in the mangroves of La Manzanilla and La Vena have been identified as cyclopoida. These small planktonic crustaceans of the subclass copepoda inhabit both freshwater and marine environments. Cyclopoids are capable of rapid movement and can

be carnivorous feeders. The planktonic Calanoida and benthic Harpacticoida may also occur in these systems. Providing an important trophic linkage between particulate matter and larval fishes zooplankton also serve as bioindicators of environmental degradation.

Zooplankton ecology has been described in several mangrove systems. Lam-Hoai (2006) found changes in taxonomic composition between wet and dry seasons in a French Guianian mangrove. Only about one third of zooplankton taxa were present during both seasons. He also found a decline in population densities during the dry season. Planktonic communities are largely driven by seasonal variation in salinity and temperature (Alongi, 1998). Bouillon (2000) found through stable isotopic signatures that phytoplankton was a primary carbon source for zooplankton despite the large amounts of mangrove detritus in the water column. Under lab conditions crab zoeae of Aratus pisonii opportunistically preyed upon copepods but did not select for them (Schwamborn 2006). Gut content and stable isotope analyses revealed that copepods in addition to crabs and shrimp were the preferred food source for zoobenthivorous and omnivorous fishes (Lugendo, 2006). Franco-Gordo (2002) noted that larval fish community composition in Bahia Tenacatita was affected by the presence of estuarine outflows suggesting preferred habitat and food availability in the form of zooplankton export.

For both study mangrove study areas development pressure may lead to increased turbidity levels that may be reflected in the zooplankton assemblages. In La Manzanilla this baseline monitoring will also be useful in recognizing changes in salinity in part due to well-based aquifer withdrawal, periodic connectivity to the sea and the expected introduction of sewage effluent. In La Vena zooplankton monitoring may prove useful in recognizing changes in local industrial (i.e. solvents, detergents etc.) effluent discharge.

Wilson (1994) suggests using different bioindicator approaches depending on the subject of monitoring. He argues for using plankton to indicate changes in salinity, ranges in species for examining contaminants, and eurytolerant species (e.g. those tolerant to wide variations in environmental conditions) when attempting to gauge system health. Distinguishing between juveniles and adults can be important in species when the salinity and turbidity optimums of the two age classes differ. One of the goals of this module is to establish a sampling regime that illustrates the baseline spatial and temporal characteristics of the current zooplankton communities.

SHRIMP

The general ecology of Palaemonid shrimp is well described in many ecosystems around the world. These shrimp were collected in the La Manzanilla and La Vena mangroves. Several studies have illustrated trophic linkages between mangrove associated shrimp populations and commercially valued fishes (Ronnback, 1999; Halliday, 1996; Primavera, 1998). Development pressures such as aquaculture, agriculture, forestry and infrastructure exerted upon mangroves continue to degrade these systems and the associated resources and services they provide (Ronnback 2000). Shrimp communities in the mangroves targeted within the scope of this research program may also be useful bioindicators of environmental disturbance (Quintanero, 2006; Gerhardt et al., 2002).

Palaemonid shrimp have developed numerous adaptations to thrive in ecologically complex and dynamic systems. In a Brazilian lagoon, detritus has been found by to be the most important food item for Palaemonid shrimp followed by chironomid larvae, odonate nymphs and the macroalgae Chara (Albertoni, 2003). During low-water periods, omnivorous-carnivorous

Palaemonids sampled from an ox-bow lake consumed zooplankton such as copepods as an alternative food source (Collins 1998). Larval forms of crabs, shrimp and fishes have been shown to be associated with floating mangrove leaves, illustrating one mechanism of larval transport for a diverse group of organisms (Schwamborn, 1996). Palaemonid females in a Spanish delta were found to be larger than males. Egg bearing females were typically found from spring to fall and peaking in abundance during May and June. Egg numbers were related to female size ranging from 318-2750. The minimum number of spawnings for a single female was two (Guerao, 1994).

Quantitative analyses correlating shrimp to fisheries production are limited. Mangrove area is highly correlated to offshore shrimp yield (Primavera 1998). Within mangroves the highest shrimp densities typically occur in areas with the greatest structural (root) complexity (Ronnback, 1999). These mangrove microhabitats are commonly used as refuges from predators and are critical for maintaining shrimp populations (Primavera, 1998). In addition, mangroves provide feeding and nursery grounds and in some instances permanent residences for invertebrates. One hypothesis used to explain the utilization of mangroves by invertebrates focuses on predator avoidances due to shallow waters, high turbidity, soft muds for burrowing and habitat complexity (Boesch and Turner, 1984; Robertson and Blaber, 1992). Shrimp abundance may not only indicate habitat availability but might be useful as indicators of pollution. One of the goals of this module is to describe whether the abundance and diversity of shrimp and zooplankton communities is associated with various forms of disturbance.

WATER QUALITY AND BIOASSAYS

Eighteen water quality samples will be collected in La Manzanilla (10 sites) and La Vena (5 sites) mangroves. One additional site is located in the bay (Fig. 1 and 2). At each site maximum depth, water clarity via Secchi depth, dissolved oxygen (DO), conductivity, specific conductivity, salinity, and pH will be measured. Using the Secchi disc, clarity and maximum depth will be measured with the rope that is marked off at 0.1m increments. DO, conductivity, specific conductivity, temperature and salinity will be measured at all surface and deep water sites using YSI-85 multi-meter. Using the pHtestr (1, 2, or 3), pH will be measured at all surface and deep water sites. For deep water samples it will be necessary to measure pH in the 1-liter raw water sample bottle that is collected.

Secchi Disc   YSI-85 multi meter   pHTestre™ 2

4

In La Manzanilla and La Vena, surface water samples will be taken at all sites. At sites M2, M5, M6, M8, V1, and V3, water samples will also be taken near maximum depth. Surface water samples will be collected manually by submerging sterile, 1-liter plastic bottles below the water's surface. Maximum depth water samples will be collected using a Van-Dorn device, placing collected water into sterile, 1-liter bottles. Samples will be taken back to the field station where they will be filtered shortly after collection.
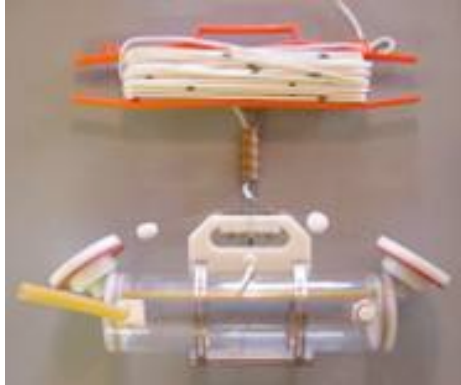
Van Dorn device

Raw water samples will be processed and filtered at the field station after collection. For total phosphorus, 60ml of unfiltered, raw mangrove water will be placed in a clean, well labeled bottle. Additional samples will be filtered using a 60ml plastic syringe, GF/F filters, and a filter attachment. With the first filter, 60ml of water will be filtered through into a 250ml sterile bottle that is labeled with site code. These filters will be removed, wrapped in aluminum foil, and stored in a small manila chlorophyll envelope. Each envelope will be labeled with the date, site code, test to be run and the amount of water filtered. Samples will be stored on ice until they can be processed at the lab.

1/12/07	1/15/07
M5	M10S
Chlorophyll	TP, SRP, NO3
30ml	NH4

Example Labels

Using a clean filter, the same sample will be filtered into the 250ml bottle until filled. When the syringe no longer filters easily, change the filters, taking care not to tear the second filter. This filter will be used for stable isotope analysis. Filters will be removed from the syringe and saved in the same manner as the previous filter, including the amount of raw water filtered. Using new filters (which will *not* be saved) continue filtering raw water into the 250mL bottle until full, leaving room for expansion when frozen.

Filtered samples, stable isotope samples, and chlorophyll samples will all be frozen at -20°C and transported to the lab for further analysis. In the lab, the samples will be analyzed for total phosphorous (TP), soluble reactive phosphorous (SRP), dissolved inorganic nitrogen (DIN), nitrate (NO_3^-), and ammonia (NH_3^+).

BIOASSAYS

Mangrove water will be collected at sites M2 and M11. One liter clear Nalgene bottles will be filled with mangrove water from 0.5 m depth with a Van Dorn sampler. The water should be screened using the zooplankton mesh net to remove zooplankton which eat algae.

Initial bioassays will determine nutrient limitations for nitrogen and phosphorus in triplicate. Therefore, each site will have a total of 12, 1-liter bottles (3 bottles for a control, 3 bottles with nitrogen, 3 bottles with phosphorous, and 3 bottles with nitrogen and phosphorous) will be required. Once full of nutrient solution and filtered water, bottles will be closed and incubated *in situ* for 3 days at 0.5m below the surface.

Incubated samples will be processed at the field station. Twenty ml of water from each bottle will be filtered for chlorophyll analysis (for procedure, see previous water quality methods section). Differences in chlorophyll a will reflect changes in algae production due to nutrient addition. A nutrient may be limiting when the omission of that nutrient results in less growth than the control bottle where all nutrients were added (Maslin and Boles, 1978). If neither nitrogen nor phosphorous are found to be limiting, limitation due to other nutrients will be tested in the future.

ZOOPLANKTON

Zooplankton samples will be collected in the La Manzanilla (3 sites) and La Vena (4 sites) mangroves. Using a zooplankton tow-net with nylon mesh size of 80 μm zooplankton will be collected at each site. For vertical tows it will be necessary to attach a weight to the tow net in order to cause it to sink. Upon collection samples will be stored in 500ml wide mouth bottles labeled with date, site code, and tow type (e.g. 5.Mar.07, M2-vertical).

In La Manzanilla, horizontal and vertical tows will be taken at M2, M5 and M8. At La Vena, horizontal tows will be taken at V1, V3 and V4 in addition to a vertical tow at V4. (Verify sites with your instructor). At each site 3 pulls will be taken and pooled into a single sample bottle. Record and sum the length of each pull. Samples will be preserved with Lugol's solution (approximately 10ml) plus sucrose at the field station and stored at room temperature. Sample bottles will be transported back to the lab for specimen identification and enumeration.

INTERDISCIPLINARY INTERSECTIONS

Development and construction on and near coastal zones adds environmental pressure on an already stressed system. How these systems respond to the pressure is, in many cases, not well understood. Mangrove systems receive water from marine and fresh sources creating a unique and complex system where water quality plays a significant role in the productivity, diversity, and health of the system. However, water quality alone does not provide the information needed to fully understand ecological processes occurring in this system. Rather, information on water sources, water fluxes, and biological diversity are equally significant in the comprehension of such processes.

The ecohydrology module studies groundwater fluxes from upper watershed as well as marine sources, measured spatially and temporally. Using this information, it is possible to determine how water quality changes based on water source. Data from ecohydrology will determine the respective inputs of fresh and saline water, generating connections between water quality in the upper watershed, the marine environment, and the mangrove itself. In reverse, water quality can inform ecohydrology about the nutrient content of each water source and its influence on the mangrove.

Fisheries are also directly related to water quality. Certain water quality characteristics such as dissolved oxygen, nutrient availability, primary production, and macroinvertebrates as a potential food source often determine which fish species may be present in a given habitat. In

mangrove systems, knowing all these parameters, which are all correlated to water source, will influence distribution, diversity, and abundance of fishes. Understanding tolerance levels of fish will also be significant as mangroves often exhibit extreme conditions such as anoxic conditions, highly turbid waters, and wide salinity gradients both vertically and horizontally through the water column. As water sources change through time and space, water quality conditions will change and, consequently, a change in fish species composition may be observed.

Mangrove trees themselves possess unique attributes that enable them to survive conditions of inundation, drought, and a range of salinity gradients typical of mangrove environments. Water quality information, such as nutrient composition, pH, temperature, and salinity will be vital in understanding the productivity and distribution of species in La Manzanilla and La Vena mangroves.

The interdisciplinary aspect of this study allows a more complete understanding of entire ecosystem processes and function and how individual components within the system are interconnected and influential on one another. Understanding each of these components may allow conservationists and developers alike to further explore and recognize how construction and development will impact mangrove health.

MATERIALS LISTS

WATER QUALITY

23 one-liter sterile bottles
Van Dorn
Secchi Disc with measured rope
YSI-85 (DO, conductivity, salinity, temperature)
pHtestr (1, 2, or 3)
Sharpie
Pencil
Lab notebook
Long pole/oar (optional)
23, 250-mL bottles
Clean filters
Syringe/Filtering device
Aluminum foil
Small manila envelopes
Storage area (-20°C)
Ziplock bags
Cooler

BIOASSAYS

16 one-liter bottles
Van-Dorn
Nitrogen nutrient solutions – $NaNO_3$, and KNO_3 (Maslin and Boles, 1984)
Phosphorous nutrient solutions – K_2HPO_4 and Na_2HPO_4 (Maslin and Boles, 1984)

Rubber policeman/bottlebrush
Weighing device
Filter or weight paper
Lab notebook
Pencil
Sharpie

ZOOPLANKTON

Tow net with 80µm nylon mesh and dolphin bucket
Rope marked at each meter
10x 500ml wide mouth sample bottles
Squirt bottle
Lugol's solution
Labeling tape
Permanent marker
Datasheets (waterproof)
Pencil
GPS

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SITE (circle site)	**Time**	**Date**	

M1 M2 M3 M4 M5 M6 M7 M8 M9 M10 M11

V1 V2 V3 V4 V5

GPS (UTM)   **OBSERVERS**

			Lab Processed
WATER QUALITY	Surface	___Depth ___Depth	(X)
Sechi Depth (m)			TP
Max. Depth (m)			SPR/DIN
pH			Chl
Conductivity 1 (mS or uSx1000)			SI
Conductivity 2 (mS or µSx1000)			
Salinity (parts per thousand)			
Temperature (Celsius)			
1L Bottle Collection Water Quality (x)			
1L Bottle Collection Ecohydrology (x)			

ZOOPLANKTON
　　Diameter of net ring
　　Mesh size
　　No. of pooled replicates　　　　1　　　2　　　3
　　Tow length/depth (m)

BIOASSAY
　　Incubation date/time
　　Retrieval date/ time
　　Amount of water filtered for chl a (ml)
　　Samples frozen and location

COMMENTS

Vegetation Module

Abstract

La Manzanilla is a small fishing community on Mexico's central pacific coast, the Costa Alegre, which supports one of the largest populations of the American Crocodile (*Crocodylus acutus*) in the state of Jalisco, Mexico. The natural resources of the La Manzanilla mangrove ecosystem are in jeopardy of being degraded by the recent rapid increase in development. The net primary productivity of the mangroves within La Manzanilla helps support the fish and crocodile populations; however, the effects of the recent development on the primary production and regeneration of mangroves is not yet known. Research is currently underway to determine if primary productivity and mangrove regeneration is affected by differences in species composition, disturbance regime, and/or water source.

Background

In recent years, there has been a dramatic rise in tourism along Mexico's central pacific coast, the Costa Alegre. As a result, many small communities along this coastline have begun to experience the ecological and economic impacts that accompany "being discovered" by the international tourism industry. One such community, La Manzanilla, is a small fishing community in the state of Jalisco. La Manzanilla, along with other communities on the Tenacatita Bay, is experiencing rapid conversion from an agricultural based economy to an economy based on commerce, real estate, tourism, and the service industry. The development accompanying this economic conversion has increased the pressures on the natural resources of the area, both marine and terrestrial. Terrestrial and aquatic species, including the American Crocodile (*Crocodylus acutus*) and the Boat-Billed Heron (*Cochlearius cochlearius*), are being affected by habitat encroachment and the biology of the local mangrove ecosystem is being altered by these anthropogenic changes.

Mangroves are the dominant coastal wetland on the Costa Alegre and are home to the largest populations of American Crocodiles in Mexico. Mangrove ecosystems are an intertidal plant community dominated by salt and flood tolerant trees and shrubs. They are widely valued for their ecological uniqueness and linkages to estuarine food webs in subtropical and tropical coastal regions (Primavera 1998); providing important rearing grounds for marine fishes and habitat for migratory and endemic bird species, reptiles, and small mammals. The mangroves and the habitat provided by the mangroves at La Manzanilla are being degraded by the direct (i.e., habitat modification) and indirect (i.e., altered hydrology, climate change) impacts of development.

Previously, information was collected that described the unique aspects (i.e., biological composition) and the disturbances (i.e., habitat encroachment and human use) to the mangroves at La Manzanilla and efforts were started to raise the awareness of the local community and tourists to the ecological and economic importance of the mangroves. Although the anthropogenic influences on the La Manzanilla mangroves are significant, the impacts are still in the early stages. Thus, this is a critical period for determining baseline conditions prior to major alterations, predicting ecosystem alterations, and developing a natural resource management plan for the lower watershed.

In order to obtain a more thorough and accurate understanding of the ecological conditions and processes occurring in the mangrove ecosystems at La Manzanilla, five research modules have been developed for further study; hydrology, vegetation, water quality, fisheries, and GIS. From the data generated through studying these modules, more objective and concise information will be given to the local community and community leaders about the major threats to the biodiversity of the mangroves and the impact on the quality of life of residents in La Manzanilla. This data may also be used to help develop strategies for the sustainable and responsible use of the natural resources of the area.

Introduction

Worldwide mangrove ecosystems are being lost at alarming rates with approximately 33% disappearing since the 1950's (Alongi 2002). Anthropogenic activities are largely responsible for the loss and degradation of mangrove ecosystems (Alongi 2002; Gunawardena and Rowan 2005; Islam and Haque 2004; Vijay et al. 2005). Development often causes alterations to hydrology, salinity and nutrient availability; three factors important for mangrove productivity. Productivity and percent cover of mangrove forests are reliable indicators for identifying the effects of anthropogenic stress (McDonald et al. 2003). Since mangrove productivity is vital to ecosystem functioning, it is important to understand the impact development may have on productivity.

Productivity of mangroves has been found to decrease when salinity is increased. In the Dominican Republic, total above ground primary productivity, biomass, and litter fall of mangroves decreased as salinity increased (Sherman et al. 2003). However, this impact may vary across species. Lovelock and Feller (2003) found that increased salinity decreased photosynthesis in white mangrove but not black mangrove. Increases in salinity may also adversely affect the reproduction of mangroves. Black mangrove seedlings were found to have higher mortality rates and a decrease in relative growth rate, leaf area, leaf longevity and number of new leaves as salinity increased (Suarez and Medina 2005). And Sherman et al. (2003) found a decrease in seed production and reproductive effort as salinity increased.

Nutrient addition, primarily nitrogen and phosphorus, has also been shown to alter the productivity of mangroves. In Florida, an impounded mangrove was found to be nitrogen limited when the addition of nitrogen increased leaf production and shoot growth of red and black mangroves but addition of phosphorus had no effect on growth (Feller et al. 2003). Red, black and white mangroves produced more root growth with low nutrient availability and increased leaf area when nutrient availability was high (McKee 1995). Mangroves are vulnerable to nutrient pollution because they are often nutrient limited (Lovelock et al. 2006). In Jamaica, mangrove productivity was found to increase as pollution/eutrophication decreased and the nitrate to phosphate ratios increased (McDonald et al. 2003).

The La Manzanilla mangroves are under pressure due to anthropogenic development. The affects that this development is having on the mangroves is unknown. This research will address whether differences in productivity and regeneration are occurring 1) in areas with different disturbance histories, 2) in areas with different water and soil characteristics, and 3) between species.

Methods

Vegetation sampling will be done at seven plots in the La Manzanilla mangroves; T1A, T1C, T1H, T1D, T2A, T2C, and T3A (Figure 1). Each plot can be located using the GPS locations listed in Table 1. The GPS point locations were taken at the entry point for each plot. From the GPS locations, follow the blue flagging into the mangroves to the center point, which is designated with blue and pink flagging. The piezometer (if they have already been installed) will be located at this center point.

Table 1: GPS point locations for the entry points to the seven plots. Note that the entry point to plots T1C and T1H are the same; flagging can be followed to each of the plots from the entry points.

PLOT	EASTING	NORTHING
T1A	522349	2132500
T1C	522202	2132561
T1H	522202	2132561
T1D	522112	2132858
T2A	522393	2134848
T2C	522337	2134916
T3A	520566	2134707

One time activities (to be completed March 2007)

Transect set up

At each plot, 10 m long transects will be ran from the center point in each of the four cardinal directions.

➢ Standing at the center point, identified by the blue and pink flagging and the piezometer (if they have been installed), use a compass to identify North.
➢ Have one member of the team remain at the center point, holding the end of the transect tape.
➢ A second member of the team will take the transect tape and measure out 10 meters to the North of the center point.
➢ An identifying post will be placed by the second team member 10 meters North of the center point to indicate the end of the transect.
➢ Repeat the above steps in each of the other cardinal directions; east, west, and south.
➢ Repeat these procedures to set up transects in each of the seven plots.

Litterbox assembly and placement

Litterboxes will be used to catch leaves and twigs (i.e., "litter") falling from mangroves throughout the year. This measurement is useful for estimating the contribution of the mangrove ecosystem to aquatic and terrestrial floor ecosystems. Six 0.25 m^2 litterboxes will be placed in each plot. These litterboxes need to be assembled and labeled prior to placement in the field. Currently, four litterboxes have been placed in the field as samples for construction and placement. Two of these litterboxes have been placed at plot T1C and two in plot T1H. Thirty-eight litterboxes need to be assembled. Follow the directions below for assembly.

➢ Cut two 14-inch pieces of wood (1 inch thick).
➢ Cut two 12-inch pieces of wood (1 inch thick).

- ➢ Arrange the four pieces of wood as shown in Figures 2 and 3.
- ➢ Place two screws in each corner as indicated by the arrows in Figure 2.
- ➢ Cut a piece of chicken wire large enough to cover the bottom and extend up the sides.
- ➢ Fold the ends of the chicken wire under to decrease sharp edges, and then use a staple gun to staple the chicken wire to the sides of the wood pieces.
- ➢ Place eye hooks in the middle of the top edge of each side; these will be used to hang the litterboxes to the trees.
- ➢ Label each litterbox using a sharpie or permanent marker. Labels will include the plot and an alphabetical identifier for the box. The 6 litterboxes at each plot will be given identifiers using the letters LB to designate litterbox and the first six letters of the alphabet; ranging from LB – A to LB – F. Some examples of labels would be T1A – LB –A, T1C – LB – C, and T2A – LB- F. See the printed labels to see more examples.
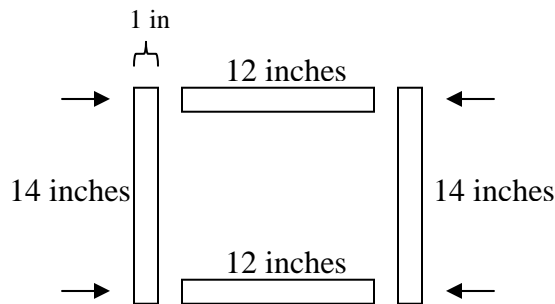
Figure 2. Schematic of how to assemble litterboxes

Figure 3: An assembled litterbox.

Litterbox placement

After assembly of the litterboxes, place six litterboxes in each plot. The litterboxes need to be distributed throughout the plot in areas that represent the canopy cover of the entire plot. If gaps, i.e., areas with few overhanging branches, are present in a plot, determine the approximate percentage of the plot that the gap covers and place a corresponding percentage of litterboxes in the gaps. For example, if 20% of the plot consists of gaps then roughly 20% of the litterboxes (one or two) should be placed in gaps. The litterboxes need to be placed high enough off of the

mangrove floor to avoid getting flooded and low enough in the canopy to be below the foliated branches. Follow the directions below for hanging the litterboxes in the field.

- ➢ Identify appropriate location for litterbox placement (see above).
- ➢ Place nails in four nearby stems/branches.
- ➢ Run wire from each nail to one of the four eye hooks on the litterbox.
- ➢ Visually level the litterbox and place flagging on the wires.
- ➢ Draw a map of the location of each litterbox with respect to the transects. This is a very important step since we do not know how legible the sharpie label will be when this box is re-visited. Remember to indicate the label of each litterbox in your drawing.
- ➢ Repeat the above steps for placement of each litter box within a plot.
- ➢ Repeat these procedures for litterbox placement at each of the seven plots.

Annual Dry Season Measurements

Sampling frequency of dry season measurements
Annual dry season measurements have been separated into two groups. The first group includes percent cover, stem density and basal area (Data sheets 1 – 3). This group will be sampled in every other March, i.e., 07, 09, etc... The second group includes the line intercept transect sampling of coarse woody debris and the belt transect sampling for regeneration (Data sheets 4-5). The second group will be sampled in March 2007 and will then be sampled annually during the March sampling effort.

Percent cover
This measurement is used to assess the density of mangrove leaves above the plot. Percent cover will be measured using a densiometer (Figure 4) at five points within each of the seven plots. The densiometer is a convex mirror divided into 24 squares. Percent cover can be determined by identifying how much of the mirror is not covered by vegetation (see below). If two species are present in the mirror, you will need to take 3 readings: %cover of species 1, % cover of species 2, and total % cover regardless of species composition. Note that the last reading is not simply the sum of the first two since you may have branches of the two species overlap.
If only one species is present, you will only need to obtain one reading since % cover of species 1 = total % cover.

- ➢ Stand at the center point facing north.
- ➢ Hold the mirror level in front of you.
- ➢ Imagine 4 uniformly spaced dots in each square.
- ➢ Count the number of dots not covered by vegetation.
- ➢ Place the count on the data sheet (Sheets 1 and 2) under center Quad 1.
- ➢ Repeat the count holding the mirror in each of the remaining cardinal directions while standing at the center point.
- ➢ If more than one species is present, repeat for cover of each species.
- ➢ Repeat the above steps at each of the four transect ends.
- ➢ Once back at base camp calculate percent cover on the data sheets by using the following equation:

$$\text{Percent cover} = 100 - (\text{count} * 1.04)$$

- ➢ Repeat these procedures for percent cover sampling at each of the seven plots.

Stem Density

Stem density will be measured using the Point Center Quarter Method (Figure 5).

- ➢ Standing at the center point, use the cardinal directions to separate the quarters.
- ➢ Start in the NE quarter, and using a transect tape measure the distance to the nearest tree (Figure 5). For multistemmed trees, take the measurement of the nearest stem.
- ➢ On the data sheet (Sheet 3) mark down the distance to that tree and the species of the tree.
- ➢ Repeat this for each of the other three quarters (Figure 5).
- ➢ Repeat the above steps at each of the four transect ends.
- ➢ Once back at base camp calculate stem density; which is the sum of the nearest neighbor distances divided by the number of quarters.
- ➢ Repeat these procedures for stem density sampling at each of the seven plots.

Figure 4: Spherical densiometer used for determining percent cover
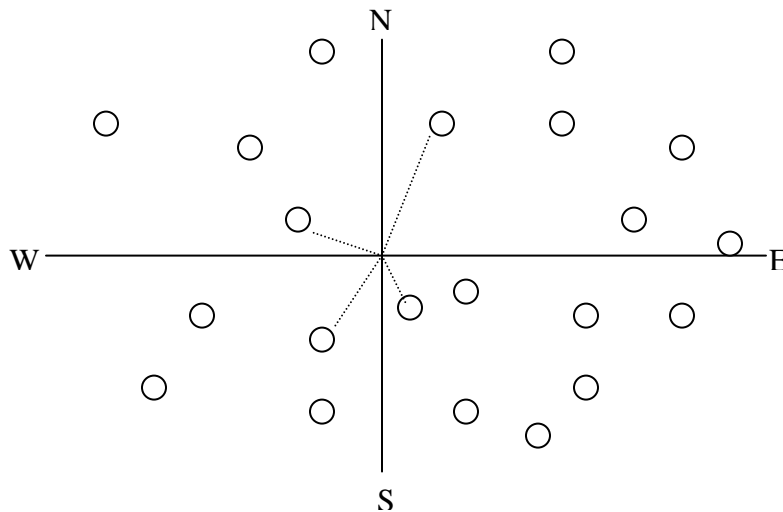
Figure 5: Schematic of Point Quarter Center Methodology. The distance to the nearest neighbor in each quarter is measured.

Basal Area

This measurement describes the amount of wood stored as trunk biomass per unit area. Basal area of each species will be measured at five points in each plot using an angle gauge (Figure 6). Basal area will be taken at the center of the plot and at each of the four transect ends. Basal area will be measured using the following protocol.

- ➢ At the center point, stand facing north.
- ➢ Place the angle gauge in one hand and the chain in the other hand. The proper distance to hold the angle gauge is determined by the length of the chain. Hold the button end of the chain touching your chin, move the angle gauge away from your face until the chain is fully extended (this should be 25 inches). Look through the upper most opening, marked with the 5 and count trees that are equal in diameter or larger in diameter than the opening.
- ➢ Rotate a full 360 degrees, keeping the angle gauge at the same location in front of you; count all live trees with diameters large enough that they fully fill the top opening (Figure 6). The distance of the tree from you is not important, the only thing that matters is that the width of the tree fills the entire opening.
- ➢ Mark down the number of trees with diameters large enough to completely fill the top opening on the data sheet (Sheet 3) under Count.
- ➢ Use the angle gauge to take the basal area measurements for each mangrove species present at the plot.
- ➢ Repeat the above steps at each of the four transect ends.
- ➢ Once back at base count add up the tally scores in each column and multiply by 5 to get the stand basal area.
- ➢ Repeat these procedures for basal area sampling at each of the seven plots.

Figure 6. Picture of a Cruz-All angle gauge. Picture from
http://www.terratech.net/product.asp?specific=jpfprqr4

Line intercept transect

A line intercept transect (Figure 7) will be used to determine the percent cover of coarse woody debris in four different diameter size classes (less than 5 cm, between 5 cm and 10 cm, larger than 10 cm but less than 30 cm, and greater than 30 cm).

- ➢ Have one team member stand at the center point of the transect; they will remain holding the transect tape at the center point during the line intercept transect sampling.

- ➢ Have a second member walk the transect tape out 10 meters to the north. If the tape can not be tied off to the end post, then that individual will need to remain at the end point holding the transect tape. The tape should be held taut above the ground.
- ➢ Using a meter stick to identify the sampling plane, walk along the line intercept transect until a piece of coarse woody debris crosses underneath the transect line (Figure 7).
- ➢ Measure the diameter of the coarse woody debris using the meter stick to identify size class.
- ➢ Measure the length of the coarse woody debris that crosses the transect.
- ➢ Continue along the length of the transect marking down the length of the different coarse woody debris size classes on the data sheets (Sheet 4).
- ➢ While the transect tape is still up, proceed to sample the belt transect to determine the density of propagules, seedlings, saplings, and suckers (see "belt transect" instructions).
- ➢ After completing the line transect and the belt transect, move to the east transect.
- ➢ Repeat the above steps for the east, west and south transects.
- ➢ Once back at base camp, add up all lengths for each category separately and divide by 1000 cm (for the length of the transect) and multiply by 100 to get the percent cover.

$$\text{Percent cover CWD (cat)} = \sum(\text{lengths})/1000*100$$

- ➢ Repeat these procedures for percent cover of coarse woody debris at each of the seven plots.
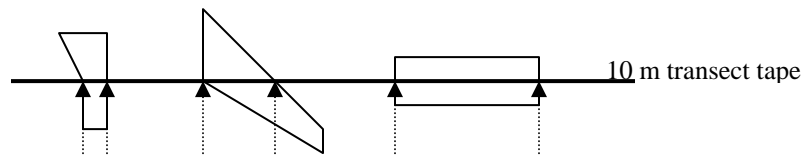
Figure 7: Schematic of a line intercept transect looking down from above. The straight solid line indicates the 10 m transect tape. The shapes are coarse woody debris. Only the length of the object crossing directly under the transect line is measured.

Belt transect

This measurement will be used to sample mangrove regeneration. A belt transect will be used to determine the density of propagules, suckers, seedlings, and saplings. The following definitions will be used to distinguish between the four sampling categories. Propagules are green and have the ability to root; if vertical, no leaves are present (Figure 8). Obviously dead propagules should not be included. Seedlings are rooted with leaves and less than 4 feet in height (Figure 8). Saplings are between 4 and 10 feet and are not attached to a tree or log. Suckers are between 4 and 10 feet in height and are attached to a tree or log.

- ➢ Proceed with the belt transect (Figure 9), as soon as the line intercept transect for coarse woody debris has been completed.
- ➢ Place a meter stick horizontal to the ground with the 50 cm mark on the transect tape, so that there is a half meter on either side of the tape.
- ➢ Run the meter stick along the transect tape and tally all the propagules, seedlings, saplings, and suckers that fall within a half meter on either side of the transect tape (Figure 9) on the data sheet (Sheet 5).
- ➢ After moving along all 10 meters of the transect move the tape to the next transect.
- ➢ Repeat the above steps for each of the four directions for a total of 4 belt transects per plot.

8

- ➢ Once back at base camp, add up the counts for each category to get the density/10 m^2.
- ➢ Repeat these procedures for propagule, seedling, sapling, and sucker density at each of the seven plots.

Figure 8: Difference between a propagule and a seedling.
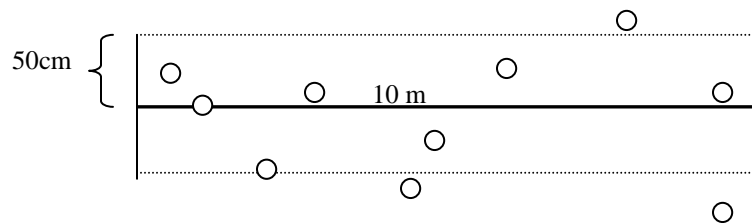
Figure 9: Schematic of a belt transect looking down from above. Circles indicate trees. The center solid line is the transect tape and the dotted lines are the 50 cm horizontal boundary. In this example the density is 7 trees/10 m^2.

Other Measurements

Litter fall

Litter fall is the primary way nutrients are recycled through the mangrove ecosystem and measurements of litter fall can be used as an estimator of primary productivity. Litter will be collected from the litterboxes at each site visit after initial installation of boxes March 07, i.e., June 07, July 07, Nov 07, etc…. It is very important that ALL the litter in the boxes be collected regardless of type, i.e., flowers, twigs, etc… should be collected along with leaves. The procedure for litterfall collection is outlined below.

- ➢ Label large (10" x13") manila envelopes using the sampling stickers provided (see appendix). Each sticker includes the plot name, e.g., T1A-LB-A and should match

the label on the litterbox. Note there are 4 replicates of each sticker. You should only need ¼ of the stickers per sampling trip.

➤ CAREFULLY empty the contents of each litterbox into the pre-labeled manila envelope. If needed, you may use more than one bag, but make sure each is labeled correctly and note on the bag that it is #1 of 2, #2 of 2 etc….

➤ Do not let any litter spill. Do double-check the identifier on the manila envelope against the litterbox label. A mislabeled sample is a lost data point. If litterbox labels are difficult to read, re-label them. If box labels are impossible to read, consult the site map drawn March 07 which includes labeled locations of each litterbox..

➤ If it is too wet out to work with manila envelopes in the field, you may want to use large LABELLED Ziploc bags for litter collection. However it is important that the sample be removed from the Ziploc and placed in the manila envelope as soon as possible to prevent mildew from forming.

➤ Spread manila envelopes out in as dry a location as possible to initiate drying of the litter.

➤ Repeat the above steps for all six litterboxes within a plot.

➤ Repeat these procedures for each of the seven plots.

➤ The litter samples will then be sent off to Mark Rains, PI USF, where they will be dried and weighed.

➤ Please write notes on the bags if there is any departure from these procedures or if anything odd is noted.

Productivity

Productivity sampling was initiated in January 2007, and will continue semi- annually at each July and Jan visit. Nine branches were chosen in each plot where the leaves were growing in a direct sun environment. The twig chosen for study had no branching in the sampling zone and the leaves showed little evidence of herbivory at the time of sampling. Since the interior of many of the plots have a full canopy, finding sun leaves that were within reach was difficult. Therefore, for plots T1C, T2A, and T2C all samples were selected on the main channel near the respective plot. Plot T1A does have 3 sampling branches on red mangroves in the interior of the plot; the remaining 6 branches are on the channel. Sampling branches for plot T3A are all along the road.

All sampling branches are marked with pink flagging, with the sampling identifier written on the flagging. A total of 63 branches were marked and sampled in January of 2007; nine branches in each plot. Each branch was given an identifying number between P1 and P63. The datasheets identify which numbered branches are at each plot. For each branch the following measurements were taken; twig length, number of leaves and the length and width of each leaf blade. The leaf consists of a petiole and a blade (Figure 10), however, only the length and width of the blade is measured. Follow the protocol below for continuing productivity sampling.

➤ Relocate each sampling branch by locating the pink flagging at each plot.

➤ Measure the length of the twig from the flag location to the apical meristem, using a metric ruler (Figure 10).

➤ Count the number of leaves including the newly emerging leaves at the tip (White mangrove leaves emerge in pairs whereas red mangroves will have a single emergent leaf).

➢ Measure the length of each leaf blade, starting at the base of the blade and not including the petiole (Figure 10) and mark measurements on the data sheet (Sheets 6-12).
➢ Measure the width of each leaf blade and its widest point and mark measurements on the data sheet (Sheets 6-12).
➢ Replace worn flagging with fresh flagging by placing it <u>in the original location</u> on the branch and label the flagging with the plot and identifying number of the branch (e.g., T1A – P2). Leave the original flagging in place if possible.
➢ Repeat the above steps for all nine productivity samples within a plot.
➢ Repeat these procedures for productivity sampling at all seven plots.
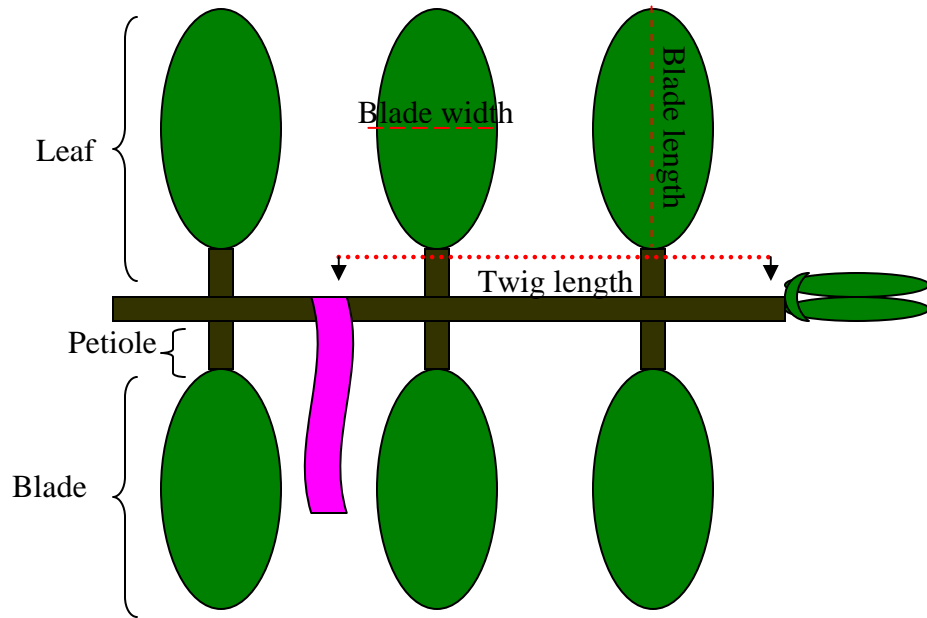
Figure 10. Schematic of productivity sampling. When measuring the length and width for the productivity samples, only the blade length and width are measured.

Interdisciplinary intersections

The trees of the mangrove ecosystem are vital to the functioning of the system. Much of the energy within the mangrove ecosystem is derived from the net primary production of the trees; although some may be inputted into the system through runoff. Leaf litter and woody debris are broken down by microbes and other detritivores (e.g., crabs and snails) which are at the base of the food web; thereby serving as a major source of food to the larger fauna within the mangrove system. Mangrove productivity is affected by nutrient availability and salinity.   Increases in nutrient availability usually are associated with an increase in productivity (Feller et al. 2003; McKee 1995) ; whereas, increases in salinity are often associated with decreases in productivity (Feller et al. 2003; Sherman et al. 2003). Hydrological and water quality changes due to anthropogenic stresses may adversely affect the productivity of the mangroves; altering the energy balance within the food web.

The mangroves are also structurally complex; with stems, prop roots, and pneumatophores. This complexity provides habitat for many different species; fish are usually abundant within mangroves and some mangroves act as nurseries for juvenile fish (Gunawardena and Rowan 2005; Verweij et al. 2006) while the prop roots and pneumatophores provide surfaces for epiphytes and algae. This structural complexity also helps increase sedimentation, thereby acting as a filter for estuarine and coral systems farther offshore.

Applications and analysis

The data collected through the vegetation module will help identify if differences in regeneration and productivity exist between plots and species in the La Manzanilla mangrove ecosystem. Differences in regeneration and productivity between plots or over time may serve to identify areas within the mangrove ecosystem that are being affected by the anthropogenic effects of development. Productivity and regeneration of mangroves may decrease if there is an increase in flood duration, salinity or a decrease in dissolved oxygen. Different anthropogenic inputs may have different effects on the mangrove ecosystem. An increase in salinity could decrease the productivity of the mangroves (Feller et al. 2003; Sherman et al. 2003). Changes in nutrient availability could also alter production. If the system is nitrogen or phosphorus limited, inputs of nutrients may increase productivity (Feller et al. 2003; McKee 1995). However, nutrient pollution could decrease productivity; for example, by altering nitrogen to phosphate ratios (McDonald et al. 2003). These changes may serve to identify areas that are under more pressure from anthropogenic activities. Understanding the impacts of development on the mangrove system is important for the local community and for maintaining a mangrove ecosystem that is not only rich in biodiversity but is economically valuable to the community.

Equipment list

One-time activities
For Transect set up (March 07)
Compass
Transect tape (>10 m)
Flagging (blue and pink)
28 marking posts for transect end points
Orange spray paint

For litterbox assembly and placement (March 07)
Saw
Drill
Screws
Screwdriver
Chicken Wire
Wire cutters
Eye hooks
Wood (1 inch thick)
Tape Measure (> 14 inches)

Wire
Nails
Hammer
Sharpie or permanent marker

Recurring activities
Percent cover (March 07, 09)
Clipboard for data sheets
7 copies of data sheets 1 and 2
Field Instruction Sheet A
Pencil/pen
Densiometer
Calculator

Stem Density (March 07, 09)
Clipboard for data sheets
7 copies of data sheet 3
Field Instruction Sheet A
Pencil/pen

Transect tape (> 10 m)
Calculator

Basal Area (March 07, 09)
Clipboard for data sheets
7 copies of data sheet 3 (same sheets as used
for stem density)
Field Instruction Sheet B
Pencil/pen
Angle gauge
Calculator

Line intercept transect (March 07, 08, 09)
Clipboard for data sheets
7 copies of data sheet 4
Field Instruction Sheet C
Pencil/pen
Transect tape (> 10 m)
Meter stick

Belt transect (March 07, 08, 09)
Clipboard for data sheets
7 copies of data sheet 5
Field Instruction Sheet C
Pencil/pen

Transect tape (>10 m)
Meter stick

Litterfall (every site visit for 2007)
Clipboard for data sheets
Field Instruction Sheet D
Pencil/pen
Sharpie/permanent marker
45 Gallon size Ziploc bags
45 Manila envelopes (10" x 13")
Pre-printed labels for litterfall (appendix)
A copy of the site map created March 07 in case
sampling points are difficult to re-locate

Productivity (July 07, Jan 08, July 08…)
Clipboard for data sheets
1 copy of data sheets 6-12
Field Instruction Sheet D
Pencil/pen
Sharpie or permanent marker
Flagging (pink) for replacing old flagging
Metric ruler
A copy of the site map in case sampling points
are difficult to re-locate

Suggested Readings

Alongi DM (2002) Present state and future of the world's mangrove forests. Environmental
    Conservation 29(3):331-349
Feller IC, Whigham DF, McKee KL, Lovelock CE (2003) Nitrogen limitation of growth and nutrient
    dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. Oecologia 134:405-414
McDonald KO, Webber DF, Webber MK (2003) Mangrove forest structure under varying
    environmental conditions. Bulletin of Marine Science 73(2):491-505

Bibliography

Alongi DM (2002) Present state and future of the world's mangrove forests. Environmental
    Conservation 29:331-349
Feller IC, Whigham DF, McKee KL, Lovelock CE (2003) Nitrogen limitation of growth and nutrient
    dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. Oecologia 134:405-414
Gunawardena M, Rowan JS (2005) Economic valuation of a mangrove ecosystem threatened by shrimp
    aquaculture in Sri Lanka. Environmental Management 36:535-550
Islam MS, Haque M (2004) The mangrove-based coastal and nearshore fisheries of Bangladesh:
    ecology, exploitation and management. Reviews in Fish Biology and Fisheries 14:153-180

Lovelock CE, Feller IC (2003) Photosynthetic performance and resource utilization of two mangrove species coexisting in a hypersaline scrub forest. Oecologia 134:455-462

Lovelock CE, Feller IC, Ball MC, Engelbrecht BMJ, Ewe ML (2006) Differences in plant function in phosphorus- and nitrogen-limited mangrove ecosystems. New Phytologist 172:514-522

McDonald KO, Webber DF, Webber MK (2003) Mangrove forest structure under varying environmental conditions. Bulletin of Marine Science 73:491-505

McKee KL (1995) Interspecific variation in growth, biomass partitioning, and defensive characteristics of neotropical mangrove seedlings: response to light and nutrient availability. American Journal of Botany 82:299-307

Primavera JH (1998) Socio-economic impacts of shrimp culture. Aquaculture Research 28:815-827

Sherman RE, Fahey TJ, Martinez P (2003) Spatial patterns of Biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. Ecosystems 6:384-398

Suarez N, Medina E (2005) Salinity effect on plant growth and leaf demography of the mangrove, Avicennia germinans L. Trees-Structure and Function 19:721-727

Verweij MC, Nagelkerken I, Wartenbergh SLJ, Pen IR, van der Velde G (2006) Caribbean mangroves and seagrass beds as daytime feeding habitats for juvenile French grunts, Haemulon flavolineatum. Marine Biology 149:1291-1299

Vijay V, Biradar RS, Inamdar AB, Deshmukhe G, Baji S, Pikle M (2005) Mangrove mapping and change detection around Mumbai (Bombay) using remotely sensed data. Indian Journal of Marine Sciences 34:310-315

APPENDIX A

Sample Locations January 2007
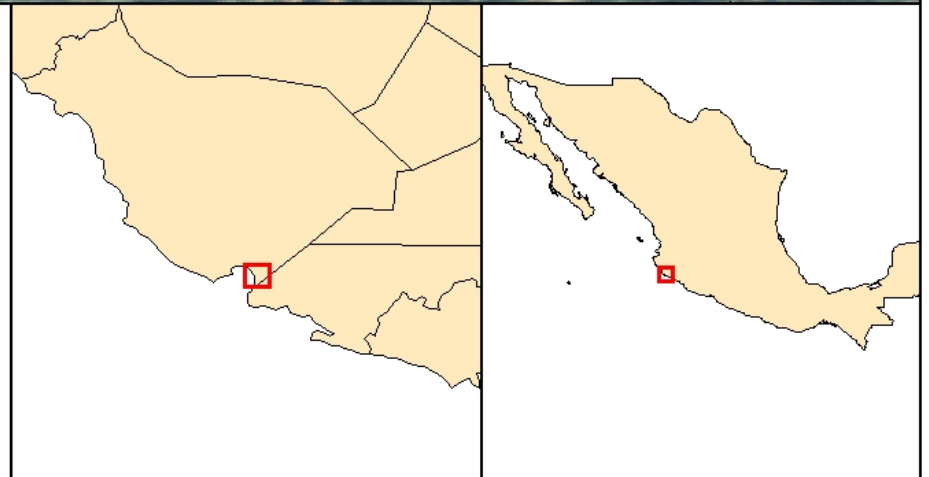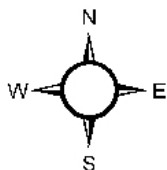
APPENDIX B

Field Instruction Sheet

Percent cover

Percent cover will be measured using a densiometer. If more than one species is present, this will be repeated for total percent cover and for percent cover of each species. Total cover is a separate measurement and cannot be obtained by adding the cover of the different species.

➤ Stand at the center point facing north.
➤ Hold the mirror level in front of you.
➤ Imagine 4 uniformly spaced dots in each square.
➤ Count the number of dots not covered by vegetation.
➤ Place the count on the data sheet (Sheets 1 and 2) under center Quad 1.
➤ Repeat the count holding the mirror in each of the remaining cardinal directions while standing at the center point.
➤ If more than one species is present, repeat for cover of each species.
➤ Repeat the above steps at each of the four transect ends.

Stem Density

Stem density will be measured using the Point Center Quarter Method.

➤ Standing at the center point, use the cardinal directions to separate the quarters.
➤ Start in the NE quarter, and using a transect tape measure the distance to the nearest tree. For multistemmed trees, take the measurement of the nearest stem.
➤ On the data sheet (Sheet 3) mark down the distance to that tree and the species of the tree.
➤ Repeat this for each of the other three quarters.
➤ Repeat the above steps at each of the four transect ends.
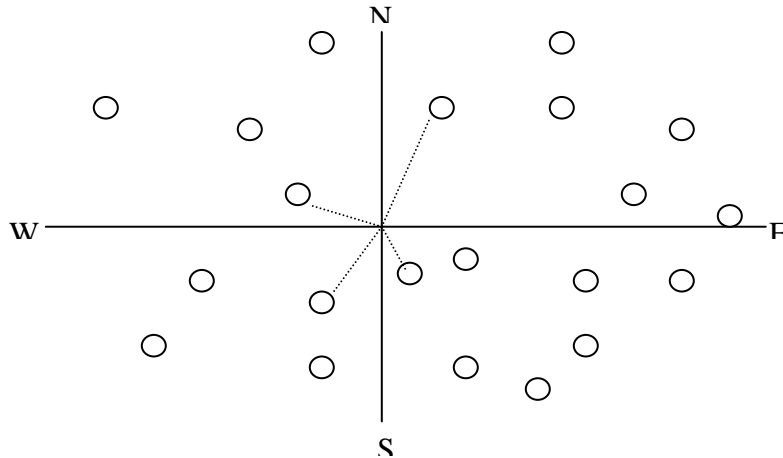
Schematic of Point Quarter Center Methodology. The distance to the nearest neighbor in each quarter is measured.

Basal Area
Basal area of each species will be measured at five points in each plot using an angle gauge.

➢ At the center point, stand facing north.

➢ Place the angle gauge in one hand and the chain in the other hand. The proper distance to hold the angle gauge is determined by the length of the chain. Hold the button end of the chain touching your chin, move the angle gauge away from your face until the chain is fully extended (this should be 25 inches). Look through the upper most opening, marked with the 5 and count trees that are equal in diameter or larger in diameter than the opening.

➢ Rotate a full 360 degrees, keeping the angle gauge at the same location in front of you; count all live trees with diameters large enough that they fully fill the top opening (Figure 6). The distance of the tree from you is not important, the only thing that matters is that the width of the tree fills the entire opening.

➢ Mark down the number of trees with diameters large enough to completely fill the top opening on the data sheet (Sheet 3) under Count.

➢ Use the angle gauge to take the basal area measurements for each mangrove species present at the plot.

➢ Repeat the above steps at each of the four transect ends.

Line intercept transect

A line intercept transect will be used to determine the percent cover of coarse woody debris in four different diameter size classes (less than 5 cm, between 5 cm and 10 cm, larger than 10 cm but less than 30 cm, and greater than 30 cm).

➢ Have one team member stand at the center point of the transect; they will remain holding the transect tape at the center point during the line intercept transect sampling.

➢ Have a second member walk the transect tape out 10 meters to the north. If the tape can not be tied off to the end post, then that individual will need to remain at the end point holding the transect tape. The tape should be held taut above the ground.

➢ Using a meter stick to identify the sampling plane, walk along the line intercept transect until a piece of coarse woody debris crosses underneath the transect line.

➢ Measure the diameter of the coarse woody debris using the meter stick to identify size class.

➢ Measure the length of the coarse woody debris that crosses the transect.

➢ Continue along the length of the transect marking down the length of the different coarse woody debris size classes on the data sheets (Sheet 4).

➢ While the transect tape is still up, proceed to sample the belt transect to determine the density of propagules, seedlings, saplings, and suckers (see "belt transect" instructions).

➢ After completing the line transect and the belt transect, move to the east transect.

➢ Repeat the above steps for the east, west and south transects.

Schematic of a line intercept transect looking down from above. The straight solid line indicates the 10 m transect tape. The shapes are coarse woody debris. Only the length of the object crossing directly under the transect line is measured.

Belt transect

➢ Proceed with the belt transect, as soon as the line intercept transect for coarse woody debris has been completed.

➢ Place a meter stick horizontal to the ground with the 50 cm mark on the transect tape, so that there is a half meter on either side of the tape.

➢ Run the meter stick along the transect tape and tally all the propagules, seedlings, saplings, and suckers that fall within a half meter on either side of the transect tape on the data sheet (Sheet 5).

➢ After moving along all 10 meters of the transect move the tape to the next transect.

➢ Repeat the above steps for each of the four directions for a total of 4 belt transects per plot.
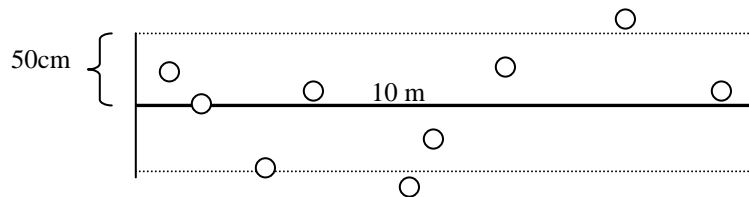
Schematic of a belt transect looking down from above. Circles indicate trees○ The center solid line is the transect tape, and the dotted lines are the 50 cm horizontal boundary. In this example the density is 7 trees/10 m^2.

Litter fall

Litter will be collected from the litterboxes at each site visit after initial installation of boxes March 07, i.e., June 07, July 07, Nov 07, etc…. It is very important that ALL the litter in the boxes be collected regardless of type, i.e., flowers, twigs, etc… should be collected along with leaves.

➢ Label large (10" x13") manila envelopes using the sampling stickers provided (see appendix). Each sticker includes the plot name, e.g., T1A-LB-A and should match the label on the litterbox. Note there are 4 replicates of each sticker. You should only need ¼ of the stickers per sampling trip.

➢ CAREFULLY empty the contents of each litterbox into the pre-labeled manila envelope. If needed, you may use more than one bag, but make sure each is labeled correctly and note on the bag that it is #1 of 2, #2 of 2 etc….

➢ Do not let any litter spill. Do double-check the identifier on the manila envelope against the litterbox label. A mislabeled sample is a lost data point. If litterbox labels are difficult to read, re-label them. If box labels are impossible to read, consult the site map drawn March 07 which includes labeled locations of each litterbox..

➢ If it is too wet out to work with manila envelopes in the field, you may want to use large LABELLED Ziploc bags for litter collection. However it is important that the sample be removed from the Ziploc and placed in the manila envelope as soon as possible to prevent mildew from forming.

➢ Spread manila envelopes out in as dry a location as possible to initiate drying of the litter.

➢ Repeat the above steps for all six litterboxes within a plot.

➢ Repeat these procedures for each of the seven plots.

➢ The litter samples will then be sent off to Mark Rains, PI USF, where they will be dried and weighed.

➢ Please write notes on the bags if there is any departure from these procedures or if anything odd is noted.

Productivity
- ➢ Relocate each sampling branch by locating the pink flagging at each plot.
- ➢ Measure the length of the twig from the flag location to the apical meristem, using a metric ruler.
- ➢ Count the number of leaves including the newly emerging leaves at the tip (White mangrove leaves emerge in pairs whereas red mangroves will have a single emergent leaf).
- ➢ Measure the length of each leaf blade, starting at the base of the blade and not including the petiole and mark measurements on the data sheet (Sheets 6-12).
- ➢ Measure the width of each leaf blade and its widest point and mark measurements on the data sheet (Sheets 6-12).
- ➢ Replace worn flagging with fresh flagging by placing it <u>in the original location</u> on the branch and label the flagging with the plot and identifying number of the branch (e.g., T1A – P2). Leave the original flagging in place if possible.
- ➢ Repeat the above steps for all nine productivity samples within a plot.

 Schematic of productivity sampling. When measuring the length and width for the productivity samples, only the blade length and width are measured.

4 replicates of litter box labels to be used in 4 separate sampling trips, eg june, july, nov, jan

Site: T1A - LB-A Date: Collector:	Site: T1A - LB-A Date: Collector:	Site: T1A - LB-A Date: Collector:
Site: T1A - LB-A Date: Collector:	Site: T1A - LB-B Date: Collector:	Site: T1A - LB-B Date: Collector:
Site: T1A - LB-B Date: Collector:	Site: T1A - LB-B Date: Collector:	Site: T1A - LB-C Date: Collector:
Site: T1A - LB-C Date: Collector:	Site: T1A - LB-C Date: Collector:	Site: T1A - LB-C Date: Collector:
Site: T1A - LB-D Date: Collector:	Site: T1A - LB-D Date: Collector:	Site: T1A - LB-D Date: Collector:
Site: T1A - LB-D Date: Collector:	Site: T1A - LB-E Date: Collector:	Site: T1A - LB-E Date: Collector:
Site: T1A - LB-E Date: Collector:	Site: T1A - LB-E Date: Collector:	Site: T1A - LB-F Date: Collector:
Site: T1A - LB-F Date: Collector:	Site: T1A - LB-F Date: Collector:	Site: T1A - LB-F Date: Collector:
Site: T1C - LB-A Date: Collector:	Site: T1C - LB-A Date: Collector:	Site: T1C - LB-A Date: Collector:
Site: T1C - LB-A Date: Collector:	Site: T1C - LB-B Date: Collector:	Site: T1C - LB-B Date: Collector:

4 replicates of litter box labels to be used in 4 separate sampling trips, eg june, july, nov, jan

Site: T1C - LB-B Date: Collector:	Site: T1C - LB-B Date: Collector:	Site: T1C - LB-C Date: Collector:
Site: T1C - LB-C Date: Collector:	Site: T1C - LB-C Date: Collector:	Site: T1C - LB-C Date: Collector:
Site: T1C - LB-D Date: Collector:	Site: T1C - LB-D Date: Collector:	Site: T1C - LB-D Date: Collector:
Site: T1C - LB-D Date: Collector:	Site: T1C - LB-E Date: Collector:	Site: T1C - LB-E Date: Collector:
Site: T1C - LB-E Date: Collector:	Site: T1C - LB-E Date: Collector:	Site: T1C - LB-F Date: Collector:
Site: T1C - LB-F Date: Collector:	Site: T1C - LB-F Date: Collector:	Site: T1C - LB-F Date: Collector:
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Site: T1H - LB-A Date: Collector:	Site: T1H - LB-B Date: Collector:	Site: T1H - LB-B Date: Collector:
Site: T1H - LB-B Date: Collector:	Site: T1H - LB-B Date: Collector:	Site: T1H - LB-C Date: Collector:
Site: T1H - LB-C Date: Collector:	Site: T1H - LB-C Date: Collector:	Site: T1H - LB-C Date: Collector:

4 replicates of litter box labels to be used in 4 separate sampling trips, eg june, july, nov, jan

Site: T1H - LB-D Date: Collector:	Site: T1H - LB-D Date: Collector:	Site: T1H - LB-D Date: Collector:
Site: T1H - LB-D Date: Collector:	Site: T1H - LB-E Date: Collector:	Site: T1H - LB-E Date: Collector:
Site: T1H - LB-E Date: Collector:	Site: T1H - LB-E Date: Collector:	Site: T1H - LB-F Date: Collector:
Site: T1H - LB-F Date: Collector:	Site: T1H - LB-F Date: Collector:	Site: T1H - LB-F Date: Collector:
Site: T1D - LB-A Date: Collector:	Site: T1D - LB-A Date: Collector:	Site: T1D - LB-A Date: Collector:
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Site: T1D - LB-C Date: Collector:	Site: T1D - LB-C Date: Collector:	Site: T1D - LB-C Date: Collector:
Site: T1D - LB-D Date: Collector:	Site: T1D - LB-D Date: Collector:	Site: T1D - LB-D Date: Collector:
Site: T1D - LB-D Date: Collector:	Site: T1D - LB-E Date: Collector:	Site: T1D - LB-E Date: Collector:

4 replicates of litter box labels to be used in 4 separate sampling trips, eg june, july, nov, jan

Site: T1D - LB-E Date: Collector:	Site: T1D - LB-E Date: Collector:	Site: T1D - LB-F Date: Collector:
Site: T1D - LB-F Date: Collector:	Site: T1D - LB-F Date: Collector:	Site: T1D - LB-F Date: Collector:
Site: T2A - LB-A Date: Collector:	Site: T2A - LB-A Date: Collector:	Site: T2A - LB-A Date: Collector:
Site: T2A - LB-A Date: Collector:	Site: T2A - LB-B Date: Collector:	Site: T2A - LB-B Date: Collector:
Site: T2A - LB-B Date: Collector:	Site: T2A - LB-B Date: Collector:	Site: T2A - LB-C Date: Collector:
Site: T2A - LB-C Date: Collector:	Site: T2A - LB-C Date: Collector:	Site: T2A - LB-C Date: Collector:
Site: T2A - LB-D Date: Collector:	Site: T2A - LB-D Date: Collector:	Site: T2A - LB-D Date: Collector:
Site: T2A - LB-D Date: Collector:	Site: T2A - LB-E Date: Collector:	Site: T2A - LB-E Date: Collector:
Site: T2A - LB-E Date: Collector:	Site: T2A - LB-E Date: Collector:	Site: T2A - LB-F Date: Collector:
Site: T2A - LB-F Date: Collector:	Site: T2A - LB-F Date: Collector:	Site: T2A - LB-F Date: Collector:

4 replicates of litter box labels to be used in 4 separate sampling trips, eg june, july, nov, jan

Site: T2C - LB-A Date: Collector:	Site: T2C - LB-A Date: Collector:	Site: T2C - LB-A Date: Collector:
Site: T2C - LB-A Date: Collector:	Site: T2C - LB-B Date: Collector:	Site: T2C - LB-B Date: Collector:
Site: T2C - LB-B Date: Collector:	Site: T2C - LB-B Date: Collector:	Site: T2C - LB-C Date: Collector:
Site: T2C - LB-C Date: Collector:	Site: T2C - LB-C Date: Collector:	Site: T2C - LB-C Date: Collector:
Site: T2C - LB-D Date: Collector:	Site: T2C - LB-D Date: Collector:	Site: T2C - LB-D Date: Collector:
Site: T2C - LB-D Date: Collector:	Site: T2C - LB-E Date: Collector:	Site: T2C - LB-E Date: Collector:
Site: T2C - LB-E Date: Collector:	Site: T2C - LB-E Date: Collector:	Site: T2C - LB-F Date: Collector:
Site: T2C - LB-F Date: Collector:	Site: T2C - LB-F Date: Collector:	Site: T2C - LB-F Date: Collector:
Site: T3A - LB-A Date: Collector:	Site: T3A - LB-A Date: Collector:	Site: T3A - LB-A Date: Collector:
Site: T3A - LB-A Date: Collector:	Site: T3A - LB-B Date: Collector:	Site: T3A - LB-B Date: Collector:

4 replicates of litter box labels to be used in 4 separate sampling trips, eg june, july, nov, jan

Site: T3A - LB-B Date: Collector:	Site: T3A - LB-B Date: Collector:	Site: T3A - LB-C Date: Collector:
Site: T3A - LB-C Date: Collector:	Site: T3A - LB-C Date: Collector:	Site: T3A - LB-C Date: Collector:
Site: T3A - LB-D Date: Collector:	Site: T3A - LB-D Date: Collector:	Site: T3A - LB-D Date: Collector:
Site: T3A - LB-D Date: Collector:	Site: T3A - LB-E Date: Collector:	Site: T3A - LB-E Date: Collector:
Site: T3A - LB-E Date: Collector:	Site: T3A - LB-E Date: Collector:	Site: T3A - LB-F Date: Collector:
Site: T3A - LB-F Date: Collector:	Site: T3A - LB-F Date: Collector:	Site: T3A - LB-F Date: Collector:
Site: - Date: Collector:	Site: - Date: Collector:	Site: - Date: Collector:
Site: - Date: Collector:	Site: - Date: Collector:	Site: - Date: Collector:
Site: - Date: Collector:	Site: - Date: Collector:	Site: - Date: Collector:
Site: - Date: Collector:	Site: - Date: Collector:	Site: - Date: Collector:

Vegetation Data Sheet

Team #: _____   Site: _____

Surveyor: _____   Date: _____

email: _____

Species present - Check which mangrove species are present

☐ **Red Mangrove -** *Rhizophora mangle*   ☐ **White Mangrove -** *Laguncularia racemosa*   ☐ **Black Mangrove -** *Avicennia germinans*

Percent (%) Cover

Take at five points; plot center and at each end of the four transects (e.g., North transect end and South transect end)

Densiometer

If more than one species is present, take densiometer readings for each species and for total percent cover. Total percent cover is a separate measurement and cannot be found by adding the species percent cover. Write species name in the space provided.

Back at base camp calculate percent cover from densiometer data: Multiply data by 1.04 and subtract from 100

Center	Total		species		species	
	Count	% cover	Count	% cover	Count	% cover
Quad 1						
Quad 2						
Quad 3						
Quad 4						
Average	-----------		-----------		-----------	

North	Total		species		species	
	Count	% cover	Count	% cover	Count	% cover
Quad 1						
Quad 2						
Quad 3						
Quad 4						
Average	-----------		-----------		-----------	

South	Total		species		species	
	Count	% cover	Count	% cover	Count	% cover
Quad 1						
Quad 2						
Quad 3						
Quad 4						

East	Total		species		species	
	Count	% cover	Count	% cover	Count	% cover
Quad 1						
Quad 2						
Quad 3						
Quad 4						

Vegetation Data Sheet

Average	----------		----------		----------		Average	-----------		----------		----------	

Team #: _____

Surveyor: _____

email: _____

Site: _____

Date: _____

Percent (%) Cover (continued)

Take at five points; plot center and at each end of the four transects (e.g., North transect end and South transect end)

Densiometer

If more than one species is present, take densiometer readings for each species and for total percent cover. Total percent cover is a separate measurement and cannot be found by adding the species percent cover. Write species name in the space provided.

Back at base camp calculate percent cover from densiometer data: Multiply data by 1.04 and subtract from 100

	West					
	Total		**species**		**species**	
	Count	**% cover**	**Count**	**% cover**	**Count**	**% cover**
Quad 1						
Quad 2						
Quad 3						
Quad 4						
Average	----------		----------		----------	

Vegetation Data Sheet

Team #: _____   Site: _____

Surveyor: _____   Date: _____

email: _____

Stem Density

Take at five points: plot center and at each end of the four transects using the Point Quarter Center Method

	Center		North		South		East		West		
	Distance	**Species**	**Distance**	**Species**	**Distance**	**Species**	**Distance**	**Species**	**Distance**	**Species**	
NE quarter											
NW quarter											
SE quarter											
SW quarter											**Plot Sum**
Distance sum		-----------		-----------		-----------		-----------		-----------	

Sum the distances in each quarter for each point (e.g., center, north) and place in distance sum.

Add up the distance sums and place in Plot Sum box.

Mean distance

Calculate[1]: **mean distance = Plot sum/20**

Basal Area

Take at five points; plot center and at each end of the four transects using the angle guage.

	Center		North		South		East		West		Ave. BA
	Count	**BA**	**Count**	**BA**	**Count**	**BA**	**Count**	**BA**	**Count**	**BA**	
Red Mangrove											
White Mangrove											
Black Mangrove											

To determine basal area (BA): multiply count by 5

To determine the average BA for each species, sum the five BA values for each species and divide by 5.

[1]Mueller-Dombois D, Ellenberg H (1974) Aims and methods of vegetation ecology. John Wiley and Sons, New York

Vegetation Data Sheet

Team #: _____   Site: _____
Surveyor: _____   Date: _____
email: _____

Percent Cover Coarse Woody Debris

Sample coarse woody debris (CWD) in four diameter size classes using line intercept transects

Mark down measurements in centimeters for each piece of CWD along the transect in the proper size category

	North	South	East	West
CWD < 5 cm				
5 cm < CWD < 10 cm				
10 cm < CWD< 30 cm				
CWD > 30 cm				

Calculations

Total: Sum values for each size class and place in the appropriate total box below
% cover = Total/1000*100
Average % cover: Sum % cover for each size class and divide by four.

	North		South		East		West		Average
	Total	% cover	Total	% cover	Total	% cover	Total	% cover	% cover
CWD < 5 cm									
5 cm < CWD < 10 cm									
10 cm < CWD < 30 cm									
CWD > 30 cm									

Vegetation Data Sheet

Team #: _____   Site: _____

Surveyor: _____   Date: _____

email: _____

Belt Transect
Place tally marks for each category in the appropriate column

	North	South	East	West
# propagules				
# seedlings (< 4 ft.)				
# saplings (> 4ft & < 10 ft)				
# suckers (> 4ft & < 10 ft)				

Density

	North	South	East	West
propagules				
seedlings				
saplings				
suckers				

Definitions

Propagule - Green and has the ability to root. If vertical to the ground, no leaves are present. No signs of decay, appears viable

Seedling - Rooted and leaves are present. Less than 4 feet in height.

Sapling - Between 4 feet and 10 feet in height and not attached to a tree or log.

Sucker - Between 4 feet and 10 feet in height and attached to a tree or log.

Vegetation Data Sheet

Team #: _____   Site: **T1A** _____

Surveyor: _____   Date: _____

email: _____

Productivity

	P1	P2	P3	P4	P5	P6	P7	P8	P9
Twig Length									
# of Leaves									
Leaf A Width (cm)									
Length (cm)									
Leaf B Width (cm)									
Length (cm)									
Leaf C Width (cm)									
Length (cm)									
Leaf D Width (cm)									
Length (cm)									
Leaf E Width (cm)									
Length (cm)									
Leaf F Width (cm)									
Length (cm)									
Leaf G Width (cm)									
Length (cm)									
Leaf H Width (cm)									
Length (cm)									
Leaf I Width (cm)									
Length (cm)									
Leaf J Width (cm)									
Length (cm)									
Leaf K Width (cm)									
Length (cm)									
Leaf L Width (cm)									
Length (cm)									

Notes: (herbivory, tree health, flagging replaced, etc.)

Vegetation Data Sheet

Team #: _____   Site: **T1C** _____

Surveyor: _____   Date: _____

email: _____

Productivity

	P10	P11	P12	P13	P14	P15	P16	P17	P18
Twig Length									
# of Leaves									
Leaf A Width (cm)									
Length (cm)									
Leaf B Width (cm)									
Length (cm)									
Leaf C Width (cm)									
Length (cm)									
Leaf D Width (cm)									
Length (cm)									
Leaf E Width (cm)									
Length (cm)									
Leaf F Width (cm)									
Length (cm)									
Leaf G Width (cm)									
Length (cm)									
Leaf H Width (cm)									
Length (cm)									
Leaf I Width (cm)									
Length (cm)									
Leaf J Width (cm)									
Length (cm)									
Leaf K Width (cm)									
Length (cm)									
Leaf L Width (cm)									
Length (cm)									

Notes: (herbivory, tree health, flagging replaced, etc.)

Sheet 7

Vegetation Data Sheet

Team #: _____

Surveyor: _____

email: _____

Site: **T1H** _____

Date: _____

Productivity

		P19	P20	P21	P22	P23	P24	P25	P26	P27
Twig Length										
# of Leaves										
Leaf A	Width (cm)									
	Length (cm)									
Leaf B	Width (cm)									
	Length (cm)									
Leaf C	Width (cm)									
	Length (cm)									
Leaf D	Width (cm)									
	Length (cm)									
Leaf E	Width (cm)									
	Length (cm)									
Leaf F	Width (cm)									
	Length (cm)									
Leaf G	Width (cm)									
	Length (cm)									
Leaf H	Width (cm)									
	Length (cm)									
Leaf I	Width (cm)									
	Length (cm)									
Leaf J	Width (cm)									
	Length (cm)									
Leaf K	Width (cm)									
	Length (cm)									
Leaf L	Width (cm)									
	Length (cm)									

Notes: (herbivory, tree health, flagging replaced, etc.)

Vegetation Data Sheet

Team #: _____

Surveyor: _____

email: _____

Site: **T1D** _____

Date: _____

Productivity

	P28	P29	P30	P31	P32	P33	P34	P35	P36
Twig Length									
# of Leaves									
Leaf A Width (cm)									
Length (cm)									
Leaf B Width (cm)									
Length (cm)									
Leaf C Width (cm)									
Length (cm)									
Leaf D Width (cm)									
Length (cm)									
Leaf E Width (cm)									
Length (cm)									
Leaf F Width (cm)									
Length (cm)									
Leaf G Width (cm)									
Length (cm)									
Leaf H Width (cm)									
Length (cm)									
Leaf I Width (cm)									
Length (cm)									
Leaf J Width (cm)									
Length (cm)									
Leaf K Width (cm)									
Length (cm)									
Leaf L Width (cm)									
Length (cm)									

Notes: (herbivory, tree health, flagging replaced, etc.)

Sheet 9

Vegetation Data Sheet

Team #: _____

Surveyor: _____

email: _____

Site: **T2A** _____

Date: _____

Productivity

	P37	P38	P39	P40	P41	P42	P43	P44	P45
Twig Length									
# of Leaves									
Leaf A Width (cm)									
Length (cm)									
Leaf B Width (cm)									
Length (cm)									
Leaf C Width (cm)									
Length (cm)									
Leaf D Width (cm)									
Length (cm)									
Leaf E Width (cm)									
Length (cm)									
Leaf F Width (cm)									
Length (cm)									
Leaf G Width (cm)									
Length (cm)									
Leaf H Width (cm)									
Length (cm)									
Leaf I Width (cm)									
Length (cm)									
Leaf J Width (cm)									
Length (cm)									
Leaf K Width (cm)									
Length (cm)									
Leaf L Width (cm)									
Length (cm)									

Notes: (herbivory, tree health, flagging replaced, etc.)

Vegetation Data Sheet

Team #: _____

Surveyor: _____

email: _____

Site: **T2C** _____

Date: _____

Productivity

	P46	P47	P48	P49	P50	P51	P52	P53	P54
Twig Length									
# of Leaves									
Leaf A Width (cm)									
Length (cm)									
Leaf B Width (cm)									
Length (cm)									
Leaf C Width (cm)									
Length (cm)									
Leaf D Width (cm)									
Length (cm)									
Leaf E Width (cm)									
Length (cm)									
Leaf F Width (cm)									
Length (cm)									
Leaf G Width (cm)									
Length (cm)									
Leaf H Width (cm)									
Length (cm)									
Leaf I Width (cm)									
Length (cm)									
Leaf J Width (cm)									
Length (cm)									
Leaf K Width (cm)									
Length (cm)									
Leaf L Width (cm)									
Length (cm)									

Notes: (herbivory, tree health, flagging replaced, etc.)

Vegetation Data Sheet

Team #: _____

Surveyor: _____

email: _____

Site: **T3A** _____

Date: _____

Productivity

	P55	P56	P57	P58	P59	P60	P61	P62	P63
Twig Length									
# of Leaves									
Leaf A Width (cm)									
Length (cm)									
Leaf B Width (cm)									
Length (cm)									
Leaf C Width (cm)									
Length (cm)									
Leaf D Width (cm)									
Length (cm)									
Leaf E Width (cm)									
Length (cm)									
Leaf F Width (cm)									
Length (cm)									
Leaf G Width (cm)									
Length (cm)									
Leaf H Width (cm)									
Length (cm)									
Leaf I Width (cm)									
Length (cm)									
Leaf J Width (cm)									
Length (cm)									
Leaf K Width (cm)									
Length (cm)									
Leaf L Width (cm)									
Length (cm)									

Notes: (herbivory, tree health, flagging replaced, etc.)

Sheet 12

APPENDIX C

Present state and future of the world's mangrove forests

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Date submitted: 28 September 2001 Date accepted: 10 April 2002

SUMMARY

Mangroves, the only woody halophytes living at the confluence of land and sea, have been heavily used traditionally for food, timber, fuel and medicine, and presently occupy about 181 000 km² of tropical and subtropical coastline. Over the past 50 years, approximately one-third of the world's mangrove forests have been lost, but most data show very variable loss rates and there is considerable margin of error in most estimates. Mangroves are a valuable ecological and economic resource, being important nursery grounds and breeding sites for birds, fish, crustaceans, shellfish, reptiles and mammals; a renewable source of wood; accumulation sites for sediment, contaminants, carbon and nutrients; and offer protection against coastal erosion. The destruction of mangroves is usually positively related to human population density. Major reasons for destruction are urban development, aquaculture, mining and overexploitation for timber, fish, crustaceans and shellfish. Over the next 25 years, unrestricted clear felling, aquaculture, and overexploitation of fisheries will be the greatest threats, with lesser problems being alteration of hydrology, pollution and global warming. Loss of biodiversity is, and will continue to be, a severe problem as even pristine mangroves are species-poor compared with other tropical ecosystems. The future is not entirely bleak. The number of rehabilitation and restoration projects is increasing worldwide with some countries showing increases in mangrove area. The intensity of coastal aquaculture appears to have levelled off in some parts of the world. Some commercial projects and economic models indicate that mangroves can be used as a sustainable resource, especially for wood. The brightest note is that the rate of population growth is projected to slow during the next 50 years, with a gradual decline thereafter to the end of the century. Mangrove forests will continue to be exploited at current rates to 2025, unless they are seen as a valuable resource to be managed on a sustainable basis. After 2025, the future of mangroves will depend on technological and ecological advances in multi-species silviculture, genetics, and forestry modelling, but the greatest hope for their future is for a reduction in human population growth.

Keywords: mangrove forest, conservation, exploitation, coastal resources, management, current state, projection

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INTRODUCTION

Mangroves are the only forests situated at the confluence of land and sea in the world's subtropics and tropics. Mangroves are trees or shrubs that develop best where low wave energy and shelter foster deposition of fine particles enabling these woody plants to establish roots and grow. Mangrove forests are architecturally simple compared to rainforests, often lacking an understorey of ferns and scrubs, and are ordinarily less species-rich than other tropical forests.

The global distribution of mangroves indicates a tropical dominance with major latitudinal limits relating best to major ocean currents and the 20°C seawater isotherm in winter (Fig.1). The latter point underscores the paramount importance of warm temperatures for the existence of mangroves. There are 9 orders, 20 families, 27 genera and roughly 70 species of mangroves occupying a total estimated area of 181 000 km² (Spalding *et al.* 1997). The most diverse biogeographical regions are in the Indo-West Pacific (Fig. 1). Indonesia, Australia, Brazil and Nigeria have roughly 43% of the world's mangrove forests.

The standing crop of mangrove forests is, on average, greater than any other aquatic ecosystem, with a decline in above-ground biomass with increasing latitude (Fig. 2). Mangrove forests around the equator can be immense, rivalling the biomass of many tropical rainforests. The biomass of mangrove forests is even greater than in Figure 2 if the biomass of living roots beneath the forest floor is included; below-ground biomass can equal the standing crop rising above-ground (Clough 1992).

Mangroves possess characteristics that, in total, make them structurally and functionally unique. Morphological and ecophysiological characteristics and adaptations of mangrove trees include aerial roots, viviparous embryos, tidal dispersal of propagules, rapid rates of canopy production, frequent absence of an understorey, absence of growth rings, wood with narrow, densely distributed vessels, highly efficient nutrient retention mechanisms, and the ability to cope with salt and to maintain water and carbon balance.
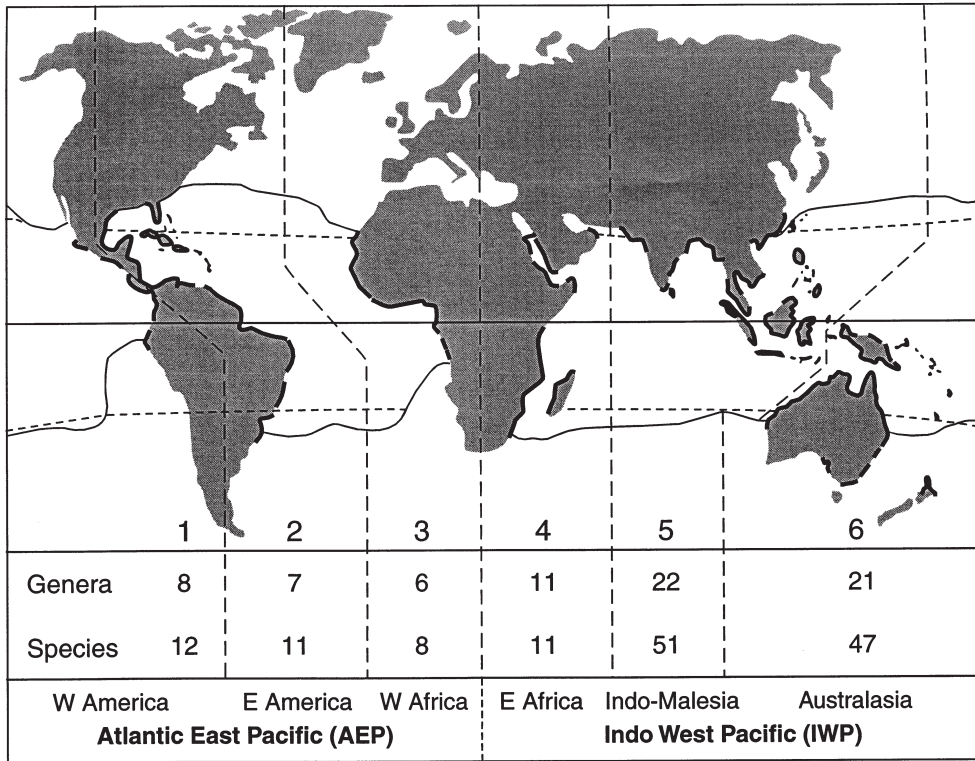
Figure 1 Distribution and biogeographical provinces of the world's mangrove forests. Forests are designated as heavy lines. The numbers of genera and species within each of the six provinces are noted below the map. Modified from Spalding *et al.* (1997) and Duke *et al.* (1998).
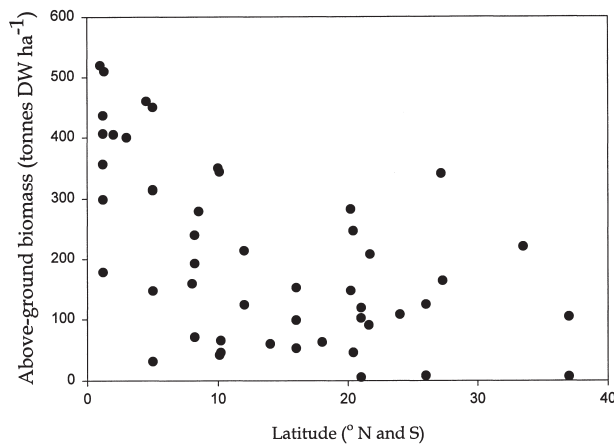
	1	2	3	4	5	6
Genera	8	7	6	11	22	21
Species	12	11	8	11	51	47
	W America	E America	W Africa	E Africa	Indo-Malesia	Australasia
	Atlantic East Pacific (AEP)			**Indo West Pacific (IWP)**		

Figure 2 Latitudinal trends in mangrove forest biomass (tonnes dry weight ha^{-1}). Modified and updated from Alongi (1998) and Fromard *et al.* (1998).

Ecosystem characteristics include comparatively simple food webs containing a mixture of marine and terrestrial species; nursery grounds and breeding sites for birds, reptiles and mammals; and accumulation sites for sediment, some contaminants, carbon and nutrients. The biology and ecology of mangroves have been recently reviewed (Hogarth 1999; Ellison & Farnsworth 2000; Kathiresan & Bingham 2001).

The objective of this review is to critically examine the present status of the world's mangrove forests and to offer a best estimate of their future to the year 2025. Such a review is necessary and timely, considering disparate threats to their existence from increasing population growth, global warming, aquaculture, and industrial and urban development. To develop a reasonable prognosis, I first consider trends and salient characteristics of mangrove ecosystems that offer best clues as to how mangroves may respond to threats in future, followed by an assessment of present threats and impacts that are most likely to continue or intensify into the future. Finally, I conclude with some advice for managers, including an analysis of important gaps in knowledge and practical actions that managers can take for the conservation of mangroves.

ENVIRONMENTAL FORCING FACTORS

Natural influences

Factors influencing the structure and function of mangrove forests vary in relation to global, regional and local scales over different time scales (Duke *et al.* 1998). At the global scale, mangroves are ultimately limited by temperature, but at the regional scale the area and biomass of mangrove forests vary in relation to rainfall, tides, waves and rivers. Various schemes have been developed to classify mangroves on local scales. However, in reality, most forests represent a continuum of geomorphological types based on their location within broader settings classified as river-dominated, tide-dominated, wave-dominated, composite wave- and river-dominated, drowned bedrock valley and carbonate

(Woodroffe 1992). Waves, tides, rivers and rainfall affect water circulation by generating turbulence, advective and longitudinal mixing and trapping coastal water, influencing the rate of erosion and deposition of sediments on which mangroves grow. Many physical and ecological variations are often expressed within a single estuary (Duke *et al.* 1998).

Mangroves are typically distributed from mean sea level to highest spring tide, and perhaps the most conspicuous feature on first glance is the sequential change of tree species parallel to shore. Many factors have been suggested to account for the apparent zonation of trees and other associated organisms across the intertidal seascape. These include salinity, soil type and chemistry, nutrient content, physiological tolerances, predation and competition (Smith 1992). Some of these factors, such as competition, remain essentially unstudied; the results of recent studies are conflicting, prohibiting generalizations about the mechanisms governing zonation. It is more likely that a few of these factors in combination come into play over different temporal and spatial scales to control mangrove distribution (Bunt 1996; Ball 1998). For an individual tree, several factors operate in tandem to regulate plant growth, including temperature, nutrients, solar radiation, oxygen and water (Clough 1992). For a mangrove ecosystem, natural changes occur on the scale of minutes to hours for microbial and physiological processes, of months to years for tree growth and replacement, and of decades to centuries for regional forest changes (Twilley *et al.* 1996).

Determination of possible impacts in future must be considered against a background of natural disturbance. Mangrove forests are often naturally disturbed by cyclones and other storms, lightning, tsunami and floods, and often take decades to recover (Smith *et al.* 1994). Cyclones are common, for instance, in the Caribbean and the Bay of Bengal regularly destroying millions of trees. Other natural events, such as disease, may be sublethal, causing stunted growth or gradual death or replacement of species. For instance, in the Sunderbans of Bangladesh, nearly 20% of *Heritiera fomes* trees have been severely affected by 'top dying', a disease that slowly kills the trees by moving from leaves, branches and twigs to the main stem (Spalding *et al.* 1997). Mangroves become more susceptible to diseases and pests when stressed by changes in salinity, tidal inundation, sedimentation and soil physicochemistry, the introduction of pollutants such as oils, herbicides, metals, sewage and acids, and damage from storms and cyclones.

Pests can have a severe impact on mangrove forests. Epidemics of bacteria, viruses, fungi, spiders and boring insects and invertebrates that destroy leaves and wood can significantly reduce forest viability. For example, caterpillars parasitize and inhibit germination of fruits of *Rhizophora* trees in northern Australia (Robertson *et al.* 1992). Various organisms such as sesarmid crabs normally chew and consume a small proportion of mangrove vegetation, especially propagules and seedlings, inhibiting replenishment of older stands (Smith 1992). General explanations of such natural phenomena are complicated by the fact that one forest can be severely disturbed by pests or predators, but an adjacent stand may not be affected at all.

The dynamics of natural gaps in mangrove forests is poorly understood, but represents a cycle of natural mortality and regeneration that must be considered when impacts are assessed, especially over the long-term (Smith 1992). Various approaches have been used to assess mangrove forest dynamics, such as traditional measurement of tree species abundance and structure over time (Clough 1992) and more recent modelling methods of simulating competition, spacing and ageing of trees (Berger & Hildenbrandt 2000). Most studies indicate that the temporal and spatial variations within mangrove forests are commonly regulated by intra- and inter-specific competition for light, space and soil nutrients that are also patchy within stands (Lugo 1997). As in other forests, these factors give rise to the so-called self-thinning line, a pattern of tree distribution with a progressive decline in density of growing trees (Clough 1992).

Terrestrial forests and mangrove forests share many of the same basic physical and ecological attributes, but other attributes of mangroves appear to be unique (see Introduction), challenging concepts such as the old-growth or late-successional forest (Lugo 1997). The apparent paradox that mangroves appear to be in steady-state despite exhibiting characteristics of establishment, thinning and transitional stage forests, can be explained by the periodic nature of disturbances (Lugo 1997). For instance, a variety of ecosystem states can develop as a result of mangrove growth and development being altered by changes in sea level, lightning, cyclones and other disturbances, resulting in a forest exhibiting a mosaic of successional characteristics. The difficulty in matching many attributes identified with terrestrial old-growth forests highlights the problem of distinguishing natural from anthropogenic-induced change in mangrove forests.

Existing human impacts and threats

Mangroves are heavily used traditionally and commercially worldwide. Local communities have always used mangroves as a source of wood for cooking and heating, and for building houses, huts, fences, matting and scaffolds (Table 1). Timber is also widely used to produce charcoal, tannins and resins for dying and leather making, furniture, bridges, poles for fish cages and traps, medicines, alcohol, boats and many other products (Kathiresan & Bingham 2001). Mangrove stands and associated waterways are important sites for gathering and small-scale cultivation of shellfish, finfish and crustaceans. Local communities are often faced with the problem of over-exploited fisheries.

Commercial practices are being increasingly adopted in developing nations due to strong pressure to increase wealth and living standards of people living in coastal areas. Commercial exploitation is commonly forced from outside the local community, and is nearly always on a scale much larger than the local forests can sustain. Examples of

commercial exploitation include felling for wood products, housing and commercial developments, and modification of natural waterways for bridges and levees (Table 1).

Felling of forests is one of the oldest forms of commercial exploitation. While much felling is unsustainable, evidence from a number of commercial operations suggests that mangrove forests can be sustainably exploited for wood. For example, production of wood from the Matang Mangrove Forest Reserve in Perak, Malaysia has been sustained since 1906 (Gan 1995). The reserve consists of roughly 40 151 ha of pure and mixed stands of *Rhizophora* and *Bruguiera*, of which only 250 ha has been lost to settlement expansion; nearly 1500 ha have been gained by natural accretion of sediment and mangrove colonization. Roughly 1050 ha of forests are clear felled annually over a 30 year rotation cycle, with an average yield of $17.4 \, t \, ha^{-1} \, yr^{-1}$ (Gan 1995). Management plans for Matang are complex and frequently revised, undoubtedly contributing to the success of the commercial operation.

The loss of mangroves for pond aquaculture is currently one of the largest threats to mangrove forests worldwide. The list of direct and indirect problems caused by pond aquaculture is long and includes:

- immediate loss of mangroves to construct ponds;
- blockage of tidal creeks;
- alteration of natural tidal flows;
- alteration of the groundwater table;
- increase in sedimentation rates and turbidity in natural waters;
- release of toxic wastes;
- overexploitation of wild seed stocks;
- development of acid sulphate soils;
- reduced water quality;
- introduction of excess nutrients; and
- alteration of natural food chains.

Other forms of aquaculture may or may not be less destructive. Cultivation of grouper and sea bass in floating cages offers an inherently less destructive form of fisheries exploitation, but the extent of impact depends upon proper planning and management, including appropriate siting of cage farms, limitations on density of cages, and methods of feeding of cage stock. The same is true for exploitation of shellfish, such as the blood cockle, on mudflats adjacent to mangrove forests (Gan 1995). Limited operations do not appear to have demonstrable impacts on other mangrove resources, but management models to predict sustainable limits are generally lacking for mangrove ecosystems.

Other abuses of mangroves are often subtle, indirect and sublethal. For instance, the encroachment and growth of human populations in coastal areas usually results in increased wastes that are often dumped into mangroves and adjacent coastal waterways. Mangrove waters can assimilate some excess nutrients, but the assimilative capacity for most waterways are unknown and likely to vary depending on the

Table 1 Current human impacts on the world's mangrove forests.

Potentially sustainable	*Unsustainable*
Food	Eutrophication
Tannins and resins	Habitat modification/ destruction/alteration for coastal development (including pond aquaculture)
Medicines and other bioproducts	
Furniture, fencing, poles (timber)	
Artisanal and commercial fishing	
Charcoal	Disruption of hydrological cycles (damming)
Cage aquaculture	Release of toxins and pathogens
Ecotourism	Introduction of exotic species
Recreation	Fouling by litter
Education	Build-up of chlorinated and petroleum hydrocarbons
	Shoreline erosion/siltation accelerated by deforestation, desertification and other poor land-use practices
	Uncontrolled resource exploitation
	Global climate change
	Noise pollution
	Mine tailings
	Herbicides and defoliants

form, type and frequency of effluent discharge, tidal range, waterway dimensions, climate, and plankton productivity and abundance (Trott & Alongi 2000). Mangrove plants and their associated microbes exhibit reduced growth when exposed to dissolved heavy metals particularly at concentrations at least five times greater than those in pristine mangrove soils (Yim & Tam 1999). The effect of some contaminants can be cumulative. Studies of oil spills in the Caribbean have shown that mangroves exhibit increased mutation rates and long (approximately 20 years) recovery times after repeated exposure (Burns *et al.* 1993; Klekowski *et al.* 1994). Physical smothering can often have as great an impact as chemical impairment of physiological performance.

Short-term climatic events may also be important environmental forcing factors. In the only known study of the impact of the El Niño-Southern Oscillation (ENSO) on mangroves, Drexler and Ewel (2001) found that in Micronesia the 1997–1998 ENSO-related drought resulted in greater soil and groundwater salinity. The most dramatic impact was a reversal of groundwater flow that sent groundwater from the mangroves upstream towards freshwater wetlands. The ecological impact of the drought was not examined, but the potential disruption to ecological processes is clear (Drexler & Ewel 2001).

IDENTIFIED LONG-TERM TRENDS

The ability to differentiate between natural and human-induced disturbance is especially challenging given the lack of long-term data for mangroves. Nevertheless, some data from a few forests can be used to identify natural changes that likely happen over time.

Natural changes in forest structure

Detection of human impacts on the structure of mangrove forests must be considered against a background of natural change in stand succession and canopy structure. Like other forests, mangrove stands follow a natural series of phases over time, from an initial pioneering stage through to rapid early growth and development, to later maturity, senescence and death (Jimenez *et al.* 1985). This natural progression is supported by data from French Guiana where Fromard *et al.* (1998) measured the structure, biomass and stand dynamics of several mangrove species. The data indicate a natural development of mangrove stands with a correlation between stem density and estimated forest age (Fig. 3).

Many stands of mangroves in the Mekong Delta were rehabilitated after the large-scale defoliation and destruction during the Vietnam War. The age of replanting and managed cutting is known, offering a rare opportunity to determine how stand structure changes with increasing age of mangrove forests (Clough *et al.* 1999). A structural analysis of various stands of *Rhizophora apiculata* indicates that tree densities decline with forest age (Fig. 4*a*), in agreement with the model of Jimenez *et al.* (1985). As in other forests, the stands become less dense due to self-thinning, as evidenced by an increase in tree girth or diameter-at-breast-height (Fig. 4*b*). Less dense but larger mature trees lead to an increase in total above-ground biomass per hectare with increasing age (Fig. 4*c*). Embedded within the long-term trend are temporal and spatial variations in individual tree growth, photosynthetic production, respiration and litterfall. In natural forests, changes in species composition occur, especially in light gaps, and with increasing distance upland.

Community structure, abundance and biodiversity

Within forest communities
Trees and bacteria dominate the biomass and productivity of mangrove forests (Fig. 5), but the structure of mangrove food

webs is unique, having both marine and terrestrial components. Data on temporal trends in mangrove food webs usually are seasonal rather than inter-annual. Abundance and biomass of organisms living in the canopy, on or beneath the forest floor and in associated waterways often vary seasonally in relation to rainfall, and spatially in response to a variety of factors that are often the same as those regulating the trees (Kathiresan & Bingham 2001).

The structure and function of mangrove food webs is ultimately driven by the production of carbon fixed mostly by the trees and by the flow of dissolved and particulate organic

Figure 4 Relationship of (*a*) stem density, (*b*) diameter at breast-height (DBH) and (*c*) above-ground biomass (tonnes dry weight ha^{-1}) to age of *Rhizophora apiculata* forests in the Mekong delta, Vietnam. Modified from Clough *et al.* (1999).

Figure 3 Colonization and development of mangrove forests over time. Data from Fromard *et al.* (1998) based on model of Jimenez *et al.* (1985).

matter within the forest and adjacent tidal waters. Within the forests, a suite of decomposer organisms directly or indirectly consumes a variable proportion of forest litter. Sesarmid, portunid, and ocypodid crabs are keystone organisms in many (but not all) forests. These crabs retain litter and recycle nutrients within forest soils, bioturbate the forest floor to stimulate microbial decomposition and, especially in the case of grapsid crabs, prey on propagules to influence the distribution, abundance and succession of tree species (Smith *et al.* 1991). It is simple to predict that losses of crabs as a result of pollution, for example, would negatively affect the growth and natural succession of mangrove forests.

The abundance and species diversity of infauna are generally low compared with other benthic habitats (Alongi & Sasekumar 1992). Low species richness may be the result of negative effects of polyphenolic acids derived from trees, low densities of surface microalgae, and the harsh physical conditions induced by tidal cycles of exposure and inundation.

The abundance and biomass of epifauna and tree-dwelling assemblages can often exceed those of the infauna. Gastropods and crustaceans are the major epifaunal groups, and exhibit clear distribution patterns related to frequency of tidal inundation, changes in sediment granulometry, water content, temperature, food sources, wave energy, salinity, anoxia, competition and predation. On the trunks, prop roots and branches of trees, most animals feed on organic debris and algae; lower on the trunks, an encrusting fauna may in turn provide a rich and mobile cryptofauna with safe refuge. These conspicuous assemblages can form a mosaic of vertically zoned organisms that are often the first residents to be harmed by pollution and other anthropogenic inputs (Alongi & Sasekumar 1992).

No attempts have been made to examine decadal trends in faunal abundance and species composition, but a few studies have examined faunal changes in relation to development and age of forests (Suzuki *et al.* 1997; Sasekumar & Chong 1998). In managed forests at different stages of the harvest cycle in Malaysia, epifaunal density and diversity was greater in a 60 year-old *R. apiculata* forest than in a recently cleared stand. The infauna showed a different pattern with greatest density and biomass in the cleared forest (Sasekumar & Chong 1998); this anomaly was attributed to greater abundance of surface algae with increasing light after canopy removal. In Thailand, an increase in benthic faunal abundance was observed in mangroves replanted in abandoned shrimp ponds (Suzuki *et al.* 1997). The sparse data indicate some impact of forest development and maturity on benthic faunal richness and diversity with a tendency toward more diverse assemblages in undisturbed and mature forests, but no forecast of long-term trends is possible.

Higher in the canopy, various species of mammals, insects and birds permanently or temporarily reside in some forests, often in dense assemblages (Kathiresan & Bingham 2001). Bird communities can be spatially and trophically complex with up to eight feeding guilds, namely granivores, frugivores, piscivores, aerial hawkers, and hovering, gleaning, flycatching and bark-foraging insectivores. A few species are nearly confined to mangroves, including several species of yellow warblers, mangrove vireo, and mangrove cuckoo. Noteworthy mammals include monkeys and flying fox, and within tidal waters, dolphins and otters. These animals are also among the first residents to flee or be harmed by human alteration of mangroves.

Pelagic communities

Pelagic food webs in mangrove waterways are usually more responsive than benthic organisms, being ordinarily affected by longitudinal and lateral mixing and trapping of water by currents, tides and waves. Plankton communities in mangrove waters do respond quickly to nutrient enrichment from aquaculture or run-off from agricultural lands, most often exhibiting an increase in growth rate and standing crop (Ayukai & Alongi 2000).

Like benthic animals, diversity and abundance of plankton is usually low and highly variable (Robertson & Blaber 1992). There is a conspicuous lack of information on the ecology of mangrove-associated microbes. The sparse data indicate abundance of bacteria and protozoa within the range of other coastal waters (Robertson & Blaber 1992), but their trophic role is more often presumed, based on relationships in other tropical coastal waters, than based on empirical data.

The ecology of zooplankton in mangrove waterways is somewhat better understood (Robertson & Blaber 1992). Species composition is influenced by seasonal variations in salinity and degree of freshwater input. Decadal studies of plankton dynamics in mangrove waters do not exist, but several annual studies indicate density peaks during summer as a result of temperature control of reproduction (McKinnon & Klumpp 1998).

Studies of nekton, especially prawns and fish, are more common and indicate the importance of mangroves as
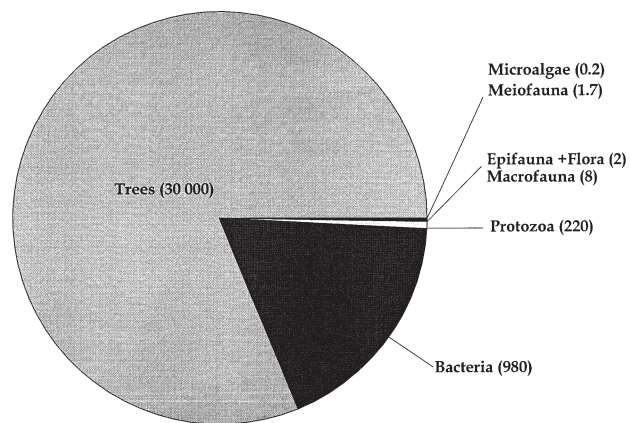

Figure 5 The distribution of living biomass (g dry weight m^{-2} to a sediment depth of 1 m) in a mature mixed *Rhizophora* forest in northern Australia. Based on data in Alongi and Sasekumar (1992) and Alongi (1998).

nursery grounds and refuges (Robertson & Blaber 1992). Many coastal species spend critical early stages of their lives in mangrove waters. The number of microhabitats is a major factor influencing community composition of fish. The number of microhabitats is however ultimately dependent upon environmental factors such as tidal amplitude, water quality and salinity (Robertson & Blaber 1992).

There are several patterns of species richness in fish communities:

- more species are usually found in large (range: 104–197 species) than in small (range: 8–128 species) estuaries;
- mangrove fish communities in the Indo-West Pacific are species-rich compared with those in some Atlantic estuaries;
- subtropical estuaries house fewer species than tropical estuaries;
- connectivity between mangroves and adjacent ecosystems (e.g. coral reefs, seagrass beds) influences community composition; and
- the nature of the offshore environment is critical in determining movements of larvae and juveniles, underscoring the fact that mangroves are not functionally divorced from adjacent coastal habitats.

Densities of juvenile fish in mangrove estuaries are high compared with other estuarine habitats. Robertson and Blaber (1992) suggest that mangroves are sources of various types of food, and provide shelter and protection.

Hypoxia, chemicals, diversion or alteration of natural tidal cycles, damming and other forms of pollution usually lower the abundance of fish and other pelagic (and benthic) organisms. Fish ordinarily escape rather than tolerate lowered water quality, but nonetheless, do not readily return to the scene of impact; the same is true for crocodiles, alligators, snakes, turtles, and lizards (Kathiresan & Bingham 2001). Recovery depends on the nature, areal extent, duration and intensity of disturbance. Recovery from a small-scale disturbance is often rapid, but there may be permanent loss from a catastrophe such as a massive oil spill (Burns *et al.* 1993). Habitat loss results in a lowering of population densities and loss of diversity of most mangrove-associated organisms.

Ecosystem function

Importance of mangrove forest production

Decadal trends in rates of mangrove primary production are unknown, as canopy production remains difficult to quantify and is often measured by indirect methods. The most reliable estimates of net primary production come from incremental measurements of biomass accumulation, but such measurements are time-consuming and laborious. The study by Day *et al.* (1996) in Mexico constitutes the longest temporal record (7 years) of mangrove net primary production. In both basin and scrub forests, Day *et al.* (1996) attributed most inter-annual variability in above-ground production and litterfall to soil salinity, minimum air temperature, and minimum rainfall, highlighting the importance of climate.

Most published estimates of primary production are derived from rapid survey measurement of light attenuation under the canopy. Estimates of net primary production using this technique range from 18–34 kg C ha^{-2} d^{-1}, but these rates are underestimates, insufficient to account for observed accumulation of biomass above-ground. A more recent method based on measurement of light transmission and measurement of net photosynthesis of leaves, indicates net daytime photosynthetic rates nearly 10 times greater than previous production estimates (Clough *et al.* 1997). If accurate, net primary production of mangroves in many regions is likely to be significantly greater than previously thought.

In a comparison of this new method and the older technique in a 22 year-old *R. apiculata* forest in Malaysia, Clough *et al.* (1997) calculated net photosynthetic rates of 155 and 13 kg C ha^{-1} d^{-1} using the new and old methods, respectively. A preliminary carbon balance for these trees (Table 2) indicates that only a small proportion of this production is allocated to above-ground biomass or lost as litterfall; most is probably lost via respiration and allocated to root production. Litterfall is often used as a proxy measure of mangrove production, but this newer data casts doubt on its appropriateness for this purpose. Litterfall is useful to examine annual reproductive patterns and the amount of organic matter potentially available for decomposition and export. Like biomass, litterfall decreases globally with distance from the equator (Saenger & Snedaker 1993).
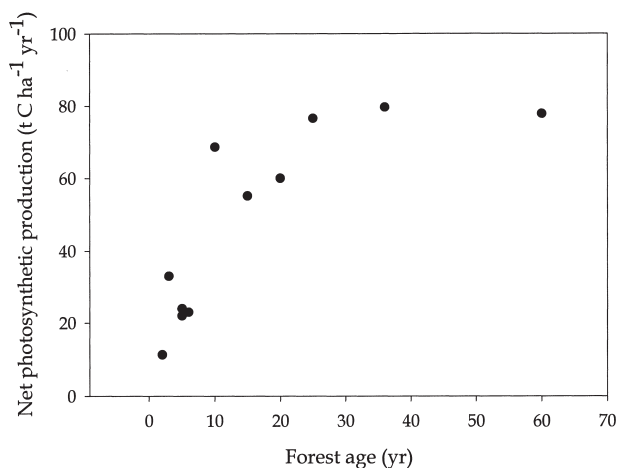
A plot of net canopy production of different aged *Rhizophora apiculata* forests in south-east Asia (Clough *et al.* 1999), shows a general trend of increase in production until 25–30 years, with the older forests maintaining rapid carbon fixation rates (Fig. 6). The high productivity of older forests shows how important mature forests are in accumulating and storing of carbon over the long-term. This characteristic of mangrove forests is likely to acquire greater relevance with the forecasted increases in atmospheric greenhouse gases this century.

Consumption, export and storage of mangrove carbon

Mangroves are among the most productive plants in the ocean (Duarte & Cebrian 1996), the recent advances in estimating photosynthetic production indicating that, on an areal basis, mangroves are usually more productive than saltmarshes, seagrasses, macroalgae, coral reef algae, microphytobenthos, and phytoplankton. Most mangroves fix carbon well in excess of ecosystem requirements, with the excess carbon representing 40% of net primary production (Duarte & Cebrian 1996). Of the mangrove carbon produced, 9% is consumed by herbivores, 30% is exported, 10% is stored in sediments, and 40% is decomposed and recycled within the system (Duarte & Cebrian 1996). Recent measurements of mangrove photosynthesis (Clough *et al.* 1997) imply that either more carbon is stored in wood and eventually decomposed within the system or more carbon is stored in sediments or exported to the adjacent coastal zone, than estimated by Duarte and Cebrian (1996).

Table 2 Carbon balance for 22-year-old *Rhizophora apiculata* trees in Malaysia (modified from Clough *et al.* 1997).

Component	Flux (t C ha^{-1} yr^{-1})
Net daytime canopy photosynthetic production	56
Carbon allocation	
Above-ground biomass accumulation	6.5
Below-ground biomass accumulation	0.6
Litter fall	4.4
Below-ground root turnover	?
Night time foliar respiration	13
Below-ground root respiration	?
Stem, branch & prop root respiration	?

Figure 6 The relationship between forest age and photosynthetic production in *Rhizophora apiculata* forests in South-east Asia (Thailand, Malaysia and Vietnam). Data compiled from Clough *et al.* (1999), Alongi and Dixon (2000) and D.M. Alongi (unpublished data from Malaysia 1999).

Levels of herbivory are known (Ellison & Farnsworth 2000), as is the proportion of organic material exported from mangroves (Robertson *et al.* 1992). There are few data on carbon storage in mangrove wood or sediments but the sparse data suggests that some forests can accumulate carbon (Twilley *et al.* 1992; Alongi *et al.* 2000, 2001). Recent information from tropical rainforests indicates that mature forests have a long-term capacity to store carbon in wood (Chambers *et al.* 2001); such may be the case for some mangrove forests, especially mature stands.

Because mangroves fix and store significant amounts of carbon, their loss may have a significant impact on global carbon budgets. In a recent analysis of the fate of fixed carbon in marine ecosystems, Cebrian (2002) estimated that a loss of about 35% of the world's mangroves has resulted in a net loss of 3.8×10^{14} gC stored as mangrove biomass. This figure is an underestimate because below-ground biomass and the more recent net canopy production estimates were not included in his calculations.

Carbon and nitrogen budgets for mangrove ecosystems: do they reflect human impacts?

Only a few studies have constructed nutrient mass balances for entire mangrove ecosystems to offer insights into what is energetically important to mangrove functioning. A comparison between a relatively young, physically dynamic mangrove ecosystem disturbed by various human activities (Sawi Bay, Thailand) and a mature, more physically quiescent, pristine ecosystem (Hinchinbrook Channel, Australia) illustrates how physical characteristics and the level of human disturbance affect rates and pathways of nutrient and energy flow (Table 3). First, both ecosystems are net autotrophic, producing more fixed carbon than they consume. This is despite the fact that the ratio of mangrove area to total ecosystem area is nearly double in Hinchinbrook Channel. The Sawi Bay mangroves are younger, smaller, but more productive, resulting in slightly more total net production than the Australian mangroves (Table 3). On an areal basis, rates of respiration, phytoplankton production and carbon burial are greater in Sawi Bay than in Hinchinbrook Channel reflecting additional inputs of carbon from the heavily used catchments bordering the bay. Tidal inputs and outwelling are greater in Hinchinbrook Channel, reflecting stronger tides and river run-off from many small rivers on the Australian mainland. A smaller proportion of carbon is buried in Sawi Bay sediments, but proportionally more carbon is lost via respiration. Carbon losses per km^2 are greater in Sawi Bay, which loses more total carbon (78%) than Hinchinbrook Channel (60%). This probably reflects greater anthropogenic inputs and lower efficiency of carbon processing, as well as greater openness of Sawi Bay to shelf waters, than semi-enclosed Hinchinbrook Channel.

The excess carbon produced by both ecosystems is fated differently, reflecting not only human influences but also differences in ecosystem maturity. Most excess carbon accumulates in tree wood and sediments in young forests lining Sawi Bay. In Hinchinbrook Channel, most carbon in excess of respiration and burial is exported (Table 3). In Sawi Bay, most of the carbon accumulating in sediments appears to be derived from land and from imported phytoplankton stimulated by inputs of inorganic nutrients from various industries within the catchment (Ayukai & Alongi 2000; Alongi *et al.* 2001).

A nitrogen budget for the Missionary Bay mangroves at the northern end of Hinchinbrook Island, Australia (Table 4) illustrates how a mature mangrove ecosystem acquires and retains nitrogen. Nitrogen enters the Missionary Bay ecosystem by nitrogen fixation, with little contribution from precipitation and groundwater (Table 4). Tidal inputs are nearly five times greater than biological fixation. Unlike most other coastal ecosystems, denitrification is a small loss compared to tidal outputs. Unlike saltmarshes, the largest inputs are in the form of dissolved organic nitrogen and net input of particulate nitrogen is negligible. This pattern reflects the import of nitrogen in dissolved form to help fuel forest production and the export to refractory nitrogen in the form of old leaf litter, pieces of branch and bark.

Mangroves have evolved efficient mechanisms to conserve nitrogen. In Missionary Bay, where water and sediment nitrogen concentrations are low, nutrients links between trees and microbes are close. The large mass of living trees and dead wood lying on the forest floor, litter processing by crabs, lower rates of denitrification than nitrogen fixation (Table 4), flushing of material in advanced stages of decomposition, all serve to retain and conserve limiting nutrients (Alongi *et al.* 1992). Inputs slightly exceed outputs, but the ecosystem is roughly in balance given the magnitude of error in extrapolating measurements to a large area. Of greater importance is how this budget demonstrates the delicate balance between the import and export of nitrogen in a mature, pristine ecosystem. This implies that such a fine balance can be easily displaced by human interference.

Nitrogen budgets on this scale for polluted mangroves do not exist, but some small-scale studies suggest that mangroves can in most cases tolerate high levels of nitrogen and phosphorus from sources such as sewage and aquaculture effluent (Boto 1992; Robertson & Phillips 1995; Trott & Alongi 2000). The level of tolerance depends on the form of nutrient and, like other types of disturbance, depends on the intensity, duration and areal extent of impact, as well as position along the tidal gradient. Several recent studies (Feller *et al.* 1999; Bouillon *et al.* 2002) suggest that mangroves, even dwarf species, can use high nitrogen and phosphorus inputs to fuel tree production as well as production of other primary producers. Further, there may be a trophic shift from assimilation of mostly mangrove-derived organic matter in pristine

Table 3 Comparison of the differences in mean rates of ecosystem-level processes between Sawi Bay and Hinchinbrook Channel (modified from Alongi *et al.* 2000).

	Sawi Bay	*Hinchinbrook Channel*
Ratio mangrove : total ecosystem area	1:5	1:2.8
Mangrove net production (mol C ha^{-1} yr^{-1})	2.8×10^6	2.3×10^6
Phytoplankton production (mmol C m^{-2} d^{-1})	43.9	22.1
Pelagic respiration (mmol C m^{-2} d^{-1})	61.0	10.0
Sediment respiration (mmol C m^{-2} d^{-1})	59.5	41.5
Sediment burial (mmol C m^{-2} d^{-1})	54.1	39.7
Percentage TOC input buried	4%	14%
Percentage TOC input respired	46% (74% including tree respiration)	20% (46% including tree respiration)
Total C inputs per km^2 (mol C km^{-2})	9.4×10^7	4.7×10^7
Total C outputs per km^2 (mol C km^{-2})	7.6×10^7	1.6×10^7
Excess C per km^2 (mol C km^{-2})	1.8×10^7	3.0×10^7
Ecosystem P/R	1.4	2.0

Table 4 Nitrogen budget of an entire mangrove ecosystem, Missionary Bay, Hinchinbrook Island, Australia (modified from Alongi 1998).

	Flux (kg N yr^{-1})
Inputs	
Precipitation	30
Groundwater	30
Nitrogen fixation	36 830
Tidal exchange	168 600
Total	205 490
Outputs	
Tidal exchange	192 430
Denitrification	2900
Sedimentation	?
Total	195 330
Net exchange	+10 160

mangroves, to use of nutrients derived from blooms of phytoplankton and macroalgae in mangrove systems receiving excess nutrients (Bouillon *et al.* 2002).

Fisheries yield

The biological importance of mangroves in terms of wood and fisheries yield is normally not reflected in ecosystem-level budgets and mass balance estimates. Mangroves are important nursery grounds despite statistical arguments to the contrary (Baran 1999). The slope of the relationship of fish and prawn landings to mangrove data differs between regions owing to differences in catch methods, structure and productivity of forests and the fisheries species in question (Chong & Sasekumar 1994).

What is unquestioned is the impact of human perturbations on fisheries' yields in mangrove-dominated regions. In south-east Asia, the growth of the trawl fishing industry has led to overfishing in many areas both as a result of, and causing, habitat destruction and environmental stress (Mohsin & Ambak 1996; Hinrichsen 1998). For instance, the long-term trend of fishing in coastal waters in Malaysia (Fig. 7) shows an unrelenting increase in catch effort. There was an increase in total landings of coastal fish in Malaysia from the late 1950s up to the mid-1980s when landings levelled off by 1986, indicating that total landings were starting to exceed estimates of maximum sustainable yield. However, there was a steep rise in total landings and catch effort into the 1990s caused by the expansion of Malaysia's fishing grounds from 160 740 km^2 to 547 200 km^2 with the establishment of the Exclusive Economic Zone (Mohsin & Ambak 1996). The probability of these coastal waters being overfished again is high given the increase in fishing effort, and will no doubt be exacerbated by any decline in the area and health of mangrove forests (Mohsin & Ambak 1996). It is often difficult to even identify such problems in mangrove-dominated waters owing to the lack of long-term data, especially from commercial operators who for a variety of reasons either do

not keep adequate records or do not accurately report their totals to government bodies.

POTENTIAL STATES IN 2025

Predicting the future of mangrove forests is problematic, given the lack of long-term data. Nevertheless, some basic prognoses can be made based on reasonable extrapolations from the salient trends and characteristics of mangroves reviewed here, likely advances in genetics and restoration ecology, and the spread of current sustainable-management practices.

Future threats

Most current uses and abuses of mangroves are unlikely to abate until after 2025. Aquaculture, mining, housing and industrial encroachment and overexploitation of resources will continue and some impacts will probably increase with concomitant growth and development of coastal settlements. Many past and current abuses are now irreversible.

Global production of farmed fish and shellfish in the coastal zone has more than doubled in the past 15 years (Naylor *et al.* 2000). Despite many unsustainable methods and a levelling off of total production, aquaculture will still result in the loss of mangrove resources; they may at best slow in some countries, but they will be maintained or even accelerated in others. As long as human populations grow in size, present impacts will not subside.

There are various threats to the future of mangrove ecosystems (Table 5), nominally divided into high-, medium- and low-level threats, based on the level of past and current impacts. Deforestation remains the single greatest threat to the survival of mangroves. Although reforestation programmes will continue and are likely to increase in future, the loss of biodiversity, especially from old-growth forests, is unlikely to be regained until at least several decades, and

Figure 7 Total annual landings of coastal fish in Malaysia, 1960–1994. Modified from Mohsin and Ambak (1996).

perhaps permanently lost if species become locally extinct due to excessive fragmentation of habitats.

Aquaculture is another major threat, being interlinked with both deforestation and overexploitation of fisheries resources. Conversion of mangrove forests and waterways for pond aquaculture will continue in some countries as depletion of natural stocks drives the need to increase dependence on farmed seafood. The upper limits of sustainability are unknown for various resources within mangrove forests, but it is likely that they will be seriously tested in future.

Technological advances are likely to result in less acute pollution such as the emission rate of thermal effluent and oil spills, but the increase in coastal development presages increased threats of low-level, chronic pollution from agriculture and industry. Contaminants seeping into groundwater may, for example, find their way into mangrove forests and adjacent waters (Field 2000). Of more immediate impact in future will be eutrophication, assuming increased boat traffic and other uses of coastal waterways. These threats will in turn increase pressure for development and alteration of waterways.

The combustion of fossil fuels combined with deforestation and other forms of land clearing are leading to an inevitable rise in atmospheric CO_2 concentrations and temperatures, giving rise in turn to an increase in sea level as polar ice melts (IPCC [Intergovernmental Panel on Climate Change] 2001). Conflicting scenarios presently being offered to predict the impact of global warming on Earth's ecosystems reflect ignorance of ecosystem functioning as well as the scale of the problem; synergistic and antagonistic effects are likely to occur as a result of natural feedbacks, complicating modelling predictions. These problems are especially critical for tropical ecosystems where there are fewer empirical data than for temperate ecosystems. Tropical terrestrial forests have recently been shown to play a greater role in determining atmospheric CO_2 concentrations than thought previously (Mahli & Grace 2000); estimates of the mangrove contribution to atmospheric carbon flux is hampered by a critical lack of information.

Global warming

By 2025, the atmospheric concentration of CO_2 is expected to rise by approximately 40 ppm, temperatures may rise by 0.5–0.9°C, and sea level may rise by 3–12 cm (IPCC 2001). What impact will these changes have on mangroves?

Over the next 25 years, average atmospheric CO_2 concentrations may increase from the 2000 average of 370 ppm to 410 ppm (IPCC 2001). Experimental evidence indicates that

Table 5 Future threats to the world's mangrove forests.

High-level threats	Intermediate threats	Low-level threats
Deforestation	Alteration of hydrology	Oil pollution
Pond aquaculture	Global warming	Thermal pollution
Overexploitation of fish and shellfish	Eutrophication	Tourism
		Noise pollution

species responses will vary; there may not be a significant overall increase in canopy photosynthesis, growth and litter-fall despite decreases in stomatal conductance and transpiration (UNEP [United Nations Environment Programme] 1994). The experiments of Ball and others (e.g. Ball *et al.* 1997) point to complex responses to elevated CO_2 concentrations. Growing *Rhizophora apiculata* and *R. stylosa* in a multifactorial combination of salinity, humidity and atmospheric CO_2, elevated CO_2 had little effect on plant growth when limited by salinity, but growth was stimulated when limited by humidity (Ball *et al.* 1997). Both species had more rapid growth under elevated CO_2 conditions at low salinity. Elevated CO_2 could alter competitive abilities along salinity–humidity gradients (Ball *et al.* 1997).

The expected rise in temperature by as much as 0.9°C (IPCC 2001) may result in expanded latitudinal limits for some species, alteration of community composition, and marginal increases in photosynthesis, respiration, litterfall, microbial decomposition, floral and faunal diversity, growth and reproduction, but reduced rates of sediment accretion (UNEP 1994). However, temperature changes in the tropics may not be as great as at higher latitudes (IPCC 2001), and there may be less seasonality due to forecasted changes in precipitation (UNEP 1994). Such changes are likely to vary greatly on local and regional scales. Nevertheless, they may induce changes in soil water content and salinity, changes in community composition of plants and animals as a result of the salinity changes, and a change in primary production if the precipitation to evaporation ratio is altered (UNEP 1994).

The presumed rise in sea level by as much as 12 cm (IPCC 2001) is difficult to evaluate owing to past and recent vari-ations in local relative sea level (Rull *et al.* 1999). Nevertheless, mangroves may progress landwards at a rate determined by the rate of sea level rise, the rate of vertical accretion, and slope and space at the landward edge. Zonal patterns of plants and animals will be altered slightly and erosion at the seaward front will increase (UNEP 1994). The ability of mangroves to accommodate future sea-level rise will likely depend on other factors such as tidal range, sediment supply and tree species composition. These factors are likely to be magnified on islands of both low- and high-relief and in the arid tropics where rates of sediment supply, available upland space and mangrove growth rates are usually low (Ellison & Stoddart 1991; Parkinson *et al.* 1994; Semeniuk 1994).

Empirical data to test the impact of sea-level rise is limited to one greenhouse study of *Rhizophora mangle* (Ellison & Farnsworth 1997). Growing seedlings in tanks simulating current conditions (control), and a 16 cm increase and a 16 cm decrease in sea level, Ellison and Farnsworth (1997) observed that plants in the increased water level treatment initially grew faster than plants in the other treatments, but slowed rapidly at the sapling stage. By the end of the 2.5-year experiment, control plants were 10–20% larger than the sea-level treatment plants. The reduced growth of *R. mangle* with changes in sea level may offset the possible stimulatory effects of increases in atmospheric CO_2 concentration.

Overall, impacts of climate change on mangrove use and exploitation are predicted to result in increased risks of flooding and erosion in low lying coasts, intrusion of salt wedge and storm surges and collateral damage (UNEP 1994). The severity of these impacts will vary in relation to regional differences in climate change (IPCC 2001).

Global losses

To make realistic prognostications of the future of mangroves, an assessment of the accuracy of the present data of losses and gains in forest area is necessary. While it is clear that large tracts of mangroves have been either severely degraded or destroyed worldwide, most data is apocryphal, reflecting inaccurate surveys, unsubstantiated claims or old estimates not based on empirical measurements (Farnsworth & Ellison 1997; Burke *et al.* 2001). For example, in Fiji total mangrove area has been reported as between 19 700 and 49 777 ha (Spalding *et al.* 1997).

Long-term changes in mangrove area (Fig. 8) show that most countries have lost mangroves, especially Vietnam, Mexico, Singapore, the Philippines and Thailand. In Singapore, the losses were incurred over nearly a century, mainly as a result of urbanization (Spalding *et al.* 1997). In other countries, losses have been sustained mostly over the past 20–30 years as a result of clearing for aquaculture, urbanization and timber products. Vietnam's losses were sustained chiefly as a result of defoliation in the 1960s and early 1970s (Hong & San 1993). Some countries, such as Papua New Guinea, Australia and Belize show no substantial change and a few countries (e.g. Cuba) have regained mangrove forests due to restoration projects (Field 2000).

Summing the empirical estimates of change in mangrove area (Spalding *et al.* 1997) and some regional estimates (Clough 1993; Diop 1993; Lacerda 1993), I calculated that approximately one-third of mangrove forests have been lost over the past 50 years. I used the above documents produced by the International Society for Mangrove Ecosystems because they appear to be the most reliable, based on empir-ical data in government forestry surveys, remotely sensed images, aerial photos and ground-truth maps. Recent publi-cations have cited a global loss figure of 50% (Burke *et al.* 2001; GESAMP [The Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection] 2001), citing reports (Kelleher *et al.* 1995) that have cited older literature containing neither empirical data nor a description of how the loss estimates were derived. Also, Spalding *et al.* (1997) found numerous inaccuracies in previous works because of what some people and organiz-ations considered mangrove forest. For example, the estimates for Venezuela were consistently gross overestimates because many surveys included non-mangrove species and adjacent swamp forest, saltmarsh or mudflat. Conversely, for Mexico, a previous estimate indicated a total mangrove area of 5315 km^2 when in fact recent high-resolution satellite images show a total mangrove area of 9328 km^2 (Spalding *et al.* 1997).
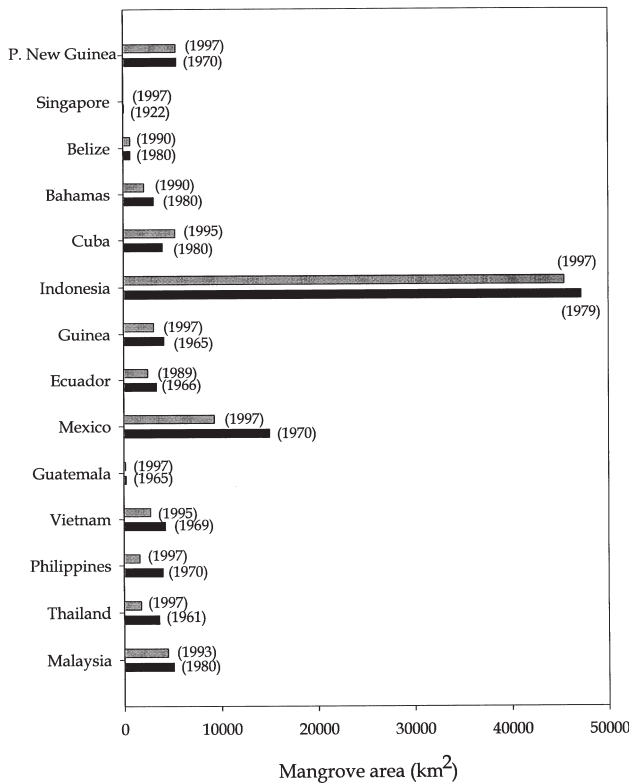
Figure 8 Long-term changes in mangrove forest areas worldwide. Compiled from data in Clough (1993); Diop (1993); Lacerda (1993); and Spalding *et al.* (1997).

Loss rates vary greatly among nations, ranging from 1 to 20% of total forest area per year (Clough 1993; Diop 1993; Lacerda 1993), making it difficult to predict global changes in forest area in future. There are enormous variations within individual countries. For instance, in Thailand losses of mangroves from 1961 to 1989 varied from 0 to 9% in central and lower Gulf of Thailand provinces to as much as 79% along the Andaman Sea coastline (Clough 1993). Similarly, Malaysia experienced an overall reduction in mangroves of approximately 12% since 1980, with greatest losses in Johor, Selangor, Negeri Sembilan and Teerengganu, but some provinces such as Malacca have increased forest area owing to restoration and sustainable management of reserves (Clough 1993). Such is true for several African and Latin American nations (Diop 1993; Lacerda 1993). In those nations that have replanted forests for a net gain, loss of biodiversity of trees and associated organisms appears to be permanent. Most restorations involve monocultures of rapidly growing species (Field 1998). Rare, slow-growing tree species are ordinarily not replaced (see below).

The future of mangroves is intimately linked to changes in forest use, which is directly tied to changes in human population growth and development. Predictions of human population change indicate most rapid growth in tropical developing nations, where the bulk of mangrove forests lie. Assuming that human populations will grow along tropical

coasts, so will anthropogenic impacts. In fact, some mangrove areas are already overfished. For example, in the Mekong delta, fish catch per unit effort has declined from the late 1970s (Fig. 9), and continues to decline, as the coastal population grows and mangroves continue to be destroyed for shrimp farming which has increased 35-fold (de Graaf & Xuan 1998). At present one hectare of mangrove supports approximately 0.45 tonnes of marine fish catch per year in the region. Increasing human pressures bring a concomitant rise in the incidence of viral and other diseases, directly impacting seed stock (de Graaf & Xuan 1998), and increasing coastal erosion and saltwater intrusion into groundwater (Hong & San 1993).

The highest-level threats to mangroves in future (Table 5) are likely to be deforestation, aquaculture and overexploitation of wood and fisheries resources. Aquaculture will remain a great threat, although aquaculture production of fish, crustaceans and molluscs in countries with mangroves appears to have levelled off (Fig. 10). This plateau indicates that a sustainable level of coastal aquaculture has been reached and that mangrove clearing for aquaculture operations has also peaked.

Assuming that the rate of deforestation does not change substantially over the next two decades, the felling of mangrove forests to construct new ponds and the discharge of wastes will continue. There have been advances in reducing waste discharge from aquaculture, but this reduction is unlikely to compensate for continued need for more space as aquaculture production per unit area is declining or remaining stable at best (Naylor *et al.* 2000; FAO [Food and Agricultural Organization of the United Nations] 2001).

It has been proposed that mangroves can be used as sinks to filter aquaculture effluent (e.g. Robertson & Phillips 1995), based on the presumption that mangroves have high capacity to tolerate and use dissolved nutrients because of their high rates of primary production. This idea has considerable merit, but maintaining a steady-state condition would be difficult. It is likely that a sustainable operation would be site-
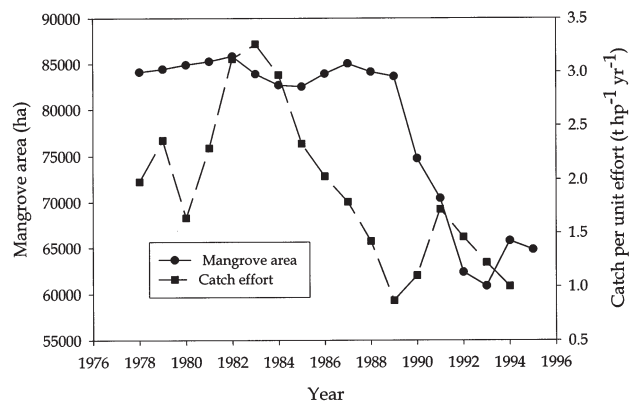

Figure 9 Changes in mangrove forest area (ha) and fisheries catch per unit effort (t hp^{-1} yr^{-1}), Minh Hai Province, Mekong Delta, Vietnam, 1977–1995. Data from deGraaf and Xuan (1998). hp = total engine capacity in horsepower.

specific, depending on the quantity and quality of waste, the proportion of particulate to dissolved waste, how and when the waste was applied to the forests, the extent of tidal flushing, and forest productivity and age (Trott & Alongi 2000). In short, no universal formula for success is forthcoming, given the lack of long-term data on the impact of aquaculture effluent discharge on mangrove forests and associated waterways. Further, an impact may be cumulative rather than immediate and overt, and may not be discernible for several years. Cage aquaculture is less destructive than ponds, but even sustaining a particular number of cages in a given area would greatly depend on hydrodynamics and coastal geomorphology, as well as the level of cultivation intensity. For both mangroves and commercial operations to be sustained, they must be properly managed and guided by national development plans.

Rehabilitation and sustainable management

Environmental degradation in many parts of the world, especially in Asia and Latin America, has led to attempts to rehabilitate and restore mangroves. Most rehabilitation and restoration projects have had mixed results, with the main reasons for failure being lack of adequate site selection and proper use of soil preparation and planting techniques (Ellison 2000). In many cases, futile attempts have been made to rehabilitate a site that is beyond restoration. In such cases, the sites are often highly saline with acid sulphate soils and with both tidal water and soils extremely low in oxygen and nutrient content; sites of shrimp faming, mining and timber harvesting are frequently in this category.

Critical to the success of a rehabilitation project is proper selection of species to be planted, and whether or not they are to regenerate naturally or artificially. Natural replenishment requires that sufficient undisturbed forests reside nearby to serve as sources of seed stock. Artificial replanting success depends on funding, time and the level of expertise available to use appropriate methods.

Figure 10 Changes in aquaculture production in all countries inhabited by mangroves, 1990–1999. Data from FAO (2001).

The technology exists to regrow trees but restoring fauna and ecosystem function is exceedingly difficult. The fact remains that most rehabilitated sites are mono-cultures or low diversity poly-cultures having little, if any, resemblance to the original habitat. Only a few species are commonly used, namely *Rhizophora apiculata*, *Rhizophora mucronata*, *Rhizophora mangle*, *Avicennia marina* and *Sonneratia apetala*. Mangrove forests can often be rehabilitated but not restored.

Mangroves are in a sense among the easiest systems to reconstruct, but the emphasis has been, and continues to be, on reintroduction of trees. It is presumed that over time animals such as crabs, fish, meiofauna and algae will recolonize replanted sites and that ecosystem linkages will be restored. The primary objectives of mangrove rehabilitation projects, in descending order of frequency, are silviculture, mitigation, coastal stabilization, ecosystem function and fisheries.

Restoration of mangrove ecosystems can theoretically be achieved, given that mangroves have been cultivated for several centuries. Mangroves can grow and thrive if hydrological and geomorphological conditions are optimal, and there is some evidence that replanted forests can approach the biomass, stand structure and productivity of undisturbed forests within 20–25 years (e.g. McKee & Faulkner 2000). However, restoration requires time, which is most often contrary to political, cultural and economic priorities. To date, extensive replanting of mangroves has been achieved only in Pakistan, Cuba and Bangladesh (Spalding *et al.* 1997).

The Bangladesh scenario is arguably the most impressive attempt to reforest mangroves along a large portion of tropical coastline (Saenger & Siddiqi 1993). Severe cyclone damage led the Bangladesh Forest Department in 1966 to initiate an afforestation programme to increase coastal protection afforded by expansion of mangrove forest. Up until 1993, nearly 120 000 ha were planted on accreting banks formed from sediment delivered to the eastern Sundarbans from the Ganges and Brahmaputra Rivers; two species, *Sonneratia apetala* and *Avicennia officinalis* were the dominant trees planted. There were some difficulties encountered with sediment stability, but the benefits have been substantial. The greatest lessons learned were: (1) to have more adaptable replanting schemes as soil salinities change over time; and (2) monospecific cultures are not a universal remedy, as they can generate problems all their own that are costly and difficult to rectify.

Most restoration projects continue to emphasize silviculture to generate production of timber, wood chips, charcoal and fuelwood (Ellison 2000). Given economic imperatives in most coastal communities in developing countries, most immediate value and emphasis is naturally placed on wood production. This trend is likely to continue to at least 2025. Indeed, the greatest success in sustainable management of mangroves has been achieved in silviculture.

Guidelines for sustainable management of mangroves have been developed by a number of organizations and agencies, and all express several commonalities:

- within a national boundary, mangroves should be assigned to one or other of the following categories: conservation reserve, forest reserve, fisheries reserve and alienable mangrove land;
- mangroves on alienable land should be maintained;
- specific management goals and practices should be clearly identified and implemented;
- appropriate laws and regulations should be enacted and enforced;
- the best available technical expertise should be used;
- there should be a buffer zone between mangroves and adjacent industry, housing and tourist development;
- pond aquaculture should not be permitted within mangrove reserves;
- within permissible areas, ponds should not be closer than 200 m to mangroves;
- an environmental impact assessment and feasibility study should be required for all development projects; and
- strict pollution controls should be established.

If these guidelines were adhered to, loss of mangroves worldwide could be minimized in future, certainly to a level not greater than an annual global loss rate of about 1% (current estimate of Kaly & Jones 1998). Fragmentation and loss of diversity, given the lack of consensus on estimating the minimum expanse of mangroves required to sustain all key processes, is still a danger (Kaly & Jones 1998).

Technological improvements, such as genetic and microbial advances, may ameliorate problems in conserving and maximizing mangrove ecosystem structure and function in rehabilitated environments. It is likely that protocols will be established for *in vitro* propagation of several key mangrove species, as can be done with *Excoecaria agallocha*, an extract of which is currently used for relief of rheumatism and treatment of ulcers (Rao *et al.* 1998). Microbes stimulate seedling growth, so culture success might be improved by inoculating seedlings with bacteria, such as nitrogen fixers, that promote plant growth (Holguin *et al.* 2001). Also, less destructive mud crab cultivation is being successfully trialled in many regions (Keenan & Blackshaw 1999), and may offer a reasonable alternative to destructive pond cultivation.

Ecological economics: towards a pragmatic solution?

If mangrove resources are to be conserved, sustainable management realistically must operate on the basis of economics (Turner *et al.* 1993). It is human nature to protect and conserve a resource that is a source of income. Economic self-interest must play a role in management if mangroves are to persist and thrive in the face of human encroachment. A few case studies indicate that the idea of conserving mangroves as economic investment is realistic (Ronnback 1999).

The mean monetary value of mangroves has recently been estimated at US$ 9990 ha^{-1} yr^{-1}, second only to the value of estuaries and seagrass beds, and greater than the economic value of coral reefs, continental shelves and the open sea

(Costanza *et al.* 1998). The commercial value of mangrove resources has been recognized since early last century. Mangrove-related fisheries resources generally are valued more highly than natural and agricultural goods, such as wood, with the value of fisheries ranging from US$ 120–3000 ha^{-1} yr^{-1} and timber from US$ 60–800 ha^{-1} yr^{-1} (Clough 1993; Diop 1993; Lacerda 1993). These figures are only indicative of their fair value; some products are worth more than others, and the same product is often worth more in one region than in another for various reasons such as quality and local market demand.

The competing demands of coastal industries and mangroves are manageable if relevant ecological information is collected and used properly to design management plans that reflect how mangrove ecosystems support fisheries. For example, until the mid-1980s, mangroves were heavily exploited in Colombia for artisanal and commercial fishing, wood extraction for poles, charcoal, paper and housing materials, with no clear national or regional plans for sustainable development (Lacerda 1993). As a result of these unsustainable losses, the National Institute for Renewable Resources and Environment started a National Mangrove Committee with the aim to formulate policies for the conservation and sustainable management of mangroves in Colombia. As a result of these policies, mangrove protective areas have been enlarged and the coastline divided into areas for protection, public interest, forestry and fisheries reserve, special management and special protection (Lacerda 1993).

On the Caribbean coast of Colombia where semi-intensive shrimp aquaculture is practised, proper environmental management plans have been drawn up as a result of an urgent need for ecologically sustainable development. The study of Larsson *et al.* (1994) is a prime example of the type of critical economic and ecological analysis necessary for sustainable management as legislated in Colombia. In their model, Larsson *et al.* (1994) first estimated the ecosystem area that is required to produce the food, clean water and nursery areas to support the shrimp farms and to assimilate their wastes. Their results show that a semi-intensive farm needs an area of mangroves 35–190 times larger than the area of the farm; for each joule of edible shrimp protein produced, approximately 295 J of ecosystem work is required. In 1990, an area equivalent to about 20–30% of Colombia's entire mangroves was required to supply the industry's entire needs for post-larval shrimp. In comparing the energetic requirements of Colombia's aquaculture industry to other food production systems, Larsson *et al.* (1994) concluded that coastal aquaculture is one of the most resource-intensive industries, and characterized it as ecologically unsustainable. To maximize use and to minimize impact, Colombia's aquaculture operations should retain natural tidal flows, locate new farms to marginal saltpans, maximize distance between farms, use vegetable instead of animal feeds, use filter feeders to naturally clarify pond waters, and improve artificial rearing methods (Larsson *et al.* 1994). It is likely that aquaculture industries in other nations would do well to take up some or all of these suggestions, where applicable.

Similar efforts to establish a clear ecological and economic link between mangroves and the value of fisheries have been difficult. Cost-benefit and multi-criteria analyses, while valuable in some circumstances, have their limitations and are often impossible to apply. In the Philippines, felling of mangroves for aquaculture has been banned since 1981, but the current decline in fish catch per unit effort has increased pressure to re-examine the protective legislation. Consequently, Janssen and Padilla (1999) compared the costs and benefits of mangrove conservation with those generated by various alternative plans of aquaculture and forestry. A comparison of net annual benefits of goods and services provided by mangroves indicates that aquaculture generates the greatest value at US$ 6793 ha^{-1} yr^{-1}, followed by forestry (US$ 150 ha^{-1} yr^{-1}) and fisheries (US$ 60 ha^{-1} yr^{-1}). Based on the trade-offs of efficiency and equity, commercial forestry delivers the most equity and semi-intensive aquaculture the most efficient alternatives; intensive aquaculture was the worst alternative. Given the limitations of not being able to value mangrove biodiversity, shore protection and flood mitigation, Janssen and Padilla (1999) concluded that semi-intensive aquaculture was the policy alternative with the highest economic value. However, they questioned whether it was possible to adequately value the impact of losses of species and ecosystems on the way of life of the indigenous people.

Several studies modelling the trade-off between mangroves and resource use argue for minimal destruction or use of forests and associated waterways, especially against the backdrop of overfishing. Using an open-access fishery model, Barbier and Strand (1998) estimated the impact of change in mangrove area on nearshore shrimp production in Campeche, Mexico. Simulating a marginal decline in mangrove forest area, their model indicated a concomitant decline in shrimp harvest and an increase in price per kg harvest and cost per vessel. Their model, however, suggested that the fishery might be sensitive to the level of mangrove exploitation; a modest decline in mangrove area may lead to a disproportionate decline in shrimp harvest and revenue if the ecosystem is deforested beyond the current levels of 2 km^2 yr^{-1} (Barbier & Strand 1998). Moreover, while mangrove deforestation contributed to a decline in the fishery so did the pervasive problem of overexploitation. It is likely that the shrimp fishery has been operating at or slightly above sustainable limits. Better management and involvement of the community in controlling overfishing is just as critical as limiting the destruction of mangrove nursery grounds.

Optimizing the trade-off between mangrove preservation and human exploitation has been modelled successfully, and these models have indicated the importance of some basic ecological variables. Employing both dynamic optimization and simulation models of the economic link between fishery production and mangrove use in Brazil, Grasso (1998) found that the optimisation model suggested how best to employ forestry and fishery workers. The worst scenario would be over-exploitation of mangrove stocks if there were no equilibrium established between forestry and fishery efforts. The

best management option in the long-term, however, was to have more workers in fisheries than forestry. Grasso (1998) suggested that clear felling of mangroves should be reduced to a minimum to avoid ecosystem collapse. The most important variable in the simulation model was the rate of forest growth, underscoring the importance of the relationship between forest age, growth and the extent of forest resource use (Grasso 1998).

The ecological ties between mangroves and adjacent environments can serve as a key for sustainable management. Resource-use models encompassing the strength of linkages between ecosystem compartments show that severe restrictions on mangrove clearing can optimize economic output. In the Bintuni Bay area of Indonesia where mangroves are heavily exploited for woodchips, and artisanal and commercial fisheries, strong economic arguments exist for limited clearing (Ruitenbeek 1994). Cost-benefit analysis of forest management options incorporating links among fishery production, mangrove use and clearance rates, erosion control and biodiversity (Ruitenbeek 1994) indicate that clear-felling of mangroves is a viable management option only when all the linkages are ignored. Assuming that clear linkages exist between mangroves and environmental functions and fisheries, a ban on cutting is optimal; if the linkages incorporate time lags on the order of years, selective cutting of 25% of total harvestable mangroves is the optimal strategy (Ruitenbeek 1994). In any case, conservative cutting appears to be a good strategy because a wrong management decision based on total ignorance would likely have severe economic and ecological consequences for several decades.

CONCLUSIONS AND MANAGEMENT

Mangroves are the only woody halophyte-dominated ecosystems situated at the confluence of land and sea. Most mangrove forests are highly productive and net autotrophic, helping to support coastal food chains, including commercially valuable fish, crustaceans and molluscs. The world's mangrove forests are economically very valuable, worth an estimated US$ 180 895 923 000 based on the valuation of Costanza *et al.* (1998).

Mangroves have traditionally been heavily used for timber, poles, food, medicines and a wide variety of other items. Most nations have lost mangroves; a few countries have gained single-species forests as a result of reforestation projects. Claims that 50% of the world's mangrove forests have disappeared over the past century (GESAMP 2001) may be exaggerated due to lack of empirical data. An analysis of current estimates (Clough 1993; Diop 1993; Lacerda 1993; Spalding *et al.* 1997) based on more reliable information suggests that cumulative losses over the past 50 years are closer to one-third. The exact losses will never be known, and even today, a precise estimate of global extent of mangrove forests is not easy (Spalding *et al.* 1997). Some countries such as Liberia, the Ivory Coast and Guinea have experienced

heavy losses, but most countries with expansive mangroves, such as Brazil and Australia, have experienced comparatively little deforestation (Spalding *et al.* 1997).

Most losses have been the direct result of felling for shrimp ponds, housing and industrial developments (Alongi 1998), but severe losses have occurred in some regions due to shoreline erosion/siltation accelerated by terrestrial defor-estation, desertification and other poor land-use practices. Herbicides and defoliants, pollution, alteration of natural tidal cycles and water flow, and uncontrolled resource exploitation, also degrade and destroy mangrove ecosystems. In future, the greatest threats to the continued existence of mangroves are deforestation, pond aquaculture and a perva-sive overexploitation of fisheries resources. Global warming and chronic eutrophication will have a lesser impact on the health of mangrove ecosystems over the next 25 years. Mangrove losses are positively related to human population density and growth; the fewer people who live at or near a forest, the less destruction and exploitation there will be.

The future is not necessarily bleak for mangroves. Lutz *et al.* (2001) estimate that the rate of world population growth is already declining, with an 85% chance that the global popu-lation will stop growing before the end of the century. The projections for sub-Sahara Africa, south Asia, Latin America, and the Asia Pacific regions show that population size will plateau by about 2050 (Lutz *et al.* 2001). Given the apparent link between the exploitation of mangroves and human popu-lation density, this implies that overexploitation will continue until 2050, but decline thereafter. Coupled with technological improvements in aquaculture, restoration ecology and genetics, hopefully the worst direct exploitation will be over by 2025. The biggest problem in future is the loss of biodiversity. Most reha-bilitation projects replant fewer species than were originally lost. Loss of biodiversity is a critical issue given that mangrove forests are less diverse than most other tropical ecosystems.

The major problem in predicting mangrove responses to human impacts is the lack of long-term data, and the ability to distinguish natural from anthropogenic change. There is a lack of knowledge of:

- gross and net canopy production;
- below-ground root production;
- tree and below-ground root respiration;
- natural successional states over time;
- whole-ecosystem mass balances for carbon, nitrogen and phosphorus;
- physiological information (water and carbon balance);
- factors regulating colonization (propagule dispersal, seedling establishment);
- secondary production;
- plant–soil–microbial relations;
- species diversity of flora and fauna;
- forestry models to determine maximum sustainable yield;
- silviculture of rare species;
- experimental effects of greenhouse gas and sea level change; and

- experimental effects of excess nutrients on mangrove growth and survival.

Actions can be taken to improve conservation of mangroves. The Charter for Mangroves put forward by the International Society for Mangrove Ecosystems (Field 1995) would be a logical first step. The charter was adopted in 1991 to complement the World Charter for Nature proclaimed by the General Assembly of the United Nations in 1982. The mangrove charter affirms that mangroves will be respected and not compromised in terms of their genetic viability, that they will be conserved where ever possible, and managed on a sustainable basis. The major stum-bling block to practical implementation of the charter remains commitment from local and national governments to provide adequate resources to implement management plans. The best example of sustained management of a mangrove ecosystem is the Matang Mangrove Forest Reserve in peninsular Malaysia. The success of this enterprise can be directly attributed to government commitment and a good relationship between government, business and the local community.

It is essential for governments and people to understand that mangroves are a valuable social and economic resource. It is a fact of human nature that we tend to preserve and protect resources that are of economic importance; aesthetics is historically not high on the list of reasons why we conserve resources. If mangrove forests are not seen as a fundamental economic and ecological resource to be treasured, they will continue to be exploited at current rates until at least 2025. The greatest hope in reducing the rate of mangrove losses is the projection that human population growth will decline, and possibly stop, later in the century.

ACKNOWLEDGEMENTS

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ECOSYSTEMS ECOLOGY

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Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida

Abstract The objectives of this study were to determine effects of nutrient enrichment on plant growth, nutrient dynamics, and photosynthesis in a disturbed mangrove forest in an abandoned mosquito impoundment in Florida. Impounding altered the hydrology and soil chemistry of the site. In 1997, we established a factorial experiment along a tree-height gradient with three zones, i.e., fringe, transition, dwarf, and three fertilizer treatment levels, i.e., nitrogen (N), phosphorus (P), control, in Mosquito Impoundment 23 on the eastern side of Indian River. Transects traversed the forest perpendicular to the shore-line, from a *Rhizophora mangle*-dominated fringe through an *Avicennia germinans* stand of intermediate height, and into a scrub or dwarf stand of *A. germinans* in the hinterland. Growth rates increased significantly in response to N fertilization. Our growth data indicated that this site is N-limited along the tree-height gradient. After 2 years of N addition, dwarf trees resembled vigorously growing saplings. Addition of N also affected internal dynamics of N and P and caused increases in rates of photosynthesis. These findings contrast with results for a *R. mangle*-dominated forest in Belize where the fringe is N-limited, but the dwarf zone is P-limited and the transition zone is co-limited by N and P. This study demonstrated that patterns of nutrient limitation in mangrove ecosystems are complex, that not all processes respond similarly to the same nutrient, and that similar habitats are not limited by the same nutrient when different mangrove forests are compared.

Introduction

Tropical and subtropical mangroves support adjacent marine communities and ecosystems, including seagrass beds and coral reefs. However, little is known about the intra-wetland processes that regulate those interactions. In salt marshes, ecological processes such as primary production and decomposition have been shown experimentally to be nitrogen (N)-limited (Valiela and Teal 1979). The few mangrove wetlands where fertilization experiments have been conducted appear to be either phosphorus (P)-limited (Feller 1995; Koch and Snedaker 1997) or differentially N- or P-limited across tidal gradients (Boto and Wellington 1983; Feller et al. 2003). Several studies have found that mangrove ecosystems have high capacity as a sink for excess nutrients and other pollutants (e.g., Nedwell 1975; Odum and Johannes 1975; Silva et al. 1990; Corredor and Morell 1994; Tam and Wong 1999). However, relatively few studies have evaluated what types of changes might occur within mangrove ecosystems in response to the ongoing process of eutrophication of the coastal zone, which are often immediately next to oligotrophic, but highly diverse, marine ecosystems (Feller et al. 1999, 2003).

The purpose of this long-term study is to examine how nutrient enrichment influences ecological processes in a mangrove system that developed in an area impacted by anthropogenic disturbance. We selected a study site in an abandoned mosquito impoundment along the Indian River Lagoon (IRL), Florida. In March 1997, we set up a fertilization experiment to determine the effects of increased nutrient availability on soil chemistry and plant growth, internal nutrient dynamics, and photosynthesis across the ecotones connecting the mangrove forests with the open water and with interior areas along a tree-height gradient. Results from this study will be compared to a parallel investigation of a pristine mangrove ecosystem on

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offshore islands in Belize associated with the Mesoamerican Barrier Reef (Feller et al. 1999, 2003; McKee et al. 2002). This study aims to test two hypotheses. H1: Essential nutrients are not uniformly distributed within mangrove ecosystems. Based on a fertilization experiment in Belize, soil fertility within mangrove forests is heterogeneous and can switch from conditions of N to P limitation along narrow spatial gradients (Feller et al. 2003). This hypothesis predicts spatial variation in plant responses (e.g., growth and photosynthesis) in response to enrichment with N and P. H2: As the availability of a limiting nutrient increases, internal nutrient dynamics and the mechanisms used by plants to use, recycle, and conserve that nutrient become less efficient (Loveless 1961; Small 1972; Stachurski and Zimka 1975; Tilton 1977; Chabot and Hicks 1982; Shaver and Melillo 1984; Vitousek 1984; Schlesinger et al. 1989; Feller et al. 1999). This hypothesis predicts that under N-limiting conditions, N will be tightly conserved via efficient internal nutrient use and cycling mechanisms. Similarly, under P-limiting conditions, P will be more efficiently used and tightly conserved.

Materials and methods

Study site

Our study was conducted at Mosquito Impoundment 23 (MI 23), a 122-ha stand of coastal mangroves located in the Avalon State Recreation Area on the lagoonal side of North Hutchinson Island, St. Lucie County, Florida (27°33'N, 80°20'W). This impoundment was originally constructed in 1966 to control populations of *Aedes taeniorrhynchus* and *A. sollicitans*, and was maintained until 1974 when its dike was breached (Rey and Kain 1991). No records are available on the pre- or post-impoundment vegetation in this area (Rey et al. 1986). Impounding, which involved construction of a dike around a wetland with material excavated from the perimeter to control flooding and water depth, altered the wetland's hydrology and pore water chemistry (Carlson et al. 1983; Rey et al. 1986, 1990, 1992). In MI 23, water connection for exchange and circulation with the IRL is through the breach and two 30" diameter culverts (James David, unpublished data). This site has not been managed for mosquito control since 1974. The soil contains dredged sand and shell fragments and has little structure.

The mangrove stand was dominated by *Avicennia germinans* L. (black mangrove) with scattered *Laguncularia racemosa* Graetn.f. (white mangrove) in the interior with *Rhizophora mangle* L. (red mangrove) confined to the periphery immediately alongside the canal. This site is characterized by a tree-height gradient, perpendicular to the shoreline. To quantify forest structure, we used the point-centered quarter method (Cintrón and Schaeffer-Novelli 1984). Measurements were taken at 20 points at regular intervals along four transects.

Experimental design

The experimental design was a randomized complete block with a factorial treatment arrangement. Transects along the tree-height gradient were replicated in three blocks, 100–150 m apart, along the western side of MI 23. In each block, three transects, 25–50 m long and ~10 m apart, were oriented perpendicular to the shoreline and subdivided into fringe, transition, and dwarf zones. Two species were targeted for fertilizer treatment: *R. mangle* in the fringe zone and *A. germinans* in the transition and dwarf zones.

Three replicate trees were selected within each zone. Trees were fertilized with 300 g of N fertilizer as urea (45:0:0), or P fertilizer as P_2O_5 (0:45:0), as described in Feller (1995). Nutrient treatment for each transect within each block was assigned randomly. A total of 81 trees (3 nutrient treatments ×3 zones ×3 blocks ×3 trees per zone) were treated and measured at 6-month intervals for 2 years. Doses (150 g) of fertilizer were placed in small holes (3 cm diameter ×30 cm deep), cored into the substrate beneath the drip line on opposing sides of the canopy of each tree, and sealed. We used this method rather than surface broadcasting to assure that the fertilizers were available to tree roots rather than lost in tidal flushing. For controls, holes were cored and sealed, but no fertilizer was added.

Plant growth and nutrient dynamics

As a bioassay of the effects of nutrient treatment on plant growth, we tracked the responses of five, initially unbranched, shoots (first order) in sunlit positions in the outer part of the canopy of each tree. To distinguish the growth produced over an interval, we labeled the leaves in the apical position on each of these shoots at each sampling period. Stem growth and leaf production were measured from the previously marked apical position to the base of the current apical bud along the main axis and any shoots. Demographic growth analysis was used to determine effect of nutrient enrichment on plant growth rates (McGraw and Garbutt 1990). Demographic absolute growth rates (DAGR) were calculated for monthly increases in stem growth for year 1 (March 1997–March 1998) and year 2 (March 1998–March 1999). Demographic relative growth rates (DRGR) were calculated for monthly rates of leaf production for year 1 and year 2, using the formula:

$$\frac{\ln(\text{No.leaves})\text{time1} - \ln(\text{No.leaves})\text{time0}}{\text{time1} - \text{time0}} = \text{DRGR(leaves/mo)}. \tag{1}$$

To determine the effects of nutrient enrichment on internal nutrient dynamics, we measured nutrient concentrations in green and senescent leaves and calculated nutrient resorption efficiency for each experimental tree. Resorption efficiency (RE) was calculated for each experimental tree as the percentage of N or P recovered from senescing leaves before leaf fall (Chapin and Van Cleve 1989):

$$\frac{\text{NorP}(mg \cdot cm^{-2})\text{greenleaves} - \text{NorP}(mg \cdot cm^{-2})\text{senescentleaves}}{\text{NorP}(mg \cdot cm^{-2})\text{greenleaves}}$$
$$\times 100 = \text{RE}(\%). \tag{2}$$

Leaf samples for analyses were harvested in January 1999. By that time, all the leaves on the targeted trees had been produced under the influence of the experimental treatment. From a sunlit position in the top of the canopy, we collected fresh, fully mature green leaves from a penapical stem position and fully senescent yellow leaves with a well-developed abscission layer from a basal position on first-order branches. Senescent leaves were collected by hand directly from the trees to eliminate nutrient loss via leaching and leaf loss by tidal flushing. We assumed that yellow leaves that could be removed from a stem with only slight pressure represented senescent leaf litter. Leaf area was determined with a Li-Cor 3000 Portable Area Meter (Li-Cor, Lincoln, Neb.). Leaf samples were dried at 70°C in a convection oven and ground in a Wiley Mill to pass through a 40 (0.38mm) mesh screen. Concentrations of carbon (C) and N were determined with a Perkin-Elmer 2400 CHN Analyzer at the Smithsonian Environmental Research Center, Edgewater, Md. Phosphorus (P) concentration was determined using an inductively coupled plasma spectrophotometer by Analytical Services, Pennsylvania State University, State College, Pa., USA.

Photosynthesis

Rates of photosynthetic electron transport on experimental trees were measured with a PAM 2000 chlorophyll fluorescence system (H. Walz, Effeltrich, Germany) during a sunny morning under light conditions saturating for photosynthesis in March 2000. These rates of photosynthetic electron transport correlate with rates of photosynthetic CO_2 assimilation (Genty et al. 1989; Krall and Edwards 1992; Lovelock and Winter 1996), although the relationship between photosynthetic electron transport and CO_2 fixation for different plant species may differ and vary between 8 and 16 electrons transported per mole of CO_2 assimilated (Krall and Edwards 1992; Lovelock and Winter 1996). In the dwarf and transition zones, rates of photosynthetic electron transport were calculated as an average of three measurements made on three most recently fully expanded leaves per plant. Mean light levels during the measurements were 1,200 μmol quanta m^{-2} s^{-1} and mean leaf temperatures were 33°C. In the fringe, the height of the canopy prevented in situ measurements of leaves developed in direct sunlight (comparable to those in the dwarf and transition zones). Thus, branches were picked using a saw on an extendable arm and transported to the laboratory. The most recently fully expanded leaf from each branch was placed in a chamber at 100% relative humidity, saturating CO_2 (supplied by breathing into the plastic chamber) and at 1,500 μmol quanta m^{-2} s^{-1}, supplied by the white actinic light source of the PAM 2000. Rates of photosynthetic electron transport were measured with the PAM 2000 on one leaf per plant. In September 1998 and June 1999, we measured rates of photosynthetic CO_2 fixation under light conditions saturating for photosynthesis in dwarf trees with a Li-Cor 6400 portable gas exchange system (Li-Cor, Lincoln, Neb., USA). Photosynthetic nutrient use efficiency (PNUE) was calculated as photosynthetic CO_2 assimilation (A) divided by the leaf N concentration (Field et al. 1983).

Hydro-edaphic measurements

Measurements of soil and porewater were conducted at each experimental tree approximately 1 m from the bole. Soil samples were collected with a piston-type corer for determination of bulk density and percent organic matter according to standard techniques. Soil redox potentials at 1 cm and 15 cm depths were measured with bright platinum electrodes equilibrated in situ for 30 min (McKee et al. 1988). Each electrode was checked before use with quinhydrone in pH 4 and 7 buffers (mV reading for quinhydrone is 218 and 40.8, respectively, at 25°C). The potential of a calomel reference electrode (+244 mV) was added to each value to calculate Eh. Interstitial water was collected from a depth of 15 cm with a probe attached to a suction device as described in McKee et al. (1988). A portion of the sample was filtered (0.45 μ) and frozen until analysis of PO_4^{2-} and NH_4^+ concentrations on a LACHAT system (QuickChem 8000 Series FIA, Zellweger Analytics, Milwaukee, Wis., USA). Analytical procedures were

checked by use of external standards and blanks as specified by instrument manufacturer. An unfiltered aliquot of each water sample was added to an equal volume of an antioxidant buffer and was analyzed for sulfide with a sulfide micro-electrode McKee et al. 1988). Additional unfiltered aliquots were used to measure pH and salinity.

Statistical analysis

Our data were analyzed by a factorial analysis of variance (ANOVA, fixed effects model) in a randomized complete block experimental design, using Systat 8.0 (Wilkinson 1996) or JMP 4.0 (SAS Institute, Cary, N.C., USA). Grouping factors were nutrient treatment (Control, N, P) × zone (fringe, transition, dwarf), in three blocks (1, 2, 3) to look for differences in variables based on harvested materials and measurements in this experiment. Physicochemical data were analyzed with repeated-measures ANOVA over four sample dates: April 1997, October 1998, March 1999, and March 2000. When significant main effects or interactions occurred, comparisons were conducted with 1 df contrast analysis. To analyze treatment effects on plant growth rates, we used repeated-measures ANOVA over two 1-year periods. When an ANOVA found a significant main effect or interaction between nutrient treatment and zone, we used Fisher's Least Significant Difference post hoc hypothesis test to examine pairwise differences within and among the treatment levels. To analyze for heteroscedasticity, probability plots of variables and ANOVA residuals were examined. For heterogeneous variances, we transformed continuous data using logarithms and transformed noncontinuous data (counts) using the square root.

Results

Forest structure

The height of the canopy at MI 23 was tallest in the fringe along the water's edge and decreased to landward (Table 1). The fringe zone was a dense but narrow stand (2–5 m wide) of uniformly tall trees (3.5–6 m), dominated by *R. mangle* with *L. racemosa* and *A. germinans* intermixed. The transition zone was 5–10 m wide and dominated by 1–3 m tall saplings of *L. racemosa* and *A. germinans*. The interior of the impoundment was 70–100 m wide and was an open stand of stunted trees (~1 m tall), dominated by *A. germinans*, referred to as the dwarf zone. Tree density and basal area (m^2·0.1 ha^{-1}) were highest in the fringe zone, with basal area 10–30 times greater than in the dwarf and transition zones, respec-

Table 1 Forest stand characteristics of the fringe, transition, and dwarf zones at Mosquito Impoundment 23, Fort Pierce, Fla.

Zone	Species	Tree height (m) (mean±1 SE)	Stand density (stems·0.1 ha^{-1})	Basal area (m^2·0.1 ha^{-1})	Relative density (%)	Relative dominance (%)	Relative frequency (%)
Fringe	*Rhizophora mangle*	3.9±0.1 (*N*=53)	3,953	6.4	66.3	56.0	48.8
	Laguncularia racemosa	3.2±0.3 (*N*=18)	1,343	3.9	22.5	33.8	33.3
	Avicennia germinans	3.8±0.3 (*N*=9)	671	1.2	11.2	10.2	17.9
Transition	*Rhizophora mangle*	–	0	0	0	0	0
	Laguncularia racemosa	1.9±0.4 (*N*=14)	2222	0.22	83.8	85.6	67.7
	Avicennia germinans	2.0±0.3 (*N*=66)	431	0.04	16.2	14.4	33.3
Dwarf	*Rhizophora mangle*	–	0	0	0	0	0
	Laguncularia racemosa	–	0	0	0	0	0
	Avicennia germinans	1.0±0.04 (*N*=81)	3,725	1.1	100	100	100

Table 2 Summary of hydro-edaphic conditions measured across the tree-height gradient by treatment (*Control*, unfertilized, *N*, nitrogen fertilized, *P*, phosphorus fertilized). Values are the mean±1 SE) of replicate (*N*=9) measurements taken four times during the study (April 1997, October 1998, March 1999, and March 2000)

Soil	Fringe			Transition			Dwarf		
	Control	N	P	Control	N	P	Control	N	P
Bulk density (g cm^{-3})	0.52 (0.09)	0.52 (0.10)	0.54 (0.11)	1.06 (0.04)	1.02 (0.04)	1.09 (0.03)	1.17 (0.03)	1.20 (0.02)	1.15 (0.04)
Organic matter (%)	14.6 (2.7)	17.3 (3.9)	14.7 (2.9)	3.3 (0.5)	3.9 (0.2)	3.4 (0.3)	1.9 (0.2)	2.0 (0.1)	1.9 (0.1)
Eh$_{1 cm}$ (mV)	155 (21)	171 (24)	202 (24)	223 (21)	183 (23)	170 (28)	192 (23)	193 (20)	173 (26)
Eh$_{15 cm}$ (mV)	30 (22)	90 (26)	51 (26)	89 (25)	35 (26)	72 (27)	95 (25)	74 (22)	49 (20)
Porewater									
Salinity (ppt)	39 (1)	40 (1)	40 (1)	41 (1)	43 (1)	42 (1)	49 (2)	57 (2)	55 (2)
pH	6.61 (0.05)	6.61 (0.05)	6.62 (0.04)	6.74 (0.04)	6.70 (0.04)	6.64 (0.04)	6.83 (0.04)	6.88 (0.05)	6.62 (0.06)

tively. Stem density and height in the transition zone were higher than in the dwarf zone, but basal area in the dwarf zone was approximately five times greater than in the transition zone.

Hydro-edaphic conditions

The soil at MI 23 had a high bulk density and a low organic matter content that varied with zone ($F_{2,70}$=102.1, P=0.0001; $F_{2, 70}$=61.8, P=0.0001), but not treatment (Table 2). Organic matter content was higher in the fringe compared to transition and dwarf zones ($F_{1,70}$=122.1, P=0.0001, 1 *df* contrast). Soil bulk density was lowest in the fringe and significantly higher in transition and dwarf zones ($F_{1, 70}$=198.2, P=0.0001, 1 *df* contrast). Soil redox potentials indicated slightly reducing conditions in all three zones that fluctuated over time ($F_{3, 70}$=63.5, P=0.0001; $F_{3, 70}$=29.9, P=0.0001 for 1 and 15 cm depths, respectively). There was no clear temporal pattern or significant differences in redox potential across zones or with treatment. The dwarf zone remained hypersaline throughout the study compared to the fringe and transition zones, which were not different ($F_{1, 70}$=3.3, P=0.001) (Table 2). Addition of N and P resulted in higher salinity in all three zones ($F_{2, 72}$=8.9, P=0.001). Sulfide was low overall, consistent with redox potentials, and was lower in the dwarf compared to fringe and transition zones ($F_{2, 72}$=10.3, P=0.002, 1 *df* contrast). Porewater pH varied only slightly across zones and treatments (Table 2). Porewater concentrations of PO_4-P and NH_4-N did not vary significantly across zones, but did show large differences with treatment, as expected ($F_{2,72}$=49.1, P=0.0001; $F_{2, 72}$=14.9, P=0.0001, respectively).

Plant growth

Nutrient treatment and zone had significant effects on growth rates (Fig. 1A–D). During both years, the N fertilizer caused a significant increase in leaf production (Fig. 1A, B) and shoot growth in each zone (Fig. 1C, D). For control trees, leaf production was highest for *R. mangle* in the fringe. Leaf production and shoot growth were significantly greater in year 2 than in year 1 ($F_{1, 70}$=9.9, P=0.002; $F_{1, 70}$=11.4, P=0.001, respectively). The P fertilizer had no effect on growth, except in the dwarf zone where leaf production increased slightly in year 1 (Fig. 1A). However, in year 2, adding P had no detectable effect on leaf production (Fig. 1B). Growth rates in years 1 and 2 were similar for the control and P-fertilized trees, but increased significantly in year 2 for the N-fertilized trees ($F_{1, 70}$=8.49, P=0.001). Data from both years indicated N-limited growth by *R. mangle* in the fringe zone and *A. germinans* in the transition and dwarf zones. During year 1, a significant block effect for DRGR ($F_{2, 70}$=7.6, P=0.001) showed that plant growth rates were not uniform at the three replicate sites.

Fig. 1 Effects of nutrient enrichment on demographic relative growth rates based on new leaves during (**A**) year 1 and (**B**) year 2; and absolute relative growth rates based on new shoot growth during (**C**) year 1 and (**D**) year 2; (**E**) N-resorption efficiency, (**F**) P-resorption efficiency, (**G**) efficiency maximum rates of photosynthetic electron transport, and (**H**) photosynthetic P use efficiency (photosynthetic electron transport rate per unit P) in fertilized mangrove trees by treatment (*Control* unfertilized, *N* nitrogen fertilized, *P* phosphorus fertilized) and zone along a tree-height gradient (fringe, transition, dwarf). Values are means ±SE. Within a zone the same lowercase letter indicates that treatment means are not significantly different; among zones the same uppercase letter indicates that treatment means are not significantly different (*P*<0.05). *N*=81 trees (3 nutrient treatments ×3 zones ×3 blocks ×3 replicate trees)
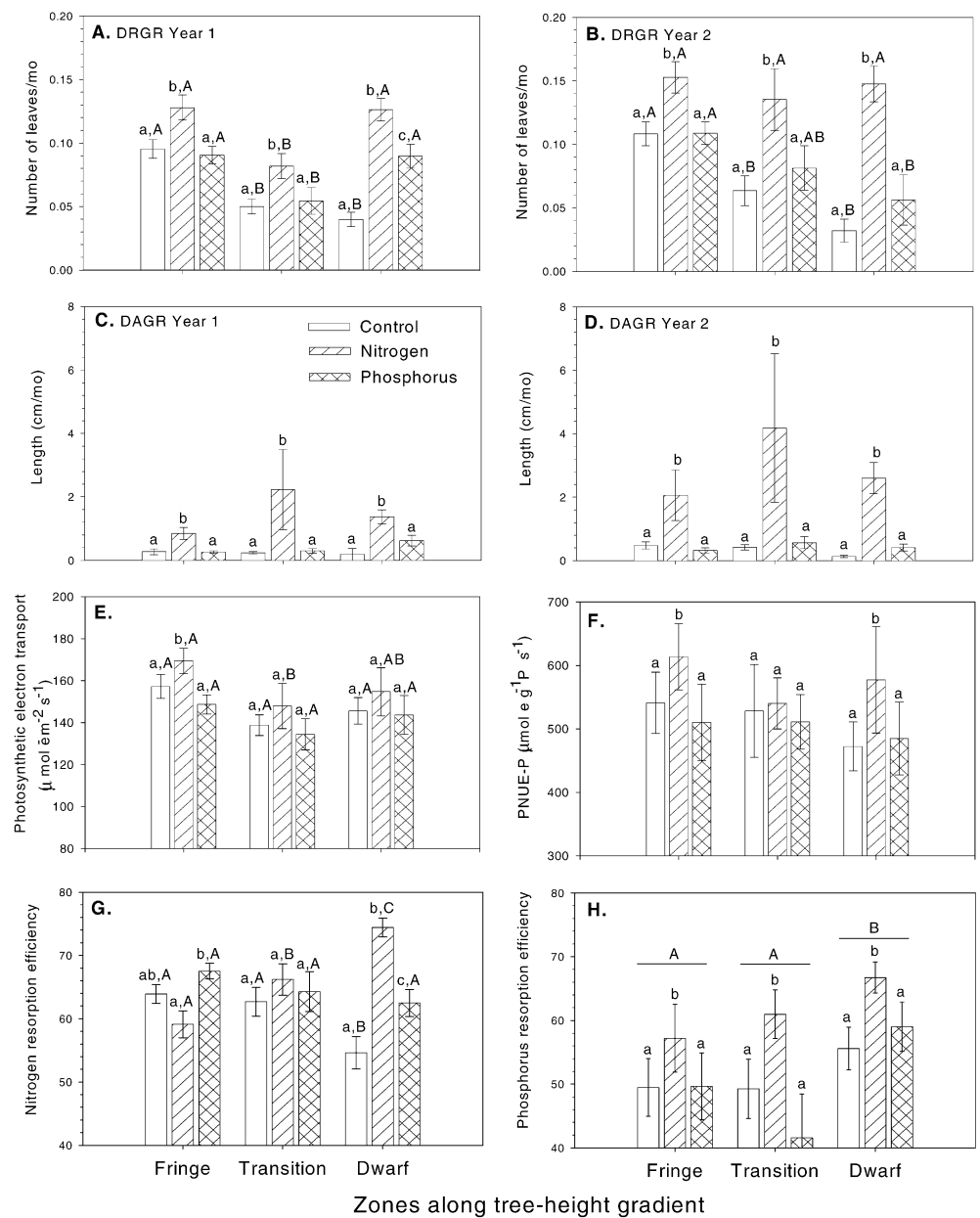
Nutrient dynamics

Nutrient enrichment and zone, but not block, had complex effects on the within-plant dynamics of N and P (Table 3). The N concentration of green leaves [N_G] from N-fertilized trees was significantly higher in all zones, and *A. germinans* had significantly higher [N_G] than *R. mangle* for all treatments (Table 3). In the dwarf zone, adding N caused a 60% increase in [N_G], compared to ~30% in fringe or transition zone. Nutrient treatment and zone also had significant effects on the N concentration of senescent leaves [N_S], with significant nutrient × zone interactions (Table 3). In controls, [N_S] was higher in *A. germinans* (transition and dwarf zones) than in *R. mangle* (fringe). Adding N caused a 36% increase in [N_S] in *R. mangle*, compared to 7% and 12% in *A. germinans* in the

transition and dwarf zones, respectively (Table 3). The P fertilizer had little effect on [N_G] or [N_S]. However, the N and P fertilizers altered N resorption efficiency, with a significant nutrient × zone interaction ($F_{4,70}$=8.8, *P*=0.001; Fig. 1G). For controls, N resorption was significantly lower in dwarf trees compared to fringe or transition trees. The greatest response was in the dwarf zone where adding N caused ~40% increase in N resorption.

Zone, but not nutrient treatment, had a highly significant effect on P concentration of green [P_G] and senescent [P_S] leaves (Table 4). The *R. mangle* in the fringe had much lower [P_G] and [P_S] than the *A. germinans* in the transition and dwarf zones (Table 3). Values for transition and dwarf zone trees were similar. Nutrient treatment and zone had significant effects on P-resorption

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Table 3 Percent nitrogen and phosphorus in green ([N$_G$], [P$_G$]) and senescent ([N$_S$], [P$_S$]) leaves from *Rhizophora mangle* in the fringe zone and *Avicennia germinans* in the transition and dwarf zones in response to treatment (*Control*, unfertilized, *N*, nitrogen fertilized, *P*, phosphorus fertilized). Values are means±(1 SE). *N* =27 trees per treatment level and 27 trees per zone. Data were arcsine square-root transformed prior to analysis

Zone	Fringe			Transition			Dwarf		
Nutrient	Control	N	P	Control	N	P	Control	N	P
[N$_G$]	1.26 (0.05)	1.56 (0.07)	1.26 (0.08)	1.66 (0.06)	2.17 (0.01)	1.60 (0.06)	1.42 (0.06)	2.27 (0.09)	1.58 (0.05)
[N$_S$]	0.44 (0.02)	0.60 (0.04)	0.40 (0.03)	0.57 (0.01)	0.61 (0.04)	0.52 (0.04)	0.59 (0.02)	0.66 (0.02)	0.60 (0.01)
[P$_G$]	0.097 (0.003)	0.104 (0.002)	0.096 (0.005)	0.147 (0.008)	0.134 (0.006)	0.147 (0.011)	0.138 (0.012)	0.135 (0.013)	0.137 (0.009)
[P$_S$]	0.047 (0.003)	0.043 (0.005)	0.047 (0.005)	0.071 (0.009)	0.055 (0.011)	0.075 (0.005)	0.057 (0.006)	0.051 (0.004)	0.057 (0.005)
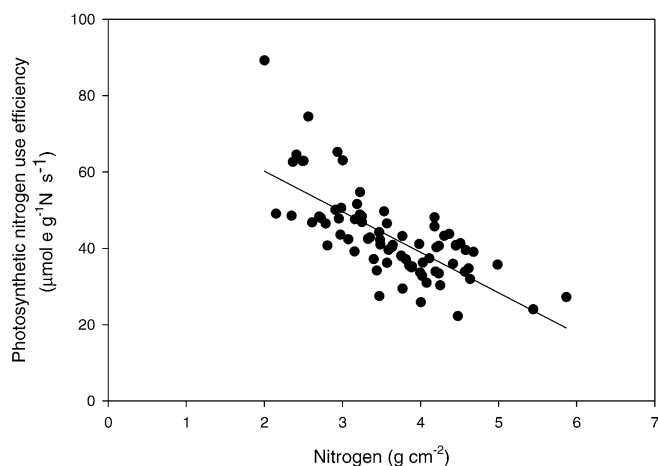
Fig. 2 The relationship between leaf nitrogen concentration per unit area (g cm^{-2}) and photosynthetic N use efficiency (μmol e g^{-1}N s^{-1}) in fertilized mangroves at MI 23. *N*=81

efficiency ($F_{2, 68}$=5.7, *P*=0.01; $F_{2, 68}$=3.9, *P*=0.02, respectively), with no significant interactions between these factors (Fig. 1H). Adding N caused a significant overall increase in P resorption efficiency, with values 10%–20% greater in N-fertilized trees than in control or P-fertilized trees. Phosphorus resorption was significantly higher in the dwarf zone than in the transition (*P*=0.01) or fringe (*P*=0.03) zones.

Photosynthesis

Nutrient enrichment had a significant effect on maximum rates of photosynthetic electron transport across zones and blocks ($F_{2, 52}$=12.2, *P*=0.02, Fig. 1E). Adding N enhanced photosynthetic electron transport of leaves relative to controls, while adding P did not. Photosynthetic CO$_2$ fixation was enhanced in N-fertilized plants in the dwarf zone in September, but not in June. However, the magnitude of the effect was influenced by block at both measurement times (September 1998, $F_{2, 18}$=11.0, *P*=0.001; June 1999, $F_{2, 18}$=10.7, *P*=0.001), with block 2 having higher rates of photosynthesis than blocks 1 or 3.

Nitrogen concentrations of the leaves used for measurement of photosynthetic electron transport were enhanced in response to the N fertilizer ($F_{2, 52}$=10.8, *P*=0.02), while leaf P concentrations were not affected by fertilizer treatments. The utilization of nutrient resources for photosynthetic processes was also significantly affected by fertilizer treatments. Adding N enhanced PNUE-P compared to controls (Fig. 1F, $F_{2, 52}$=21.5, *P*=0.01). Fertilizer treatments did not significantly alter the photosynthetic N use efficiency, but over all trees, PNUE-N was negatively correlated with N concentrations in leaves (Fig. 2).

Table 4 Results of three-way ANOVAs performed on percent nitrogen (N) and phosphorus (P) concentration in green and senescent leaves from *Rhizophora mangle* and *Avicennia germinans* by nutrient treatment, Nt (*Control*, unfertilized, *N*, nitrogen fertilized, *P*, phosphorus fertilized) and Zone (fringe, transition, dwarf), blocked at three sites at Mosquito Impoundment 23, Fort Pierce, FL. Values are *F*-ratios. *N*=27 trees per nutrient treatment; *N*=27 trees per zone. Data were arcsine square-root transformed

Source of variation	df	N$_{green}$	N$_{senescent}$	P$_{green}$	P$_{senescent}$
Nutrient (Nt)	2	51.644 ***	14.424***	0.059 ns	2.621 ns
Zone	2	36.498***	19.399***	25.735***	8.480***
Block	2	0.499 ns	0.876 ns	0.163 ns	1.197 ns
Nt × Zone	4	3.414**	2.621 ns	0.524 ns	0.569 ns

* $P \le 0.05$; ** $P \le 0.01$; *** $P \le 0.001$; ns, not significant

Discussion

The tidal forest at MI 23 was characterized by a spatial gradient in both species dominance and tree stature. Tall *R. mangle* dominated a narrow fringe along the man-made channel, but was virtually absent from the interior portions of the forest, which were dominated by stunted *A. germinans* and *L. racemosa*. Such spatial variability of species zonation, primary production, tree stature, and growth rates within a mangrove forest has been correlated with many environmental variables, including salinity, nutrient availability, flooding frequency, oxidation-reduction status of soil, sulfide concentrations, and surface hydrology (MacNae 1968; Lugo and Snedaker 1974; Onuf et al.1977; Boto and Wellington 1983; Cintrón et al.1978;1985; Lugo 1990; Jimenez and Sauter1991; Clough et al.1982; McKee 1993;1995). Growth response to fertilization indicated that the mangrove forest at MI 23 was N-limited along the entire tree-height gradient. These data partially support Hypothesis 1, i.e., that nutrient availability limits growth, but does not shift from N to P limitation.

Results from this study contrast with a parallel investigation of a pristine mangrove ecosystem on offshore islands in Belize (Twin Cays), associated with the Mesoamerican Barrier Reef System (Feller 1995; Feller et al. 1999, 2003; McKee et al. 2002). The Belize site is characterized by a height gradient in *R. mangle* from fringe to interior, whereas the Florida site exhibits a switch in species dominance to landward. In contrast with the Belize site where the soil in dwarf forests is strongly reducing with sulfide accumulation, the Florida interior forest is drained for most of the year and is hypersaline. Both forests were characterized by a distinctive tree-height gradient of relatively tall trees in the fringe, with tree height decreasing to landward. The hinterlands at both sites were dominated by extensive stands of stunted trees but with different dominant species. The dwarf zone in Belize is dominated by *R. mangle* compared to *A. germinans* in MI 23. In contrast with the Belize site where the soil in the interior areas is waterlogged, the hinterland in Florida site is drained for most of the year. These sites also differed in age and disturbance history. The Florida site is heavily disturbed, and the forest is young (<30 years old). The Belize site is pristine and has been a mangrove system for 7,000–10,000 years (Macintyre et al. 1995).

This site also has not witnessed a severe hurricane since 1961 or experienced conspicuous anthropogenic damage throughout its Holocene history (Rützler and Feller 1996).

MI 23 has direct contact with the Indian River Lagoon that receives large amounts of nutrient input from coastal runoff and canals and rivers draining into the IRL from agricultural and urban developments (http://www.epa.-gov/OWOW/oceans/lagoon/impacte.html). Even with potentially high nutrient inputs, all measurements of growth and productivity were still nutrient limited at MI 23. The N fertilizer caused a significant increase in photosynthetic electron transport, shoot growth, and leaf production in all zones. Additionally, photosynthetic CO_2 fixation was significantly enhanced in the N-fertilized dwarf trees compared to control and P-fertilized trees. Temporal differences in responses to N enrichment were due to patterns of leaf aging (Lovelock and Feller 2003).

The greatest responses to N enrichment occurred in the dwarf and transition zones, while the response of photosynthetic electron transport to the N enrichment was similar across all zones. Infrequent tides sufficient to flood the dwarf and transitions zones and the absence of sedimentation indicated that relatively few external nutrients reach the interior portions of the forest. Sedimentation rate along the shoreline averages 0.88±0.33 cm year^{-1}, but little of this reaches the interior forest (0.09±0.03 cm year^{-1}) (McKee, unpublished data). The significantly higher growth rates for control trees in the fringe zone may be partly due to greater sedimentation and nutrient input compared to transition and dwarf zones. The consistent response to addition of N fertilizer along the tree-height gradient at MI 23 was in sharp contrast to the pattern of nutrient limitation detected in the mangrove forests at Twin Cays, Belize (Feller et al. 2003; McKee et al. 2002). In that forest, tree growth was N-limited in the fringe and P-limited in the interior dwarf stands, which were less than 50 m inland. McKee et al. (2002) hypothesized that the nutrient switching pattern observed in Belize reflected the interaction of external supply of nutrients with internal demand, which was influenced by other environmental stress factors that varied spatially. The tree-height gradient in Belize was characterized by spatial variation in flooding stresses as well as relative availability of N and P. Flooding-related stress may increase plant demand for P, whereas salinity stress may increase demand for N. Where availability of P

relative to N was lowest (in the dwarf zone), plants responded strongly to fertilization with P, but not with N (Feller et al. 2003). In Florida at MI 23, the trees responded significantly to addition of N (Fig. 1A–D). However, the response to N was greatest in the dwarf zone where salinity stress (and the requirement for N) was highest. In both cases, low relative availability of N (Florida) or P (Belize) coincided with the occurrence of other stresses which may have increased the requirement for the limiting nutrient. This effect may partly explain the switch from N to P limitation across Belizean island forests where flooding depth and duration increases with distance from the shoreline (Feller et al. 2003). Flooding and salinity stresses may also directly affect plant growth or ability to acquire limiting nutrients. For example, flooding may restrict root exploration of soil and/or decrease root surface area, which strongly influences acquisition of immobile ions such as phosphate (McKee 2001). Furthermore, the addition of N and P caused an increase in salinity (Table 2). Presumably, higher rates of transpiration caused accumulation of ions excluded from uptake in the transpiration stream, as described in Passioura et al. (1992).

As the availability of a limiting nutrient increases, do the mechanisms used by plants to recycle and conserve that nutrient become less efficient? Our results from MI 23 and Twin Cays for nutrient resorption efficiency and nutrient use efficiency for growth and photosynthetic electron transport indicate that increased availability of a limiting nutrient did change nutrient use and conservation patterns in mangrove forests. However, the patterns exhibited were complex. Our data suggest that responses depended not only on the nature of nutrient limitations but also on interspecific differences. In our second hypothesis, we predicted that under N-limiting conditions, N would be more tightly conserved via efficient internal nutrient cycling mechanisms than under N-enriched conditions. Contrary to these predictions, at MI 23 where growth was N-limited throughout the forest, increased N availability caused N resorption *to increase* in *A. germinans* in the dwarf zone but *to decrease* in *R. mangle* in the fringe. Addition of N also resulted in increased resorption of P in all three zones. These differences in nutrient conservation in response to fertilization may be related to interspecific physiological differences between *A. germinans* and *R. mangle* in their relative tolerance of environmental conditions (Ball 1996). In our study, adding N led not only to increased growth but also to enhanced nutrient conservation of both N and P by *A. germinans* in hypersaline conditions. The mangrove trees at MI 23 were proficient at resorbing N, the growth-limiting nutrient. Nutrient concentrations in senescent leaves suggest that under N-limiting conditions resorption of N by *R. mangle* and *A. germinans* is complete and reaches the maximal physiological levels proposed by Killingbeck (1996). In Belize, increased N availability had no effect on *R. mangle*'s ability to conserve N along an N to P limitation gradient, even in the fringe zone where growth was N-limited (Feller et al. 2003).

Although adding P had only a slight effect on growth rates at MI 23 during year 1, it caused a 13% increase in N resoption in P-fertilized dwarf trees. This result contrasts sharply with >60% increase in N resorption by P-fertilized trees in the dwarf zone at the Belize site.

Many factors, including salinity, may be influential in determining the local dominance and productivity of mangrove species (Smith 1992). At MI 23, salinity was 40–50% higher in the dwarf zone than in either the transition or fringe zones. Salt tolerance in *A. germinans* is energy and nutrient demanding because it involves salt excretion through leaf salt glands and synthesis of N-based compounds for osmoregulation (Popp 1984; Popp et al. 1988; Popp and Polania 1989). The physiological effects of salinity and interactions between salinity and N nutrition have also been documented for *Spartina alterniflora,* which employs similar mechanisms for salt tolerance. The tree-height and salinity gradients at MI 23 are somewhat analogous to *S. alternifloria*-dominated marshes in temperate latitudes. In those systems, as salinity increases, the amount of N required to sustain growth also increases (Bradley and Morris 1992). Sea salts also competitively inhibit uptake of NH_4, which diminishes *S. alterniflora*'s ability to osmoregulate (Bradley and Morris 1992). At MI 23, porewater salinity appears to contribute to the low stature and stunted growth of the dwarf trees in the interior of the forest, consistent with observations by Lin and Sternberg (1992). The results from our fertilization experiment at MI 23 suggest that growth limitation is due to interacting stressors, including salinity and nutrient availability.

Addition of the N fertilizer did not significantly alter the photosynthetic N use efficiency. Higher N concentrations in leaves (which were significantly enhanced by the N fertilizer) were associated with a decline in the efficiency with which N is used for photosynthesis, indicating allocation of N to other metabolic processes when N is no longer limiting. Fertilization with N significantly enhanced the utilization of P for photosynthesis. Thus, by relieving N limitation in leaf tissues, more P can be incorporated into the photosynthetic apparatus. At the level of individual leaves, addition of limiting nutrients appears to reduce the efficiency by which the limiting nutrient, in this case N, is used, while improving the utilization of other resources (e.g., P), which supports our second hypothesis.

Nitrogen limitation in MI 23 contrasts with a well-documented pattern of P-limitation in mangrove and other tidal and non-tidal wetlands elsewhere in Florida (Brown 1981; Caraco et al. 1990; Craft and Richardson 1997; Koch and Snedaker 1997; Chen and Twilley 1999; Daoust and Childers 1999; Chiang et al. 2000; Pant and Reddy 2001). We hypothesize that the mangrove forest at MI 23 is not P-limited because of direct or indirect physical or chemical impacts caused by impounding. Overall, our experiments in Belize and Florida show that essential nutrients were not uniformly distributed within or among mangrove ecosystems and provide experimental evidence

that not all ecological and physiological processes within an ecosystem were limited by the same nutrient.

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MANGROVE FOREST STRUCTURE UNDER VARYING ENVRIONMENTAL CONDITIONS

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ABSTRACT

Vegetation assessments were carried out in three mangrove forests undergoing different levels of anthropogenic stress and varying environmental factors. These forests were in Hunts Bay, Fort Rocky Lagoon (part of the Port Royal mangroves on the south shore of Kingston Harbour), and Wreck Bay (Hellshire). The vegetation assessments included the determination of species composition, floristics, and leaf litter production of the mangrove trees. Selected environmental and biological conditions were also investigated at each site. The hypothesized gradient of environmental factors, eutrophication and disturbance was Hunts Bay > Fort Rocky Lagoon > Wreck Bay. With the exception of light on the forest floor, the soil and water column parameters were all significantly different among sites, but the values did not always follow the expected environmental gradient. For example, nitrate/nitrite values were maximum at Wreck Bay (34.4 µM), followed by Hunts Bay (12.41 µM) and Fort Rocky Lagoon (10.0 µM), and phosphates ranked with maximum at Fort Rocky Lagoon (9.69 µM), then Hunts Bay (4.41 µM) and Wreck Bay (1.24 µM). Of the vegetation characteristics, only average leaf litter production and percentage cover were significantly different among sites, with a ranking similar to the hypothesis (i.e., Hunts Bay > Fort Rocky Lagoon > Wreck Bay). The most important factors influencing the distribution of productivity and percentage cover among forests were soil salinity, soil NO_3, especially the nitrate to phosphate ratio, soil moisture content and soil temperature with R^2 values of 0.77 for litter production and 0.64 for percentage cover. Other factors such as diameter at breast height and tree height were not significantly different among forests and showed a weak relationship with edaphic factors. Overall results indicated that the forests were very different with respect to physicochemical and edaphic factors, and there was a clear gradient of eutrophication. However, the effect of anthropogenic stress and varying environmental conditions is most reliably demonstrated in the productivity and percentage cover of the forests.

The influence of man on mangrove forest structure is intensive, non-selective, and non-specific. Worldwide it is estimated that as many as one million hectares of mangroves are lost every year (Bossi and Cintron, 1990). Although there are no figures for the Caribbean as a whole, there is need for concern. Mangrove areas in Jamaica tend to be smaller and easily cleared or converted to other uses. These losses are often irreversible (Bossi and Cintron, 1990). In cases involving reclamation for garbage disposal, there are problems not only with the loss of wetlands, but increased pollution potential as well. Such reclamations can result in the fringe zone being destroyed; the pollution load in the waterway increased; the tidal ventilation reduced; and velocity of runoff increased, resulting in increased siltation and less incoming ocean water to reduce the pollutants present in the estuary (Mangroves, 1998a). Shoreline development has replaced mangroves with marinas, dredged channels, airports, filled lots, sea walls, and other commercial and residential constructions. Of shallow water open mangroves in the upper Florida Keys, 60% were lost between 1965–1985 and 40% of that was due to dredging and filling of mangroves (Mangroves, 1999). While extensive documentation exists on the effect of these obvious activities on mangrove systems, there is a paucity of studies on the more subtle

effect of nutrient enrichment and eutrophication on mangrove forests. Organic effluents can substantially alter a mangrove ecosystem by causing depletion of dissolved oxygen, DO, and increases in nutrient levels in the water (Mangroves, 1998b). There is need to examine the effects on Jamaican mangrove forests as well as to determine the forest parameters and variables, which are useful indicators of eutrophication effects on mangrove forests. To achieve this objective, assessments were conducted in three different mangrove forests between January and August 1999.

Two mangrove areas were selected in Kingston Harbour, one in Hunts Bay and the other on the south shore of the Harbor in an area of Port Royal Mangroves (Fort Rocky Lagoon). A third station was sited in Wreck Bay, a pristine bay along the Hellshire coast. This was regarded as a 'control' station, being far removed from the influence of Kingston Harbour and other major sources of eutrophication (Webber, 1990).

Hunts Bay, according to Ranston (1998), supports generally 'unhealthy' ruinate mangrove swamps along its shores. The Soapberry swamp lies along the north shore of the bay and the mangrove swamps on the north and northeastern shores taper gradually into nearby residential and industrial sectors (Ranston, 1998). From initial general observations, this site was deemed representative of an area of mangroves influenced by a high volume of fresh water and a high level of eutrophication as well as disturbance from direct human activity. The site is situated between the Duhaney River and the Sandy Gully, thus should receive large quantities of fresh water and sediments especially during periods of high rainfall. The observed species composition is depauperate with *Laguncularia racemosa* and *Avicennia germinans* accounting for the majority of the vegetation, and *Rhizophora mangle* occurring in very small patches and being in very poor health where they occurred. This site may be classified on the basis of Lugo and Snedaker (1974) as a riverine forest. Hunts Bay mangroves can also be classified according to Asprey and Robbins (1953) as silt/mud mangroves. The soil here is predominantly anaerobic so that pneumatophores, or breathing roots are critical to survival; therefore, Hunts Bay is dominated by *A. germinans* and *L. racemosa* along with the occasional *R. mangle* tree.

Fort Rocky Lagoon represents an area of moderate disturbance, which is indirectly influenced by the polluted waters of Kingston Harbour. It is part of the Port Royal mangrove swamp, which is an area of mangrove lagoons and channels between large islands of mangrove forests. The most obvious sign of impact on the mangrove forests on the south shore of Kingston Harbour is the build up of solid waste deposited on the forest floor in areas adjacent to the open waters (Green and Webber, 1996), on the windward side of the mangrove islands. The mangrove areas adjacent to the lagoon (the leeward side of the mangrove islands) are not influenced by any major fluvial inputs, but due to the indirect influence of Kingston Harbour, the site is ranked next to Hunts Bay with respect to pollution. The site can be classified as a fringe forest and the area sampled can best be described as typical of an associes of mature *R. mangle* and *L. racemosa* with *R. mangle* dominant. Alleng (1990) found that most of the trees were tall and light penetration was minimal. The 27 km coastline of Hellshire consists of a variety of bays that are under different influences (Lindo, 1991). Wreck Bay is situated within the northeastern sector of the Hellshire coastline, and is a shallow (1–5 m) bay protected by reefs and sand banks to varying degrees. There is significant fresh water input from an underground source that has been observed percolating through fissures in the porous limestone rocks on the shallow bay floor (Webber, 1990). Due to the distance of Wreck Bay from the
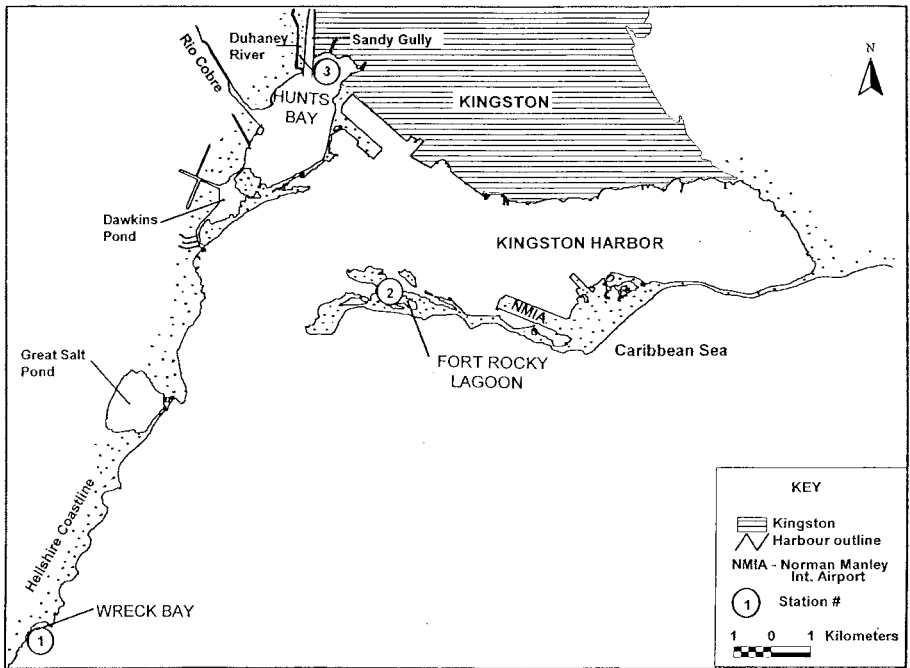
Figure 1. Map showing the location of the three forests investigated during the study.

mouth of the Kingston Harbour, and that it is relatively exposed to the open ocean, it was deemed a pristine site. The mangals in this area have a sand substrate and the mangrove species, notably an abundance of *R. mangle*, are interspersed with other coastal plant species in the zone nearest to land, but the *R. mangle* plants were observed to be in their typical zone along the fringe (seaward edge) of the forest. The area can thus be classified according to Asprey and Robbins (1953) as a sand mangrove and according to Lugo and Snedaker (1974) as a fringe forest. This area was chosen to be the site least influenced by anthropogenic stress whether industrial, domestic, or otherwise.

MATERIALS AND METHODS

VEGETATIVE SURVEY

The mangrove vegetation and associations at each site were described according to the methods of Lugo and Snedaker (1974) and Snedaker and Snedaker (1984). The classification of five major forest types: fringe, overwash, riverine, basin and dwarf forests, was used to describe the different mangrove communities under investigation at the four locations.

Vegetation Profiles.—A representative portion of the forest vegetation at each site was chosen and sampled using a belt transect. The transects all started from the lagoon end (Datum point), but the exact area sampled varied in each of the forests as follows: Hunts Bay: 40 m in length × 4 m in width, Fort Rocky Lagoon: 50 m in length × 2 m in width and Hellshire: 25 m in length × 2 m in width.

During sampling several characteristics (floristic features) were recorded for all the plants encountered within the belt transect. Diameter at breast height (dbh) was determined with the use of the Haglof caliper. Tree height, which was taken as the linear vertical distance between the ground

and the tip of the tree crown (Cintron and Schaeffer-Novelli in Snedaker and Snedaker, 1984), was measured directly where possible. Where direct measurement was impossible, an inclinometer was used to obtain this value of height. Visual estimates of percentage cover were made for the individual plants sampled. Generally, plant species composition was determined with the aid of the Vegetative Key to Mangroves referred to by Tomlinson (1994).

Leaf Litter Production.—The levels of leaf litter were determined as an indication of primary productivity at the three sampling sites. To measure productivity, leaf litter traps were deployed at the beginning of the transect (datum point) and at successive 5 m intervals. The traps were constructed of 0.5×0.5 m (0.25 m^2) wooden frames with 0.25 m^2 of nylon netting (mesh aperture size 2.0 mm) attached to one side. The litter from these traps was collected after a two-week period. The collected material was allowed to dry to a constant weight at 55°C before weighing. Productivity was determined using the following formula:

$$\text{Productivity } (g\ m^{-2} d^{-1}) = \frac{\text{Dry weight } (g\ m^{-2}) \text{ of litter over a 1 m}^2 \text{ area}}{\text{Time } (d)}$$

ENVIRONMENTAL, EDAPHIC AND PHYSICOCHEMICAL VARIABLES

Environmental variables were measured in the lagoon immediately adjacent to the forest and in any standing water on the forest floor. These included: salinity, temperature (°C), dissolved oxygen (mg L^{-1}), Redox potential (mV) and pH. These measurements were taken at mid-depth in the lagoon immediately adjacent to the study sites, and where the entire forest floor was permanently inundated by sea water or had fresh water present, measurements were taken at the beginning of the transect and at every successive 5 m interval. The instrument used to measure these variables was the Hydrolab H$_2$0 Water Quality Multiprobe. Nutrients were also measured (NO$_3$ and PO$_4$) via water samples, which were collected at mid-depth from the lagoon adjacent to each site as well as at the beginning and each successive 5 m interval along the transect in instances where the forest floor was covered with fresh/sea water. These water samples were preserved using chloroform (to produce a 10% chloroform solution) within a maximum time of three hrs after collection to maintain the quality and status of the samples.

Field Measurements.—Light available under the forest canopy (Lux) was measured at breast height at datum point and every successive 5 m intervals along the transect at each sampling area, using a Davis® Light Meter (Model 0198).

Soil cores were collected at the same intervals, stored in Ziploc™ bags and placed in coolers until taken to the laboratory later that day. The samples were analyzed for soil salinity and pH, as well as interstitial water, nitrate and phosphate levels. Soil temperature was determined in situ using a Reotemp soil temperature probe.

Laboratory Procedures.—Soil moisture content was determined gravimetrically using the conventional drying temperature of 60°C to a constant weight and calculated as the difference between fresh and dry weight as a percentage of the original (fresh weight).

Soil organic matter was also determined gravimetrically with the oven dried soil being ashed in a muffle furnace for three hrs at 550° C. The total organic matter in the soil samples was obtained by difference between dry weight and ash weight and reported as a % of the original (dry weight).

Soil nutrient analyses first involved extraction of soil pore water from soil cores collected along each transect. 80 ml of deionized water was added to a volume of approximately 160–180 mL of soil to form a 2:1 soil to water solution. This mixture was stirred vigorously until the soil lumps had completely disintegrated, at which time chloroform was added. The solution was allowed to settle for a few minutes after which it was vacuum filtered using cellulose filter paper with a pore size of 0.7 µm. and the filtrate frozen for further analysis (i.e., determination of nitrates and phosphates) using an autoanalyzer. Seawater, fresh water and soil water samples preserved in the field were filtered and stored as above. Soil water salinity (± 0.5) was determined using the American Optical

Refractometer (Model No. 88CO). The pH ($\pm$ 0.5) of the samples was determined using an Orion pH Tester.

The Cadmium Reduction method was used to determine nitrate-N concentrations. This was measured colorimetrically at a wavelength of 550 nm using a Technicon™ autoanalyser (Technicon Instruments Corporation, 1972b).

Concentrations of ortho-phosphate were determined using a molybdenum complex. This was measured colorimetrically at a wavelength of 880 nm also using a Technicon™ autoanalyser (Technicon Instruments Corporation, 1972a).

Statistical Analyses.—Tests for significant differences in environmental characteristics among the forests were using analysis of variance (ANOVA) with sites as the main effect. The grouping and ranking of sites was done using the multiple range/ post hoc test, Tukey's Honest Significant Difference (HSD) test. Stepwise variable selection multiple regression was used to determine the relationship between the physico-chemical variables and the vegetation parameters of the combined results for the three sites. The stepwise variable selection multiple regression model was used to determine the parameters that were most important in explaining the variations in vegetation parameters between sites.

<center>RESULTS AND DISCUSSION</center>

LAGOON ENVIRONMENTAL PARAMETERS

The variation in temperature, salinity and pH of the lagoons adjacent to the three mangrove forests sampled showed a similar pattern (Fig. 2). Mean temperatures of 29.59º C were recorded in Fort Rocky Lagoon, 28.79º C in Wreck Bay and 26.11º C in Hunts Bay. Fort Rocky lagoon had an average salinity of 34.2, Wreck Bay 33.6 and Hunts Bay lagoon 5.5. The lowered salinity and temperature of the Hunts Bay lagoon was due to fresh water influence in the lagoon from the rivers and gullies, which drain into Hunts Bay. The lagoon adjacent to the Wreck Bay mangroves was slightly less saline than Fort Rocky due to the direct influence of a small fresh water spring. Fort Rocky lagoon has no such direct sources of fresh water. The pattern in temperature is probably due to degree of shading as well as inputs of cold fresh water. The pH seemed to be affected by relative amounts of fresh water and seawater as pH of the lagoons followed a similar pattern to temperature and salinity: pH values of 9.5 for Fort Rocky Lagoon, 9.32 for Wreck Bay and 9.01 for Hunts Bay.

Dissolved oxygen values in the adjacent lagoons were highest for Wreck Bay with a value of 10.43 mg L^{-1} followed by Fort Rocky Lagoon with 5.62 mg L^{-1} and then Hunts Bay which had the lowest value of 4.57 mg L^{-1} (Fig. 2D). This trend suggests that as the level of eutrophication decreases, the dissolved oxygen increases.

Redox potential increased with decreasing eutrophic conditions, being the highest (257 mV) at Wreck Bay, 223 mV at Fort Rocky Lagoon and extremely low (9 mV) at Hunts Bay (Fig. 2E). Redox potential and dissolved oxygen are useful indicators of water quality and these two variables show similar trends with high values for Redox potential relating to good dissolved oxygen conditions at Wreck Bay, and the converse at Hunts Bay.

The nitrate content of the lagoons adjacent to the mangrove forests did not show the expected eutrophication gradient (Fig. 2F). Hunts Bay lagoon had a mean value of 22 µM, Fort Rocky Lagoon had a value of 9.5 µM and Wreck Bay had a value of 31 µM. The expected gradient may have been observed, but for an exceptionally high value at Wreck Bay. This high value was probably due to the influence of a fresh water stream in the
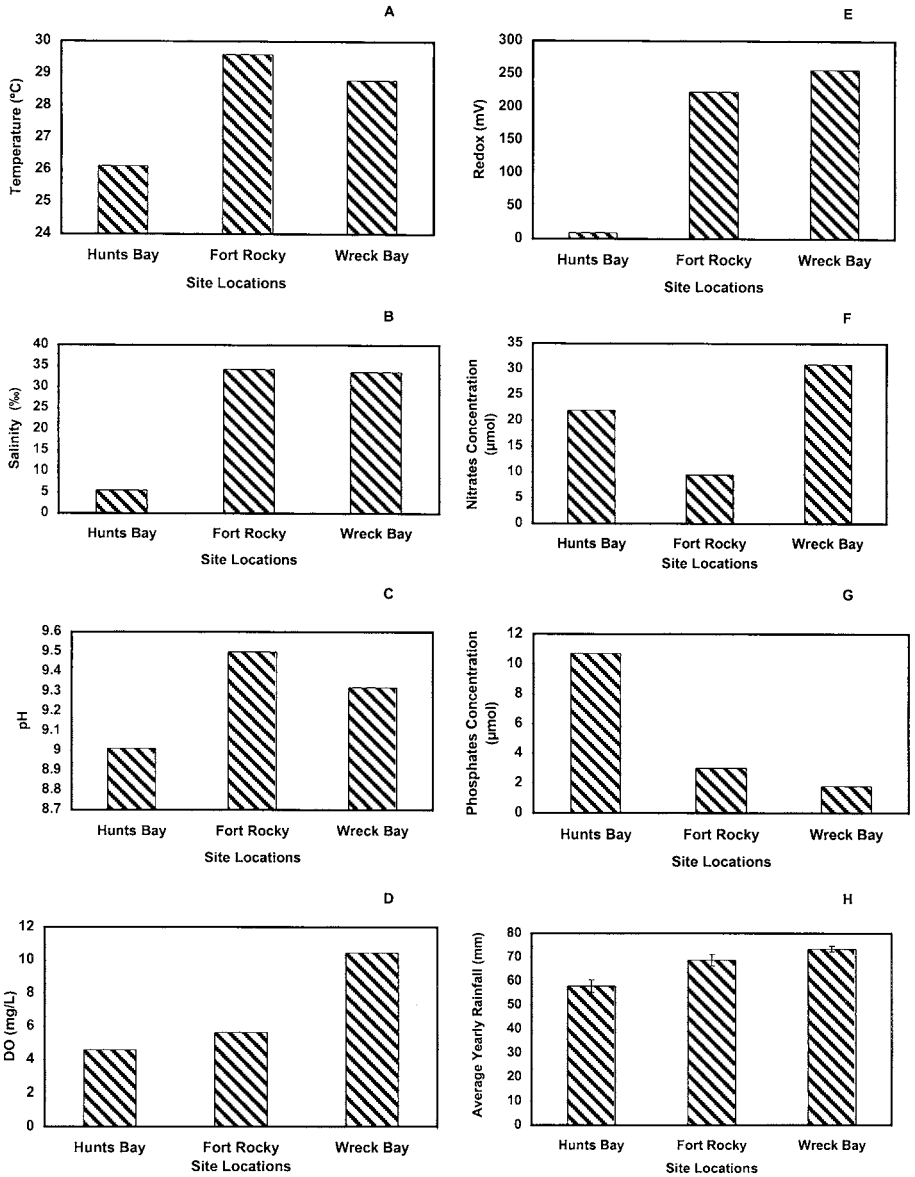
Figure 2. Physicochemical parameters and variables determined for the lagoon adjacent to each forest (A-Temperature, B- Salinity, C- pH, D- Dissolved Oxygen, E- Redox potential, F- Nitrates, G- Phosphates as well as, H- Average annual rainfall influencing the three areas sampled).

forest, which had a very high NO_3 content. Hunts Bay lagoon also had a high NO_3 content and this is due to the heavy nutrient loads deposited in the lagoon by the rivers that enter the lagoon as well as the storm water gully. Additionally, all the outputs from land (sewage and otherwise), which enter the harbor, would influence the nutrient content of the Hunts Bay lagoon.

The mean phosphate content of Hunts Bay was 10.7 µM, Fort Rocky Lagoon had a value of 3 µM and Wreck Bay had a value of 1.8 µM (Fig. 16). The distribution of PO_4 in the lagoons manifested the hypothesized eutrophication gradient, (i.e., Hunts Bay > Fort Rocky Lagoon > Wreck Bay). When examined in relation to the nitrate values at all sites it is clear that phosphate values are extremely high and indicate enrichment and eutrophication. However, only at Wreck Bay was the ratio of nitrate to phosphate (17:1) close to that required (15:1) for optimal algal growth (Redfield, 1934) and greater than ratios considered optimal (8:1) for higher plant growth (Clarkson, 1985). While values were high at Hunts Bay and Fort Rocky Lagoon, nitrate to phosphate ratios were never in excess of 3:1 suggesting nitrogen limitation.

FOREST ENVIRONMENTAL/PHYSICOCHEMICAL PARAMETERS

Average soil temperature decreased from 27.24º C at Wreck Bay to 26.27º C at Fort Rocky Lagoon forest, and Hunts Bay accounted for the lowest soil temperature on average with a value of 24.44º C (Fig. 3A). Average soil temperature was significantly different among sites (Table 1). This trend in soil temperature could be due to an increase in level of exposure to oceanic water renewal, with Wreck Bay being the most exposed site and Hunts Bay being the least. It could also be due to canopy cover as average soil temperatures for the forests showed an inverse trend to average percentage cover (Fig. 5).

Soil salinity was highest for Fort Rocky with a mean value of 22.36, Hunts Bay had a value of 15 and Wreck Bay had the lowest soil salinity of 6.4 (Fig. 3B). Average soil salinity varied significantly among the sites (Table 1). Soil salinity decreased with increasing direct freshwater influence at these sites so that the site with the lowest freshwater influence (Fort Rocky) had the highest salinity and Wreck Bay, where the stream flowed through the forest, had greatest direct freshwater influence and the lowest soil salinity. Despite the fact that the lagoon adjacent to the Wreck Bay mangrove forest had a high salinity, which should influence the soil pore water salinity in the forest, the stream saturated the soil with freshwater, resulting in very low values for soil water salinity.

The average soil pH was highest for Wreck Bay with a value of 7.74, then Hunts Bay with a value of 6.83, and Fort Rocky Lagoon forest with a value of 6.18 (Fig. 3C). Average soil pH values varied significantly among the three sites (Table 1). Soil pH increased with decreasing eutrophication for the respective sites. This may be due to eutrophic conditions increasing microbial activity, which result in a decrease in pH. Alternatively, pH on the forest floor may be affected by the degree of saline intrusion. The forest with the greatest saline intrusion would be expected to have the highest pH due to the slightly alkaline nature of sea water and its buffering capacity. However, the importance of this is negated by the fact that Fort Rocky lagoon, which has the highest soil salinity, is the forest with the lowest pH and Wreck Bay, with the lowest soil salinity, has the highest pH.

Average soil moisture content for the Fort Rocky forest was 80.47%, Wreck Bay had a value of 72.83% and Hunts Bay had a value of 52.23% (Fig. 3D). Average soil moisture content values varied significantly among the sites (Table 1). Soil moisture content was highest at Fort Rocky Lagoon because of the high amount of roots of *R. mangle* in the substratum, which created a mat into which soil was admixed; thus, conferring a spongy nature to the substrate and high water holding capacity. The same situation existed for Wreck Bay except the soil comprising that portion of the substrate was sandy so that this sandy soil combined with the intertwining roots of *R. mangle* did not confer as high a
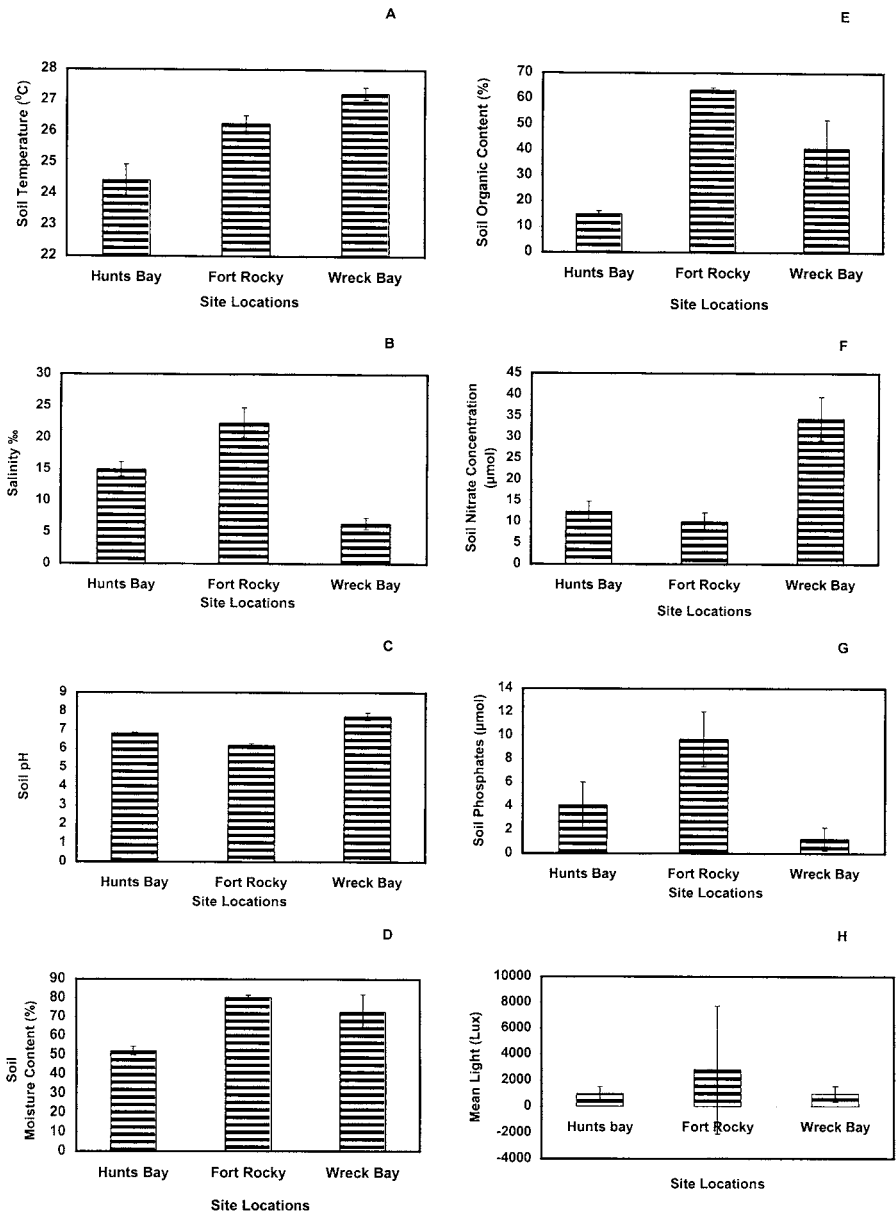
Figure 3. Edaphic features measured for each forest.

water holding capacity. Hunts Bay was lowest because the soil there was quite coarse and there were very few *R. mangle* trees, hence a loss of the intertwining roots of this species.

Soil organic content showed similar trends to soil moisture content for Hunts Bay, Fort Rocky Lagoon and Wreck Bay (Fig. 3E). This is because water-holding capacity is conferred onto the soil by an increase in soil organic content. An increase in soil organic content leads to the creation of more small soil particles, which then increases the capacity of the soil to hold water. Soil organic content values were highest for Fort Rocky

Table 1. Results of ANOVA tests for significance between sites using physicochemical parameters/variables and floristics. Ranking was done using Tukey HSD post hock test.

Independent variable	Dependent variable	P value	df	Ranking
Sites	Soil salinity	< 0.001	2,70	3-1-2
	Soil temperature	0.01	2,70	1-2-3
	Soil pH	< 0.001	2,23	2-1-3
	Soil moisture content	< 0.001	2,70	1-3-2
	Soil organic content	< 0.001	2,70	1-3-2
	Soil nitrates	< 0.001	2,70	2-1-3
	Soil phosphates	< 0.001	2,70	3-1-2
	Light variability	0.60	2,70	Not significant
	Diameter at breast height	0.19	2,70	Not significant
	Tree height	0.10	2,70	Not significant
	Percentage cover	< 0.001	2,70	3-2-1
	Productivity	< 0.001	2,70	1-2-3

Lagoon forest (63.5%), followed by Wreck Bay (40.79%) and then Hunts Bay with a value of 15.07%. Average soil organic content was significantly different between each site (Table 1). Soil organic content was expected to be highest for the sites with greater numbers of individuals of the species *R. mangle* (i.e., Wreck Bay and Fort Rocky Lagoon). This is because *R. mangle* species have much higher rates of leaf fall than other species. Hunts Bay had few individuals of the species *R. mangle* and had the lowest value for soil organic content. The leaves of *R. mangle* falling to the forest floor greatly increases surface organic matter content of the soil as does the matted root system of this same species (Tomlinson, 1994).

Wreck Bay had an average soil NO_3 content of 34.4 µM, Hunts Bay 12.41 µM, and Fort Rocky lagoon 10 µM (Fig. 3F). Average soil NO_3 at Wreck Bay was significantly higher than the other two sites (Table 1). The observed pattern was not what was expected. Hunts Bay, deemed the most eutrophic, was expected to have the highest value for soil NO_3 content and Wreck Bay was expected to have the least. The high values seen at Wreck Bay are probably due to the presence of the fresh water stream, which transports these nutrients from land and this serves as a nutrient rich land runoff source. This high NO_3 value reflects the complex vegetation structure. This result is similar to findings made by Pool et al. (1977) in that areas which receive large amounts of fresh water and nutrients will have taller trees and overall a complex, well developed forest.

Soil PO_4 content at Hunts Bay had an average value of 4.1 µM, Fort Rocky 9.69 µM, and Wreck Bay1.24 µM (Fig. 3G). There were significant differences in average soil PO_4 content among sites. Again, the pattern observed was not what was expected, as Hunts Bay was expected to have the highest concentration of soil PO_4. Instead, the Fort Rocky Lagoon forest had the highest value for soil PO_4 content, although the Hunts Bay mean value was higher than that for Wreck Bay. These PO_4 values must be interpreted with care since low oxygen concentrations in mangrove soils can lead to phosphate release particularly at pH less than 7 (Patrick and Mahapatra, 1968).

Light available to the forest floor was not significantly different among forests, although the average at Fort Rocky was more than twice that at the other stations (Fig. 3H). There was very high within forest variation and this may have reduced the significance of the between forest variation.
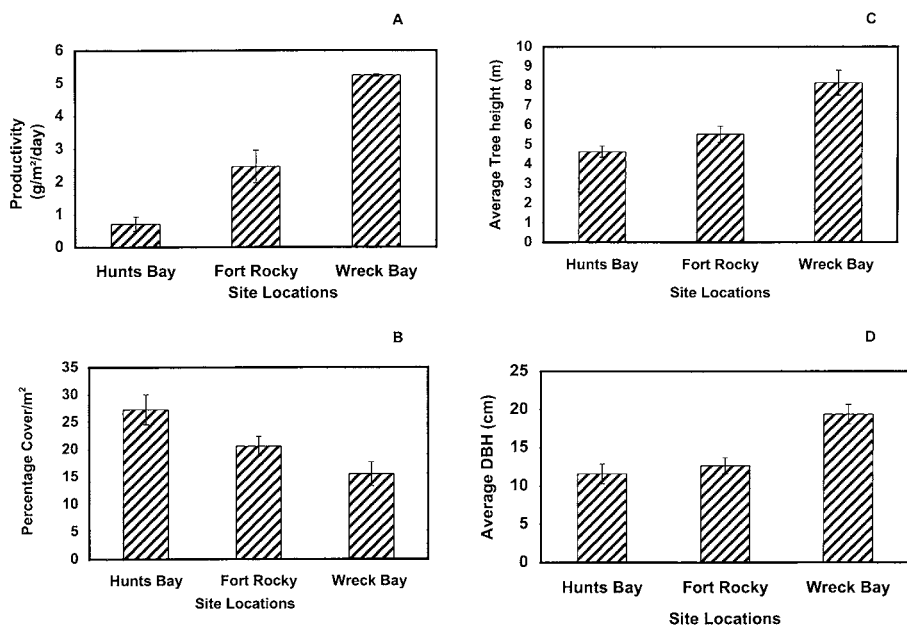
Figure 4. Vegetation characteristics/ floristics (A- Average tree height, B- Average D.B.H., C- Average productivity and D- Percentage cover) for the three forests sampled.

FOREST STRUCTURE

Leaf Litter Production.—Average leaf litter production was highest for the Wreck Bay forest, which had a value of 5.24 g $m^{-2}d^{-1}$. The Fort Rocky Lagoon site had an average value of 2.46 g $m^{-2}d^{-1}$, and Hunts Bay had the lowest value for average productivity with a value of 0.71 g $m^{-2}d^{-1}$ (Fig. 4A). There was a significant difference in productivity at all the sites (Table 1): productivity decreased with increasing pollution/eutrophication.

Litter production in these mangrove forests of different structures (Hunts Bay- riverine mangrove forest, Fort Rocky Lagoon- fringe mangrove forest and Wreck Bay- fringed mangrove forest) is similar to that produced by forests of similar structure within the tropics (Snedaker, 1982).

The maximum leaf litter production at the Wreck Bay site may be explained by the presence of fresh water and high nitrate to phosphate ratios, which optimizes growth conditions so that more leaves are produced, which would imply a higher rate of leaf fall. The trend seen in the other sites (i.e., a decrease from Fort Rocky Lagoon to Hunts Bay) is likely due to increasing eutrophic conditions, especially phosphate availability, but nitrate limitation at each site. This trend could also be due to a reduction in the density of the species *R. mangle*, which produces leaf litter in copious amounts.

There is greater than a 95% probability that 77% of the variation in leaf litter production in the different forests is due to the location of the forest, variations in soil temperature, variations in soil NO_3 content and light availability to the forest floor (Table 2). All these parameters exhibit a strong positive correlation with litter production with the exception of soil temperature, which shows a strong negative correlation.

Percentage Cover.—Average percentage cover for the Fort Rocky Lagoon site was 20.57% m^{-2}. Percent cover increased with increasing eutrophication/disturbance: Wreck

Table 2. Multiple regression results showing the significant physicochemical and edaphic parameters/variables (independent variables) deemed to be determinants for the variation in vegetational parameters between sites.

Dependent variable	Adjusted R^2	Independent variables	P value
Productivity	0.77	Sites	< 0.001
		Soil temperature	0.034
		Soil NO_3 content	0.008
		Light available to the forest floor	0.020
Percentage cover	0.64	Sites	< 0.001
		Soil salinity	0.043
		Soil moisture content	0.002
		Light available to the forest floor	< 0.001

Bay had a value of 15.5% m^{-2} while Hunts Bay had the highest value of 27.29% m^{-2} (Fig. 4B).

There were significant differences in average percentage cover between sites (Table 1). Percentage cover is a function of forest structure and complexity. Hunts Bay had the highest value for average percentage cover because it is highly disturbed and composed of a large number of small trees, creating multiple layers in the canopy. Fort Rocky Lagoon was next in disturbance level, followed by Wreck Bay.

There is greater than a 95% probability that 64% of the variation in percentage cover in the different forests is due to the location of the forests, variations in soil salinity, soil moisture content and light availability to the forest floor (Table 2).

Tree Height.—The trees at the Wreck Bay were the tallest, with an average height of 8.15 m, while those at the Fort Rocky Lagoon had an average height of 5.53 m, and those at Hunts Bay had the lowest height of 4.63 m (Fig. 4C). Tree height is usually greatest in areas receiving large amounts of fresh water and nutrients (Smith, III, 1992). The forest at Wreck Bay had the lowest soil salinity and highest soil nitrates; yielding the tallest trees and with greatest productivity. Hunts Bay had low salinity in the lagoon but not necessarily in the forest. Nitrates were also low in the forest soil and this coupled with large amounts of organic and other pollutants being introduced (evidenced by very low Redox potential) in the runoff from Kingston, which had negative effects on the forest. Generally, Hunts Bay had stunted trees with multiple layers from frequent and indiscriminate cutting, and low productivity due to the high disturbance and eutrophication/pollution levels. The trend in tree height, although consistent with that predicted, was not significantly different among sites (Table 1).

According to Snedaker (RSMAS, Univ. Miami, pers. comm.) the maximum height for the three species of mangrove trees depends wholly on local growing conditions particularly with regard to limiting factors such as physical composition of the substrate (e.g., rock versus silt or clay), fertility, water availability and other such factors. Within the Caribbean region, hurricanes also play a major role in altering tree height (McCoy et al., 1996). Along the Pacific coasts of Costa Rica and Panama, areas outside the Hurricane belt support *R. mangle* trees, which can reach heights in excess of 30 m (Pool et al., 1977). Furthermore, the species under study (i.e., *L. racemosa, A. germinans* and *R. mangle*) can exist in a dwarf form, which is defined by a decurrent architecture. In the dwarf form, the species seldom reach a height above 1.2–1.5 m, which can be assumed to be the
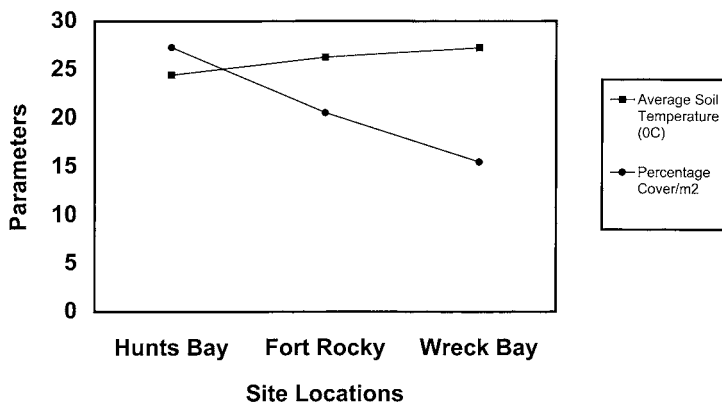
Figure 5. Comparison of average soil temperature and average percentage cover for the three mangrove forests sampled.

minimum height for a reproductively mature tree. This height limit is typical throughout the world where dwarf mangroves occur.

The occurrence of the tallest trees at Wreck Bay may be explained by the small, but constant inputs of fresh water, optimal nitrate to phosphate ratios and the lack of disturbance in the area. The decrease in height from Fort Rocky Lagoon to Hunts Bay is more likely explained by the high phosphate dominated eutrophication and anthropogenic disturbance at Hunts Bay. This suggests that the positive contribution of riverine inputs to the lagoon is being negated by disturbance and pollution, and since the more eutrophic areas tend to be those with significant riverine inputs, tree height is probably not a reliable indicator of stress in mangrove forests.

Diameter at Breast Height (DBH).—Maximum DBH was recorded at the Wreck Bay site and was 19.36 cm. This was followed by DBH at the Fort Rocky lagoon site (12.62 cm) while the Hunts Bay site had a value of 11.58 cm (Fig. 4D). However, although there was no significant difference among sites (Table 1), average DBH showed a similar trend to average tree height and that could be accounted for in the same manner as was done for average tree height. Based on findings by Smith III (1992), an increase in basal area (or DBH) is consistent with forests, which are influenced by large amounts of fresh water.

According to Snedaker (RSMAS, Univ. Miami, pers. comm.), *R. mangle* can reach DBH's in excess of 1 m under the most ideal growing conditions. Hunts Bay had low values for DBH since it is very disturbed by removal of trees for charcoal burning and has a high density of small diameter trees.

EVALUATION OF THE LEVEL OF EUTROPHICATION/ENVIRONMENTAL STRESS AT EACH SITE

Hunts Bay.—Of the three forests studied, the Hunts Bay mangrove forest has undergone the highest levels of human disturbance mainly through the harvesting of mature trees for the purpose of charcoal burning. This forest is also impacted by human influence via encroachment on the forest for residential as well as industrial purposes. Industrial and domestic waste enters Hunts Bay via five major gullies, which originate and run through the city of Kingston.

Terrigenous sources, which drain into the lagoon adjacent to the forest, are a major source of organic and inorganic pollution. These sources supply pollutants in the form of

solid wastes, sewage, dead plants and animals as well as vast amounts of sediments. These contributing factors result in the highly eutrophic status and subsequently high levels of stress experienced by this mangrove forest. The level of stress is also mirrored in the vegetation, for example in the form of species composition and species density as well as other vegetation characteristics of the forest, such as DBH, percentage cover of the canopy and height of lowest living limb. The trends in these parameters are obviously due to high levels of stress. Some environmental factors measured for the lagoon (for example DO levels, Redox potential and salinity) are also indicators of the status of the Hunts Bay mangroves. The bay is characterized as having eutrophic nutrient levels, but low nitrate to phosphate ratios and low salinity.

Fort Rocky Lagoon.—The Fort Rocky Lagoon mangrove forest ranks next after Hunts Bay with respect to anthropogenic disturbance and eutrophication. It is used by a few people for relatively nondestructive purposes, which is obvious from the footpaths observed through the vegetation. Major damage in this regard is reflected in the trampling of seedlings and the damaging of prop roots.

The Port Royal mangrove forest is greatly influenced by the polluted waters of the Kingston Harbour in which this forest is situated. The level of stress, due to eutrophication, experienced at this site is second highest of the three forests studied. This site is characterized as having high salinity, moderate nitrate levels, but high phosphate availability due to the low pH and dissolved oxygen concentrations.

Wreck Bay.—The Wreck Bay mangrove forest is the least influenced by anthropogenic disturbances of the three sites. There is a footpath through the vegetation as well as a quantifiable amount of solid wastes at the most landward edge of the forest. However, this mangrove forest is relatively pristine and is not influenced by pollution of an industrial or domestic nature due to its location, far from areas of high population density. This directly implies a reduction in pollution by human and other terrigenous sources. Wreck Bay is also deemed to be pristine due to its distance from the negative influences of Kingston Harbour.

The vegetation comprising this forest is very successful in terms of growth and development and exhibits the characteristics and complexity of a mangrove forest existing under the most ideal conditions for mangrove growth. It is owing to this fact that the Wreck Bay mangrove forest can be described as the site characterized by ideal conditions for the successful development of mangrove forests: low salinity and moderate to high nutrient levels in near optimal ratios.

It can be concluded that the vegetation type and floristics of the three forests are different and that differences between forests are driven by various environmental/edaphic factors. The environmental factors most responsible for variations in forest structure are soil and lagoon salinity, soil and lagoon NO_3 absolute concentration and ratio with PO_4 concentration, soil moisture, and soil temperature. From this study, the most useful vegetation parameters for differentiating between mangrove forests are litter production and percentage cover. Diameter at breast height and tree height can be positively or negatively affected by different aspects of anthropogenic stress and so can be confounding.

It is difficult to interpret with confidence the relative importance of each factor to productivity, percentage cover and growth owing to the complexity of interactions between all factors and the influence of anthropogenic stress. However, the quantification of environmental factors of importance and identifying the most demonstrable forest attribute to ob-

serve and record environmental influences provides a significant tool towards conceptualizing and interpreting functional relationships within mangrove systems.

ACKNOWLEDGEMENTS

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Fisheries Module

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ABSTRACT

An interdisciplinary team has been established to investigate the eco-hydrology, water quality, mangrove ecology, and fish communities of La Manzanilla, Mexico. The primary goal of the fisheries team is to assess the spatial and temporal patterns in fish communities of La Manzanilla, Mexico in order to better understand ecosystem structure and function and to assess the effects of anthropogenic impacts on the mangrove ecosystem. In January 2007, the fisheries team sampled four aquatic habitats (mangrove, bay, reef, and upland stream) to generate species lists and determine species diversity and relative abundance. Sampling methods included the use of beach seines, cast nets, minnow traps, long lines, and local knowledge interviews. The marine fish community is highly diverse, comprising at least twenty species, while the mangrove and inland fish communities appear less diverse, composed of a small assemblage of mollies, sleepers, mullet, and snook. In total, eight species were found in the mangrove and four species were found in the freshwater system. We recommend the use of beach seining and minnow traps to sample mangrove fish species. We also recommend the use of long-lining and minnow traps to determine their potential use in this study. Reef surveys should be conducted at least twice times per year. We recommend conducting three transect line surveys and one RDT survey to monitor changes in fish abundance, species assemblages, bottom cover, and overall reef health over time. Lastly we recommend sampling La Vena mangrove in order to gain insight into the species composition and abundance of fish in a dramatically different mangrove ecosystem.

BACKGROUND AND LITERATURE REVIEW

General Overview

Mangroves are among the most productive ecosystems in the world (Alongi 2002, Eong 1993, Kathiresan 2001). Because of their high productivity, local communities traditionally use mangroves for food, timber, fuel, and medicine (Alongi 2002). Ecologically, mangroves have been shown to export dissolved and particulate materials into the coastal zone; these materials are thought to stimulate coastal productivity and increase fishery yields (Sheridan & Hays 2003). In addition, mangrove ecosystems provide food, shelter, and refuge for fishes. As such, mangroves are believed to serve as important nursery habitats for coastal and reef fishes (Alongi 2002, Barbier 2000, Laegdgaard & Johnson 2001, Sheridan & Hays 2003).

Over the past fifty years, approximately one-third of the world's mangroves have been lost. Reasons for decline include urban encroachment, wood cutting/harvesting, agriculture, pond aquaculture, road building, and modification of natural waterways for bridges and levees (Alongi 2002). In Mexico, about 70,000 ha of mangroves have been lost between 1993 and 2000 (Holguin etal. 2006). Because mangroves serve as an important habitat for many birds, fishes, and reptiles, destruction of mangroves harms local communities that underestimate its value as an economic resource, such as using it for ecotourism or improving coastal fisheries (Ellison and Farnsworth 1996).
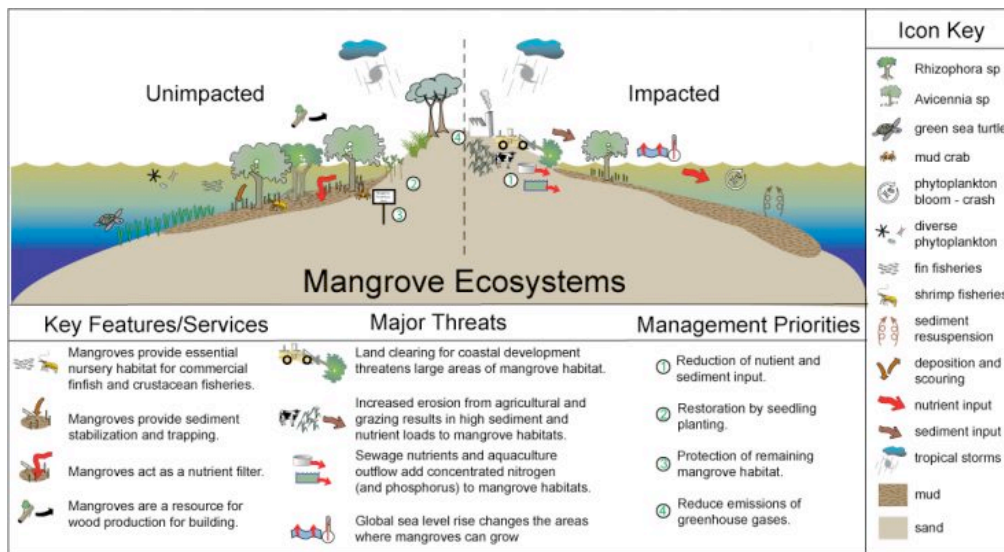

Figure 1. A conceptual diagram of a mangrove ecosystem.

The La Manzanilla mangrove, located in La Manzanilla on the Pacific Coast of Mexico, is no exception. It serves as an important breeding site for a number of migratory birds, in addition to being a unique sanctuary for the second largest population of American crocodiles on the Pacific Coast. However, population growth and urbanization threaten this fragile ecosystem. Homes are being built along the beach between the mangrove and bay, bisecting a corridor commonly used by crocodiles. In addition, roads built through the mangrove have fragmented the habitat. Another threat is a nearby vacation resort that pumps large amounts of groundwater in order to irrigate its golf course. Lastly, a sewage overflow station is located directly at the mangrove's edge. A sewage overflow could cause a dramatic shift in water quality and

productivity. The combination of these factors continually threatens the function and dynamics of this unique ecosystem.

Interestingly, the La Manzanilla mangrove does not function as a typical mangrove system. Fed mainly by freshwater and blocked by a sandbar, the mangrove is rarely connected to the marine environment, with the exception of possible groundwater influences. Therefore, the system likely functions as a sink for sediments and nutrients filtered from the uplands. Because of these unique characteristics, the fish communities of the La Manzanilla mangrove are likely unusual compared to other mangrove systems. Mangroves are traditionally thought to serve as nurseries for juvenile fishes from the coast; however, the La Manzanilla mangrove likely supports juveniles and adults of species with freshwater and marine origins. As such, the fishes could serve as an important food source for crocodiles and birds.

Sampling Aquatic Ecosystems

A variety of methods can be used to sample aquatic ecosystems. A beach seine is one method commonly used in shallow water beach areas of lakes, lagoons, and oceans (Edgar and Shaw 1995; Simier 2004). A seine is simply a large cloth net with a weighted line, which is dragged along the bottom substrate, and a float line that keeps the net vertical in the water column. The seine is strung out in the water parallel to the shore and then the two ends are dragged towards the beach and pulled together, enclosing all fishes within the circle. A gill net, which often consists of numerous pieces of plastic mesh with varying sizes, is another commonly used sampling method. Gill nets can be set at varying depths within the water column and the varying mesh sizes allow for selection of different size classes (Vetemaa et al. 2006). The nets are usually left out over night and collected the next morning. In wide open water channels a circular cast net can also be utilized by a skilled individual.

Minnow traps are used for sampling small fish and invertebrates in aquatic ecosystems. Minnow traps can be made from a range of materials including metal mesh and old plastic soda bottles (Jackson and Harvey 1997). They are designed so that fish swim into the funnel-shaped ends and are not able to find their way out. This method is most effective for small fish when numerous traps are left out overnight.

Figure 2. A minnow trap.

Electroshocking is yet another method, but instead of entangling or trapping the fish, an electroshocker temporally stuns them for ease of collection. This method is useful because the all size classes can be sampled and quantified. However, electroshocking can only be used in relatively shallow freshwater; saline water is too conductive, and fishes will not be properly stunned.

While the methods listed above are the most commonly used in freshwater habitats, not all would be effective when employed in thickly vegetated, saline, crocodile infested habitats such as the La Manzanilla mangrove. Several sampling methods have been developed to effectively sample fish in heavily vegetated areas. A square shaped drop net, which is deployed from above, is one method that has been utilized in heavily vegetated mangroves in the southern everglades (Lorenz et al. 1997, Green et al. 2006). While this method is effective, it requires the building of walkways in order to reach and deploy the nets, as well as the use of poison to kill the entrapped fish for easy removal. Therefore, this method may not be desirable for our purposes. Another method used to sample in heavy vegetation is the throw trap. Throw traps are nets sewn into a rectangular box. They are thrown into the water and quickly pressed into the substrate (Jordan and Texler 1997, Green et al. 2006). This method may be more plausible in the La Manzanilla mangrove because we would not need to construct to walkways and the nets are cleared with dip nets and bar seines instead of poison. However, the presence of mangrove root systems underwater may make it difficult to press such a trap into the substrate.

Sampling Coral Reefs

In order to evaluate the condition of a reef ecosystem, managers typically monitor bottom cover, species composition, and the abundance and size distribution of fish assemblages. A change in any one of these factors often indicates an underlying change within the reef (Reese 1977; Hughes 1996; Schmitt et al. 2002). In the past, poisoning was the primary method for surveying fish populations within a reef. While poisoning yielded extremely accurate and comprehensive results, the irreversible damage to fish populations and other reef organisms far out weighed the benefits (Randall 1963; Ackerman and Bellwood 2002).

Several less destructive methods, such as SCUBA divers, underwater photography, and sonar, have recently been employed to monitor reef conditions. Visual surveys and censuses using SCUBA divers and snorkelers have quickly become the preferred method because they are easily repeatable, have minimal impacts on the reef, and with short, intense training even volunteers can produce scientifically valid surveys (Hatcher et al. 1989; Schmitt et al. 2002; Foster-Smith and Evans 2002; Pattengill-Semmens and Semmens 2003). However, visual surveys are prone to underestimating fish populations due to overlooking species, such as those which are cryptic or nocturnal (Edgar et al. 2004; Willis 2001). One type of visual survey uses belt transect lines to monitor reef conditions. The transect lines are often made of plastic rope or chain, usually 20m-50m long, which are laid out on the bottom of the reef. Divers or snorkelers then swim along the transect, noting bottom cover and fish species abundance occurring within a 1m-10m wide belt along the transect line. The width of the transect belt will vary depending on the target species being surveyed; smaller widths are used to count small or cryptic species, while larger transects are more appropriate for the larger, easier to count species (AIMS 1996; Cheal 1997). In addition to fish abundance, divers can be trained to accurately estimate fish length while conducting the survey (Bell 1985; Schmitt et al. 2002). Fish length and abundance

can then be converted into a number representing total fish biomass which can be a good indicator of changes occurring within the reef, such as overfishing.

Another type of visual survey is a roving diver transect (RDT). Using this method, a divers or snorkelers swim around an entire reef (size dependent of course) for an average time of 45-60 minutes. During this time, the diver takes note of coral cover, damage from boats/anchors, and coral bleaching. In addition, every fish the divers observe during the time interval is counted. This technique is useful because it gives managers a good indication of what fishes are present in the given area in a shorter amount of time. RDT also increases the chance of seeing more of the uncommon fishes that may be overlooked by surveying only small areas, as with transect lines (Schmitt et al. 2002). This type of survey can also be done by towing a diver behind a motorized boat, called a manta tow; however, the noise of the motor may scare fish away from the area, resulting in inaccurate counts.

With technological advances in the electronics field, video cameras can now function dependably underwater. This is a relatively non-intrusive way to peek into the underwater world. Video cameras can be used gather a variety of information on factors such as fish populations, bottom cover, and coral health. Cameras can be carried by a diver during transect or RDT surveys, or be mounted and left, either baited or unbaited, to record passing fish (Watson et al. 2005). Studies testing whether video recording techniques are more accurate than traditional slate recording methods have shown that slate recordings are typically more accurate (Tessier et al. 2005). On the other hand, mounted and baited cameras allowed for more accurate abundance estimates of cryptic species (Pfister and Goulet 1999).

Objectives

The primary objective of January 2007 sampling was to gather baseline information on species composition and abundance and suggest topics for further study. The long-term goal of the fisheries component is to establish a repeatable monitoring project that can measure the effects of human impacts on the systems associated with the La Manzanilla mangrove. In doing so, we hope to provide the local community with a better understanding of the importance of their mangroves and fish communities, and the organisms that depend on them.

Study Site

The La Manzanilla mangrove, located in La Manzanilla, Mexico, encompasses an area approximately 6 km². The vegetation is largely dominated by the White mangrove (*Laguncularia racemosa*). The mangroves are bordered by the town of La Manzanilla to the south, the beach of Tenacatica Bay to the west, and farmland and mountains to the north and east (Appendix 2). The main channel of the mangrove is largely unattached to Tanacatica Bay, although there may some groundwater influence. As a result, La Manzanilla mangrove is less saline than typical mangrove systems because most water inputs come from small upland streams and rainfall. The ecosystem hosts a wide variety of migratory and resident birds, small mammals, reptiles, fishes, and one of the largest populations of American crocodiles on the Pacific Coast of Mexico. Tenacatica Bay and the reef adjacent to the bay are of particular interest because of the rapid development of houses and resorts along the coastline. Monitoring

these habitats is important because the literature suggests there are strong linkages between mangroves, upland streams, reefs, and coastal marine ecosystems (Gillanders, et al. 2003).

METHODS

Mangrove

The objectives of the mangrove sampling are to 1) compare fish species composition and abundance between the upper, middle, and lower mangrove, 2) compare fish species composition and abundance in the lower versus upper water column of the main channel, and 3) compare fish species composition and abundance between the main channel and within the mangrove trees. To fully understand the spatial distribution of fish communities throughout the mangrove, we sampled longitudinal, horizontal, and vertical aspects of the mangrove habitat. To compare fishes longitudinally (coast to upland), sites were chosen to include the upper, middle, and lower ends of the mangrove. Three methods were used at each site; the "stacker", "spreader", and long-line (see instructional Powerpoint for a graphical description of the methods).

To compare fishes vertically in the water column we constructed a stacked minnow trap apparatus. To accomplish this, three minnow traps, baited with dog food, were vertically aligned from top to bottom of the water column and centered in the main channel of the mangrove. A small-link chain, 4 meters in length, was used to attach the minnow traps. One trap was attached to the chain at the bottom, one in the middle, and one at the top. Traps were affixed to the chain using common bailing wire and were equally spaced along the chain. Distance between the traps depended on depth of the water column at each location. A twenty pound weight was used to anchor the chain while empty plastic bottles were attached to the top link, which served as buoys to hold the apparatus vertical.

A waypoint was taken at each sampling site using a handheld GPS in NAD83 coordinates. The minnow traps were set during the afternoon and gathered the next morning. Fish were placed into three separate bottles numbered with the depth they were collected (i.e. top trap = #1, middle trap = #2, & bottom trap = #3). In the lab, individuals were identified to the species level and measurements of lengths (mm) and weights (g) were recorded. All data were recorded on a datasheet (Appendix 3) and entered into the computer as soon as possible.

Subsequently, a long-line was set adjacent to the vertical minnow traps. Using a 4 meter small-link chain, a rope was tied to one end and a 10 lb. anchor to the other. One hook was placed every eighth chain link, alternating small and large hooks (19 total). Hooks were baited with salami one time and Pacific mollies the other. The roped-end of the long-line was affixed to the nearest large branch. The long-line was extended out perpendicular to the main channel of the mangrove, setting the line in a sloped position from the water surface to the bottom of the channel. GPS coordinates from the stacked minnow traps were used for location identification. During collection, hook size was noted and fish were placed into separate bottles for each meter of chain link (i.e. 4 separate bottles; top meter is "meter 1" and bottom meter is "meter 4"). All data was recorded on datasheets (Appendix 3) and entered into a computer as soon as possible.

Next, minnow traps were set to gain knowledge of species composition horizontally across the mangrove (from bank to main channel) within the trees. Four minnow traps, baited with dog food, were placed perpendicular to main channel beginning at the waters edge extending inward to the fringe of the main channel at equally spaced distances. Traps were tied to a branch using bailing wire; the location of each trap was marked with flagging tape for ease

of relocating the traps. Traps were numbered 1-4, with trap #1 being closest to the dry zone and trap #4 being set on the fringe of the main channel. Again, traps were set in the afternoon and collected the following morning. Fish were placed into separated bottles and labeled with the trap number they were collected from. Again, all data was recorded on datasheets (Appendix 3) and entered into a computer.

Due to lack of prior knowledge of fish communities in the mangrove, a 100 foot beach seine was set in the lagoon at the mouth of the mangrove to collect specimens for identification. A total 7 species were identified from the beach seine. 200 individuals from 2 of the 7 species collected, the Pacific molly (*Poecilia butleri*) and the snouted mullet (*Chaenomugil proboscideus*), were measured for length (mm) and weight (g). In addition, random cast-netting was used throughout the mangrove to collect a representative sample of species within the mangrove. A total of two species were collected using this method, Pacific fat sleeper (*Dormitator latifrons*) and Pacific molly (*Poecilia butleri*).

Bay

In order to obtain fish abundance and diversity outside of mangrove, we sampled Tanacatica Bay using a 100 foot beach seine. We used a standard "u" pattern method. This method requires one person to walk one end of the seine out into the surf perpendicular to the beach. A second person follows the same line with the other end of the seine. Once the lead individual is out a distance the length of the seine from the beach, that person makes a 90° turn and walks the seine parallel with the beach the distance of the seine again. The second individual stops where the first made the turn. Once the seine is parallel with the beach, both individuals pull it back into the shore, being careful to drag the lead line along the bottom to prevent fishes from escaping. Because of our lack of knowledge of coastal marine fishes of Mexico, we separated the catch into groups of similar appearance. Once individuals were confidently identified to the species level, we measured the lengths (mm) of 50 individuals from each species for a representative sample of the catch. After 50 individuals were measured, the remaining fish were counted for abundance.

Reef

In order to gather data on species composition and general reef health, we conducted a transect survey of the reef approximately 1 mile south of La Manzanilla. A 75ft plastic chain, divided into 3 ft long segments with colored plastic zip-ties, was laid down on the reef floor and carefully anchored, as not to harm the reef. A snorkel surveyor swam along the line and classified bottom cover type (rock, gravel, sand, coral or algae) for every segment. A recorder in a boat listed the substrate type the snorkeler called out.

Once substrate classification was completed, four surveyors, two on each side of the transect line, slowly swam the transect line and counted individuals of all fish species occurring within 3 meters of the transect line. The number of species observed was called out to the recorder in the boat. All data was recorded on datasheets (Appendix 4) and entered into a computer.

Freshwater

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Our sampling of the upland freshwater stream was simply an attempt to assess species presence. A small 20 ft. beach seine was pulled downstream in several pools. At two deep pools, where it was too deep to use a seine, a cast-net was thrown several times. Data was recorded on datasheets (Appendix 3) and entered into a computer.
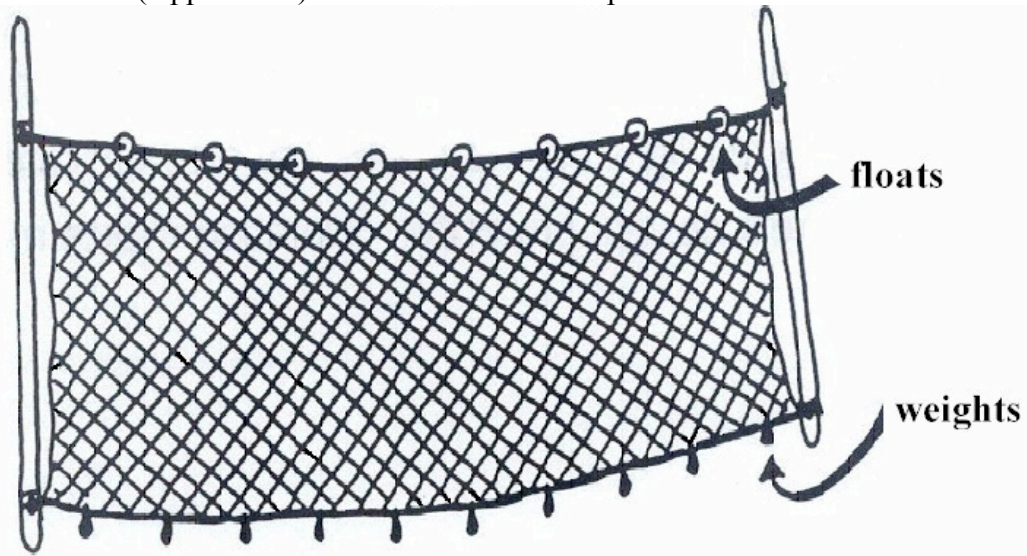

Figure 3. A large seine net was used to sample the bay and mangrove. A smaller seine, like the net shown here, was used to sample to pools and riffles of the upland stream.

Species Identification

For the mangrove and freshwater species, we used Miller's "Freshwater Fishes of Mexico" (2005). Fishes collected from the bay and reef were identified using Allen & Robertson's "Fishes of the Tropical Eastern Pacific" (1994) and Humann & Deloach's "Reef Fish Identification: Baja to Panama" (2004).
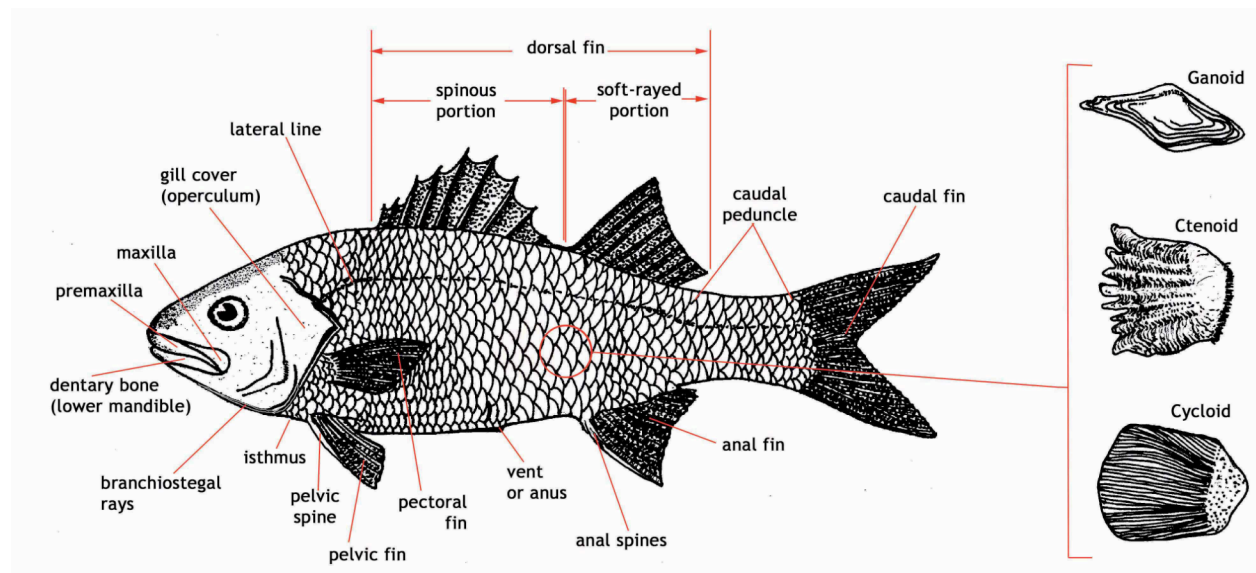

Figure 4. A labeled diagram of a generic fish.

We preserved five individuals of each species in 10% formaldehyde for future references. Each bottle was labeled with the location of collection, method of collection, date, and species.

INSTRUMENTATION

<u>**Materials**</u>
Sampling:

Small 20ft. seine
2 cast nets (small & large)
1 gill net
1 100ft beach seine
12 minnow traps total
Handheld GPS unit
Stacker
- 4m chain
- Bailing wire
- 4 minnow traps
- 20 lb. weight
- Buoys
- Dog food

Long line
- 4m chain
- 19 hooks, sizes 12 and 8
- Bait (chunks of fish)
- Rope
- 10 lb. weight
- 6 lb. fishing line

Reef Transect
- 75ft. plastic chain
- 5lb. weights (2)
- Zip ties
- Underwater slates
- Snorkels, masks, fins

Lab/fish processing:

Microscope
Fish board
Scale
1 L bottles
200 ml jars
10% Formaldehyde
4 pairs of forceps

RESULTS

Species in the Mangrove

Eight species of fish were found in La Manzanilla mangrove (Table 3). Based on initial sampling, La Manzanilla mangrove is home to far fewer species than other Mexican mangroves which reportedly harbor upwards of 75 species (Flores-Verdugo et al. 1990). Mangroves typically support a high diversity of fish in part because of the link between mangroves and marine environments including tidal channels, bays, reefs, and coastal lagoons. We hypothesize that due to 1) the sporadic levels of connectivity with the ocean and 2) poor water quality, fish species within La Manzanilla mangrove are hardy fish with broad environmental tolerances able to survive their entire lives within this mangrove ecosystem. In this paper we define "hardy" fish as those species tolerant to varying water temperatures, pH levels, and water quality. Because pH levels are between 6.2 and 8.1 and temperatures can reach 28.2 °C, we presume the fish species in the La Manzanilla mangrove are likely well adapted to conditions such as high salinity and low dissolved oxygen; however, there was no information in the literature to support this claim.

Three of the eight fish species found in the mangrove are mainly described as marine species: the Pacific sleeper, snouted mullet, and the graceful herring (Faunce and Serafy 2006). The rest of the fish inhabit freshwater to brackish and estuarine systems. All the fishes collected from the mangrove and freshwater systems commonly utilize these habitats for nurseries and as juveniles, with the exception of the Pacific molly which spend all of their life in freshwater or estuaries. Two fish in the La Manzanilla mangrove are carnivorous, the Pacific sleeper and the eleotridae species. These species primarily prey upon insects and terrestrial source inputs. It is unclear whether these species prey on other fish species within the system. The remaining species collected are herbivores, feeding primarily on algae and detritus.

Table 1: Species found in La Manzanilla Mangrove January 2007. Minnow traps, cast-netting, and beach seine were utilized to capture the fish. Note that * indicates unknown.

Common Name	Scientific Name	Distribution	Resilience	Temp. Tolerance	Diet
Pacific Molly	Poecilla butleri	Central America; Mexico to Panama	High	23-27C	algae and other vegetation
Pacific Fat Sleeper	Dormitator latifrons	Gulf of California to Northern Peru	High	25-33C	detritus
Blackfin Snook	Centropomus medius	Central Gulf of California to Colombia	High	24-?C	*
Pacific Sleeper	Gobiomorus maculates	Central and South America	Medium	24-33C	Crustaceans and fish
Graceful Herring	Lile gracilis	East Central Pacific to South America	High	*	*
Snouted Mullet	Chaenomugil probosicdeus	Revillagigedo Islands and Mexico to Panama	Medium	*	algae
*	Poeciliopis	Central Mexico to South America	High	23-28C	algae, diatoms detritus
*	Eleotridae	Tropics		*	Carnivorous

Pacific mollies have a broad geographical range in Mexico, from the Pacific to the Atlantic, utilizing both freshwater and estuarine systems. They are a non-migratory freshwater species that have a pH tolerance range of 7.0 to 7.8. Maximum total length is 7.0 cm for males and 8.0 cm for females. They occur in the water column instead of the benthic region.

Pacific Molly

The Pacific fat sleepers have a distribution from the Gulf of California to Tumbes in Northern Peru (Massay and Mosquera 1992). Similar to the Pacific molly, they are a pelagic, or water column, species found at a maximum depth of 1 meter. They have a higher pH range than the Pacific molly ranging from 7.5 to 9.5 and a temperature tolerance 25-33°C. Their maximum total length is 650mm (IGFA).

Pacific fat sleeper

The blackfin snook have a distribution from Baja California and Gulf of California, Mexico, southward to Buenaventura Colombia (Bussing 1995). They have a threshold tolerance of 15-24 °C for temperature, which coincides with the northern and southern limits of their distribution, respectively (Rivas 1986). Snook are diadromous, moving from freshwater to the ocean to spawn. They are estuarine-dependent and euryhaline, meaning they have a high tolerance for salinity. Movement is seasonal and, when occurring in the sea, they stay in shallow water close to shore, not straying far from estuaries (Rivas, 1986). The largest known blackfin snook is 558mm total length.


Blackfin snook

The Pacific sleeper occurs from Central America to South America (Bussing W.A. 1998). The Pacific sleeper is a freshwater and marine species. It is believed that reproduction occurs in marine or brackish environments due to the number of juveniles found in these habitats. They

have a medium resilience, with a temperature tolerance of 24-33 °C. They have a maximum total length of 270mm (Bussing W.A. 1998).

Pacific sleeper

The snouted mullet has a maximum total length of 220mm and are herbivorous, mainly feeding on algae (Harrison I. J. et al. 1995). They have a distribution encompassing Eastern Central Mexico ranging from Revillagigedo Islands in Mexico to Panama. They are a marine species, typically found inhabiting rocky littoral areas. However, the snouted mullet was the only species that we found in both the mangrove and bay.
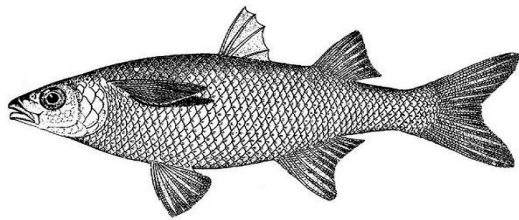
Snouted mullet

The graceful herring is another marine species with a maximum length of 8.0 cm. They are found in the pelagic region and have a distribution from Eastern Central Pacific to Mexico (Whitehead and Rodriguez-Sanchez 1995). We were not able to classify the *Eleotridae* species found in the mangrove, but have collected information on the family as a whole. There are 35 genera and 150 species. The majority lives in brackish or fresh water. Only a few species are truly marine, but many have a marine larval stage and return inland as juveniles. Most species are carnivorous and can tolerate warm water temperatures. They are also common residences of mangroves (Allen and Robertson 1994).

Graceful herring

Table 2: Species list of fish found in freshwater January 2007. Fish were captured using seine net and cast-net. Note that * indicates unknown.

Common Name	Scientific Name	Distribution	Resilience	Temp. tolerance	Diet
Pacific Molly	Poecilla butleri	Central America; Mexico to Panama	High	23-27C	algae and other veg.
Mountain Mullet	Agonostomus monticola	North America to Colombia and Venezuela, including West Indies	High	21-31C	zoobenthos
*	Gobiidae	World Wide	*	*	omnivores, herbivores, and carnivores
*	Poeciliopsis	*	*	*	*

Species in the freshwater stream

Mountain mullet are one of the only species in the mulledia family that ascends far inland and spends all of their adult life in freshwater. They are catadromous and pelagic with a maximum total length of 360mm.

Gobiidae has 212 genera and 1,875 species making them the largest marine fish family. They are found worldwide in fresh, brackish, and saltwater. They are also found in mangrove swamps and certain species can climb out of water for extended periods to forage (Bohlke and Chaplin 1994). There are approximately 200 freshwater species of gobies. They are extremely successful in freshwater habitats and provide a vital link in many food chains.

Table 3: Species list of fish found in the bay by the outflow of La Manzanilla mangrove January 2007. Fish were caught using a beach seine. Note that * indicates unknown.

Common Name	Scientific Name	Distribution	Resilience	Habitat Preference	Diet
Yellow fin herring	Pliosteostoma lutipinnis	Eastern Central Pacific: Mexico to Ecuador	High	Coastal waters	*
Snouted Mullet	Chaenomugil proboscidues	Revillagigedo Islands and Mexico to Panama	Medium	Inhabits rocky littoral zones	algae
Flat iron herring	Harengula thrissina	Eastern Pacific: California to Peru	High	Coastal waters	Planktonic crustaceans
Blue Bobo	Polydactylus approximas	Eastern Pacific: Baja Cal. to Peru	High	Shallow water near coasts	Omnivores
*	Pomadasys spp.	Atlantic and Pacific Mexico	*	*	*

DISCUSSION

Mangroves commonly form integrated ecosystems of high productivity (Ronnback 1999); fish species richness in these systems has been reported as high as 200 species (Robertson and Blaber 1992). However, we found that the La Manzanilla mangrove contains few fish species, possibly because this mangrove is rarely connected to the bay. The system likely serves as a sink for nutrients and has a high residence time. In the dry season, temperature, pH, and primary productivity rates likely increase, while dissolved oxygen decreases. We believe certain water quality parameters, in addition to lack of connectivity to the bay, are the primary reasons we observed low fish diversity.

Data collected by the water quality team showed temperature ranges from 22.1 to 28.2°C and pH ranged from 6.2 to 8.1, which fell within the relative tolerance ranges for the Pacific molly and the Pacific fat sleeper. We were unable to determine tolerance ranges for the other

remaining species found in the mangrove from the scientific literature; however, given the harsh conditions observed in the La Manzanilla mangrove, we can infer they are highly tolerant as well.

Species Structure and abundance

The Pacific fat sleeper and the Pacific Molly were the only fish caught using the spreader method; no fish were caught at the upper site. Due to the varying number of species collected in the traps (0 to 106), we were unable to run an analysis of variance for differences within each location. We were, however, able to compare catches between sites. Using a one way analysis of variance, there was no significant difference (p= 0.387 and p= 0.062) in the total length of fish sampled between the middle and lower sites of the mangrove. Histograms of were created for each species for a visual representation of size distributions (Appendix 1). Using this type of analysis in the future will enable us to compare fish communities within the mangrove.

Based on the literature, it is apparent that the seven species found in our mangrove have not reached their maximum size; we question if they ever will. This could be attributed to sampling error or it could be that there are only small fish in the mangrove. We formulated three hypotheses to address why we only observed small fish in the mangrove: 1) lack of connectivity between the ocean and the mangrove, 2) lack of productivity and food for fishes in the mangrove, and 3) stunted growth due to stressful conditions. However, one interesting observation is that, despite the small size of the fish, overall biomass appeared relatively high. Still, we question whether the fishes in the La Manzanilla mangrove are sufficient enough in numbers or biomass to supplement the diet of crocodiles. If not, what are the crocodiles eating? Further research on the ecology of crocodiles and the fish communities is needed to answer this important question.

Hindell and Jenkins (2005) concluded that water depth was not a good indicator of fish abundance, species richness, or biomass, but did find that faunal interactions are most important in shaping patterns of zonation of fish within mangroves. We found similar results using the stacker method; we were unable to trap fish at varying depths. Single minnow traps set in transects placed in the upper water column achieved greater success. This indicates most fish utilize only the upper several centimeters of the water column. Therefore, water depth may be a good indicator of fish abundance in the La Manzanilla mangrove.

Previous research on mangroves has presented conflicting data of species assemblages in mangroves. Vance et al. (1996) found higher abundance of fish along the mangrove fringe than at sites inside the mangrove forest. However Ronnback et al. (1999) and Hindell and Jenkins (2005) found differences in fish assemblages between microhabitats within the mangrove forests and richer assemblages inside the forest than along the edge. Hindell and Jenkins' (2005) results indicated strong differences in fish assemblages between the edge and interior of the mangrove forest, suggesting differences between mangroves concerning species assemblages and abundance. In the La Manzanilla mangrove, we observed fish throughout the upper, middle and lower sections, inhabiting the open water and interior parts of the mangrove. Unfortunately, we were only able to capture fish in the open water using a cast-net, thrown randomly, and therefore we were unable to quantitatively compare the relative abundance of fish in this habitat between sites.

The methods we chose to sample the fishes in La Manzanilla were exploratory. Therefore, based on our results, we make the following recommendations to improve upon our methods:

Sampling Method Recommendations

Overview

We recommend the use of beach seining and minnow traps to sample mangrove fish species. We also recommend the use of long-lining and minnow traps to determine their potential use in this study. Reef surveys should be conducted at least twice times per year. We recommend conducting three transect line surveys and one RDT survey to monitor changes in fish abundance, species assemblages, bottom cover, and overall reef health over time. Lastly we recommend sampling La Vena mangrove in order to gain insight into the species composition and abundance of fish in a dramatically different mangrove ecosystem.

Mangrove

In addition to using the stacker method, we recommend performing eight "quality" cast-net throws in the same location where the stacker is placed. With the boat facing parallel to the main channel, two casts should be thrown from the front of the boat, two from the rear, and two from each side. Samples can be pooled into one bottle labeled "cast-net" with the corresponding site location and date. This should be done before the stacker is taken from the water to minimize disturbance of the fishes in the area. A short lesson on throwing the cast-net should be given prior to performing this method in the field. This way, we can insure "quality" throws are used to sample for maximum efficiency. In addition, we seemed to have greater catch success with the spreader method when the entrances to the minnow traps were placed just below the water surface (2-5 cm). Also, due to the lack of minnow traps available, we set the spreader only on one side of the main channel. We recommend buying four more traps to set on the opposite side of the main channel as well (i.e. the spreader method will include a total of 8 traps; 4 on one side of the main channel and 4 on the other side). Numbering of the traps should continue across the main channel; so, trap #5 will be on the fringe of the channel opposite from trap #4 and traps #6-8 will be equally spaced from the fringe, inland to the waters edge. We also had no success catching fish with the long-line. This might have been attributed to using salami as bait the first time it was performed; however, the second time we tried it we did use small whole fishes, but this was also unsuccessful. We believe this method is worth trying again, but we recommend using chunks of fish which might attract the piscivorous fishes.

In order to assess food web dynamics, we recommend taking the stomach contents of 7-10 individuals of each size class (small, medium, & large) for each species. In addition, muscle tissue should be sampled from all individuals for stable-isotope analysis. By coupling the isotopic signatures from the fish tissue with aquatic vegetation and invertebrates, we can assess the carbon source for each trophic level and the trophic structure of the mangrove food web.

Bay

Because diel variation of fish communities within bays can be great (Flores-Verdugo et al. 1990), one beach seine should be set in the morning, before the wind picks up, and another should be set in the evening hours. This does not have to be done on the same day. Morning and

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evening samples should be processed the same way, but kept separate from each other (i.e. label bottles and datasheet "beach seine, bay, morning", and "beach seine, bay, evening" with the date). In addition, we believe there were many species from the bay that were not caught using the beach seine method. Therefore, we recommend speaking with the local fishermen who were observed gill-netting at different locations in the bay every morning (Appendix 8). Ideally, we would like one or two volunteers to go out with at least one of these fishermen twice to record species, species lengths, and number of individuals for each species. If there are certain species the fishermen do not wish to keep, ask if we can bottle the samples and bring them back to be processed the same way the catch from the beach seine was (the bottles and datasheets should be labeled "gill net, bay" with the date).

Reef

We recommend conducting three transect line surveys and one RDT survey in the La Manzanilla reef. In doing so, our goals are to monitor changes in fish abundance, species assemblages, bottom cover, and overall reef health over time. We recommend that a 45 minute RDT survey be conducted upon arrival at the reef. This would give volunteers an opportunity to gain an idea of reef topography as well as to ask any questions about fish identification before line transects begin. Each surveyor, or pair of surveyors, should be given an underwater slate for recording species abundance. We have provided a list of 15 species to monitor in the reef (Table 2). These species should be listed on each surveyor's slate and a tally taken during the RDT survey.

Once the RDT survey is complete, transect line surveys can then be performed. To do so, lay a 75ft plastic chain on the reef floor, anchored as well as possible while avoiding damage to the reef coral. A GPS point should be recorded at each transect line. Once the line is anchored, surveyors swim two passes along the transect line. During the first pass, surveyors count all large species occurring within 3 ft on either side of the line. One the second pass, surveyors count all individuals of the small species occurring within 1.5 ft on either side of the line. Once fish surveys are complete, bottom cover can be classified. For each 3 ft. segment of the chain, surveyors classify the bottom cover as predominately rock, gravel, sand, coral or algae. Two more transect line surveys are performed the same way in separate sections of the reef. Results are to be recorded on datasheets immediately after transects are completed. Upon returning to camp, all data should be entered into a computer immediately to ensure any questions about data are cleared up while the information is still fresh in the surveyors mind. Suggested methods of analysis for reef survey data can be found in Schmitt et al. (2002).

Freshwater stream

Our current goal for sampling the freshwater stream is to monitor the fish assemblages (i.e. what species are present). Therefore, we recommend pulling the small beach seine at several locations and sampling all habitat types (riffles, runs, and pools). However, during the dry season, there is not enough flow in the stream to seine the riffle and run sections; only the pools can be successfully sampled. During the wet season we assume the stream is larger, allowing us to successfully sample the riffle and runs with a seine. In the riffle and run sections, the two people hold the ends of the seine close to the waters edge and pull it downstream about 30m, keeping the lead line on the bottom. In the pools, we recommend pulling the seine

downstream through the entire pool and throwing the cast net several times to get a representative sample of the species present. In addition, a D-net would be useful to try to catch some of the smaller fishes. If possible, we also recommend electroshocking the stream. This is a highly effective sampling method for acquiring all species and size classes.

La Vena mangrove

The La Vena mangrove occurs on the opposite end of Tenacatica Bay. This mangrove is dramatically different from the La Manzanilla mangrove because it is always connected to the bay and is dominated by the Red mangrove. For these reasons, we believe the water quality and fish communities are significantly different as well. Because of time constraints we were not able to sample the La Vena mangrove. However, we believe it could serve as a "control" treatment because it does not face the same threats from urbanization as the La Manzanilla mangrove does. Therefore, we recommend setting the stacker, spreader, and long–line in the La Vena mangrove at both ends of the mangrove (two separate locations). Use the same methods described above. This will take two days to complete. Cast-nets should be thrown as well (using the method described above) when the stacker and long-line are collected.

INTERDISCIPLINARY INTERSECTIONS

A collaborative effort between hydrologists, plant ecologists, limnologists, and fisheries ecologists is essential to try and understand the dynamics of the La Manzanilla mangrove. From the fisheries point of view, groundwater data collected from the hydrologists can explain the mangrove's connection, or lack there of, with the marine system, in addition to the amount of freshwater flowing in from underground. Knowing how much saline water and freshwater flows into the mangrove is essential for explaining why we might observe marine or freshwater species. Furthermore, plant ecologists are studying primary production in the mangrove which gives us an idea of productivity for the entire mangrove. Because mangrove trees can serve as important habitats for fishes, it is necessary to know the trees' status. Most importantly, the water quality and aquatic invertebrate data collected by limnologists will be used directly by fisheries ecologists to understand food web dynamics and conditions of the aquatic habitat. Knowing the temperature, salinity, DO, and pH, we can infer why we are observing tolerant, or less tolerant, species.

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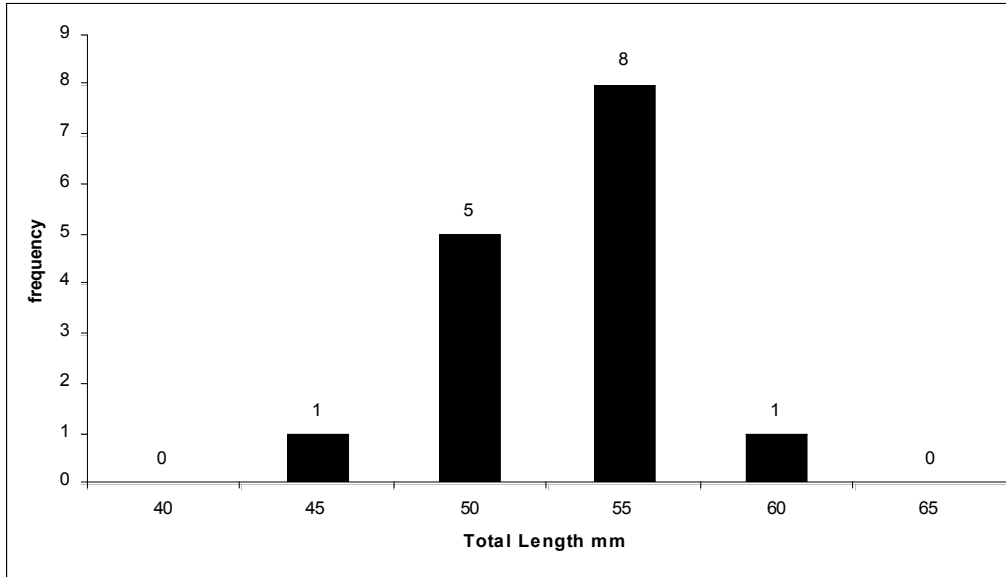Cienc. Del. Mar. Y Limnol. Univ. Nal. Autón. México 4(1):125-140.

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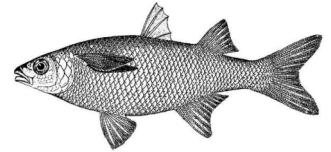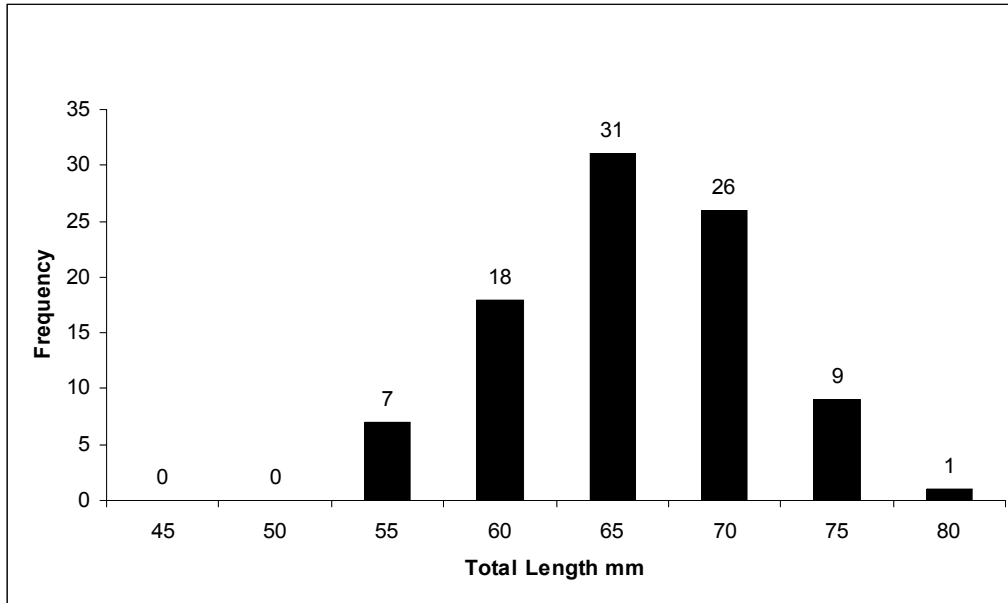
Snouted mullet frequency histogram. Samples obtained from seine sampling at the mouth of the mangrove.
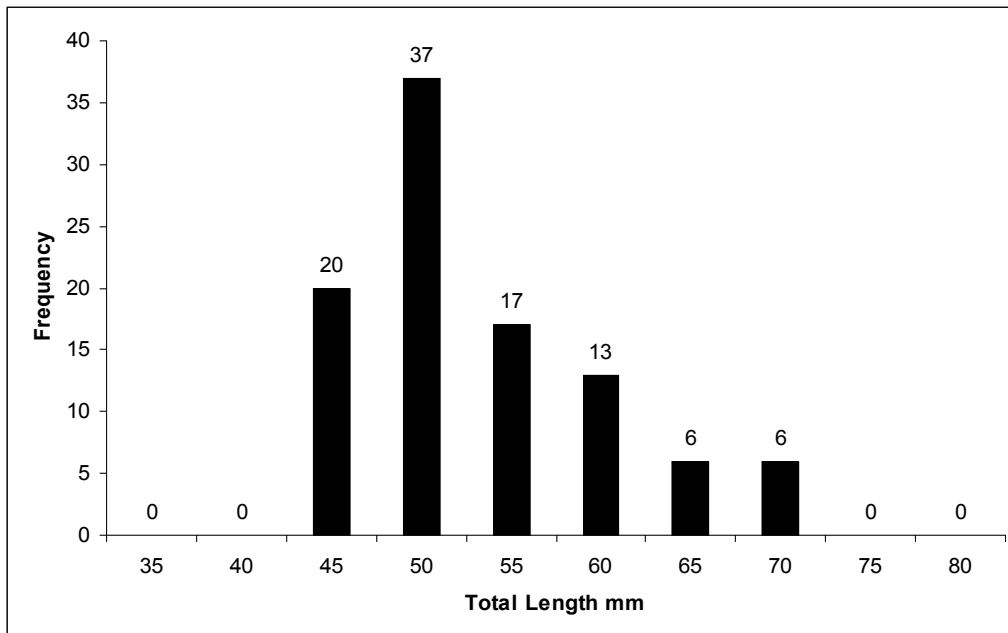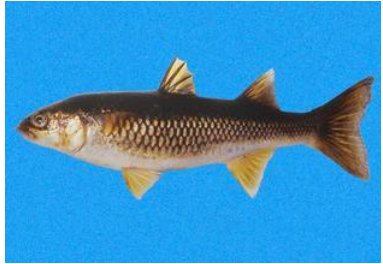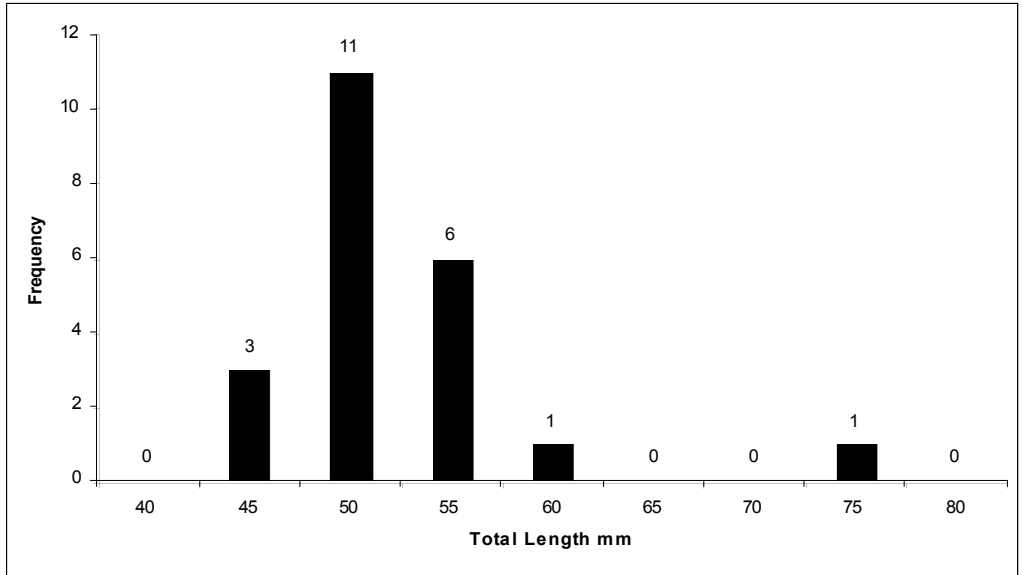

Pacific molly frequency histogram. Samples obtained from seining in the mangrove at the mouth of the mangrove.

Graceful herring total length histogram. Samples were obtained from beach seining at the mouth of the mangrove.
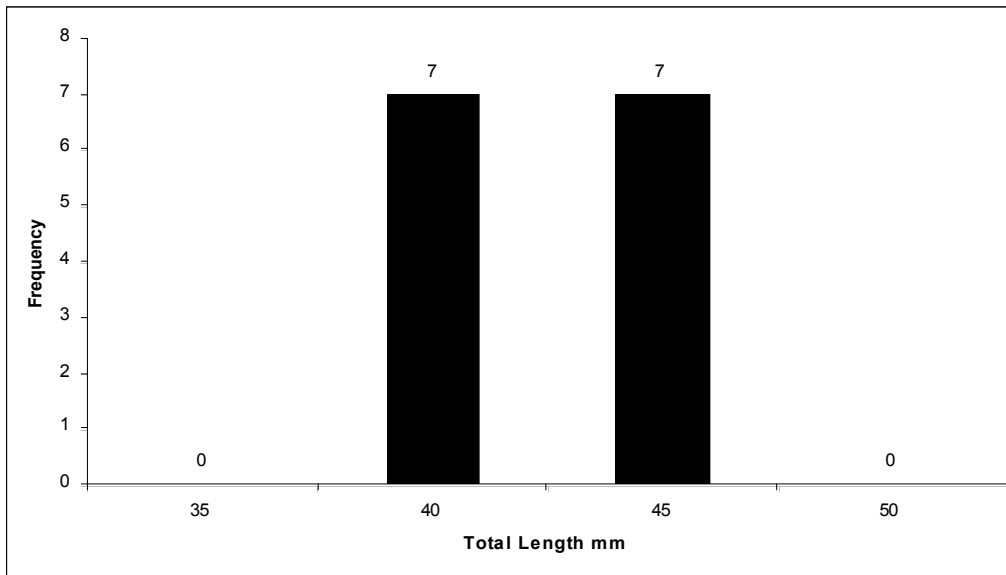
Blackfin snook total length histogram. Samples were obtained from beach seining at the mouth of the mangrove.

Mountain mullet total length histogram. Samples were obtained from seining the freshwater system.

Appendix 2

Map of La Manzanilla mangrove and surrounding area.

Appendix 3

Map of study sites within the mangrove

Appendix 4

Reef Monitoring Data Sheet

Date: Time: Surveyors:

Locality: La Manzanilla   Tenacatita

Method: RDT   Transect: 1   2   3

Depth Range:

Visibility:

Bottom Coverage Data:

ROCK
GRAVEL
CORAL
SAND
ALGAE

Fish Data:

Reef Species	# of individuals
Acapulco Damselfish	
Scissortail Damselfish	
Giant Damselfish	
Cortez Rainbow Wrasse	
Balloonfish	
Spotted Boxfish	
Spotted Porcupinefish	
Mexican Hogfish	
Flag Cabrilla	
Panamic Fanged Blenny	
Yellowtail Surgeonfish	
King Angelfish	
Reef Cornetfish	
Panamic Sergeant Major	
Threebanded Butterflyfish	

Comments:

Appendix 5

DATE:
TIME:
CREW:
SITE LOCATION: **Upper**   **Middle**   **Lower**   **Bay**   **Freshwater**
SAMPLING
METHOD: **Stacker**   **Spreader**   **Seine**   **Cast Net**
CAGE/THROW #:   **1**   **2**   **3**   **4**   **5**   **6**   **7**   **8**
UTM COORDINATES   Zone   Easting
**NAD83**   Northing

HABITAT DESCRIPTION:

*For Long line indicate which meter in comments

|	SPECIES	STANDARD L (mm)	TOTAL L (mm)	WEIGHT(grams)	COMMENTS
1					
2					
3					
4					
5					
6					
7					
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33					

Appendix 6

How to throw a Cast Net*

Throwing a cast net is just like learning anything new. It will be a little shaky at first, but with a little practice you'll be throwing that net like a pro every time. The key is **practice.** Practice throwing your cast net in the yard at home. The following instructions are assuming that you are right handed. If you are left handed, just do the opposite.
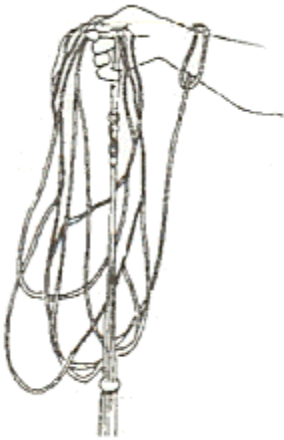
Make a wrist loop in the end of the hand line and place it over your right wrist. Then make a number of loops in your right hand collecting the hand line.
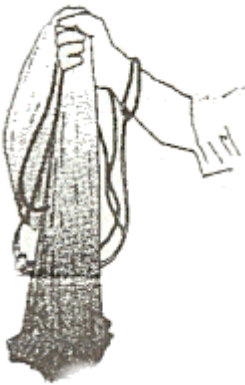
Check the draw strings to make sure they are hanging straight. Then grasp the entire net about 1/3 of the way down.
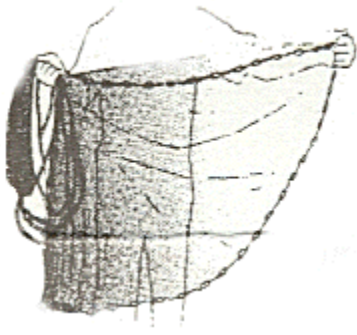
Grasp lead line in both hands and check it to make sure it is not twisted or tangled.

Make a smooth, full counter-clockwise turning cast. Practice in the yard will help you get the best results. Distance will come with experience.

*Cast net instructions from: http://www.texasgulfcoastfishing.com/castnets.htm

Appendix 7
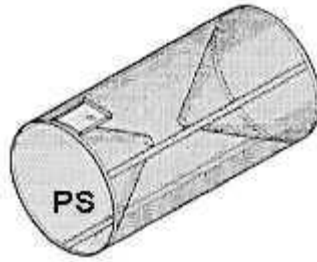
Cylinder Fish Trap*

The cylinder fish trap is constructed from woven, galvanized mesh, zinc coated screws and steel/aluminum rivets. Mesh size is 1/8". A waterproof sealer is added to prevent jagged edges, rust or corrosion. Each trap features an easy slide door, conveniently located for fast unloading. Cylinder traps features a cone-shaped funnel on each end. The "B" trap has a long, rectangular slot in the side for fish/minnow entrance.

* Instructions taken from: http://www.pondsolutions.com/traps.htm

Appendix 8

Interview questions for La Manzanilla fishers

1. How many fishermen are there in La Manzanilla (boats/day)?

2. How many fishermen are there in Tenacatita Bay (estimate)?

3. What is the average catch?

4. Does the catch vary seasonally?

5. What are the most common species? Do the most common species vary seasonally?

6. Has the number of fishermen changed over the past 30 years? How so?

7. Has the catch/fishermen changed over the past 30 years? How so?

8. Have fish stocks changed over the past 30 years? How so?

9. Which species seem less common now than 30 years ago?

10. What are some of the reasons that these species have declined?

11. Which species of fish live in La Manzanilla mangrove?

12. Do people ever fish in La Manzanilla mangrove? Now? In the past?

13. Is there a link between the mangrove and the bay? Can fish move back and forth?

14. How many fishermen/people feed the crocodiles/day? What do the crocs eat besides fish given to them by fishermen?

15. Do people ever harvest fish from the freshwater streams around La Manzanilla?

Additional questions for La Vena fishermen:

1. How many fish species occur in La Vena mangrove?

2. Are the fish in the mangrove the same species as in the ocean?

3. Is there a link between the mangrove fishery and the fishery in the bay?

4. Has the fish harvest from the mangrove increased or decreased over the past 10 years?

5. What are the main threats to the fish in La Vena mangrove?

Green Kingfisher *(Chloroceryle americana)* Collarejo Martin-pescador Verde

American Blackbirds & Orioles *(Icteridae)*
+*Yellow-winged Cacique *(Amblycercus h. holosericeus)* Cacique Mexicana
+Streak-backed Oriole *(Icterus pustulatus)* Bolsero Dorsirrayado
+Great-tailed Grackle *(Quiscalus mexicanus)* Zanata Mayor

Tyrant-flycatchers *(Tyrannidae)*
+Social Flycatcher *(Myiozetetes similis)* Luis Gregario
Great Kiskadee *(Pitangus sulphuratus)* Luis Grande
Tropical Kingbird *(Tyrannus melancholicus)* Tirano Tropical

Wrens *(Troglodytidae)*
*Sinaloa Wren *(Thyrothorus sinaloa)* Saltapared Sinaloense

Kites, Hawks, Eagles, and Allies *(Accipitridae)*
Mangrove Black Hawk *(Buteogallus subtilis)* Aguililla Negra Menor
Great Black Hawk *(Buteogallus urubitinga ridwayi)* Aguililla Negra Mayor
Grey Hawk *(Buteo nitidus)* Aguililla Gris

Piculets and Woodpeckers *(Picidae)*
*Golden-cheeked Woodpecker *(Centurus chrysogenys)* Carpintero Cachetidorado
Lineated Woodpecker *(Dryocopus lineatus)* Carpintero Lineado
Pale-billed Woodpecker *(Campephilus guatemalensis)* Carpintero Piquiclaro

Pigeons and Doves *(Columbidae)*
White-tipped Dove *(Leptotila verreauxi)* Paloma Arroyera
Red-billed Pigeon *(Columba flavirostrus)* Paloma Morada
White-winged Dove *(Zenaida asiatica)* Paloma Aliblanca

Cotingas *(Cotingidae)*
Rose-throated Becard *(Pachyramphus aglaiae)* Cabezón Degollado

Cuckoos *(Cuculidae)*
Groove-billed Ani (*Crotophaga sulcirostris)* Garrapatero Pijuy
Mangrove Cuckoo *(Coccyzus minor)* Cuco Manglero
Squirrel Cuckoo *(Piaya cayana)* Cuco Ardilla

Hummingbirds *(Trochilidae)*
Plain-capped Starthroat *(Heliomaster constantii)* Picolargo Coronioscuro

Frigatebirds *(Fregatidae)*
Magnificent Frigatebird *(Fregata magnificens)* Fragata Magnífica

Boobies and Gannets (*Sulidae*)
Brown Booby *(Sula leucogaster)* Bobo Vientre-blanco

New World Vultures *(Cathartidae)*
Black Vulture *(Coragyps atratus)* Zopilote Negro
Turkey Vulture *(Cathartes aura)* Aura Cabercirroja

Neotropcial Migratory: 11 species

American Blackbirds & Orioles *(Icteridae)*
Baltimore Oriole *(Icterus galbula)*   Bolsero de Baltimore
Orchard Oriole *(Icterus spurius)*   Bolsero Castaño

Ibises and Spoonbills *(Threskiornithidae)*
White-faced Ibis *(Plegadis chihi)*   Ibis Cariblanco
Roseate Spoonbill *(Platalea ajaja)*   Espátula Rosada

Storks *(Ciconidae)*
Wood Stork *(Mycteria americana)*   Cigueña Americana

Kingfishers *(Alcedinidae)*
Belted Kingfisher *(Ceryle alcyon)*   Martin-pescador
                                                                 Norteño

Wood Warblers *(Parulinae)*
Black-and-White Warbler *(Mniotilta varia)*   Chipe Trepador
Northern Waterthrush *(Seiurus noveboracensis)*   Chipe-suelero
                                                                 Charquero
Common Yellowthroat *(Geothlypus trichas)*   Mascarita
                                                                 Común
Yellow Warbler *(Dendroica petechia)*   Chipe Amarillo

Stilts and Avocets *(Recurvirostridae)*
American Avocet *(Recurvirostra Americana)*   Avoceta Americana

Appendix 3, 4 and 5—SEE ATTACHMENTS

ANALYSIS

The ecological basis for economic value of seafood production supported by mangrove ecosystems

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Abstract

The undervaluation of natural products and ecological services generated by mangrove ecosystems is a major driving force behind the conversion of this system into alternative uses. This trend of undervaluation is partly due to the difficulty involved in placing a monetary value on all relevant factors, but lack of ecological knowledge and a holistic approach among those performing the evaluation may be even more important determinants. This article identifies and synthesizes ecological and biophysical links of mangroves that sustain capture fisheries and aquaculture production. Fish, crustacean and mollusc species associated with mangroves are presented and the ecology of their direct use of this system is reviewed. Through a coastal seascape perspective, biophysical interactions among mangroves, seagrass beds and coral reefs are illustrated. The life-support functions of mangrove ecosystems also set the framework for sustainable aquaculture in these environments. Estimates of the annual market value of capture fisheries supported by mangroves ranges from US\$750 to 16 750 per hectare, which illustrates the potential support value of mangroves. The value of mangroves in seafood production would further increase by additional research on subsistence fisheries, biophysical support to other ecosystems, and the mechanisms which sustain aquaculture production. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Mangroves; Coastal seascape; Ecological services; Capture fisheries; Aquaculture; Economic evaluation

1. Introduction

In an ecologically illiterate world, the economic value of natural products and ecosystem services generated by mangrove forests is generally underestimated (Saenger et al., 1983; Hamilton and Snedaker, 1984; Hamilton et al., 1989; Lal, 1990; Barbier, 1994). As a consequence mangrove ecosystems have become prime candidates for conversion into large scale development activities,

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Table 1

Natural products and ecological services of mangrove ecosystems[a]

Natural products

Fuel
  Firewood
  Charcoal
  Alcohol
Construction
  Timber for scaffolds and heavy construction
  Beams, poles, flooring, panelling, etc.
  Boat building
  Dock piling
  Thatch, matting
Fishing
  Poles for fish traps
  Fish attracting shelters
  Fishing floats
  Fish poison
  Tannins for net and line preservation
Food and beverages
  Fish
  Crustaceans
  Molluscs
  Other fauna
  Vegetables from propagules, fruit and leaves
  Sweetmeats from propagules
  Condiments from bark
  Sugar
  Honey
  Cooking oil
  Tea substitutes
  Alcohol
  Vinegar
  Fermented drinks
Household items
  Furniture
  Glue
  Wax
  Household utensils
  Incense
  Matchsticks
Textiles, leather
  Fur, skins
  Synthetic fibres (e.g. rayon)
  Dye for cloth
  Tannins for leather preservation
Other products
  Fish, shellfish and mangrove roots for aquarium trade
  Medicines from bark, leaves, fruits and seeds
  Fodder for cattle, goats and camels
  Fertilisers
  Lime
  Paper
  Raw material for handicraft
  Cigarette wrappers

Table 1 (Continued)

Ecological services

Protection against floods, hurricanes and tidal waves
Control of shoreline and riverbank erosion
Biophysical support to other coastal ecosystems
Provision of nursery, breeding and feeding grounds
Maintenance of biodiversity and genetic resources
Storage and recycling of organic matter, nutrients and pollutants
Export of organic matter and nutrients
Biological regulation of ecosystem processes and functions
Biological maintenance of resilience
Production of oxygen
Sink for carbon dioxide
Water catchment and groundwater recharge
Topsoil formation, maintenance of fertility
Influence on local and global climate
Habitat for indigenous people
Sustaining the livelihood of coastal communities
Heritage values
Cultural, spiritual and religious values
Artistic inspiration
Educational and scientific information
Recreation and tourism

[a] Sources: Saenger et al., 1983; Hamilton and Snedaker, 1984; Ruitenbeek, 1994; Costanza et al., 1997.

such as agriculture, aquaculture, forestry, salt extraction and infrastructure. More than 50% of the world's mangroves have been removed (World Resources Institute, 1996), and for the Asia-Pacific region an annual deforestation rate of 1% is considered to be a conservative measure (Ong, 1995). Mangroves formerly occupied ≈ 75% of tropical coasts and inlets (Farnsworth and Ellison, 1997), but today they only line ≈ 25% of the world's tropical coastlines (World Resources Institute, 1996). Evaluation of the importance of mangroves for society requires insight into the flow of products and services within the social system of coastal communities, and how they are linked and influenced by domestic and international markets and institutions. It also requires insight into the biophysical links within and between mangroves and other ecosystems for the generation of natural products and ecological services, many of which are harvested or enjoyed outside the mangrove system. Although it will not be possible to place a monetary value on all relevant factors, they must be recognized explic-

itly and incorporated into the discussion of management alternatives for mangrove forests.

Mangroves provide a wide range of ecological services like protection against floods and hurricanes, reduction of shoreline and riverbank erosion, maintenance of biodiversity, etc. (Table 1). These services are key features which sustain economic activities in coastal areas throughout the tropics. In addition to the multiple ecological services provided by mangrove ecosystems, ranges of direct and indirect natural products from mangroves are vital to subsistence economies and provide a commercial base to local and national economies (Table 1). Commercial and traditional products range from timber to charcoal, and from tannins to medicines. Moreover, a number of food products are harvested directly within the mangrove system through hunting, gathering, and fishing operations.

Capture fisheries production is believed to constitute the major value of marketed products from an unexploited mangrove forest (Hamilton et al., 1989), and the support to commercial, recreational and subsistence fisheries is well documented. For instance, 80% of all marine species of commercial or recreational value in Florida, USA, have been estimated to depend upon mangrove estuarine areas for at least some stage in their life cycles (Hamilton and Snedaker, 1984). In Fiji (Hamilton and Snedaker, 1984) and in India (Untawale, 1986), approximately 60% of the commercially important coastal fish species are directly associated with mangrove environments. The relative contribution of mangrove-related species to total fisheries catch can also be significant, constituting 67% of the entire commercial catch in eastern Australia (Hamilton and Snedaker, 1984), 49% of the demersal fish resources in the southern Malacca Strait (Macintosh, 1982), 30% of the fish catch and almost 100% of shrimp catch in ASEAN countries (Singh et al., 1994). Positive correlations have also been demonstrated between mangrove cover and municipal fisheries landings (Camacho and Bagarinao, 1987) as well as penaeid shrimp catches (Turner, 1977; Staples et al., 1985; Pauly and Ingles, 1986). In addition to commercial fisheries, coastal subsistence economies in many developing countries are heavily dependent upon sustainable harvest of fish and shellfish from mangroves. The median fisherman density of about 5.6 fishermen per km^2 in mangrove environments is considerably higher than in other fished systems as is the yield per unit area (Matthes and Kapetsky, 1988). Because a large portion of the world's human population lives in coastal or estuarine areas, e.g. 70% of the population in South East Asia (Pauly and Chua, 1988), the importance of fishery activities as a source of food and income cannot be overstated.

Another aspect of mangroves as life-support systems is their role in sustaining mollusc, fish, and shrimp aquaculture. Land based pond farming of fish and crustaceans in former mangrove areas has a long tradition in many countries, and dates back some 500 years to rearing of milkfish (*Chanos chanos*) in Indonesia (Schuster, 1952). In recent decades, aquaculture activities have intensified dramatically, particularly for high-value crops like penaeid shrimps. Conversion of mangrove forests into shrimp farms has grown to such an extent that today it constitutes the main threat to mangroves in many countries (Hamilton et al., 1989; Primavera, 1998). Ironically, the productivity of these aquaculture systems is heavily dependent on surrounding mangroves which provide seed, food inputs, clean water, etc. (Hamilton and Snedaker, 1984; Larsson et al., 1994; Beveridge et al., 1997). Failure to acknowledge this life-support function of mangroves is one explanation for the boom-and-bust pattern of shrimp aquaculture. The lifespan of most semi-intensive and intensive ponds seldom exceeds 5–10 years (Gujja and Finger-Stich, 1996), and 70% of previously productive ponds have been abandoned in Thailand (Stevenson, 1997).

This article identifies and synthesizes ecological and biophysical links of mangroves that sustain seafood production (Fig. 1). By illuminating the 'hidden' support of mangroves to capture fisheries and aquaculture, these human activities are put into an ecosystem framework. Without this understanding it is difficult, if not impossible, to sustainably manage mangroves and the natural products and ecological services associated with this coastal ecosystem. This ecological knowledge

can also serve as a conceptual framework for economic evaluations of mangrove ecosystems in supporting seafood production. First, I identify fish, crustacean and mollusc species associated with mangroves and review the ecology of their direct use of mangroves. This is followed by a section on biophysical interactions between mangroves and other coastal ecosystems, relations often forgotten in mangrove management. The ecological goods and services constituting a prerequisite for sustainable aquaculture in mangrove environments are outlined before discussing economic valuations of seafood production supported by this system. To illustrate the potential support value of mangroves in fish and shellfish production, productivity and market value of some fisheries are presented. The undervaluation

of mangroves, originating in ecological illiteracy and in the difficulties involved in placing a monetary value on generated natural products and ecological services, is also discussed.

2. Fish, crustaceans and molluscs associated with mangroves

Fishery species which use mangroves as habitat can be classified into permanent residents, spending their entire life cycle in mangrove systems, and temporary residents, associated with mangroves during at least one stage in their life cycle (Ogden and Gladfelder, 1983). The latter can be divided into obligate or incidental users. The broad application of these definitions has been widely de-
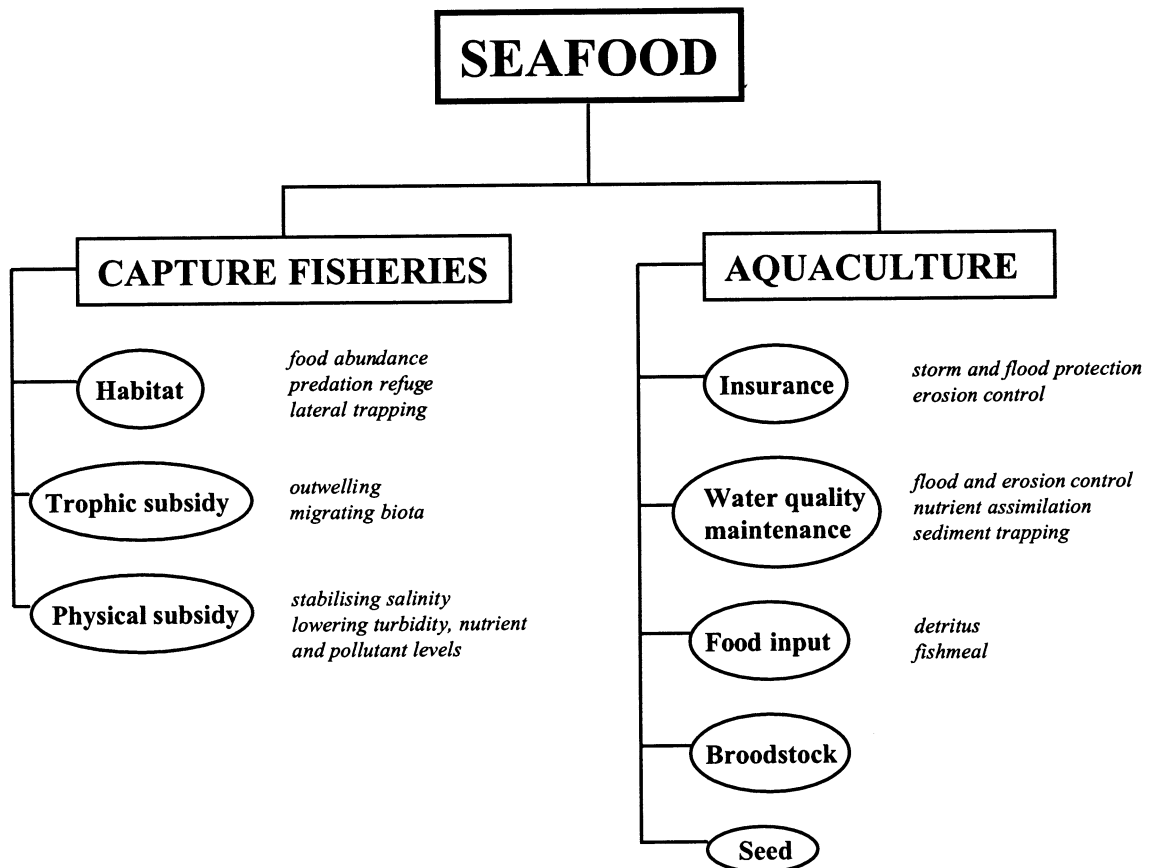
Fig. 1. Seafood production generated by mangrove ecosystems: direct biophysical support to capture fisheries, and natural products and ecological services sustaining aquaculture.

bated and criticised (Potter et al., 1990). In addition to the difficulty involved in defining the degree of dependence, fish and shellfish species associated with mangroves are in some cases not confined to particular families or even genera (Robertson and Blaber, 1992). For instance, many genera contain closely related species whose adults co-occur offshore, but which do not all use mangroves as nursery. The importance of mangroves to economically important organisms was highlighted through a biogeographic analysis by Matthes and Kapetsky (1988), which associated particular life stages of these organisms to mangrove environments. This kind of information is, however, limited in many areas due to lack of adequate research.

2.1. Fish

Few fish species are permanent residents in mangroves, but numerous marine species use mangroves as nursery grounds (Robertson and Blaber, 1992). Fish species richness has been reported to be as high as almost 200 species in mangrove-dominated estuaries and embayments in Australia and India (reviewed by Robertson and Blaber, 1992). A large number of teleost (bony fish) species that utilise mangrove areas as larvae, juveniles, or adults are captured by fishermen either inshore or offshore (economically important families are listed in Table 2). Highly valued food and game fish that have a close association with mangroves in the Indo-West Pacific include mullets (*Liza*, *Mugil*), groupers (*Epinephelus*), snappers (*Lutjanus*), tarpons (*Megalops*), sea-perch (*Lates*, *Centropomus*) and catfish (e.g. *Arius*, *Tachysurus*) (Macintosh, 1982). In addition to teleosts, a great number of shark and ray species can also be found in mangrove environments (Matthes and Kapetsky, 1988).

2.2. Crustaceans

Mangroves are important nursery areas for many commercially important shrimp and crab species throughout the tropics (Macnae, 1974; Dall et al., 1990). In terms of value per unit catch and total value of catch, the penaeid shrimps are

Table 2
Fish families that utilise mangroves as habitat during their life cycle and are of economic importance to fisheries[a]

Megalopidae (tarpons)
Chanidae (milkfish)
Clupeidae (herrings, sardines, pilchards)
Engraulidae (anchovies)
Ariidae (sea catfishes)
Plotosidae (eel catfishes)
Mugilidae (mullets)
Centropomidae (barramundi, snooks)
Serranidae (groupers, sea basses)
Sillaganidae (sillagos)
Carangidae (king fishes)
Leiognathidae (soapies)
Lutjanidae (snappers)
Gerridae (mojarras)
Haemulidae (rubberlips, grunts)
Sparidae (breams)
Polynemidae (threadfins)
Scianidae (drums, croakers)
Mullidae (goat fishes)
Cichlidae (cichlids)
Gobiidae (gobies)
Scatophagidae (scatties)
Siganidae (rabbit fishes)
Sphyraeinidae (barracudas)
Stromateidae (ruffs)
Cynoglossidae (tonguefishes)

[a] Sources: Macnae, 1974; Hamilton and Snedaker, 1984; Matthes and Kapetsky, 1988; Singh et al., 1994.

among the most important resources for coastal fisheries worldwide (Dall et al., 1990). Many species of palaemonid shrimps are also associated with mangroves, including the commercially important giant freshwater shrimp, *Macrobrachium rosenbergii* (Macnae, 1974; Matthes and Kapetsky, 1988; Singh et al., 1994). Mangroves also support vast numbers of small shrimp of which *Acetes* spp. (Sergestidae) are the most important to fisheries (Macnae, 1974; Macintosh, 1982). These shrimps are partially dried and made into a fermented paste that forms a key ingredient in South East Asian cooking.

The mangrove crab fauna is of major ecological and economic importance (Macnae, 1974; Macintosh, 1982; Matthes and Kapetsky, 1988), including the high-priced mangrove mud crab, *Scylla serrata*. Distributed from eastern Africa to the central Pacific, this crab is abundant enough to

support local fisheries and aquaculture operations throughout the Indo-West Pacific region. In addition to *S. serrata* there are minor fisheries for some of the larger species of mangrove sesarmid crabs in Burma and Thailand. In the Eastern Pacific, Twilley et al. (1993) reported that in Ecuadorian mangroves the ocypodid crab, *Ucides occidentalis*, occupies a similar fishery niche as *S. serrata* in the Indo-West Pacific.

2.3. Molluscs

Mangrove estuarine areas often support an abundance of mollusc species that are largely sessile in nature and constitute an important in-situ fishery (Macnae, 1974; Macintosh, 1982; Hamilton and Snedaker, 1984; Matthes and Kapetsky, 1988; personal observation). Edible species of oysters, mussels, cockles, and gastropods are collected extensively for local consumption, usually by the families of local fishermen. Mangrove roots and lower parts of trunks provide substrate for oysters and mussels. Because these animals are filter feeders, they are confined to microhabitats below mean high water, and are usually only abundant in areas adjacent to open water (Macintosh, 1982; Menzel, 1991). The blood clam, *Anadara granosa*, and other cockles can be found in large numbers in mudflats on mangrove strands, where it lies partially buried in the sediment (Macintosh, 1982).

Historically the natural stocks of molluscs have been more than sufficient to meet market demands, resulting in no incentive for culturing molluscs like oysters, mussels and cockles (Macintosh, 1982; Hamilton and Snedaker, 1984). However, this situation has changed dramatically in many countries, due to overcollection and loss of previously productive mollusc beds through habitat destruction, pollution, etc. In many areas the harvestable yields are augmented by the provision of artificial substrates in the form of rafts, simple stakes, or ropes placed in the shallow waters of mangrove estuaries for settlement and growth of bivalve molluscs (Hamilton and Snedaker, 1984).

3. Mangroves as habitat for fish and shellfish

Mangroves dominate the intertidal zone of tropical deltas, lagoons, and estuarine coastal systems that receive significant inputs of exogenous material, but they can also be found colonizing the shoreline of carbonate platforms, developing from little or no terrestrial run-off (Duke, 1992; Twilley et al., 1993, 1996). Local variations in topography and hydrology result in the differentiation of ecological types of mangroves such as riverine, fringe, basin, overwash and dwarf forest (Lugo and Snedaker, 1974). The combination of different geomorphological settings, each with a variety of ecological types, contributes to the diversity of mangrove ecosystems, and their specific characteristics of structure and function (Duke, 1992; Twilley et al., 1993, 1996).

Mangroves are characterized by high abundance of fish, crustaceans and molluscs. Fish standing stock, ranging from 4 to 25 g m^{-2} in intertidal mangrove habitat (reviewed by Rönnbäck et al., 1999), is much higher in mangrove habitat compared to adjacent coastal habitats (Robertson and Duke, 1987; Thayer et al., 1987; Blaber et al., 1989; Morton, 1990; Robertson and Duke, 1990). For instance, Robertson and Duke (1987) found mangroves in northern Australia to contain four to ten times higher fish abundance compared to adjacent seagrass habitats, and Thayer et al. (1987) reported fish to be 35 times more abundant in Florida mangroves compared to adjacent seagrass beds.

Several complementary hypotheses have been proposed to explain why many fish and invertebrate species utilise mangroves during at least one stage of their life cycle. The three most widely accepted explanations relate to food abundance, shelter from predation, and the hydrodynamic ability of mangroves to retain immigrating larvae and juveniles (Fig. 1). Spatiotemporal variations in the availability of food and shelter, and retention capacity, affect the quality of individual mangrove microhabitats for fish and shellfish. Identification of prime nursery and feeding grounds is therefore of central importance to mangrove conservation and management.

3.1. Food abundance

Because of the high primary productivity in mangrove systems (Birkeland, 1985; Robertson and Blaber, 1992), it has been suggested that fish and invertebrates occupying mangrove habitats do so mainly to utilise the food resource (Boesch and Turner, 1984; Robertson and Blaber, 1992; Singh et al., 1994). Primary production can be attributed to several sources: the trees themselves, their associated epiphytes (ongrowth), other larger plants, phytoplankton (microscopic, floating plants), and benthic microalgae. Carbon fixed by the trees is likely to be the main carbon source for fauna in systems with turbid waters and a relatively high proportion of forest to open water (Robertson et al., 1992). Where mangroves occur as fringing vegetation along coastal lagoons, or on small islands in relatively clear water, food webs are likely to be more complex (Robertson et al., 1992).

A crucial argument for the food supply hypothesis is that mangrove forests provide a higher abundance of food than adjacent coastal ecosystems. This was proven to be the case in a mangrove-lined estuary in northeastern Australia (reviewed by Robertson et al., 1992). During the major recruitment period of most fish into the system, zooplankton-feeding fish dominated the fish community. The diet of most juvenile fish caught during this recruitment period was dominated by crab larvae, which were two orders of magnitude more abundant in mangrove waterways compared to adjacent nearshore habitats.

Odum and Heald (1975) suggested that the principal flow in mangrove food web was mangrove leaf litter → saprophytic community (microbial decomposition) → detritus consumers → lower carnivores → higher carnivores. Annual leaf litterfall can be substantial; in northeastern Australia litterfall has been estimated at 8–10 t dry weight per ha, with a maximum of up to 20 t dry weight per ha (Clough, 1992). The mangrove crab fauna can consume or store 30–80% of this litterfall (Robertson et al., 1992). These crabs are consumed by fishes, and therefore constitute an important link at the primary consumer level in food webs, beginning with mangrove plant production

and leading to higher level consumers harvested by humans. Small-sized sergestid and palaemonid shrimp, which feed mostly on mangrove detritus (Odum and Heald, 1972; Macintosh, 1982), are other key organisms in mangrove food webs by virtue of their immense abundance and their importance as prey for fish and shellfish (Xiao and Greenwood, 1993).

Stable isotope studies have indicated that seagrass, macroalgae and phytoplankton might be more important than mangrove leaf detritus as carbon source for some fish and invertebrate species (Primavera, 1996; Loneragan et al., 1997). For these species the role of mangroves as habitat may be more a result of the predation refuge offered or the lateral trapping capacity, rather than the food abundance.

3.2. Predation refuge

Mangrove environments function as predation refuges for larvae and juveniles of many fish and invertebrates (Boesch and Turner, 1984; Robertson and Blaber, 1992; Singh et al., 1994). For penaeid shrimps the major cause of mortality in estuaries and coastal areas is predation rather than food supply or physico-chemical factors (Dall et al., 1990). Minello et al. (1989) concluded that the number of postlarvae entering estuaries only partially explained the variability in recruitment of brown shrimp, *Penaeus aztecus*, to the fishery. Rather, the mortality of young life stages within the nursery habitat appeared critical in determining recruitment levels.

Juvenile fish and shrimp have been found to move substantial distances into the mangrove forest habitat at high tide (Vance et al., 1996; Rönnbäck et al., 1999), where they gain protection from predation by larger fish, which remain in or near mangrove waterways (Vance et al., 1996). The structural complexity resulting from mangrove roots, debris, and other vegetational structures of the intertidal habitat enhances the refuge aspect. Shelter is also created through shallow environments, high turbidity, and soft muds suitable for burrowing, all as a result of the sediment-trapping capacity of mangroves. These physical characteristics should be of major impor-

tance in reducing predation rates on ebb tides, when juvenile fish and shrimp concentrate in the open water of mangrove waterways. The shelter function of mangroves has also been attributed to lower abundance of large carnivorous fish compared to coral reef ecosystems (Section 4.1).

3.3. Lateral trapping

About 70% of all marine invertebrate larvae are pelagic, and these adaptations facilitate dispersal and colonization (Thorson, 1950). Planktonic larvae spawned offshore, but utilising mangroves as nursery habitats, e.g. many penaeid shrimp, face the problem of recruitment to and retention in this coastal ecosystem. The lateral trapping hypothesis focuses on the role of mangroves as a retention area for immigrating early life stages that would otherwise be swept away by currents and tidal action (Chong, 1995; Chong et al., 1996). The presence of mangroves greatly increases the residence time of the water, which is particularly prominent in the upper reaches of flat, wide mangrove forests with high-complexity waterways (Wolanski and Ridd, 1986). This reflects the need for extensive and wide mangrove forests in retaining immigrating young stages of fish and invertebrates of direct and indirect importance to fisheries and aquaculture.

4. Biophysical interactions with other coastal ecosystems

Although mangroves, seagrass beds, and coral reefs can exist in isolation from each other, they commonly form integrated ecosystems of high productivity that generate a diversity of ecological services (Moberg and Folke, this issue). Many of these ecological services constitute an important support to the productivity and sustainability of capture fisheries and aquaculture operations. A coastal seascape perspective, where the biophysical interactions among mangroves, seagrass beds and coral reefs are acknowledged (Fig. 1), is therefore a prerequisite for the management and economic evaluation of seafood production from individual systems.

4.1. Animal migrations

The larvae and juveniles of many fish and shellfish species utilise mangroves or seagrass beds as nursery grounds, whereafter they emigrate to other systems as adults or subadults (Ogden and Gladfelder, 1983; Parrish, 1989). This strategy should increase the survival rates and recruitment success of commercially valuable species harvested in other ecosystems, such as coral reefs and pelagic zones (Parrish, 1989). In this respect, the ability of mangroves to passively retain or actively attract immigrating larvae and juveniles is of critical importance to capture fisheries.

Given the high abundance of young organisms and their relative vulnerability during migrations, larger carnivorous fish are attracted to mangroves from surrounding systems such as coral reefs (Ogden and Gladfelder, 1983). Coral reef fish and invertebrate communities also include herbivores, whose feeding migrations are quantitatively important wherever reefs and vegetated habitats co-occur (Birkeland, 1985; Parrish, 1989; see also Holmlund and Hammer, in this issue).

4.2. Outwelling

Much of the mangrove leaf production is unexploited by terrestrial animals and instead becomes available to surrounding waters through litterfall (Robertson et al., 1992). Large amounts of leaf litter are normally retained within the forest, but the rest is exported to nearshore areas as organic carbon and nutrients. This outwelling has long been considered to play an important role in enhancing production in other systems in the coastal seascape, and has been widely used as an argument for mangrove conservation (Parrish, 1989; Lee, 1995). However, mangrove leaf detritus is relatively refractory to decomposition and direct assimilation by fauna, and thus its importance to the productivity of surrounding systems has also been questioned (Rodelli et al., 1984; Birkeland, 1985; Lee, 1995).

The magnitude and direction of material fluxes between mangroves and adjacent coastal systems depends on the geomorphological setting, hydrodynamics, soil and vegetation types, the time

frame of observation, and the substance in question (Robertson et al., 1992). Estimates of dissolved material fluxes between mangroves and nearshore areas vary widely and range from net imports of 73 kg/ha per year to exports of 443 kg/ha per year (reviewed by Robertson et al., 1992). In a detailed study in tropical Australia, the annual export of particulate organic matter was found to be 3322 kg/ha (reviewed by Robertson et al., 1992). However, this estimate does not include the movement of animal biomass, an aspect usually overlooked in mangrove mass balance studies (Robertson et al., 1992). Those species which spend their larval and juvenile phase in the mangroves but migrate to other habitats as adults may represent one important source of carbon input originating from mangrove primary production (see also Holmlund and Hammer, this issue). This is the case in north-eastern Australia, where many clupeid species, of no or low importance to capture fisheries, become prey for commercially important fish species like mackerel, once they leave their mangrove nursery (Robertson and Duke, 1990).

4.3. Physical interactions

Mangroves, seagrasses, and coral reefs interact by modifying their physical environment. Reefs function as a hydrodynamic barrier, dissipating wave energy and creating waters of low energy on the landward side (Ogden and Gladfelder, 1983; Birkeland, 1985; Ogden, 1997). This is of major importance to seagrass beds and mangroves, which thrive in the presence of those barriers. The reciprocal dependence on mangroves relates to the ability of this system to control coastal water quality (Ogden and Gladfelder, 1983; Birkeland, 1985; Ogden, 1997). The long residence time of water inside mangrove environments buffers the magnitude and frequency of salinity fluctuations in the coastal zone. Fresh water stored in mangroves may be lost through evapotranspiration as well as dissolving excess salt in mangrove sediment, reducing the volume of undiluted freshwater that

reaches the coast. Another important feature of mangroves, and to a lesser degree also seagrass beds, is the trapping of particulate matter and assimilation of nutrients in river run-off. Mangroves also influence coastal water quality, while functioning as a flood control mechanism and as an effective binder of shoreline and riverbank sediments, thereby reducing erosion or scouring by waves and currents.

The influence of mangroves in stabilising water quality in the coastal zone can be of major importance to the functioning of nearby coral reefs. Sediments and accompanying nutrients are a major threat to coral reefs, which require oligotrophic (nutrient poor) waters of low turbidity for vigorous growth (Kühlmann, 1988; Goureau et al., 1997). The clearing of watersheds for agriculture, industry and tourism, and the destruction of coastal estuaries, seagrass beds and mangrove forests, acting as sediment traps, are therefore among the most damaging influences on coral reefs around the world (Ogden, 1997).

Do mangroves function as a net source or sink of particulate matter and nutrients? As mentioned previously, mangroves export part of their primary production as organic carbon and nutrients and thus fertilise adjacent waters, but at the same time mangroves are said to control water quality by trapping and assimilating sediments, organic material, and nutrients. The possible confusion about whether mangrove forests are net exporters or importers generally results from observations at different time scales (Robertson et al., 1992). The export of particulate carbon from mangrove systems can be substantial. During dry periods, with insignificant river run-off, the export of mangrove detritus could be important in sustaining production in adjacent systems. On the other hand, during periods of significant run-off, the trapping and assimilating functions of mangroves reduce fluctuations in salinity, turbidity and nutrient levels in coastal waters, and thus lower the stress on adjacent coastal ecosystems. This illustrates the importance of understanding and accounting for the spatiotemporal dynamics of the ecosystem that generates a flow of essential products and services.

5. The role of mangroves in sustaining aquaculture production

Mangroves support various types of aquaculture through a wide variety of mechanisms (Fig. 1). They help control erosion and protect against floods and hurricanes, and thus help protect aquaculture operations against these natural disturbances. The importance of these ecological services to aquaculture production depends upon the vulnerability of the site to disturbances and may be extremely valuable in certain areas, creating an incentive to preserve mangrove greenbelts along shorelines and riverbanks.

Deteriorating water quality in mangrove environments can have serious impacts on the marketability and sustainability of mollusc (Menzel, 1991; Beveridge et al., 1997) and shrimp aquaculture (Macintosh and Phillips, 1992; Beveridge et al., 1997). Therefore, the ability of mangroves to maintain good water quality, i.e. to abate fluctuations in salinity and turbidity, reduce concentrations of pollutants, and control nutrient levels in coastal waters cannot be overstated. Larsson et al. (1994) estimated the mangrove ecosystem area needed to sustain a Colombian semi-intensive shrimp farm. The area of mangrove lagoons providing clean water to the ponds was estimated to be seven times larger than the shrimp pond, a figure that would increase with higher intensity of the farming system. Robertson and Phillips (1995) estimated that 22 ha of mangrove forest would be required to filter the nitrogen and phosphorus loads from effluents produced per hectare of intensive shrimp pond. However, it should be stressed that the environmental effects of this loading are virtually unknown, suggesting the use of the precautionary principle on this matter (Troell et al., 1999). Furthermore, the establishment of shrimp aquaculture usually results in massive mangrove deforestation and degradation in the area. As a consequence, the size of remaining mangroves are too small to assimilate all nutrients released, which increases the risk of self-pollution and subsequent collapse of the shrimp farm. The filtering capacity of mangroves can only be used successfully if the density of shrimp ponds is sufficiently low and ponds are located either towards the landward edge of the forest or on terrestrial areas inland.

The high productivity of mangrove forests provides food inputs to aquaculture systems. Organic material and nutrients can either be exported to adjacent open water habitat, where they enhance the production of cultured molluscs, or they can serve as a more direct input to landbased farming systems with suitable logistics. Larsson et al. (1994) estimated that bacterial and fungal films on mangrove leaf detritus made up 30% of shrimp food, corresponding to a mangrove area four times the size of the semi-intensive pond. Fish and invertebrates dependent on mangroves can also serve as feed inputs to aquaculture, either as direct 'trash fish' input or as ingredients in formulated feeds.

Perhaps the most important link between mangroves and aquaculture is the natural production of larvae and juveniles—or seed as they are known to the aquaculturist—of farmed species (FAO/NACA, 1995). Some countries have developed hatcheries for seed production of certain species, whereas many countries still depend on wild seed for stocking. Wild seed is either collected from natural habitat and subsequently placed in aquaculture systems, or allowed to enter farming systems naturally through tidal entry of fish and crustaceans into land-based systems, or by settling of mollusc seed on artificial substrates.

The productivity of mangrove mollusc culture can be severely limited by low availability of seed (Hamilton and Snedaker, 1984; Menzel, 1991), which is aggravated by the destruction and deterioration of natural spatfall (larvae production) areas, i.e. mangroves. For milkfish, *C. chanos*, the principal tropical marine fish species reared in coastal mangrove ponds, shortage of wild seed can also be a serious constraint to increased production (Macintosh, 1982). In the Larsson et al. study, the largest support system by far was the mangrove nursery area for shrimp postlarvae, which ranged between ten and 160 times the area of a semi-intensive shrimp farm, depending on the quantity of wild-caught postlarvae, stocking densities in ponds and larval density in the mangrove. Therefore, the destruction of mangrove habitat will exacerbate existing shortages of postlarval

shrimp, which is the primary constraint on increased production of cultured shrimp in many countries (FAO/NACA, 1995). The development of hatcheries for cultured shrimp and fish species may have reduced the dependence on mangroves to produce seed, but has increased demand for wild-caught female spawners instead. The deforestation of mangroves has also led to a shortage of broodstock, resulting in movements of animals (including exotic strains and species) within and between countries and with implications for spread of disease and dilution of wild genetic material (Beveridge et al., 1997).

6. The economic significance of mangroves in seafood production

6.1. Capture fisheries

Below I review economic evaluations of mangroves in sustaining capture fisheries production. Studies which fail to provide adequate information on how the value was derived or lack reasonable methodology are not included. Original calculations, based on productivity estimates for some fisheries, are also presented. The objective is to outline the potential of some fisheries, rather than assigning an economic value to all mangrove-associated fisheries. Economic values predominantly represent gross financial benefits, and are calculated by using market prices to assign values.

Comparing market values from previous studies needs to be done with some caution, due to differences in inflation rates and in market prices of the same fishery products between countries. Therefore, the productivity by biomass should be included in the presentation, but unfortunately this is not always the case. Economic valuation is also context-specific. To ask about the value of a hectare of mangrove without relating it to a specific decision situation is not very meaningful from a standard economic perspective (Barbier et al., 1994).

One major weakness of previous evaluations of mangroves and capture fisheries production is the number and type of fisheries included in the analysis. The economic value of mangroves is usually underestimated, since only one or a few species of commercial importance are included in the evaluation, not acknowledging the large number of fish and shellfish species associated with mangroves. This is in part due to the fact that many species are harvested outside mangrove environments, even if they are dependent upon this system during early life stages. Hence, the important link between mangroves and harvested fish and shellfish is not always perceived. Another reason is that a significant proportion of the fisheries catch is non-marketed subsistence harvest, which is not included in national fishery statistics. Due to lack of reliable catch data, the actual value of subsistence fisheries is usually underestimated. However, some studies have illuminated its significant importance. The contribution of subsistence fisheries to total catch supported by mangroves was estimated to 10–20% in Sarawak (Bennett and Reynolds, 1993), 56% in Fiji (Lal, 1990), and 90% in Kosrae (Naylor and Drew, 1999). Therefore, any economic analysis trying to estimate the value of mangroves to fisheries, without recognizing their contribution to subsistence economies, will be incomplete.

6.1.1. Penaeid shrimp

Penaeid shrimps are the most economically valuable fishery resource associated with mangroves, due to their abundance and very high market price. Positive correlations between offshore yield of shrimps and amount of mangrove forest in the nursery area have been demonstrated throughout the tropics (Table 3). Turner (1977) and Pauly and Ingles (1986) found a correlation between latitude and penaeid catch, with increasing catches towards the equator. Turner (1977) attributed this to temperature, food availability, and changes in the amount of time needed for shrimp growth in estuaries. Moreover, Pauly and Ingles (1986) found a logarithmic relationship between mangrove area and shrimp production, implying that the shrimp fisheries impact of reducing mangrove area becomes greater as the remaining area is reduced. Estimates of annual economic value per hectare of mangrove ranges from US$91 (1 ha of mangrove supports a penaeid fishery

Table 3

Annual production, market price and economic value per hectare mangrove for fisheries species utilising this habitat, linked with penaeid shrimp trawling or supported by mangrove outwelling

Area	Production (kg/ha/yr)	Market price (US$/kg)	Value (US$/ha)	Source
Crustaceans				
Penaeid shrimp				
Indonesia	16–165	7.00[f]	112–1155	Martosubroto and Naamin (1977)
Worldwide survey	13–756[a]	7.00[f]	91–5292	Turner (1977)
Peninsular Malaysia	515	7.00[f]	3.605	Gedney et al. (1982)
Philippines	130–350	7.00[f]	910–2450	Pauly and Ingles (1986)
Java, Indonesia	161	7.00[f]	1.127	Naamin (1990)
Irian Jaya, Indonesia	18	7.00[f]	126	Ruitenbeek (1994)
Perak, Malaysia	670	7.00[f]	4.690	Singh et al. (1994); Chan et al. (1993)
Sumatra, Indonesia	274	7.00[f]	1.918	Hambrey (1996)
Sergestid shrimp				
Peninsular Malaysia	63	0.30[f]	19	Gedney et al. (1982)
Malaysia	29[b]	0.30[f]	9	
Philippines	113[b]	0.30[f]	34	
Thailand	89[b]	0.30[f]	27	
Mangrove mud crab				
Kowie, South Africa	34	3.00[f]	102	Hill (1975)
Chanthaburi, Thailand	13	3.00[f]	39	Christensen (1982)
Peninsular Malaysia	15	3.00[f]	45	Gedney et al. (1982)
Andrah Pradesh, India	17	3.00[f]	51	Macintosh (1982)
India, Madagaskar, Thailand	17–23	3.00[f]	51–69	Sivasubramaniam and Angell (1992)
Kosrae, Micronesia	64	5.50	352	Naylor and Drew (1999)
Fish				
Peninsular Malaysia	549	1.00[f]	549	Gedney et al. (1982)
Fiji	257	1.85	475	Lal (1990)
Queensland, Australia	5,840[c]		5330[h]	Morton (1990)
Perak, Malaysia	900	0.80	713	Singh et al. (1994); Chan et al. (1993)
Molluscs				
Blood cockles				
Perak, Malaysia	500–750	0.28[g]	140–210	Macintosh (1982)
Edible molluscs				
Negros Oriental, Philippines	979	0.28[g]	274	NRMC and NMC (1986)
Fish subsidised by penaeid trawlers	87–5,040[d]	1.00[f]	87–5040	
Discarded catch in penaeid fisheries	68–3,931[e]	0.10[f]	7–393	
Fish production from outwelling	3–33	1.00[f]	3–33	

[a] Multiplied by a factor of 1.6 to convert 'head-off' to 'head-on' values (Pauly and Ingles, 1986).
[b] Mean catch (1992–1996) of sergestid shrimps (FAO, 1998) related to mangrove cover (Spalding et al., 1997).
[c] Fish standing stock.
[d] Trawl catch subsidised by penaeid shrimp fishery (667 kg fish:100 kg shrimp) (Turner, 1977).
[e] Catch ratio, 520 kg discarded catch:100 kg shrimps (Alversson et al., 1994).
[f] Assumed market price at present.
[g] Average market value of mussels in Southeast Asia in 1992 (FAO, 1995).
[h] Includes only large-sized marketable fish (valued at Australian $8380).

production of 13 kg) to US$5292 (1 ha supports 756 kg) (Table 3). This high variability in shrimp productivity can be attributed to regional variations in the quality of the mangrove nursery, underreporting of fisheries catch, underdeveloped or overdeveloped shrimp fisheries. In addition, shrimps landed in one area may have been caught in another, and thus the shrimp productivity in the landing area may be overestimated. The average annual penaeid production, based on 43 data sets (summarized in Table 3), is 162 kg/ha mangrove, estimated at US$1134 (based on a market price of US$7.00/kg). Moreover, because penaeid shrimp sales generate most of the revenues from mechanized trawling in developing countries, shrimps (and indirectly mangroves) effectively subsidise commercial fish harvesting efforts by these vessels, including fish species not using mangroves as habitat (Turner, 1977; Bennett and Reynolds, 1993). Trawl catch ratio between marketed fish and penaeids in Indonesia was 667 kg of fish for every 100 kg of shrimps trawled (Turner, 1977). In addition, the discarded catch from shrimp trawling has a potential value if landed and utilised for human consumption or processed into fish meal. The mean ratio of discarded to landed weight in shrimps is 5.20 globally, with a maximum recorded ratio of 14.7 for Trinidadian shrimp trawling (reviewed by Alversson et al., 1994). Roughly speaking, 1 ha of mangrove generating a penaeid fishery production of 162 kg, sustains a market value of US$2340 from penaeid shrimp fishery (US$1134), discarded catch (US$126), and subsidised trawl fisheries (US$1080) alone.

6.1.2. Fish

The market value of commercial fish species utilising mangroves as habitat ranges from US$475 to 5330 ha/year (Table 3). Morton (1990) based his calculations on field sampling from a subtropical mangrove in eastern Australia. Twice a month during a whole year, the same 3340-m^2 area of *Avicennia marina* was sampled with block nets. The total biomass of fish caught over the year was as high as 5840 kg/ha. From the total annual catch Morton (1990)

made a conservative estimate of the market value, which equaled US$5330/ha mangrove. However, this value only included marketed fish value, and did not account for the numerous commercially important juveniles caught in the study. In Perak, Malaysia, 39 000 t of mangrove-dependent fish were landed in 1990, valued commercially at US$31 million (Singh et al., 1994). Divided by the areal extent of mangrove in this state (Chan et al., 1993), the annual production of fish would be 900 kg/ha, supporting a market value of US$713.

6.1.3. Coastal seascape perspective

Through biophysical interactions, mangroves also support fisheries where the harvested species themselves never visit mangrove environments. The export of organic carbon and nutrients from mangroves constitutes a trophic subsidy to fisheries production. In an estuarine-lagoon system, the ratio of potential maximum sustainable fish yield to primary production by weight ranges from 0.0008 to 0.01 (Marten and Polovina, 1982). The potential fish yield supported by mangrove outwelling ranges from 3 to 33 kg/ha (Table 3), based on this ratio and a particulate carbon export of 3300 kg/ha per year (Robertson et al., 1992). The role of mangroves in maintaining coastal water quality indirectly supports the functioning and fisheries production of other ecosystems like coral reefs. Reefs have high fish standing stocks, and annual fisheries production has been estimated to be as high as 370 kg/ha (Alcala, 1988). Reef fisheries harvest many high-valued species, resulting in high market value for these fisheries. An excellent example of how to address the impact of sedimentation on coastal ecosystems is seen in a case study of resource-use conflicts, logging versus fisheries and tourism, carried out in Palawan, Philippines (Hodgson and Dixon, 1988). The competition between these industries was indirect through major ecosystem links. Erosion from coastal logging operations produced negative downstream effects on the marine ecosystem via sedimentation, and posed a threat to the viability of the coral reef tourism and the fishery industries. The results of

this study were striking, with the gross revenues under the no-logging-option more than doubling those of the continued-logging-option (Hodgson and Dixon, 1988).

6.2. Aquaculture

The economic profit from aquaculture systems in mangrove environments is dependent on the support capacity of mangroves (Fig. 1). However, this 'free' support is not internalised in the market price of the product. The erosion control and protection against floods and hurricanes provided by mangroves could be valued by using the replacement cost of building hard protective structures in its place. In peninsular Malaysia, Chan et al. (1993) estimated this cost at US$3 million per kilometre coastline. Costanza et al. (1997) estimated the disturbance regulation to be worth US$1800/ha mangrove annually.

The susceptibility to self-pollution and subsequent collapse of aquaculture systems can be reduced if pond operation logistics enables the assimilation of effluents by surrounding mangroves. The value of this service should be compared with the cost involved in nitrogen and phosphorous reduction in conventional water treatment systems. The overall waste treatment function of mangroves has been estimated at US$6700/ha per year (Costanza et al., 1997).

Products like seed, broodstock and fishmeal ingredients have a market price, and if the productivity of these organisms is known, an economic value per mangrove area can be estimated. The opportunity cost of wild seed collection, resulting from discarded bycatch, should be included in an economic analysis of this activity. The collection of larvae and juveniles can be substantial in many countries. For instance, around 50 000 persons are involved in penaeid postlarvae collection in West Bengal, India (FAO/NACA, 1995). The favoured species for shrimp culture, i.e. *Penaeus monodon*, constitutes a very small proportion (down to 0.1%) of fish and invertebrate larvae in seed collector's catch (Primavera, 1998). Thus, the bycatch can be substantial, having significant negative impacts on biodiversity and capture fisheries production in the area.

7. Conclusion

This article illustrates the essential role of mangrove ecosystem in sustaining such human activities as capture fisheries and aquaculture. The amount of seafood production that can be supported by mangroves shows spatiotemporal variations throughout the tropics and subtropics. Therefore, when evaluating mangroves for seafood production or discussing management from a fisheries perspective, mangroves have to be viewed as dynamic ecosystems with non-linearities, thresholds and discontinuities (Costanza et al., 1993).

For crustaceans (penaeid shrimp, sergestid shrimps and mangrove mud crab), fish and molluscs that use mangroves as habitat the annual market value of fisheries per hectare mangrove ranges from US$750 to 11 280. If discarded catch in shrimp fisheries and other trawl fisheries subsidised by the penaeid fishery are included, the marketed value of fisheries dependent on mangroves ranges from US$850 to 16 750/ha per year. This value is eight to 170 times higher than previous capture fisheries values in the order of US$100 often used in cost-benefit analysis of management alternatives for mangroves (Christensen, 1982; Ruitenbeek, 1994; Janssen and Padilla, 1997). These lower market values must be considered as grave underestimates, given the information outlined in this article. Unfortunately, undervaluation is a major driving force behind the conversion of mangroves into alternative uses like shrimp pond farming. In part, this trend of undervaluation is due to the difficulty involved in placing a monetary value on some of the mangrove-related fisheries. Lack of ecological knowledge and a holistic approach among those performing the evaluation may be even more important determinants. Additional research is needed to identify fishery species directly or indirectly associated with mangroves, and to obtain reliable catch data for these. Estimates of fisheries production from mangroves have mainly focussed on penaeid shrimps, and there is a severe lack of good productivity estimates for other fishery species. Another serious shortcoming of economic valuations has been the inability to acknowledge

the biophysical support from mangroves to seafood production in other systems. Recognizing the importance of mangroves to subsistence economies should also be self-evident when evaluating the production of fish and shellfish. However, the failure to take this non-commercial direct use value into account is often a major factor behind policy decisions that lead to overexploitation of mangroves (Barbier, 1994).

The life-support functions of mangroves set the framework for sustainable aquaculture in the tropical coastal seascape. Ecological illiteracy has, however, often caused the development of aquaculture systems like intensive shrimp farming, known for their ecological and socio-economic unsustainability (Macintosh and Phillips, 1992; Primavera, 1998). Ecological services, including flood and storm protection, erosion control, and water quality maintenance are crucial for the sustainability of aquaculture systems. In addition, low availability of seed or broodstock is a serious constraint to increased aquaculture production in many systems. Ironically, this is aggravated by the destruction of mangroves to accommodate aquaculture activities. Although the economic profit from aquaculture systems in mangrove environments depends on the support capacity of mangroves, the market price of the cultured product does not capture most of the goods and services provided by the mangrove ecosystems. These 'free' goods and services would require considerable amounts of energy and money if they were to be substituted with human technology based on fossil fuels. By internalising this 'free' support from mangroves, the market price of the product would increase significantly, thereby jeopardizing the economic sustainability of the aquaculture system itself.

Finally, it should be emphasized that this article has only focused on seafood production supported by mangrove ecosystems. Additional efforts to evaluate natural products and ecosystem services generated by mangroves (Table 1) would further demonstrate the dynamics of this system, and highlight its value and support to subsistence, local, and national economies. With increasing ecological and socio-economic knowledge, the conversion of mangroves into development activities whose social costs far outweigh their benefits should be reduced.

Acknowledgements

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Present state and future of the world's mangrove forests

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SUMMARY

Mangroves, the only woody halophytes living at the confluence of land and sea, have been heavily used traditionally for food, timber, fuel and medicine, and presently occupy about 181 000 km² of tropical and subtropical coastline. Over the past 50 years, approximately one-third of the world's mangrove forests have been lost, but most data show very variable loss rates and there is considerable margin of error in most estimates. Mangroves are a valuable ecological and economic resource, being important nursery grounds and breeding sites for birds, fish, crustaceans, shellfish, reptiles and mammals; a renewable source of wood; accumulation sites for sediment, contaminants, carbon and nutrients; and offer protection against coastal erosion. The destruction of mangroves is usually positively related to human population density. Major reasons for destruction are urban development, aquaculture, mining and overexploitation for timber, fish, crustaceans and shellfish. Over the next 25 years, unrestricted clear felling, aquaculture, and overexploitation of fisheries will be the greatest threats, with lesser problems being alteration of hydrology, pollution and global warming. Loss of biodiversity is, and will continue to be, a severe problem as even pristine mangroves are species-poor compared with other tropical ecosystems. The future is not entirely bleak. The number of rehabilitation and restoration projects is increasing worldwide with some countries showing increases in mangrove area. The intensity of coastal aquaculture appears to have levelled off in some parts of the world. Some commercial projects and economic models indicate that mangroves can be used as a sustainable resource, especially for wood. The brightest note is that the rate of population growth is projected to slow during the next 50 years, with a gradual decline thereafter to the end of the century. Mangrove forests will continue to be exploited at current rates to 2025, unless they are seen as a valuable resource to be managed on a sustainable basis. After 2025, the future of mangroves will depend on technological and ecological advances in multi-species silviculture, genetics, and forestry modelling, but the greatest hope for their future is for a reduction in human population growth.

Keywords: mangrove forest, conservation, exploitation, coastal resources, management, current state, projection

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INTRODUCTION

Mangroves are the only forests situated at the confluence of land and sea in the world's subtropics and tropics. Mangroves are trees or shrubs that develop best where low wave energy and shelter foster deposition of fine particles enabling these woody plants to establish roots and grow. Mangrove forests are architecturally simple compared to rainforests, often lacking an understorey of ferns and scrubs, and are ordinarily less species-rich than other tropical forests.

The global distribution of mangroves indicates a tropical dominance with major latitudinal limits relating best to major ocean currents and the 20°C seawater isotherm in winter (Fig.1). The latter point underscores the paramount importance of warm temperatures for the existence of mangroves. There are 9 orders, 20 families, 27 genera and roughly 70 species of mangroves occupying a total estimated area of 181 000 km² (Spalding *et al.* 1997). The most diverse biogeographical regions are in the Indo-West Pacific (Fig. 1). Indonesia, Australia, Brazil and Nigeria have roughly 43% of the world's mangrove forests.

The standing crop of mangrove forests is, on average, greater than any other aquatic ecosystem, with a decline in above-ground biomass with increasing latitude (Fig. 2). Mangrove forests around the equator can be immense, rivalling the biomass of many tropical rainforests. The biomass of mangrove forests is even greater than in Figure 2 if the biomass of living roots beneath the forest floor is included; below-ground biomass can equal the standing crop rising above-ground (Clough 1992).

Mangroves possess characteristics that, in total, make them structurally and functionally unique. Morphological and ecophysiological characteristics and adaptations of mangrove trees include aerial roots, viviparous embryos, tidal dispersal of propagules, rapid rates of canopy production, frequent absence of an understorey, absence of growth rings, wood with narrow, densely distributed vessels, highly efficient nutrient retention mechanisms, and the ability to cope with salt and to maintain water and carbon balance.
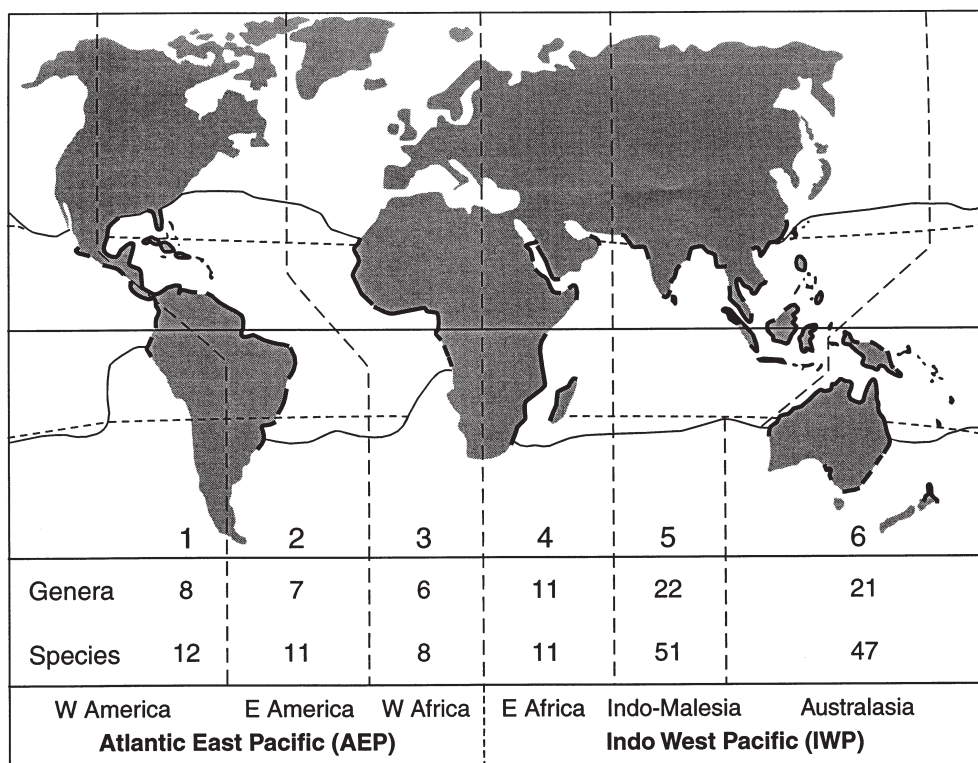
Figure 1 Distribution and biogeographical provinces of the world's mangrove forests. Forests are designated as heavy lines. The numbers of genera and species within each of the six provinces are noted below the map. Modified from Spalding *et al.* (1997) and Duke *et al.* (1998).
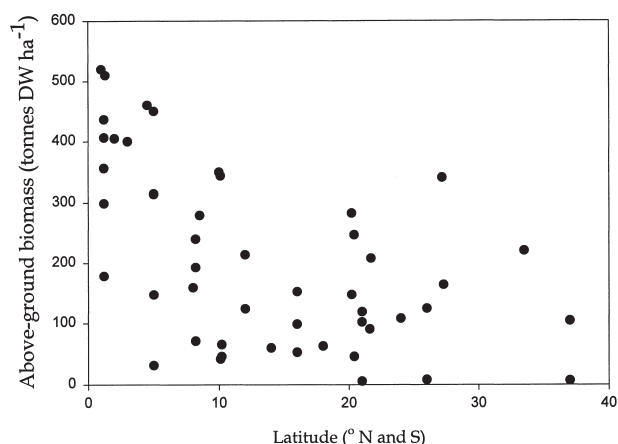

Figure 2 Latitudinal trends in mangrove forest biomass (tonnes dry weight ha^{-1}). Modified and updated from Alongi (1998) and Fromard *et al.* (1998).

Ecosystem characteristics include comparatively simple food webs containing a mixture of marine and terrestrial species; nursery grounds and breeding sites for birds, reptiles and mammals; and accumulation sites for sediment, some contaminants, carbon and nutrients. The biology and ecology of mangroves have been recently reviewed (Hogarth 1999; Ellison & Farnsworth 2000; Kathiresan & Bingham 2001).

The objective of this review is to critically examine the present status of the world's mangrove forests and to offer a best estimate of their future to the year 2025. Such a review is necessary and timely, considering disparate threats to their existence from increasing population growth, global warming, aquaculture, and industrial and urban development. To develop a reasonable prognosis, I first consider trends and salient characteristics of mangrove ecosystems that offer best clues as to how mangroves may respond to threats in future, followed by an assessment of present threats and impacts that are most likely to continue or intensify into the future. Finally, I conclude with some advice for managers, including an analysis of important gaps in knowledge and practical actions that managers can take for the conservation of mangroves.

ENVIRONMENTAL FORCING FACTORS

Natural influences

Factors influencing the structure and function of mangrove forests vary in relation to global, regional and local scales over different time scales (Duke *et al.* 1998). At the global scale, mangroves are ultimately limited by temperature, but at the regional scale the area and biomass of mangrove forests vary in relation to rainfall, tides, waves and rivers. Various schemes have been developed to classify mangroves on local scales. However, in reality, most forests represent a continuum of geomorphological types based on their location within broader settings classified as river-dominated, tide-dominated, wave-dominated, composite wave- and river-dominated, drowned bedrock valley and carbonate

(Woodroffe 1992). Waves, tides, rivers and rainfall affect water circulation by generating turbulence, advective and longitudinal mixing and trapping coastal water, influencing the rate of erosion and deposition of sediments on which mangroves grow. Many physical and ecological variations are often expressed within a single estuary (Duke *et al.* 1998).

Mangroves are typically distributed from mean sea level to highest spring tide, and perhaps the most conspicuous feature on first glance is the sequential change of tree species parallel to shore. Many factors have been suggested to account for the apparent zonation of trees and other associated organisms across the intertidal seascape. These include salinity, soil type and chemistry, nutrient content, physiological tolerances, predation and competition (Smith 1992). Some of these factors, such as competition, remain essentially unstudied; the results of recent studies are conflicting, prohibiting generalizations about the mechanisms governing zonation. It is more likely that a few of these factors in combination come into play over different temporal and spatial scales to control mangrove distribution (Bunt 1996; Ball 1998). For an individual tree, several factors operate in tandem to regulate plant growth, including temperature, nutrients, solar radiation, oxygen and water (Clough 1992). For a mangrove ecosystem, natural changes occur on the scale of minutes to hours for microbial and physiological processes, of months to years for tree growth and replacement, and of decades to centuries for regional forest changes (Twilley *et al.* 1996).

Determination of possible impacts in future must be considered against a background of natural disturbance. Mangrove forests are often naturally disturbed by cyclones and other storms, lightning, tsunami and floods, and often take decades to recover (Smith *et al.* 1994). Cyclones are common, for instance, in the Caribbean and the Bay of Bengal regularly destroying millions of trees. Other natural events, such as disease, may be sublethal, causing stunted growth or gradual death or replacement of species. For instance, in the Sunderbans of Bangladesh, nearly 20% of *Heritiera fomes* trees have been severely affected by 'top dying', a disease that slowly kills the trees by moving from leaves, branches and twigs to the main stem (Spalding *et al.* 1997). Mangroves become more susceptible to diseases and pests when stressed by changes in salinity, tidal inundation, sedimentation and soil physicochemistry, the introduction of pollutants such as oils, herbicides, metals, sewage and acids, and damage from storms and cyclones.

Pests can have a severe impact on mangrove forests. Epidemics of bacteria, viruses, fungi, spiders and boring insects and invertebrates that destroy leaves and wood can significantly reduce forest viability. For example, caterpillars parasitize and inhibit germination of fruits of *Rhizophora* trees in northern Australia (Robertson *et al.* 1992). Various organisms such as sesarmid crabs normally chew and consume a small proportion of mangrove vegetation, especially propagules and seedlings, inhibiting replenishment of older stands (Smith 1992). General explanations of such natural phenomena are complicated by the fact that one forest can be severely disturbed by pests or predators, but an adjacent stand may not be affected at all.

The dynamics of natural gaps in mangrove forests is poorly understood, but represents a cycle of natural mortality and regeneration that must be considered when impacts are assessed, especially over the long-term (Smith 1992). Various approaches have been used to assess mangrove forest dynamics, such as traditional measurement of tree species abundance and structure over time (Clough 1992) and more recent modelling methods of simulating competition, spacing and ageing of trees (Berger & Hildenbrandt 2000). Most studies indicate that the temporal and spatial variations within mangrove forests are commonly regulated by intra- and inter-specific competition for light, space and soil nutrients that are also patchy within stands (Lugo 1997). As in other forests, these factors give rise to the so-called self-thinning line, a pattern of tree distribution with a progressive decline in density of growing trees (Clough 1992).

Terrestrial forests and mangrove forests share many of the same basic physical and ecological attributes, but other attributes of mangroves appear to be unique (see Introduction), challenging concepts such as the old-growth or late-successional forest (Lugo 1997). The apparent paradox that mangroves appear to be in steady-state despite exhibiting characteristics of establishment, thinning and transitional stage forests, can be explained by the periodic nature of disturbances (Lugo 1997). For instance, a variety of ecosystem states can develop as a result of mangrove growth and development being altered by changes in sea level, lightning, cyclones and other disturbances, resulting in a forest exhibiting a mosaic of successional characteristics. The difficulty in matching many attributes identified with terrestrial old-growth forests highlights the problem of distinguishing natural from anthropogenic-induced change in mangrove forests.

Existing human impacts and threats

Mangroves are heavily used traditionally and commercially worldwide. Local communities have always used mangroves as a source of wood for cooking and heating, and for building houses, huts, fences, matting and scaffolds (Table 1). Timber is also widely used to produce charcoal, tannins and resins for dying and leather making, furniture, bridges, poles for fish cages and traps, medicines, alcohol, boats and many other products (Kathiresan & Bingham 2001). Mangrove stands and associated waterways are important sites for gathering and small-scale cultivation of shellfish, finfish and crustaceans. Local communities are often faced with the problem of over-exploited fisheries.

Commercial practices are being increasingly adopted in developing nations due to strong pressure to increase wealth and living standards of people living in coastal areas. Commercial exploitation is commonly forced from outside the local community, and is nearly always on a scale much larger than the local forests can sustain. Examples of

commercial exploitation include felling for wood products, housing and commercial developments, and modification of natural waterways for bridges and levees (Table 1).

Felling of forests is one of the oldest forms of commercial exploitation. While much felling is unsustainable, evidence from a number of commercial operations suggests that mangrove forests can be sustainably exploited for wood. For example, production of wood from the Matang Mangrove Forest Reserve in Perak, Malaysia has been sustained since 1906 (Gan 1995). The reserve consists of roughly 40 151 ha of pure and mixed stands of *Rhizophora* and *Bruguiera*, of which only 250 ha has been lost to settlement expansion; nearly 1500 ha have been gained by natural accretion of sediment and mangrove colonization. Roughly 1050 ha of forests are clear felled annually over a 30 year rotation cycle, with an average yield of $17.4\,t\,ha^{-1}\,yr^{-1}$ (Gan 1995). Management plans for Matang are complex and frequently revised, undoubtedly contributing to the success of the commercial operation.

The loss of mangroves for pond aquaculture is currently one of the largest threats to mangrove forests worldwide. The list of direct and indirect problems caused by pond aquaculture is long and includes:

- immediate loss of mangroves to construct ponds;
- blockage of tidal creeks;
- alteration of natural tidal flows;
- alteration of the groundwater table;
- increase in sedimentation rates and turbidity in natural waters;
- release of toxic wastes;
- overexploitation of wild seed stocks;
- development of acid sulphate soils;
- reduced water quality;
- introduction of excess nutrients; and
- alteration of natural food chains.

Other forms of aquaculture may or may not be less destructive. Cultivation of grouper and sea bass in floating cages offers an inherently less destructive form of fisheries exploitation, but the extent of impact depends upon proper planning and management, including appropriate siting of cage farms, limitations on density of cages, and methods of feeding of cage stock. The same is true for exploitation of shellfish, such as the blood cockle, on mudflats adjacent to mangrove forests (Gan 1995). Limited operations do not appear to have demonstrable impacts on other mangrove resources, but management models to predict sustainable limits are generally lacking for mangrove ecosystems.

Other abuses of mangroves are often subtle, indirect and sublethal. For instance, the encroachment and growth of human populations in coastal areas usually results in increased wastes that are often dumped into mangroves and adjacent coastal waterways. Mangrove waters can assimilate some excess nutrients, but the assimilative capacity for most waterways are unknown and likely to vary depending on the

Table 1 Current human impacts on the world's mangrove forests.

Potentially sustainable	*Unsustainable*
Food	Eutrophication
Tannins and resins	Habitat modification/ destruction/alteration for coastal development (including pond aquaculture)
Medicines and other bioproducts	
Furniture, fencing, poles (timber)	
Artisanal and commercial fishing	
Charcoal	Disruption of hydrological cycles (damming)
Cage aquaculture	
Ecotourism	Release of toxins and pathogens
Recreation	Introduction of exotic species
Education	Fouling by litter
	Build-up of chlorinated and petroleum hydrocarbons
	Shoreline erosion/siltation accelerated by deforestation, desertification and other poor land-use practices
	Uncontrolled resource exploitation
	Global climate change
	Noise pollution
	Mine tailings
	Herbicides and defoliants

form, type and frequency of effluent discharge, tidal range, waterway dimensions, climate, and plankton productivity and abundance (Trott & Alongi 2000). Mangrove plants and their associated microbes exhibit reduced growth when exposed to dissolved heavy metals particularly at concentrations at least five times greater than those in pristine mangrove soils (Yim & Tam 1999). The effect of some contaminants can be cumulative. Studies of oil spills in the Caribbean have shown that mangroves exhibit increased mutation rates and long (approximately 20 years) recovery times after repeated exposure (Burns *et al.* 1993; Klekowski *et al.* 1994). Physical smothering can often have as great an impact as chemical impairment of physiological performance.

Short-term climatic events may also be important environmental forcing factors. In the only known study of the impact of the El Niño-Southern Oscillation (ENSO) on mangroves, Drexler and Ewel (2001) found that in Micronesia the 1997–1998 ENSO-related drought resulted in greater soil and groundwater salinity. The most dramatic impact was a reversal of groundwater flow that sent groundwater from the mangroves upstream towards freshwater wetlands. The ecological impact of the drought was not examined, but the potential disruption to ecological processes is clear (Drexler & Ewel 2001).

IDENTIFIED LONG-TERM TRENDS

The ability to differentiate between natural and human-induced disturbance is especially challenging given the lack of long-term data for mangroves. Nevertheless, some data from a few forests can be used to identify natural changes that likely happen over time.

Natural changes in forest structure

Detection of human impacts on the structure of mangrove forests must be considered against a background of natural change in stand succession and canopy structure. Like other forests, mangrove stands follow a natural series of phases over time, from an initial pioneering stage through to rapid early growth and development, to later maturity, senescence and death (Jimenez *et al.* 1985). This natural progression is supported by data from French Guiana where Fromard *et al.* (1998) measured the structure, biomass and stand dynamics of several mangrove species. The data indicate a natural development of mangrove stands with a correlation between stem density and estimated forest age (Fig. 3).

Many stands of mangroves in the Mekong Delta were rehabilitated after the large-scale defoliation and destruction during the Vietnam War. The age of replanting and managed cutting is known, offering a rare opportunity to determine how stand structure changes with increasing age of mangrove forests (Clough *et al.* 1999). A structural analysis of various stands of *Rhizophora apiculata* indicates that tree densities decline with forest age (Fig. 4*a*), in agreement with the model of Jimenez *et al.* (1985). As in other forests, the stands become less dense due to self-thinning, as evidenced by an increase in tree girth or diameter-at-breast-height (Fig. 4*b*). Less dense but larger mature trees lead to an increase in total above-ground biomass per hectare with increasing age (Fig. 4*c*). Embedded within the long-term trend are temporal and spatial variations in individual tree growth, photosynthetic production, respiration and litterfall. In natural forests, changes in species composition occur, especially in light gaps, and with increasing distance upland.

Community structure, abundance and biodiversity

Within forest communities
Trees and bacteria dominate the biomass and productivity of mangrove forests (Fig. 5), but the structure of mangrove food

webs is unique, having both marine and terrestrial components. Data on temporal trends in mangrove food webs usually are seasonal rather than inter-annual. Abundance and biomass of organisms living in the canopy, on or beneath the forest floor and in associated waterways often vary seasonally in relation to rainfall, and spatially in response to a variety of factors that are often the same as those regulating the trees (Kathiresan & Bingham 2001).

The structure and function of mangrove food webs is ultimately driven by the production of carbon fixed mostly by the trees and by the flow of dissolved and particulate organic
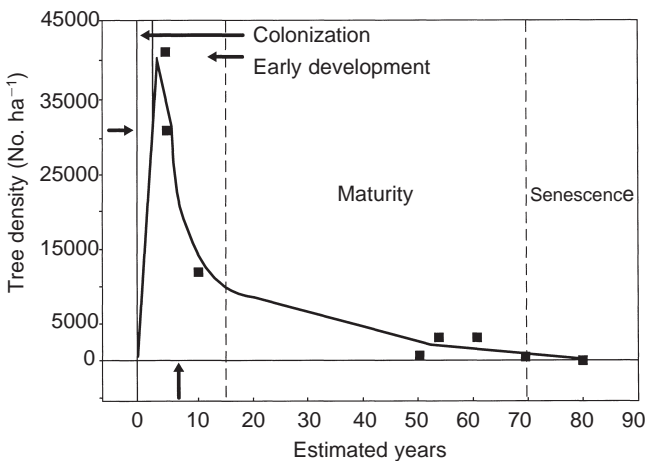
Figure 4 Relationship of (*a*) stem density, (*b*) diameter at breast-height (DBH) and (*c*) above-ground biomass (tonnes dry weight ha^{-1}) to age of *Rhizophora apiculata* forests in the Mekong delta, Vietnam. Modified from Clough *et al.* (1999).

Figure 3 Colonization and development of mangrove forests over time. Data from Fromard *et al.* (1998) based on model of Jimenez *et al.* (1985).
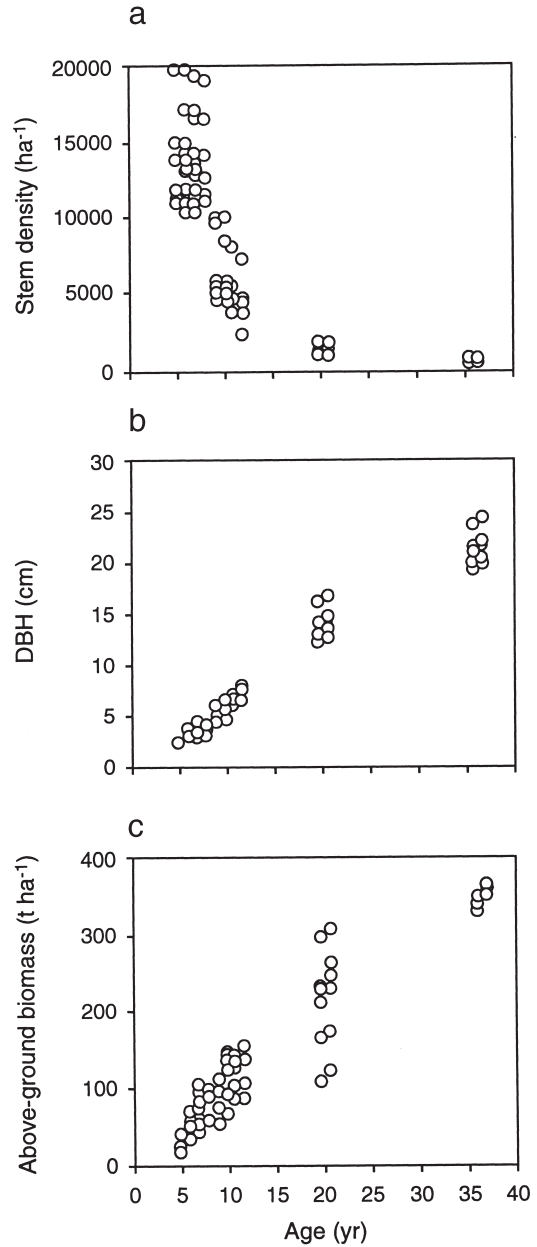
matter within the forest and adjacent tidal waters. Within the forests, a suite of decomposer organisms directly or indirectly consumes a variable proportion of forest litter. Sesarmid, portunid, and ocypodid crabs are keystone organisms in many (but not all) forests. These crabs retain litter and recycle nutrients within forest soils, bioturbate the forest floor to stimulate microbial decomposition and, especially in the case of grapsid crabs, prey on propagules to influence the distribution, abundance and succession of tree species (Smith *et al.* 1991). It is simple to predict that losses of crabs as a result of pollution, for example, would negatively affect the growth and natural succession of mangrove forests.

The abundance and species diversity of infauna are generally low compared with other benthic habitats (Alongi & Sasekumar 1992). Low species richness may be the result of negative effects of polyphenolic acids derived from trees, low densities of surface microalgae, and the harsh physical conditions induced by tidal cycles of exposure and inundation.

The abundance and biomass of epifauna and tree-dwelling assemblages can often exceed those of the infauna. Gastropods and crustaceans are the major epifaunal groups, and exhibit clear distribution patterns related to frequency of tidal inundation, changes in sediment granulometry, water content, temperature, food sources, wave energy, salinity, anoxia, competition and predation. On the trunks, prop roots and branches of trees, most animals feed on organic debris and algae; lower on the trunks, an encrusting fauna may in turn provide a rich and mobile cryptofauna with safe refuge. These conspicuous assemblages can form a mosaic of vertically zoned organisms that are often the first residents to be harmed by pollution and other anthropogenic inputs (Alongi & Sasekumar 1992).

No attempts have been made to examine decadal trends in faunal abundance and species composition, but a few studies have examined faunal changes in relation to development and age of forests (Suzuki *et al.* 1997; Sasekumar & Chong 1998). In managed forests at different stages of the harvest cycle in Malaysia, epifaunal density and diversity was greater in a 60 year-old *R. apiculata* forest than in a recently cleared stand. The infauna showed a different pattern with greatest density and biomass in the cleared forest (Sasekumar & Chong 1998); this anomaly was attributed to greater abundance of surface algae with increasing light after canopy removal. In Thailand, an increase in benthic faunal abundance was observed in mangroves replanted in abandoned shrimp ponds (Suzuki *et al.* 1997). The sparse data indicate some impact of forest development and maturity on benthic faunal richness and diversity with a tendency toward more diverse assemblages in undisturbed and mature forests, but no forecast of long-term trends is possible.

Higher in the canopy, various species of mammals, insects and birds permanently or temporarily reside in some forests, often in dense assemblages (Kathiresan & Bingham 2001). Bird communities can be spatially and trophically complex with up to eight feeding guilds, namely granivores, frugivores, piscivores, aerial hawkers, and hovering, gleaning, flycatching and bark-foraging insectivores. A few species are nearly confined to mangroves, including several species of yellow warblers, mangrove vireo, and mangrove cuckoo. Noteworthy mammals include monkeys and flying fox, and within tidal waters, dolphins and otters. These animals are also among the first residents to flee or be harmed by human alteration of mangroves.

Pelagic communities

Pelagic food webs in mangrove waterways are usually more responsive than benthic organisms, being ordinarily affected by longitudinal and lateral mixing and trapping of water by currents, tides and waves. Plankton communities in mangrove waters do respond quickly to nutrient enrichment from aquaculture or run-off from agricultural lands, most often exhibiting an increase in growth rate and standing crop (Ayukai & Alongi 2000).

Like benthic animals, diversity and abundance of plankton is usually low and highly variable (Robertson & Blaber 1992). There is a conspicuous lack of information on the ecology of mangrove-associated microbes. The sparse data indicate abundance of bacteria and protozoa within the range of other coastal waters (Robertson & Blaber 1992), but their trophic role is more often presumed, based on relationships in other tropical coastal waters, than based on empirical data.

The ecology of zooplankton in mangrove waterways is somewhat better understood (Robertson & Blaber 1992). Species composition is influenced by seasonal variations in salinity and degree of freshwater input. Decadal studies of plankton dynamics in mangrove waters do not exist, but several annual studies indicate density peaks during summer as a result of temperature control of reproduction (McKinnon & Klumpp 1998).

Studies of nekton, especially prawns and fish, are more common and indicate the importance of mangroves as
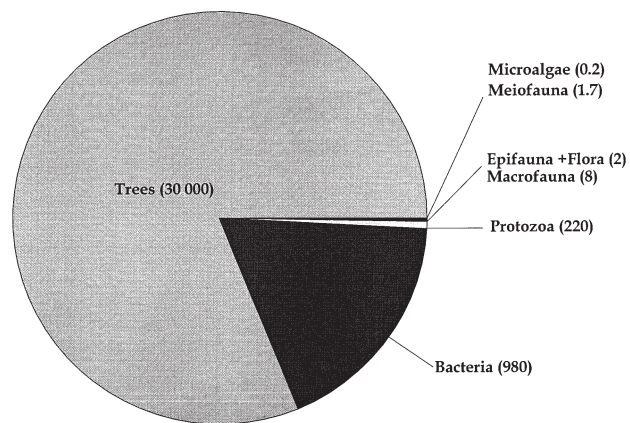

Figure 5 The distribution of living biomass (g dry weight m^{-2} to a sediment depth of 1 m) in a mature mixed *Rhizophora* forest in northern Australia. Based on data in Alongi and Sasekumar (1992) and Alongi (1998).

nursery grounds and refuges (Robertson & Blaber 1992). Many coastal species spend critical early stages of their lives in mangrove waters. The number of microhabitats is a major factor influencing community composition of fish. The number of microhabitats is however ultimately dependent upon environmental factors such as tidal amplitude, water quality and salinity (Robertson & Blaber 1992).

There are several patterns of species richness in fish communities:

- more species are usually found in large (range: 104–197 species) than in small (range: 8–128 species) estuaries;
- mangrove fish communities in the Indo-West Pacific are species-rich compared with those in some Atlantic estuaries;
- subtropical estuaries house fewer species than tropical estuaries;
- connectivity between mangroves and adjacent ecosystems (e.g. coral reefs, seagrass beds) influences community composition; and
- the nature of the offshore environment is critical in determining movements of larvae and juveniles, underscoring the fact that mangroves are not functionally divorced from adjacent coastal habitats.

Densities of juvenile fish in mangrove estuaries are high compared with other estuarine habitats. Robertson and Blaber (1992) suggest that mangroves are sources of various types of food, and provide shelter and protection.

Hypoxia, chemicals, diversion or alteration of natural tidal cycles, damming and other forms of pollution usually lower the abundance of fish and other pelagic (and benthic) organisms. Fish ordinarily escape rather than tolerate lowered water quality, but nonetheless, do not readily return to the scene of impact; the same is true for crocodiles, alligators, snakes, turtles, and lizards (Kathiresan & Bingham 2001). Recovery depends on the nature, areal extent, duration and intensity of disturbance. Recovery from a small-scale disturbance is often rapid, but there may be permanent loss from a catastrophe such as a massive oil spill (Burns *et al.* 1993). Habitat loss results in a lowering of population densities and loss of diversity of most mangrove-associated organisms.

Ecosystem function

Importance of mangrove forest production

Decadal trends in rates of mangrove primary production are unknown, as canopy production remains difficult to quantify and is often measured by indirect methods. The most reliable estimates of net primary production come from incremental measurements of biomass accumulation, but such measurements are time-consuming and laborious. The study by Day *et al.* (1996) in Mexico constitutes the longest temporal record (7 years) of mangrove net primary production. In both basin and scrub forests, Day *et al.* (1996) attributed most inter-annual variability in above-ground production and

litterfall to soil salinity, minimum air temperature, and minimum rainfall, highlighting the importance of climate.

Most published estimates of primary production are derived from rapid survey measurement of light attenuation under the canopy. Estimates of net primary production using this technique range from 18–$34\,kg\,C\,ha^{-2}\,d^{-1}$, but these rates are underestimates, insufficient to account for observed accumulation of biomass above-ground. A more recent method based on measurement of light transmission and measurement of net photosynthesis of leaves, indicates net daytime photosynthetic rates nearly 10 times greater than previous production estimates (Clough *et al.* 1997). If accurate, net primary production of mangroves in many regions is likely to be significantly greater than previously thought.

In a comparison of this new method and the older technique in a 22 year-old *R. apiculata* forest in Malaysia, Clough *et al.* (1997) calculated net photosynthetic rates of 155 and $13\,kg\,C\,ha^{-1}\,d^{-1}$ using the new and old methods, respectively. A preliminary carbon balance for these trees (Table 2) indicates that only a small proportion of this production is allocated to above-ground biomass or lost as litterfall; most is probably lost via respiration and allocated to root production. Litterfall is often used as a proxy measure of mangrove production, but this newer data casts doubt on its appropriateness for this purpose. Litterfall is useful to examine annual reproductive patterns and the amount of organic matter potentially available for decomposition and export. Like biomass, litterfall decreases globally with distance from the equator (Saenger & Snedaker 1993).
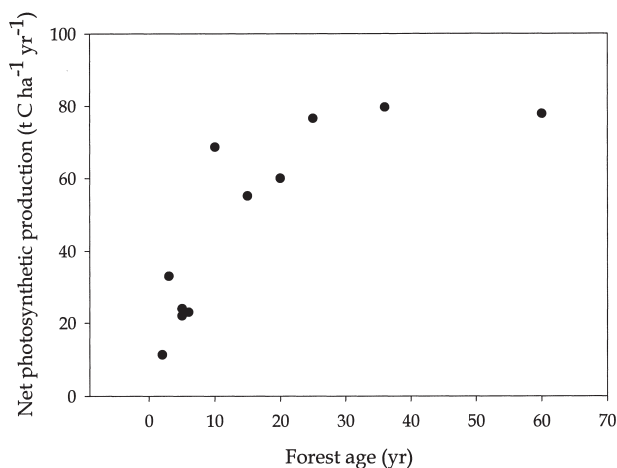
A plot of net canopy production of different aged *Rhizophora apiculata* forests in south-east Asia (Clough *et al.* 1999), shows a general trend of increase in production until 25–30 years, with the older forests maintaining rapid carbon fixation rates (Fig. 6). The high productivity of older forests shows how important mature forests are in accumulating and storing of carbon over the long-term. This characteristic of mangrove forests is likely to acquire greater relevance with the forecasted increases in atmospheric greenhouse gases this century.

Consumption, export and storage of mangrove carbon

Mangroves are among the most productive plants in the ocean (Duarte & Cebrian 1996), the recent advances in estimating photosynthetic production indicating that, on an areal basis, mangroves are usually more productive than saltmarshes, seagrasses, macroalgae, coral reef algae, microphytobenthos, and phytoplankton. Most mangroves fix carbon well in excess of ecosystem requirements, with the excess carbon representing 40% of net primary production (Duarte & Cebrian 1996). Of the mangrove carbon produced, 9% is consumed by herbivores, 30% is exported, 10% is stored in sediments, and 40% is decomposed and recycled within the system (Duarte & Cebrian 1996). Recent measurements of mangrove photosynthesis (Clough *et al.* 1997) imply that either more carbon is stored in wood and eventually decomposed within the system or more carbon is stored in sediments or exported to the adjacent coastal zone, than estimated by Duarte and Cebrian (1996).

Table 2 Carbon balance for 22-year-old *Rhizophora apiculata* trees in Malaysia (modified from Clough *et al.* 1997).

Component	Flux (t C ha^{-1} yr^{-1})
Net daytime canopy photosynthetic production	56
Carbon allocation	
Above-ground biomass accumulation	6.5
Below-ground biomass accumulation	0.6
Litter fall	4.4
Below-ground root turnover	?
Night time foliar respiration	13
Below-ground root respiration	?
Stem, branch & prop root respiration	?

Figure 6 The relationship between forest age and photosynthetic production in *Rhizophora apiculata* forests in South-east Asia (Thailand, Malaysia and Vietnam). Data compiled from Clough *et al.* (1999), Alongi and Dixon (2000) and D.M. Alongi (unpublished data from Malaysia 1999).

Levels of herbivory are known (Ellison & Farnsworth 2000), as is the proportion of organic material exported from mangroves (Robertson *et al.* 1992). There are few data on carbon storage in mangrove wood or sediments but the sparse data suggests that some forests can accumulate carbon (Twilley *et al.* 1992; Alongi *et al.* 2000, 2001). Recent information from tropical rainforests indicates that mature forests have a long-term capacity to store carbon in wood (Chambers *et al.* 2001); such may be the case for some mangrove forests, especially mature stands.

Because mangroves fix and store significant amounts of carbon, their loss may have a significant impact on global carbon budgets. In a recent analysis of the fate of fixed carbon in marine ecosystems, Cebrian (2002) estimated that a loss of about 35% of the world's mangroves has resulted in a net loss of 3.8×10^{14} gC stored as mangrove biomass. This figure is an underestimate because below-ground biomass and the more recent net canopy production estimates were not included in his calculations.

Carbon and nitrogen budgets for mangrove ecosystems: do they reflect human impacts?

Only a few studies have constructed nutrient mass balances for entire mangrove ecosystems to offer insights into what is energetically important to mangrove functioning. A comparison between a relatively young, physically dynamic mangrove ecosystem disturbed by various human activities (Sawi Bay, Thailand) and a mature, more physically quiescent, pristine ecosystem (Hinchinbrook Channel, Australia) illustrates how physical characteristics and the level of human disturbance affect rates and pathways of nutrient and energy flow (Table 3). First, both ecosystems are net autotrophic, producing more fixed carbon than they consume. This is despite the fact that the ratio of mangrove area to total ecosystem area is nearly double in Hinchinbrook Channel. The Sawi Bay mangroves are younger, smaller, but more productive, resulting in slightly more total net production than the Australian mangroves (Table 3). On an areal basis, rates of respiration, phytoplankton production and carbon burial are greater in Sawi Bay than in Hinchinbrook Channel reflecting additional inputs of carbon from the heavily used catchments bordering the bay. Tidal inputs and outwelling are greater in Hinchinbrook Channel, reflecting stronger tides and river run-off from many small rivers on the Australian mainland. A smaller proportion of carbon is buried in Sawi Bay sediments, but proportionally more carbon is lost via respiration. Carbon losses per km^2 are greater in Sawi Bay, which loses more total carbon (78%) than Hinchinbrook Channel (60%). This probably reflects greater anthropogenic inputs and lower efficiency of carbon processing, as well as greater openness of Sawi Bay to shelf waters, than semi-enclosed Hinchinbrook Channel.

The excess carbon produced by both ecosystems is fated differently, reflecting not only human influences but also differences in ecosystem maturity. Most excess carbon accumulates in tree wood and sediments in young forests lining Sawi Bay. In Hinchinbrook Channel, most carbon in excess of respiration and burial is exported (Table 3). In Sawi Bay, most of the carbon accumulating in sediments appears to be derived from land and from imported phytoplankton stimulated by inputs of inorganic nutrients from various industries within the catchment (Ayukai & Alongi 2000; Alongi *et al.* 2001).

A nitrogen budget for the Missionary Bay mangroves at the northern end of Hinchinbrook Island, Australia (Table 4) illustrates how a mature mangrove ecosystem acquires and retains nitrogen. Nitrogen enters the Missionary Bay ecosystem by nitrogen fixation, with little contribution from precipitation and groundwater (Table 4). Tidal inputs are nearly five times greater than biological fixation. Unlike most other coastal ecosystems, denitrification is a small loss compared to tidal outputs. Unlike saltmarshes, the largest inputs are in the form of dissolved organic nitrogen and net input of particulate nitrogen is negligible. This pattern reflects the import of nitrogen in dissolved form to help fuel forest production and the export to refractory nitrogen in the form of old leaf litter, pieces of branch and bark.

Mangroves have evolved efficient mechanisms to conserve nitrogen. In Missionary Bay, where water and sediment nitrogen concentrations are low, nutrients links between trees and microbes are close. The large mass of living trees and dead wood lying on the forest floor, litter processing by crabs, lower rates of denitrification than nitrogen fixation (Table 4), flushing of material in advanced stages of decomposition, all serve to retain and conserve limiting nutrients (Alongi *et al.* 1992). Inputs slightly exceed outputs, but the ecosystem is roughly in balance given the magnitude of error in extrapolating measurements to a large area. Of greater importance is how this budget demonstrates the delicate balance between the import and export of nitrogen in a mature, pristine ecosystem. This implies that such a fine balance can be easily displaced by human interference.

Nitrogen budgets on this scale for polluted mangroves do not exist, but some small-scale studies suggest that mangroves can in most cases tolerate high levels of nitrogen and phosphorus from sources such as sewage and aquaculture effluent (Boto 1992; Robertson & Phillips 1995; Trott & Alongi 2000). The level of tolerance depends on the form of nutrient and, like other types of disturbance, depends on the intensity, duration and areal extent of impact, as well as position along the tidal gradient. Several recent studies (Feller *et al.* 1999; Bouillon *et al.* 2002) suggest that mangroves, even dwarf species, can use high nitrogen and phosphorus inputs to fuel tree production as well as production of other primary producers. Further, there may be a trophic shift from assimilation of mostly mangrove-derived organic matter in pristine

Table 3 Comparison of the differences in mean rates of ecosystem-level processes between Sawi Bay and Hinchinbrook Channel (modified from Alongi *et al.* 2000).

	Sawi Bay	*Hinchinbrook Channel*
Ratio mangrove : total ecosystem area	1:5	1:2.8
Mangrove net production (mol C ha^{-1} yr^{-1})	2.8×10^6	2.3×10^6
Phytoplankton production (mmol C m^{-2} d^{-1})	43.9	22.1
Pelagic respiration (mmol C m^{-2} d^{-1})	61.0	10.0
Sediment respiration (mmol C m^{-2} d^{-1})	59.5	41.5
Sediment burial (mmol C m^{-2} d^{-1})	54.1	39.7
Percentage TOC input buried	4%	14%
Percentage TOC input respired	46% (74% including tree respiration)	20% (46% including tree respiration)
Total C inputs per km^2 (mol C km^{-2})	9.4×10^7	4.7×10^7
Total C outputs per km^2 (mol C km^{-2})	7.6×10^7	1.6×10^7
Excess C per km^2 (mol C km^{-2})	1.8×10^7	3.0×10^7
Ecosystem P/R	1.4	2.0

Table 4 Nitrogen budget of an entire mangrove ecosystem, Missionary Bay, Hinchinbrook Island, Australia (modified from Alongi 1998).

	Flux (kg N yr^{-1})
Inputs	
Precipitation	30
Groundwater	30
Nitrogen fixation	36 830
Tidal exchange	168 600
Total	205 490
Outputs	
Tidal exchange	192 430
Denitrification	2900
Sedimentation	?
Total	195 330
Net exchange	+10 160

mangroves, to use of nutrients derived from blooms of phytoplankton and macroalgae in mangrove systems receiving excess nutrients (Bouillon *et al.* 2002).

Fisheries yield

The biological importance of mangroves in terms of wood and fisheries yield is normally not reflected in ecosystem-level budgets and mass balance estimates. Mangroves are important nursery grounds despite statistical arguments to the contrary (Baran 1999). The slope of the relationship of fish and prawn landings to mangrove data differs between regions owing to differences in catch methods, structure and productivity of forests and the fisheries species in question (Chong & Sasekumar 1994).

What is unquestioned is the impact of human perturbations on fisheries' yields in mangrove-dominated regions. In south-east Asia, the growth of the trawl fishing industry has led to overfishing in many areas both as a result of, and causing, habitat destruction and environmental stress (Mohsin & Ambak 1996; Hinrichsen 1998). For instance, the long-term trend of fishing in coastal waters in Malaysia (Fig. 7) shows an unrelenting increase in catch effort. There was an increase in total landings of coastal fish in Malaysia from the late 1950s up to the mid-1980s when landings levelled off by 1986, indicating that total landings were starting to exceed estimates of maximum sustainable yield. However, there was a steep rise in total landings and catch effort into the 1990s caused by the expansion of Malaysia's fishing grounds from 160 740 km^2 to 547 200 km^2 with the establishment of the Exclusive Economic Zone (Mohsin & Ambak 1996). The probability of these coastal waters being overfished again is high given the increase in fishing effort, and will no doubt be exacerbated by any decline in the area and health of mangrove forests (Mohsin & Ambak 1996). It is often difficult to even identify such problems in mangrove-dominated waters owing to the lack of long-term data, especially from commercial operators who for a variety of reasons either do

not keep adequate records or do not accurately report their totals to government bodies.

POTENTIAL STATES IN 2025

Predicting the future of mangrove forests is problematic, given the lack of long-term data. Nevertheless, some basic prognoses can be made based on reasonable extrapolations from the salient trends and characteristics of mangroves reviewed here, likely advances in genetics and restoration ecology, and the spread of current sustainable-management practices.

Future threats

Most current uses and abuses of mangroves are unlikely to abate until after 2025. Aquaculture, mining, housing and industrial encroachment and overexploitation of resources will continue and some impacts will probably increase with concomitant growth and development of coastal settlements. Many past and current abuses are now irreversible.

Global production of farmed fish and shellfish in the coastal zone has more than doubled in the past 15 years (Naylor *et al.* 2000). Despite many unsustainable methods and a levelling off of total production, aquaculture will still result in the loss of mangrove resources; they may at best slow in some countries, but they will be maintained or even accelerated in others. As long as human populations grow in size, present impacts will not subside.

There are various threats to the future of mangrove ecosystems (Table 5), nominally divided into high-, medium- and low-level threats, based on the level of past and current impacts. Deforestation remains the single greatest threat to the survival of mangroves. Although reforestation programmes will continue and are likely to increase in future, the loss of biodiversity, especially from old-growth forests, is unlikely to be regained until at least several decades, and

Figure 7 Total annual landings of coastal fish in Malaysia, 1960–1994. Modified from Mohsin and Ambak (1996).

perhaps permanently lost if species become locally extinct due to excessive fragmentation of habitats.

Aquaculture is another major threat, being interlinked with both deforestation and overexploitation of fisheries resources. Conversion of mangrove forests and waterways for pond aquaculture will continue in some countries as depletion of natural stocks drives the need to increase dependence on farmed seafood. The upper limits of sustainability are unknown for various resources within mangrove forests, but it is likely that they will be seriously tested in future.

Technological advances are likely to result in less acute pollution such as the emission rate of thermal effluent and oil spills, but the increase in coastal development presages increased threats of low-level, chronic pollution from agriculture and industry. Contaminants seeping into groundwater may, for example, find their way into mangrove forests and adjacent waters (Field 2000). Of more immediate impact in future will be eutrophication, assuming increased boat traffic and other uses of coastal waterways. These threats will in turn increase pressure for development and alteration of waterways.

The combustion of fossil fuels combined with deforestation and other forms of land clearing are leading to an inevitable rise in atmospheric CO_2 concentrations and temperatures, giving rise in turn to an increase in sea level as polar ice melts (IPCC [Intergovernmental Panel on Climate Change] 2001). Conflicting scenarios presently being offered to predict the impact of global warming on Earth's ecosystems reflect ignorance of ecosystem functioning as well as the scale of the problem; synergistic and antagonistic effects are likely to occur as a result of natural feedbacks, complicating modelling predictions. These problems are especially critical for tropical ecosystems where there are fewer empirical data than for temperate ecosystems. Tropical terrestrial forests have recently been shown to play a greater role in determining atmospheric CO_2 concentrations than thought previously (Mahli & Grace 2000); estimates of the mangrove contribution to atmospheric carbon flux is hampered by a critical lack of information.

Global warming

By 2025, the atmospheric concentration of CO_2 is expected to rise by approximately 40 ppm, temperatures may rise by 0.5–0.9°C, and sea level may rise by 3–12 cm (IPCC 2001). What impact will these changes have on mangroves?

Over the next 25 years, average atmospheric CO_2 concentrations may increase from the 2000 average of 370 ppm to 410 ppm (IPCC 2001). Experimental evidence indicates that

Table 5 Future threats to the world's mangrove forests.

High-level threats	Intermediate threats	Low-level threats
Deforestation	Alteration of hydrology	Oil pollution
Pond aquaculture	Global warming	Thermal pollution
Overexploitation of	Eutrophication	Tourism
fish and shellfish		Noise pollution

species responses will vary; there may not be a significant overall increase in canopy photosynthesis, growth and litter-fall despite decreases in stomatal conductance and transpiration (UNEP [United Nations Environment Programme] 1994). The experiments of Ball and others (e.g. Ball *et al.* 1997) point to complex responses to elevated CO_2 concentrations. Growing *Rhizophora apiculata* and *R. stylosa* in a multifactorial combination of salinity, humidity and atmospheric CO_2, elevated CO_2 had little effect on plant growth when limited by salinity, but growth was stimulated when limited by humidity (Ball *et al.* 1997). Both species had more rapid growth under elevated CO_2 conditions at low salinity. Elevated CO_2 could alter competitive abilities along salinity–humidity gradients (Ball *et al.* 1997).

The expected rise in temperature by as much as 0.9°C (IPCC 2001) may result in expanded latitudinal limits for some species, alteration of community composition, and marginal increases in photosynthesis, respiration, litterfall, microbial decomposition, floral and faunal diversity, growth and reproduction, but reduced rates of sediment accretion (UNEP 1994). However, temperature changes in the tropics may not be as great as at higher latitudes (IPCC 2001), and there may be less seasonality due to forecasted changes in precipitation (UNEP 1994). Such changes are likely to vary greatly on local and regional scales. Nevertheless, they may induce changes in soil water content and salinity, changes in community composition of plants and animals as a result of the salinity changes, and a change in primary production if the precipitation to evaporation ratio is altered (UNEP 1994).

The presumed rise in sea level by as much as 12 cm (IPCC 2001) is difficult to evaluate owing to past and recent variations in local relative sea level (Rull *et al.* 1999). Nevertheless, mangroves may progress landwards at a rate determined by the rate of sea level rise, the rate of vertical accretion, and slope and space at the landward edge. Zonal patterns of plants and animals will be altered slightly and erosion at the seaward front will increase (UNEP 1994). The ability of mangroves to accommodate future sea-level rise will likely depend on other factors such as tidal range, sediment supply and tree species composition. These factors are likely to be magnified on islands of both low- and high-relief and in the arid tropics where rates of sediment supply, available upland space and mangrove growth rates are usually low (Ellison & Stoddart 1991; Parkinson *et al.* 1994; Semeniuk 1994).

Empirical data to test the impact of sea-level rise is limited to one greenhouse study of *Rhizophora mangle* (Ellison & Farnsworth 1997). Growing seedlings in tanks simulating current conditions (control), and a 16 cm increase and a 16 cm decrease in sea level, Ellison and Farnsworth (1997) observed that plants in the increased water level treatment initially grew faster than plants in the other treatments, but slowed rapidly at the sapling stage. By the end of the 2.5-year experiment, control plants were 10–20% larger than the sea-level treatment plants. The reduced growth of *R. mangle* with changes in sea level may offset the possible stimulatory effects of increases in atmospheric CO_2 concentration.

Overall, impacts of climate change on mangrove use and exploitation are predicted to result in increased risks of flooding and erosion in low lying coasts, intrusion of salt wedge and storm surges and collateral damage (UNEP 1994). The severity of these impacts will vary in relation to regional differences in climate change (IPCC 2001).

Global losses

To make realistic prognostications of the future of mangroves, an assessment of the accuracy of the present data of losses and gains in forest area is necessary. While it is clear that large tracts of mangroves have been either severely degraded or destroyed worldwide, most data is apocryphal, reflecting inaccurate surveys, unsubstantiated claims or old estimates not based on empirical measurements (Farnsworth & Ellison 1997; Burke *et al.* 2001). For example, in Fiji total mangrove area has been reported as between 19 700 and 49 777 ha (Spalding *et al.* 1997).

Long-term changes in mangrove area (Fig. 8) show that most countries have lost mangroves, especially Vietnam, Mexico, Singapore, the Philippines and Thailand. In Singapore, the losses were incurred over nearly a century, mainly as a result of urbanization (Spalding *et al.* 1997). In other countries, losses have been sustained mostly over the past 20–30 years as a result of clearing for aquaculture, urbanization and timber products. Vietnam's losses were sustained chiefly as a result of defoliation in the 1960s and early 1970s (Hong & San 1993). Some countries, such as Papua New Guinea, Australia and Belize show no substantial change and a few countries (e.g. Cuba) have regained mangrove forests due to restoration projects (Field 2000).

Summing the empirical estimates of change in mangrove area (Spalding *et al.* 1997) and some regional estimates (Clough 1993; Diop 1993; Lacerda 1993), I calculated that approximately one-third of mangrove forests have been lost over the past 50 years. I used the above documents produced by the International Society for Mangrove Ecosystems because they appear to be the most reliable, based on empirical data in government forestry surveys, remotely sensed images, aerial photos and ground-truth maps. Recent publications have cited a global loss figure of 50% (Burke *et al.* 2001; GESAMP [The Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection] 2001), citing reports (Kelleher *et al.* 1995) that have cited older literature containing neither empirical data nor a description of how the loss estimates were derived. Also, Spalding *et al.* (1997) found numerous inaccuracies in previous works because of what some people and organizations considered mangrove forest. For example, the estimates for Venezuela were consistently gross overestimates because many surveys included non-mangrove species and adjacent swamp forest, saltmarsh or mudflat. Conversely, for Mexico, a previous estimate indicated a total mangrove area of 5315 km^2 when in fact recent high-resolution satellite images show a total mangrove area of 9328 km^2 (Spalding *et al.* 1997).
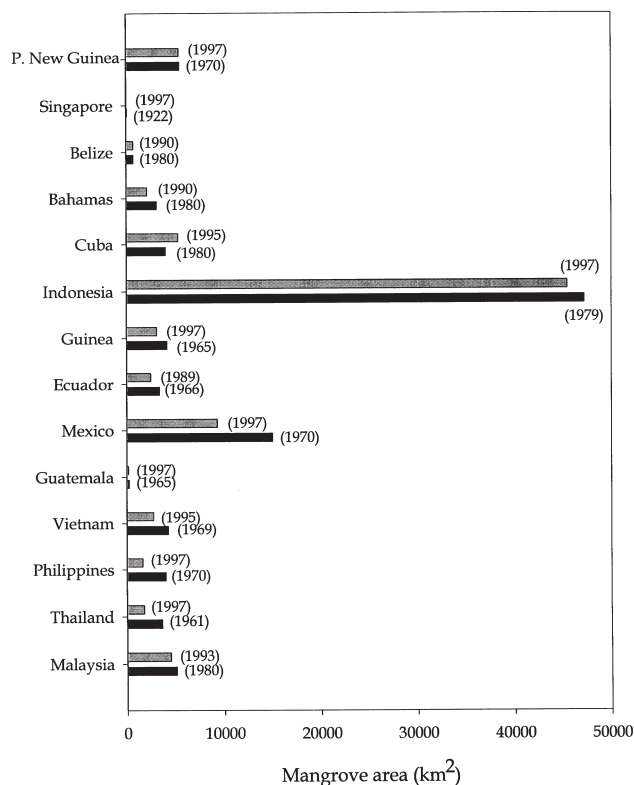
Figure 8 Long-term changes in mangrove forest areas worldwide. Compiled from data in Clough (1993); Diop (1993); Lacerda (1993); and Spalding *et al.* (1997).

Loss rates vary greatly among nations, ranging from 1 to 20% of total forest area per year (Clough 1993; Diop 1993; Lacerda 1993), making it difficult to predict global changes in forest area in future. There are enormous variations within individual countries. For instance, in Thailand losses of mangroves from 1961 to 1989 varied from 0 to 9% in central and lower Gulf of Thailand provinces to as much as 79% along the Andaman Sea coastline (Clough 1993). Similarly, Malaysia experienced an overall reduction in mangroves of approximately 12% since 1980, with greatest losses in Johor, Selangor, Negeri Sembilan and Teerengganu, but some provinces such as Malacca have increased forest area owing to restoration and sustainable management of reserves (Clough 1993). Such is true for several African and Latin American nations (Diop 1993; Lacerda 1993). In those nations that have replanted forests for a net gain, loss of biodiversity of trees and associated organisms appears to be permanent. Most restorations involve monocultures of rapidly growing species (Field 1998). Rare, slow-growing tree species are ordinarily not replaced (see below).

The future of mangroves is intimately linked to changes in forest use, which is directly tied to changes in human population growth and development. Predictions of human population change indicate most rapid growth in tropical developing nations, where the bulk of mangrove forests lie. Assuming that human populations will grow along tropical

coasts, so will anthropogenic impacts. In fact, some mangrove areas are already overfished. For example, in the Mekong delta, fish catch per unit effort has declined from the late 1970s (Fig. 9), and continues to decline, as the coastal population grows and mangroves continue to be destroyed for shrimp farming which has increased 35-fold (de Graaf & Xuan 1998). At present one hectare of mangrove supports approximately 0.45 tonnes of marine fish catch per year in the region. Increasing human pressures bring a concomitant rise in the incidence of viral and other diseases, directly impacting seed stock (de Graaf & Xuan 1998), and increasing coastal erosion and saltwater intrusion into groundwater (Hong & San 1993).

The highest-level threats to mangroves in future (Table 5) are likely to be deforestation, aquaculture and overexploitation of wood and fisheries resources. Aquaculture will remain a great threat, although aquaculture production of fish, crustaceans and molluscs in countries with mangroves appears to have levelled off (Fig. 10). This plateau indicates that a sustainable level of coastal aquaculture has been reached and that mangrove clearing for aquaculture operations has also peaked.

Assuming that the rate of deforestation does not change substantially over the next two decades, the felling of mangrove forests to construct new ponds and the discharge of wastes will continue. There have been advances in reducing waste discharge from aquaculture, but this reduction is unlikely to compensate for continued need for more space as aquaculture production per unit area is declining or remaining stable at best (Naylor *et al.* 2000; FAO [Food and Agricultural Organization of the United Nations] 2001).

It has been proposed that mangroves can be used as sinks to filter aquaculture effluent (e.g. Robertson & Phillips 1995), based on the presumption that mangroves have high capacity to tolerate and use dissolved nutrients because of their high rates of primary production. This idea has considerable merit, but maintaining a steady-state condition would be difficult. It is likely that a sustainable operation would be site-
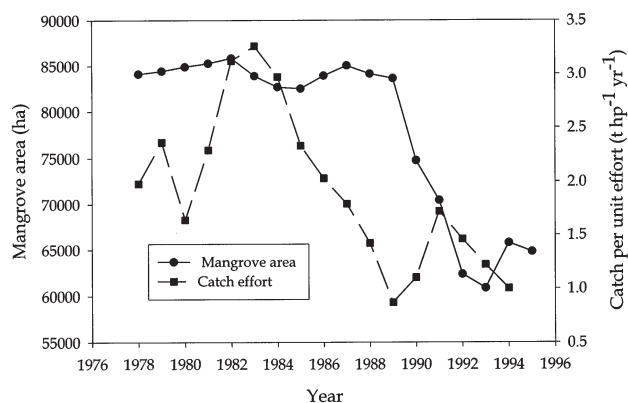

Figure 9 Changes in mangrove forest area (ha) and fisheries catch per unit effort (t hp^{-1} yr^{-1}), Minh Hai Province, Mekong Delta, Vietnam, 1977–1995. Data from deGraaf and Xuan (1998). hp = total engine capacity in horsepower.

specific, depending on the quantity and quality of waste, the proportion of particulate to dissolved waste, how and when the waste was applied to the forests, the extent of tidal flushing, and forest productivity and age (Trott & Alongi 2000). In short, no universal formula for success is forthcoming, given the lack of long-term data on the impact of aquaculture effluent discharge on mangrove forests and associated waterways. Further, an impact may be cumulative rather than immediate and overt, and may not be discernible for several years. Cage aquaculture is less destructive than ponds, but even sustaining a particular number of cages in a given area would greatly depend on hydrodynamics and coastal geomorphology, as well as the level of cultivation intensity. For both mangroves and commercial operations to be sustained, they must be properly managed and guided by national development plans.

Rehabilitation and sustainable management

Environmental degradation in many parts of the world, especially in Asia and Latin America, has led to attempts to rehabilitate and restore mangroves. Most rehabilitation and restoration projects have had mixed results, with the main reasons for failure being lack of adequate site selection and proper use of soil preparation and planting techniques (Ellison 2000). In many cases, futile attempts have been made to rehabilitate a site that is beyond restoration. In such cases, the sites are often highly saline with acid sulphate soils and with both tidal water and soils extremely low in oxygen and nutrient content; sites of shrimp faming, mining and timber harvesting are frequently in this category.

Critical to the success of a rehabilitation project is proper selection of species to be planted, and whether or not they are to regenerate naturally or artificially. Natural replenishment requires that sufficient undisturbed forests reside nearby to serve as sources of seed stock. Artificial replanting success depends on funding, time and the level of expertise available to use appropriate methods.
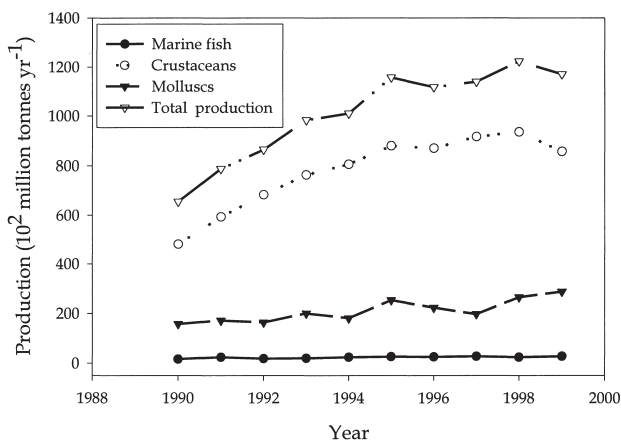

Figure 10 Changes in aquaculture production in all countries inhabited by mangroves, 1990–1999. Data from FAO (2001).

The technology exists to regrow trees but restoring fauna and ecosystem function is exceedingly difficult. The fact remains that most rehabilitated sites are mono-cultures or low diversity poly-cultures having little, if any, resemblance to the original habitat. Only a few species are commonly used, namely *Rhizophora apiculata*, *Rhizophora mucronata*, *Rhizophora mangle*, *Avicennia marina* and *Sonneratia apetala*. Mangrove forests can often be rehabilitated but not restored.

Mangroves are in a sense among the easiest systems to reconstruct, but the emphasis has been, and continues to be, on reintroduction of trees. It is presumed that over time animals such as crabs, fish, meiofauna and algae will recolonize replanted sites and that ecosystem linkages will be restored. The primary objectives of mangrove rehabilitation projects, in descending order of frequency, are silviculture, mitigation, coastal stabilization, ecosystem function and fisheries.

Restoration of mangrove ecosystems can theoretically be achieved, given that mangroves have been cultivated for several centuries. Mangroves can grow and thrive if hydrological and geomorphological conditions are optimal, and there is some evidence that replanted forests can approach the biomass, stand structure and productivity of undisturbed forests within 20–25 years (e.g. McKee & Faulkner 2000). However, restoration requires time, which is most often contrary to political, cultural and economic priorities. To date, extensive replanting of mangroves has been achieved only in Pakistan, Cuba and Bangladesh (Spalding *et al.* 1997).

The Bangladesh scenario is arguably the most impressive attempt to reforest mangroves along a large portion of tropical coastline (Saenger & Siddiqi 1993). Severe cyclone damage led the Bangladesh Forest Department in 1966 to initiate an afforestation programme to increase coastal protection afforded by expansion of mangrove forest. Up until 1993, nearly 120 000 ha were planted on accreting banks formed from sediment delivered to the eastern Sundarbans from the Ganges and Brahmaputra Rivers; two species, *Sonneratia apetala* and *Avicennia officinalis* were the dominant trees planted. There were some difficulties encountered with sediment stability, but the benefits have been substantial. The greatest lessons learned were: (1) to have more adaptable replanting schemes as soil salinities change over time; and (2) monospecific cultures are not a universal remedy, as they can generate problems all their own that are costly and difficult to rectify.

Most restoration projects continue to emphasize silviculture to generate production of timber, wood chips, charcoal and fuelwood (Ellison 2000). Given economic imperatives in most coastal communities in developing countries, most immediate value and emphasis is naturally placed on wood production. This trend is likely to continue to at least 2025. Indeed, the greatest success in sustainable management of mangroves has been achieved in silviculture.

Guidelines for sustainable management of mangroves have been developed by a number of organizations and agencies, and all express several commonalities:

- within a national boundary, mangroves should be assigned to one or other of the following categories: conservation reserve, forest reserve, fisheries reserve and alienable mangrove land;
- mangroves on alienable land should be maintained;
- specific management goals and practices should be clearly identified and implemented;
- appropriate laws and regulations should be enacted and enforced;
- the best available technical expertise should be used;
- there should be a buffer zone between mangroves and adjacent industry, housing and tourist development;
- pond aquaculture should not be permitted within mangrove reserves;
- within permissible areas, ponds should not be closer than 200 m to mangroves;
- an environmental impact assessment and feasibility study should be required for all development projects; and
- strict pollution controls should be established.

If these guidelines were adhered to, loss of mangroves worldwide could be minimized in future, certainly to a level not greater than an annual global loss rate of about 1% (current estimate of Kaly & Jones 1998). Fragmentation and loss of diversity, given the lack of consensus on estimating the minimum expanse of mangroves required to sustain all key processes, is still a danger (Kaly & Jones 1998).

Technological improvements, such as genetic and microbial advances, may ameliorate problems in conserving and maximizing mangrove ecosystem structure and function in rehabilitated environments. It is likely that protocols will be established for *in vitro* propagation of several key mangrove species, as can be done with *Excoecaria agallocha*, an extract of which is currently used for relief of rheumatism and treatment of ulcers (Rao *et al.* 1998). Microbes stimulate seedling growth, so culture success might be improved by inoculating seedlings with bacteria, such as nitrogen fixers, that promote plant growth (Holguin *et al.* 2001). Also, less destructive mud crab cultivation is being successfully trialled in many regions (Keenan & Blackshaw 1999), and may offer a reasonable alternative to destructive pond cultivation.

Ecological economics: towards a pragmatic solution?

If mangrove resources are to be conserved, sustainable management realistically must operate on the basis of economics (Turner *et al.* 1993). It is human nature to protect and conserve a resource that is a source of income. Economic self-interest must play a role in management if mangroves are to persist and thrive in the face of human encroachment. A few case studies indicate that the idea of conserving mangroves as economic investment is realistic (Ronnback 1999).

The mean monetary value of mangroves has recently been estimated at US$ 9990 ha^{-1} yr^{-1}, second only to the value of estuaries and seagrass beds, and greater than the economic value of coral reefs, continental shelves and the open sea

(Costanza *et al.* 1998). The commercial value of mangrove resources has been recognized since early last century. Mangrove-related fisheries resources generally are valued more highly than natural and agricultural goods, such as wood, with the value of fisheries ranging from US$ 120–3000 ha^{-1} yr^{-1} and timber from US$ 60–800 ha^{-1} yr^{-1} (Clough 1993; Diop 1993; Lacerda 1993). These figures are only indicative of their fair value; some products are worth more than others, and the same product is often worth more in one region than in another for various reasons such as quality and local market demand.

The competing demands of coastal industries and mangroves are manageable if relevant ecological information is collected and used properly to design management plans that reflect how mangrove ecosystems support fisheries. For example, until the mid-1980s, mangroves were heavily exploited in Colombia for artisanal and commercial fishing, wood extraction for poles, charcoal, paper and housing materials, with no clear national or regional plans for sustainable development (Lacerda 1993). As a result of these unsustainable losses, the National Institute for Renewable Resources and Environment started a National Mangrove Committee with the aim to formulate policies for the conservation and sustainable management of mangroves in Colombia. As a result of these policies, mangrove protective areas have been enlarged and the coastline divided into areas for protection, public interest, forestry and fisheries reserve, special management and special protection (Lacerda 1993).

On the Caribbean coast of Colombia where semi-intensive shrimp aquaculture is practised, proper environmental management plans have been drawn up as a result of an urgent need for ecologically sustainable development. The study of Larsson *et al.* (1994) is a prime example of the type of critical economic and ecological analysis necessary for sustainable management as legislated in Colombia. In their model, Larsson *et al.* (1994) first estimated the ecosystem area that is required to produce the food, clean water and nursery areas to support the shrimp farms and to assimilate their wastes. Their results show that a semi-intensive farm needs an area of mangroves 35–190 times larger than the area of the farm; for each joule of edible shrimp protein produced, approximately 295 J of ecosystem work is required. In 1990, an area equivalent to about 20–30% of Colombia's entire mangroves was required to supply the industry's entire needs for post-larval shrimp. In comparing the energetic requirements of Colombia's aquaculture industry to other food production systems, Larsson *et al.* (1994) concluded that coastal aquaculture is one of the most resource-intensive industries, and characterized it as ecologically unsustainable. To maximize use and to minimize impact, Colombia's aquaculture operations should retain natural tidal flows, locate new farms to marginal saltpans, maximize distance between farms, use vegetable instead of animal feeds, use filter feeders to naturally clarify pond waters, and improve artificial rearing methods (Larsson *et al.* 1994). It is likely that aquaculture industries in other nations would do well to take up some or all of these suggestions, where applicable.

Similar efforts to establish a clear ecological and economic link between mangroves and the value of fisheries have been difficult. Cost-benefit and multi-criteria analyses, while valuable in some circumstances, have their limitations and are often impossible to apply. In the Philippines, felling of mangroves for aquaculture has been banned since 1981, but the current decline in fish catch per unit effort has increased pressure to re-examine the protective legislation. Consequently, Janssen and Padilla (1999) compared the costs and benefits of mangrove conservation with those generated by various alternative plans of aquaculture and forestry. A comparison of net annual benefits of goods and services provided by mangroves indicates that aquaculture generates the greatest value at US\$ 6793 ha^{-1} yr^{-1}, followed by forestry (US\$ 150 ha^{-1} yr^{-1}) and fisheries (US\$ 60 ha^{-1} yr^{-1}). Based on the trade-offs of efficiency and equity, commercial forestry delivers the most equity and semi-intensive aquaculture the most efficient alternatives; intensive aquaculture was the worst alternative. Given the limitations of not being able to value mangrove biodiversity, shore protection and flood mitigation, Janssen and Padilla (1999) concluded that semi-intensive aquaculture was the policy alternative with the highest economic value. However, they questioned whether it was possible to adequately value the impact of losses of species and ecosystems on the way of life of the indigenous people.

Several studies modelling the trade-off between mangroves and resource use argue for minimal destruction or use of forests and associated waterways, especially against the backdrop of overfishing. Using an open-access fishery model, Barbier and Strand (1998) estimated the impact of change in mangrove area on nearshore shrimp production in Campeche, Mexico. Simulating a marginal decline in mangrove forest area, their model indicated a concomitant decline in shrimp harvest and an increase in price per kg harvest and cost per vessel. Their model, however, suggested that the fishery might be sensitive to the level of mangrove exploitation; a modest decline in mangrove area may lead to a disproportionate decline in shrimp harvest and revenue if the ecosystem is deforested beyond the current levels of 2 km^2 yr^{-1} (Barbier & Strand 1998). Moreover, while mangrove deforestation contributed to a decline in the fishery so did the pervasive problem of overexploitation. It is likely that the shrimp fishery has been operating at or slightly above sustainable limits. Better management and involvement of the community in controlling overfishing is just as critical as limiting the destruction of mangrove nursery grounds.

Optimizing the trade-off between mangrove preservation and human exploitation has been modelled successfully, and these models have indicated the importance of some basic ecological variables. Employing both dynamic optimization and simulation models of the economic link between fishery production and mangrove use in Brazil, Grasso (1998) found that the optimisation model suggested how best to employ forestry and fishery workers. The worst scenario would be over-exploitation of mangrove stocks if there were no equilibrium established between forestry and fishery efforts. The

best management option in the long-term, however, was to have more workers in fisheries than forestry. Grasso (1998) suggested that clear felling of mangroves should be reduced to a minimum to avoid ecosystem collapse. The most important variable in the simulation model was the rate of forest growth, underscoring the importance of the relationship between forest age, growth and the extent of forest resource use (Grasso 1998).

The ecological ties between mangroves and adjacent environments can serve as a key for sustainable management. Resource-use models encompassing the strength of linkages between ecosystem compartments show that severe restrictions on mangrove clearing can optimize economic output. In the Bintuni Bay area of Indonesia where mangroves are heavily exploited for woodchips, and artisanal and commercial fisheries, strong economic arguments exist for limited clearing (Ruitenbeek 1994). Cost-benefit analysis of forest management options incorporating links among fishery production, mangrove use and clearance rates, erosion control and biodiversity (Ruitenbeek 1994) indicate that clear-felling of mangroves is a viable management option only when all the linkages are ignored. Assuming that clear linkages exist between mangroves and environmental functions and fisheries, a ban on cutting is optimal; if the linkages incorporate time lags on the order of years, selective cutting of 25% of total harvestable mangroves is the optimal strategy (Ruitenbeek 1994). In any case, conservative cutting appears to be a good strategy because a wrong management decision based on total ignorance would likely have severe economic and ecological consequences for several decades.

CONCLUSIONS AND MANAGEMENT

Mangroves are the only woody halophyte-dominated ecosystems situated at the confluence of land and sea. Most mangrove forests are highly productive and net autotrophic, helping to support coastal food chains, including commercially valuable fish, crustaceans and molluscs. The world's mangrove forests are economically very valuable, worth an estimated US\$ 180 895 923 000 based on the valuation of Costanza *et al.* (1998).

Mangroves have traditionally been heavily used for timber, poles, food, medicines and a wide variety of other items. Most nations have lost mangroves; a few countries have gained single-species forests as a result of reforestation projects. Claims that 50% of the world's mangrove forests have disappeared over the past century (GESAMP 2001) may be exaggerated due to lack of empirical data. An analysis of current estimates (Clough 1993; Diop 1993; Lacerda 1993; Spalding *et al.* 1997) based on more reliable information suggests that cumulative losses over the past 50 years are closer to one-third. The exact losses will never be known, and even today, a precise estimate of global extent of mangrove forests is not easy (Spalding *et al.* 1997). Some countries such as Liberia, the Ivory Coast and Guinea have experienced

heavy losses, but most countries with expansive mangroves, such as Brazil and Australia, have experienced comparatively little deforestation (Spalding *et al.* 1997).

Most losses have been the direct result of felling for shrimp ponds, housing and industrial developments (Alongi 1998), but severe losses have occurred in some regions due to shoreline erosion/siltation accelerated by terrestrial deforestation, desertification and other poor land-use practices. Herbicides and defoliants, pollution, alteration of natural tidal cycles and water flow, and uncontrolled resource exploitation, also degrade and destroy mangrove ecosystems. In future, the greatest threats to the continued existence of mangroves are deforestation, pond aquaculture and a pervasive overexploitation of fisheries resources. Global warming and chronic eutrophication will have a lesser impact on the health of mangrove ecosystems over the next 25 years. Mangrove losses are positively related to human population density and growth; the fewer people who live at or near a forest, the less destruction and exploitation there will be.

The future is not necessarily bleak for mangroves. Lutz *et al.* (2001) estimate that the rate of world population growth is already declining, with an 85% chance that the global population will stop growing before the end of the century. The projections for sub-Sahara Africa, south Asia, Latin America, and the Asia Pacific regions show that population size will plateau by about 2050 (Lutz *et al.* 2001). Given the apparent link between the exploitation of mangroves and human population density, this implies that overexploitation will continue until 2050, but decline thereafter. Coupled with technological improvements in aquaculture, restoration ecology and genetics, hopefully the worst direct exploitation will be over by 2025. The biggest problem in future is the loss of biodiversity. Most rehabilitation projects replant fewer species than were originally lost. Loss of biodiversity is a critical issue given that mangrove forests are less diverse than most other tropical ecosystems.

The major problem in predicting mangrove responses to human impacts is the lack of long-term data, and the ability to distinguish natural from anthropogenic change. There is a lack of knowledge of:

- gross and net canopy production;
- below-ground root production;
- tree and below-ground root respiration;
- natural successional states over time;
- whole-ecosystem mass balances for carbon, nitrogen and phosphorus;
- physiological information (water and carbon balance);
- factors regulating colonization (propagule dispersal, seedling establishment);
- secondary production;
- plant–soil–microbial relations;
- species diversity of flora and fauna;
- forestry models to determine maximum sustainable yield;
- silviculture of rare species;
- experimental effects of greenhouse gas and sea level change; and
- experimental effects of excess nutrients on mangrove growth and survival.

Actions can be taken to improve conservation of mangroves. The Charter for Mangroves put forward by the International Society for Mangrove Ecosystems (Field 1995) would be a logical first step. The charter was adopted in 1991 to complement the World Charter for Nature proclaimed by the General Assembly of the United Nations in 1982. The mangrove charter affirms that mangroves will be respected and not compromised in terms of their genetic viability, that they will be conserved where ever possible, and managed on a sustainable basis. The major stumbling block to practical implementation of the charter remains commitment from local and national governments to provide adequate resources to implement management plans. The best example of sustained management of a mangrove ecosystem is the Matang Mangrove Forest Reserve in peninsular Malaysia. The success of this enterprise can be directly attributed to government commitment and a good relationship between government, business and the local community.

It is essential for governments and people to understand that mangroves are a valuable social and economic resource. It is a fact of human nature that we tend to preserve and protect resources that are of economic importance; aesthetics is historically not high on the list of reasons why we conserve resources. If mangrove forests are not seen as a fundamental economic and ecological resource to be treasured, they will continue to be exploited at current rates until at least 2025. The greatest hope in reducing the rate of mangrove losses is the projection that human population growth will decline, and possibly stop, later in the century.

ACKNOWLEDGEMENTS

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ORIGINAL ARTICLE

Aaron M. Ellison

Macroecology of mangroves: large-scale patterns and processes in tropical coastal forests

Abstract Macroecology is an emerging subdiscipline within ecology that explores effects of large-scale processes on local, regional, and global patterns of species diversity and taxon-independent scaling of structural and functional relationships. Statistical analysis of these patterns yields hypotheses concerning the processes determining population, community, and ecosystem-level patterns, which have been the historical focus of most ecological research, including that done in mangroves. The majority of studies of mangrove forests have aimed to better understand the causes of local (within-forest) ecological patterns (e.g. zonation, tolerance to salinity and hypoxia, litterfall and production), with little attention to the larger environmental, historical and evolutionary contexts that can influence local processes. I argue that a focus on the larger-scale contexts that constrain local processes (a "macroecology of mangroves") will provide us with new insights into the structure and function of mangrove ecosystems. Further, such analyses can be used to determine if mangroves follow similar general rules that have been identified for upland forested ecosystems. I consider two examples: relationships between local species richness and latitude, longitude and regional diversity; and structural coordination of leaf traits. I present data and analyses of these macroecological patterns in mangrove forests, and illustrate points of agreement and disagreement between these and upland ecosystems. I suggest that ecological theory developed in upland forests can be readily applied to mangrove forests. Such a conclusion should lead to advances in ecological research of mangroves and better predictions of how they will respond to global climate change.

Keywords Biogeography · Leaf traits · Macroecology · Mangroves · Zonation

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"To do science is to search for repeated patterns, not simply to accumulate facts..."

(R.H. MacArthur 1972)

Introduction

"Macroecology" is concerned with the statistical analysis of large-scale patterns of the distribution, abundance and diversity of species (Brown and Maurer 1989; Brown 1995), and with the scaling among species of structural and functional relationships (e.g. Enquist et al. 1999, 2000; Enquist and Niklas 2001; Niklas and Enquist 2001). Many ecological patterns that are observed and measured on one or a few species at single study sites are controlled or constrained by general processes common to many taxa or operating at much larger spatial and temporal scales. However, it is rarely possible to conduct replicated, manipulative experiments on many species simultaneously at large scales. Humans are affecting ecosystems at regional and global scales but responses of ecosystems to small-scale perturbations at single study sites are not easily extrapolated to large-scale impacts on whole ecosystems. Guidance is needed on how to scale the results of studies conducted on single species at single sites for short periods of time, to multiple species at large spatial and temporal scales (Farnsworth 1998).

Mangrove forests are distributed worldwide on sheltered, tropical coastlines (Ellison and Farnsworth 2001), and consist of 50–75 species in 20–26 genera in 16–20 families (contrasting numbers from different circumspections of "mangrove" by Tomlinson 1986; Duke 1992; Kathiresan and Bingham 2001). Mangroves are a good ecological group to use for macroecological investigations because they include a large number of taxonomically unrelated species in which convergent properties have been well documented (Ellison and Farnsworth 2001). Further, mangroves are restricted to a small number of habitat types (intertidal eutrophic to oligotrophic estuaries) constrained by geomorphology (Thom 1982; Twilley 1995), so dramatic differences in "habitat com-

plexity" – a common bugbear of macroecology – are minimized among mangrove forests. Thus, large-scale patterns in the structure and function of mangrove forests should be readily apparent and straightforward to interpret.

Here, I illustrate two examples of macroecological analyses of mangroves. First, I describe relationships among species richness patterns of mangroves at local, regional, and global scales. Understanding the relationships between small- and large-scale patterns of species richness is the starting point for any macroecological analysis. Second, I examine relationships among mangrove leaf traits and compare these relationships to those seen for plant taxa across a range of temperate and tropical biomes. Such relationships can be used to model regional- and global-scale patterns of productivity, distribution, and dynamics of vegetation (Leuning et al. 1995; Aber et al. 1996; Reich et al. 1999).

I illustrate how macroecological analyses of mangroves can provide inferences about large-scale processes from small-scale patterns and simultaneously yield new insights regarding the structure and dynamics of mangrove forests. These analyses also illustrate that the many processes that structure mangroves are similar to those that structure upland forests, and that general ecological theory is applicable to mangrove forests. Mangroves do not exist in isolation, but occur at the boundary between terrestrial and marine environments. Integrating regional and global patterns of mangrove species richness with general ecophysiological processes into a comprehensive "macroecology of mangroves" could lead to more reliable predictions of the responses of mangrove and upland forests to global climate change. This integration is a major challenge for mangrove ecologists.

Large amounts of existing data on mangrove ecosystems can be brought to bear in macroecological analyses, and new data are being published at an exponential rate (Fig. 1). A cynical mangrove macroecologist could observe that at the current rates of deforestation (1–2%/year; Farnsworth and Ellison 1997a; Ellison and Farnsworth 2001), and in response to rising sea levels (Ellison 1993, 1994; Ellison and Farnsworth 1996b, 1997) mangrove forests will be virtually gone by the year 2100, and during that same year 4.3 million papers will be published about them.

Developers of ecological databases and models of responses of ecosystems to global change are not drawing on available data from mangrove forests. For example, recent compilations of data on forest species diversity (Waide et al. 1999), leaf-level trait, phenology, and climate relationships (Reich et al. 1992, 1999; Reich 1995), global ecosystem net primary productivity (Esser et al. 2000), and tropical forest production (Clark et al. 2001) do not include data from any mangrove forest, despite the existence of these data in the published, indexed literature. The absence of mangroves in these databases may be related to the observation (Fig. 1) that studies of mangroves appear to contribute little to developing fundamental ecological theories or applied ecological
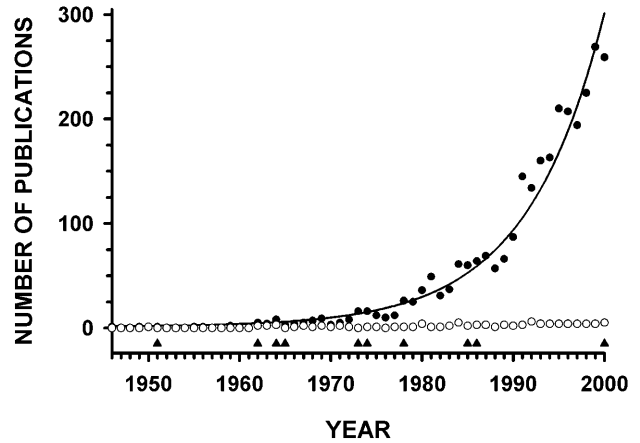

Fig. 1 Publication rate of papers on mangroves. *Solid circles* illustrate total number of papers per year with the word "mangrove" or "mangroves" in the title, abstract, or keywords that occurred in ISI's Science Citation Index of >5,700 peer-reviewed scientific journals (ISI, Philadelphia). The line is the best-fit nonlinear regression (r^2=0.97). *Open circles* are the total number of papers per year published in international "high-impact" ecological journals (*Ecology, Ecological Monographs, Ecological Applications, Journal of Ecology, Journal of Animal Ecology, Journal of Applied Ecology, Oecologia, Oikos* and *American Naturalist*). The annual number of high-impact mangrove papers is roughly constant over the 55-year period surveyed and never exceeds 5 per year. *Triangles* indicate years in which a single mangrove-related letter or paper (two in 1974) was published in *Science, Nature,* or *Proceedings of the National Academy of Sciences, USA*

models. The macroecological analyses described here show that mangrove forests and upland forests are structured similarly. However, relationships among ecophysiological leaf traits of mangroves are different enough to suggest that current models of responses of global vegetation to climate change may need to be adjusted to account for unique properties of woody halophytes.

Example 1: patterns of mangrove species richness

Describing and interpreting species distributions of mangrove trees has preoccupied mangrove researchers for centuries (see reviews in Ball 1988; Smith 1992; Duke et al. 1998; Ellison et al. 1999). These studies have focused either on the local (within stand or forest) patterns of mangrove species "zonation" (e.g., Snedaker 1982) or on the biodiversity "anomaly" of global mangrove species richness (e.g., Ricklefs and Latham 1993). In contrast, regional patterns of species richness have received significantly less attention (but see Schaeffer-Novelli et al. 1990; Duke 1992; Duke et al. 1998). In this review, a region is the area whose species complement (or species pool, Caley and Schluter 1997) could contribute to local species richness. This lacuna is curious, since in general, regional richness can strongly influence local richness (see review in Srivastava 1999), and is the raw information that is used for determining global diversity patterns.

Local patterns of mangrove species richness

Species zonation patterns – the predictable and discrete ordering of species with respect to one or several environmental gradients – have been described for dozens of individual mangrove swamps (reviews in Macnae 1968; Snedaker 1982; Smith 1992; Bunt 1996). Virtually all such descriptions are based in some way on the classification first presented in Watson's (1928) monograph on mangroves of the Malaysian peninsula, in which he suggested that restrictions of given mangrove species to certain portions of a swamp are determined by their tolerance to tidal inundation. Tidal inundation is a nearly ideal proxy for the wide variety of environmental conditions that affect plant growth, including soil salinity, redox potential, and waterlogging (Adams 1963; Snow and Vince 1984; Bertness and Ellison 1987; Ukpong 1994), and degree of tidal inundation largely derives from local geomorphology (Thom 1967, 1982). Nevertheless, Watson's proposed inundation classes were "entirely arbitrary" (Watson 1928, p 130) and the species distribution map he produced (Watson 1928, p 128) is "entirely imaginary" (Watson 1928, p 130). Smith (1992, p 103) reprints this map, but claims it represents Watson's "synthesis of zonation" rather than the "typical, but by no means inevitable distribution of the more important mangrove species" (Watson 1928, p 128). Finally, the "imaginary" zonation and "arbitrary" inundation categories described by Watson (1928) were, he stated, only applicable for the west coast of Malaysia, in the neighborhood of Port Swettenham.

Watson's description of local patterns of species distributions in mangroves epitomize those that follow: they are qualitative, not quantitative, and they are site-specific. Although Watson did not discuss succession of mangroves (the concept of succession being relatively young in 1928), he did consider mangroves to be land-builders (cf. Davis 1940), and zones to be (in modern terms) equilibrium communities. An evaluation of ≈50 years of observations on zonation and succession in mangrove forests reviewed by Lugo (1980) led to the conclusion that zonation represents an equilibrium, steady-state condition, but not a successional one. Studies on disturbance and gap dynamics in mangrove forests (Wadsworth and Englerth 1959; Roth 1992; Ellison and Farnsworth 1993, 1996a; Smith et al. 1994; Imbert et al. 1996; McCoy et al. 1996), however, often fail to support even the idea that they are equilibrium communities.

This qualitative, site-specific approach to documenting zonation, and the implicit assumption that mangroves are equilibrium communities (whether successional or not) permeated many subsequent studies of the associations between mangrove distribution patterns and local edaphic conditions (summarized in Macnae 1968; Smith 1992; Ellison and Farnsworth 2001). Despite the availability since the early 1970s of statistical tests for zonation (reviewed by Dale 1999), the fundamental assumption that species in mangrove forests are, in fact, zoned with respect to these edaphic conditions, has been tested explicitly only in the last 5 years (Bunt 1996, 1999; Bunt and Bunt 1999; Bunt and Stieglitz 1999; Ellison et al. 2000). These studies, conducted in the species-rich forests of northeastern Australia and the Sundarbans of Bangladesh, have failed to support the hypothesis that species occur in distinct (or even indistinct) zones.

Why was zonation not detected quantitatively? Possible explanations for the lack of zonation observed in these studies include: (1) the use of inappropriate statistical methods for testing for zonation in mangrove forests; (2) these investigators focused on an inappropriate spatial scale of observation and analysis for detecting zonation; (3) human impacts on the forests have disrupted zonation patterns; and (4) the "null hypothesis" that zonation does not actually exist in mangrove forests. Explanation 1 is unlikely, as statistical methods for testing species distributions across environmental gradients are well-developed (Dale 1999), and different statistical tests have yielded similar results (see comparison of methods in Ellison et al. 2000). Explanation 2 is contradicted by Ellison et al.'s (2000) study that explicitly looked at species distributions as a function of spatial scale. Human impacts (explanation 3) were minimized at all sites studied in Australia and Bangladesh, but it is virtually impossible to find a mangrove swamp anywhere on the planet that has not been altered substantially by human activities. Jackson (1997) has warned about drawing conclusions about ecological (especially marine) systems based on a "shifting baseline" of assumptions. Current intensive studies of mangrove swamps are being conducted on fragmented remnants of these forests that may bear little structural or functional resemblance to the mangrove forests of centuries past, yet we often consider our study sites to be "representative". Thus, we cannot rule out that these forests were once zoned, but are no longer because of previous, undocumented anthropogenic disturbance(s).

Researchers should consider seriously the last explanation, however: the "null" hypothesis that true zonation does not occur in mangrove forests. Profile diagrams based on dominant species do not reflect distributions of all the species in a given forest, and so generally are not usable to test hypotheses regarding zonation. Without statistical testing, such diagrams convey only the investigator's idealized notion of forest structure, a pattern little changed since Watson (1928). Considering the distribution of mangrove species across the intertidal in terms of overlapping species arrayed along an environmental gradient(s) (cf. Whittaker 1956; Ball 1998; Ball and Sobrado 1998) may lead to a better understanding of mechanisms promoting species segregation and coexistence in mangrove forests. In addition, alternative hypotheses generated by applying basic theory regarding the relationship between regional richness (availability of species) and local richness (Srivastava 1999) can suggest mechanisms determining mangrove forest structure. Relationships between regional and local richness fall within the domain of macroecology.

Fig. 2 Local-regional richness plot for mangrove swamps around the world. Solid line is the best-fit linear regression (r^2=0.592; P=1×10^{-9}), and dotted line is the best-fit saturating (power) function (r^2=0.595; P=1×10^{-9}) No significant improvement in fit (P=0.15, F-test) is provided by the power function, which suggests that these forests are not saturated with species
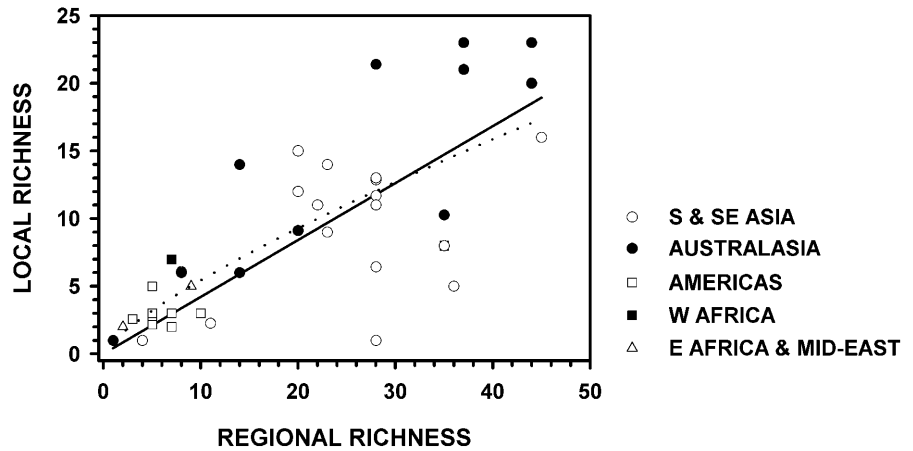
A macroecology of local richness

A macroecological analysis of local richness begins with the axiom that species that occur at a given site are a subset of a regional pool of species that are available to colonize the site (Caley and Schluter 1997; Grace 2001a). For example, of the 22 mangrove species that are known from Bangladesh (Spalding et al. 1997), a maximum of 11 occurred in any of the sites described in Ellison et al. (2000). The absence of the full complement of 22 species at any given site could result from edaphic conditions that favor some species over others, but it could also result from: (1) the failure of some species to colonize the site (e.g., Rabinowitz 1978a); (2) the competitive exclusion of some species by others at the site (e.g., Ball 1980; Ellison and Farnsworth 1993); or (3) preferential predation of propagules (e.g., Smith et al. 1989). A simple correlation analysis could support the hypothesis that species occurrences result from associations with edaphic factors, but this result would not rule out propagule sorting, competition, or preferential predation as mechanisms causing species to occur or not occur in a given site.

An appropriate null hypothesis is that any species that is available in the regional pool could be found in the local assemblage (Caley and Schluter 1997). This is the appropriate null hypothesis because only after species have colonized a site could edaphic sorting, competitive interactions, or propagule predation occur. One way to test this null hypothesis is to examine the relationship between regional and local species richness (Srivastava 1999). A linear relationship between total regional richness and the number of species in a given forest implies that local areas are "unsaturated". That is, local species richness is controlled by ecological factors such as colonization ability and dispersal, and evolutionary factors such as speciation and fixation of mutations that allow species to establish at a given site. A curvilinear (or asymptotic) relationship between regional and local richness implies that there is an upper limit to local species richness that is set by ecological factors such as niche availability (edaphic tolerance), niche partitioning (competition), or exclusion (due to competition or predation).

Thus, if species richness is determined by random colonization and evolutionary diversification, then the number of species in a given swamp should increase consistently with the number of species available for colonization. Alternatively, if species richness is limited by niche availability, as implied by zonation models that restrict species to particular edaphically or competitively determined niches, then the number of species in a given swamp should be independent of the total number of species available in the region.

I examined the relationship between local and regional species richness for 44 study sites around the world for which I could obtain complete species lists from the literature.[1] Local species richness values were determined from these species lists, which were based on 100–200 m transects, 0.1 ha, or 1.0 ha plots. Regional species richness values were taken from Spalding et al. (1997), with additions for China from Li and Lee (1997). Country-wide richness totals were used as regional species pools for all sites except for those in Australia and India, which were divided into sub-regions by Spalding et al. (1997), and for countries in the Neotropics that have both Pacific and Atlantic (or Caribbean) coastlines. A common difficulty with analyzing local versus regional patterns of species richness is an independent measure of the species pool (Grace 2001b). However, the existence of independent lists of regional species (Spalding et al. 1997), and data on the long-range dispersability of mangrove propagules (Rabinowitz 1978a; Steinke 1986; Komiyama et al. 1992; Smith 1992; Clarke 1993; McGuinness 1997) suggests that the species pools used are appropriate for these analyses. Linear and non-linear (power) functions were fit to the data using S-Plus version 6.0 (Insightful, Seattle, Wash., USA). Relative fits of the models were compared using an F-test (Draper and Smith 1981; Hilborn and Mangel 1997).

Regional species richness explains nearly 60% of the variance in within-site species richness (Fig. 2), and a linear relationship provides as good a fit to these data as

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[1] The full dataset and literature citations are available on request from the author

does an asymptotic saturating relationship. Since the saturating relationship has one more parameter than the linear relationship and there is no significant difference in fit, parsimony suggests that we accept the linear relationship as the true relationship between local and regional species richness. Such a linear relationship implies that mangrove forests are unsaturated with species, and that controls on local species richness are best looked for at regional scales. This relationship is independent of biogeographic province [as defined by Spalding et al. (1997): South and Southeast Asia, Australasia (including the eastern Pacific), the Americas, West Africa, and East Africa and the Middle East; Fig. 2].

Global distribution of mangrove species

Species richness of mangrove forests is highest in the Indo-West Pacific and declines relatively smoothly with distance from ≈100°E, the longitude of peak species richness (Fig. 3; Ellison et al. 1999). This distribution pattern is similar to that seen in reef-building corals and seagrasses, (McCoy and Heck 1976), reef-fishes (Bellwood and Hughes 2001), and mangrove-inhabiting snails (Ellison et al. 1999). After nearly 100 years of discussion, a consensus is emerging that for mangroves, this pattern is best explained by a combination of continental drift and in situ species diversification (reviews in Ellison et al. 1999; Ellison and Farnsworth 2001). The extent and structure of mangrove ecosystems in geological time have been determined by tectonic activity (Ellison et al. 1999) and changing sea levels (Woodroffe and Grindrod 1991; Ellison 1993, 1994).

Less has been written about latitudinal patterns of mangrove species richness (but see Schaeffer et al. 1990; De Lange and de Lange 1994; Duke et al. 1998). In contrast to their "anomalous" longitudinal distribution pattern, latitudinal gradients in mangrove species richness are quite similar to those seen for other taxa. Species richness is highest at the equator and tails off smoothly to the north and south (Fig. 3). There is a vast literature on such patterns, and hundreds of mechanisms have been hypothesized to explain them (Huston 1994; Palmer 1994; Colwell and Lees 2000).

The "mid-domain effect" provides one appropriate null model for such patterns (Colwell and Lees 2000). The mid-domain model accounts for the joint effects of observed latitudinal midpoints and extents of species' geographic ranges and their potential geographic ranges as determined by biogeographic barriers [winter seawater isotherm ≈20°C and winter minimum air temperature >0°C; Duke et al. (1998)]. This model depends on a geometric constraint: species whose range midpoints occur towards the edge of a geographic boundary (here the northern and southern climatic boundaries) must have relatively smaller latitudinal ranges than species whose range midpoints occur towards the center of a groups' distribution (here, the equator). Colwell and Lees (2000) showed that these geometric constraints on range size
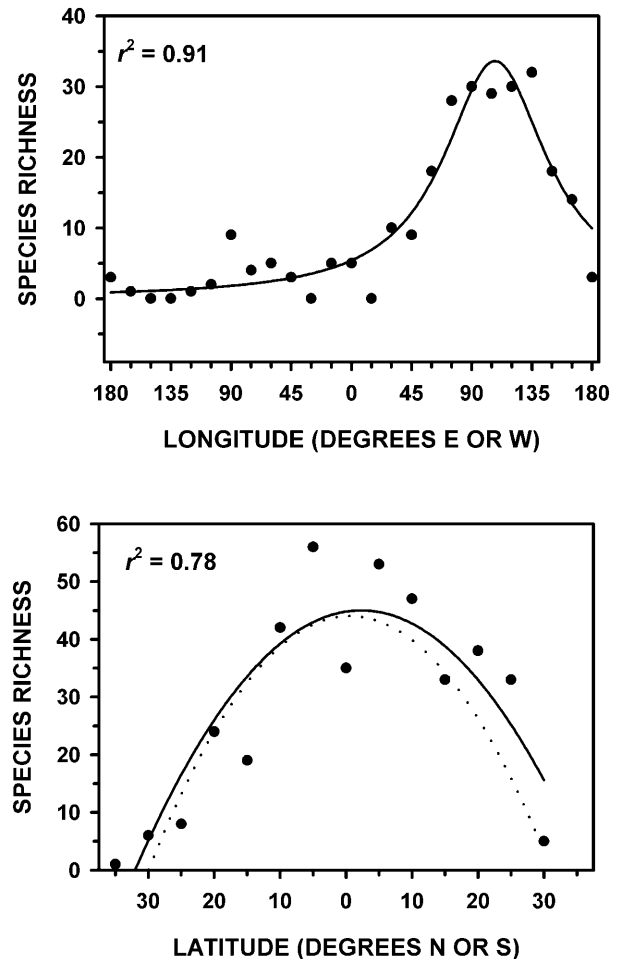

Fig. 3 Species richness of mangroves as a function of longitude (*upper panel*) and latitude (*lower panel*). Lines are best fit non-linear regressions. On the richness vs. latitude plot (*lower panel*) the solid line is the observed relationship, and the dotted line is the expected relationship for all mangrove species with observed latitudinal midpoints and randomized latitudinal ranges. The expected distribution was generated using RangeModel 3.0 (Colwell 2000)

lead to a peak in species richness at the center, even in the absence of environmental gradients correlated with latitude. By comparing the observed pattern of species richness with that expected under the mid-domain ("null") model (Lees et al. 1999; Lyons and Willig 1999; Veech 2000), one can test whether global patterns of species distribution can be explained simply by spatial geometry, or whether other processes need to be considered.

I used RangeModel 3.0 (Colwell 2000) to generate, using Monte Carlo simulations, 1,000 distributions of all mangrove species [those listed Spalding et al. (1997) along with the Chinese endemics listed in Li and Lee (1997)]. Country-by-country data (Spalding et al. 1997) were used to determine latitudinal mid-points and ranges of these mangroves. The observed distribution (Fig. 3, solid line) was compared with a null distribution in which latitudinal midpoints were those actually observed and range sizes were chosen at random (Fig. 3, dotted

line). This is a reasonable null model if modern species essentially evolved in situ (Ellison et al. 1999). The actual latitudinal distribution did not differ from this null distribution (P=0.26, two-sample Kolmogorov-Smirnov test), and explained nearly 80% of the variance in latitudinal species richness. Thus, simple geometric constraints, notably habitat area, perhaps interacting with regional climatic variables, are sufficient to explain latitudinal patterns in mangrove species richness.

What determines regional richness of mangrove species?

The analysis of the local-regional richness plot (Fig. 2) suggests that regional processes are critical determinants of local species richness. Similarly, a null model analysis indicates that regional variables, especially available habitat area, also play a significant role in determining global patterns of species richness with respect to both latitude and longitude (Fig. 3). These results illustrate that a macroecological approach can lead to better understanding of factors that control species richness of mangroves at intermediate (regional) scales.

In the most complete study to date of regional species richness patterns, Duke and his colleagues (Duke 1992; Duke et al. 1998) concluded that environmental factors such as rainfall, tidal variation, estuary length, and catchment area contribute significantly to observed intra-regional differences in species richness. Similarly, Schaeffer-Novelli et al. (1990) attributed intra-regional differences in species composition of Brazilian mangroves to local topography and edaphic factors operating within the constraints set by climate and hydrology.

Because habitat area has an strong effect on species richness (Connor and McCoy 1979), it is important to remove its effects before attributing observed patterns of species richness to edaphic factors, topography, and rainfall. Using geographic data in Spalding et al. (1997), I examined the relationship between regional species richness and area occupied by mangroves. Area alone explains 28% of the variance in species richness across regions (Fig. 4A). Stepwise multiple regression analysis further indicates that annual rainfall (Fig. 4B) and biogeographic province (categories of Fig. 2) explain an additional 23% and 13%, respectively, of the overall variance in inter-regional species richness, but there is no additional significant effect of either latitude or longitude. Thus, variables identified by Schaeffer-Novelli et al. (1990) and Duke (1992; Duke et al. 1998) do affect regional species richness, but less so than available area.

The lack of discrete latitudinal or longitudinal effects also is observed at global scales (Ellison et al. 1999). The latitudinal pattern shown in Fig. 3 is due almost entirely to total mangrove area at a given latitude, which accounts for 78% of the variance in latitudinal species richness patterns (Fig. 4C). Similarly, mangrove area explains 88% of the variance in species richness across the five large biogeographic provinces (South and Southeast
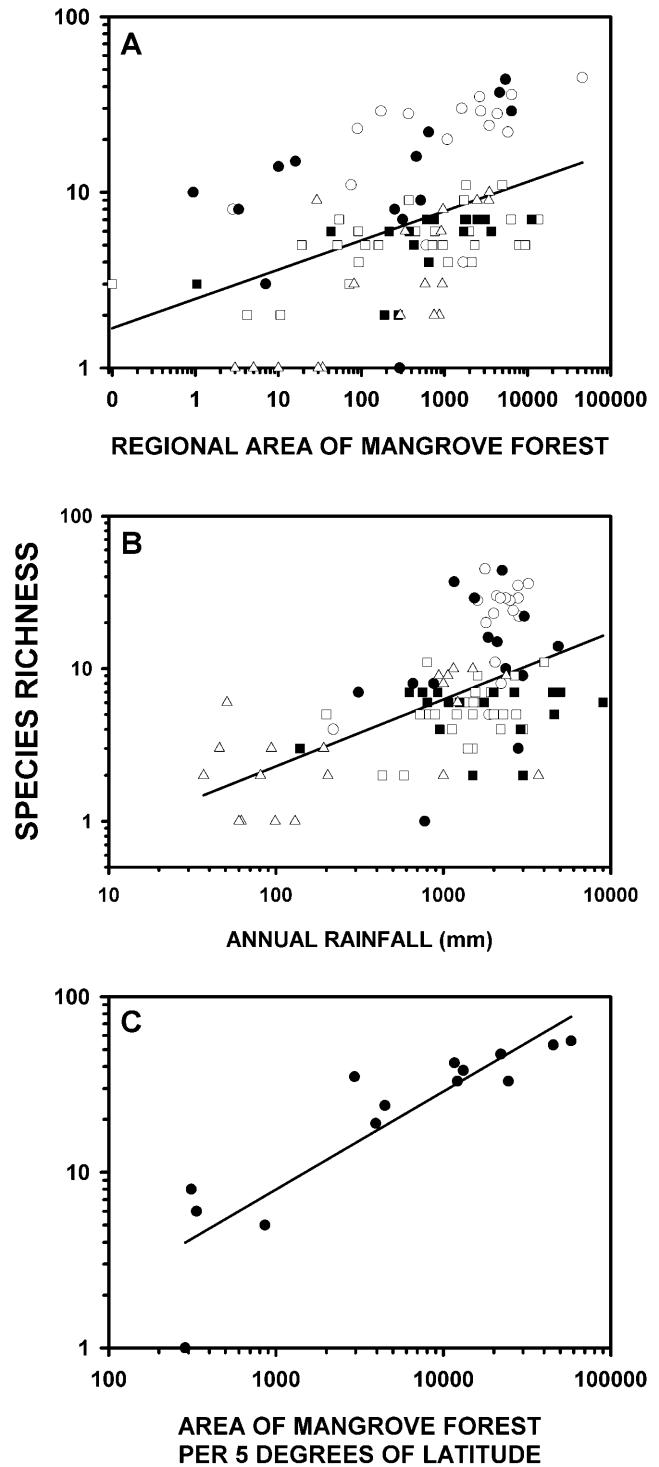

Fig. 4A–C Species richness of mangroves as a function of area and rainfall. **A** Richness as a function of regional (country or region within country) area (symbols as in Fig. 2); **B** richness as a function of regional rainfall (symbols as in Fig. 2); **C** richness for a given 5° interval of latitude as a function of area at that latitude

Asia, Australasia and the Pacific Islands, the Americas, West Africa, and East Africa and the Middle East) in which mangroves occur (Ellison et al. 1999). A similarly large effect of habitat area in these regions was found for coral reef fishes (Bellwood and Hughes 2001), which

have latitudinal and longitudinal patterns of species richness nearly identical to that of mangroves.

This macroecological analysis of mangrove species richness leads to three conclusions. First, we can identify regional species pools and use them to predict local species richness. This alone may help us to determine whether a given forest is or has been impacted by anthropogenic activities. Second, we can construct more accurate models of large-scale forest compositing that can be used in models of forest productivity and nutrient cycling. Third, this approach can be used for mangrove associates such as invertebrates (Ellison et al. 1999), fish, birds, or fungi. As more taxa are studied, the global pattern of mangrove species distribution becomes less anomalous.

Considering species within mangroves to be distributed broadly among overlapping gradients as opposed to in discrete zones can inform our understanding of how local processes filter regional species pools to result in the structure and composition of a specific forest. Within individual swamps, it is as important to ask why available species do not occur as it is to determine edaphic limits of currently occurring species. For example, predation of propagules prior to dispersal (Farnsworth and Ellison 1997b) may reduce significantly the colonization of some mangroves to a given site. Similarly, dispersed propagules are consumed in large numbers, and often in density- or frequency-dependent numbers once they wash up on shore (Smith 1987; Smith et al. 1989; Sousa and Mitchell 1999). Data available on post-predation recruitment and early seedling success (Ellison and Farnsworth 1993; Clarke 1995; McKee 1995; Kathiresan et al. 1996; O'Grady et al. 1996; Koch 1997; Osunkoya and Cresse 1997) have focused on locally-occurring species (as opposed to the entire species pool). Only Rabinowitz (Rabinowitz 1978b) experimentally examined the interaction of seedling growth, dispersal, and local distribution patterns, and her results are not applicable to the Indo-West Pacific, where within- and between-forest diversity is much higher (Smith 1992). Interspecific interactions – notably interspecific competition – have been little studied in mangroves (Ball 1980; Smith 1988; Rey 1994), despite their overwhelming importance in determining plant species distributions in terrestrial uplands (Gurevitch et al. 1992), freshwater wetlands (Keddy 2000), and salt marshes (Bertness and Ellison 1987).

Example 2: functional relationships among mangrove leaf traits

Local species richness by itself is not the same as zonation. Edaphic conditions vary across the intertidal creating environmental stressors that are linked to species distributions through their effects on plant physiological processes (Ball 1988; Ball and Sobrado 1998). Mangroves are a model system for studying effects of hypoxia and salinity on water relations and photosynthesis in stressful habitats. Yet, as with the studies of mangrove distributions described above, there have been few attempts to integrate mangrove ecophysiology with broader patterns and trends across the plant kingdom (but see notable exceptions in Ball 1996; Farnsworth and Farrant 1998; Farnsworth 2000).

Recent research has shown that relationships among key ecophysiological traits of leaves – lifespan, specific area, nitrogen content, photosynthetic and diffusive conductance rates – are similar across a taxonomically diverse range of plants in upland biomes ranging from the Arctic tundra to the tropical rain forests (Reich et al. 1992, 1997, 1999). This generality could allow for the modeling of regional- and global-scale productivity, distribution, and dynamics of vegetation given a small set of easily measured leaf traits (Leuning et al. 1995; Aber et al. 1996; Reich et al. 1999). Many of these leaf traits may be measurable for mangroves using remote-sensing technologies (Ramsey and Jensen 1996; Green et al. 1997; Blasco et al. 1998; Mumby et al. 1999), leading to better predictions of the responses of mangroves to global climate change and other large-scale stressors. In light of this potential, and to determine if existing models might need adjustments to account for the unique ecophysiological traits associated with adaptations for dealing with hypoxia and salinity, I compared relationships among mangrove leaf traits with those published for upland biomes (Reich et al. 1999) and temperate wetlands (Shipley and Lechowicz 2000).

Data of the kind used by Reich et al. (1999) and Shipley and Lechowicz (2000) to examine the generality of relationships among leaf-trait never have been collected simultaneously from a single mangrove plant. Therefore, for comparative exploratory analyses, I extracted values for leaf lifespan (months), specific leaf area (SLA: cm^2/g), photosynthetic rates [either area-based (A_{area}: $\mu mol\ CO_2\ m^{-2}\ s^{-1}$) or mass-based ($A_{mass}$: $nmol\ CO_2\ g^{-1}\ s^{-1}$), foliar nitrogen content [either area-based (N_{area}: g/m^2) or mass-based (N_{mass}: mg/g)], and leaf diffusive conductance (G_s: $mmol\ H_2O\ m^{-2}\ s^{-1}$) from the published literature and created "composite mangrove" leaves by pooling traits across studies (Table 1)[2]. In general, published photosynthetic rates for mangroves are area-based, and I derived A_{mass} as $A_{area} \times SLA$ ($\mu mol\ CO_2\ m^{-2}\ s^{-1} \times cm^2\ g^{-1}/10 = nmol\ CO_2\ g^{-1}\ s^{-1}$). I then plotted the "composite mangrove" data alongside field data published by Reich et al. (1999) for 105 species from six upland biomes in the Americas and data published by Shipley and Lechowicz (2000) for 40 species of freshwater wetland herbs from eastern North America that were grown in a common garden. Regression analyses were done separately for the mangrove species, the wetland herbs, and the upland species (in S-Plus). Model I and model II regressions gave similar results, and for consistency with Reich et al. (1999), I report the results of the model I regressions.

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[2] The full dataset from which these "composite mangroves" were created, along with literature citations, is available on request from the author

Table 1 Leaf traits of "composite mangroves" used in the comparative analysis of leaf-trait relationships (Fig. 5). Variables used and their units are: leaf lifespan (months); specific leaf area (*SLA*) (cm²/g); mass-based photosynthetic rate (A_{mass}) (nmol CO_2 g⁻¹ s⁻¹); mass-based leaf nitrogen content (N_{mass}) (mg/g); leaf diffusive conductance (G_s) (mmol H_2O m⁻² s⁻¹). (*n.a.* no data available)

Species	Leaf lifespan	SLA	N_{mass}	A_{mass}	G_s
Aegiceras corniculatum	24	n.a.	n.a.	n.a.	138.00
Avicennia germinans	10	64.80	16.00	41.15	270.00
Avicennia marina	13.7	42.20	13.54	54.31	200.00
Bruguiera gymnorrhiza	32.7	75.13	6.50	71.37	160.00
Ceriops tagal	36.5	52.85	7.72	15.58	43.75
Cocoloba uvifera	n.a.	n.a.	9.60	n.a.	300.00
Conocarpus erectus	5	65.80	8.55	32.70	196.67
Kandelia candel	12	n.a.	14.95	n.a.	n.a.
Laguncularia racemosa	4	67.50	8.85	50.56	182.00
Rhizophora apiculata	19.5	67.20	15.30	51.41	69.25
Rhizphora mangle	9	80.00	18.00	74.05	163.25
Rhizopora mucronata	17	n.a.	10.50	n.a.	44.00
Rhizophora stylosa	19	59.07	9.22	62.02	114.00

Table 2 Summary of Model I regression analyses for leaf traits illustrated in Fig. 5. Reich et al.'s (1999) dataset includes field data from six biomes of the Americas: alpine tundra-subalpine forest ecotone, cold temperate forest-prairie ecotone, montane cool temperate forest, desert shrubland, subtropical forest, and tropical rainforest. The data for eastern North American wetlands are from plants grown in a common garden by Shipley and Lechowizc (2000). Species used in the mangrove analysis are: *Avicennia germinans, Avicennia marina, Bruguiera gymnorrhiza, Ceriops tagal, Conocarpus erectus, Laguncularia racemosa, Rhizophora apiculata, Rhizophora mangle,* and *Rhizophora stylosa.* Variables and units as in Table 1. All regressions were done on log₁₀-transformed data. Shipley and Lechowicz do not provide data for leaf lifespan. (*n.a.* no data available)

Upland biomes of the Americas		Mangroves		Eastern North American Wetlands	
Regression equation	r^2	Regression equation	r^2	Regression equation	r^2
SLA=2.42–0.46×Leaf lifespan	0.57	SLA=1.85–0.05×Leaf lifespan	0.05	n.a.	
A_{mass}=2.56–0.66×Leaf lifespan	0.78	A_{mass}=1.77–0.10×Leaf lifespan	0.03	n.a.	
N_{mass}=1.57–0.34×*Leaf lifespan*	0.59	N_{mass}=1.18–0.12×Leaf lifespan	0.06	n.a.	
G_s=2.8–0.33×Leaf lifespan	0.30	Gs=2.65–0.49×Leaf lifespan	0.31	n.a.	
A_{mass}=–0.20+1.06×SLA	0.74	A_{mass}=–0.11+0.99×SLA	0.15	A_{mass}=1.24+0.44×SLA	0.13
N_{mass}=0.13+0.56×SLA	0.55	N_{mass}=0.91+0.07×SLA	0.001	N_{mass}=1.09+0.08×SLA	0.01
G_s=2.03+0.23×SLA	0.06	G_s=1.28+0.48×SLA	0.03	G_s=4.40–0.95×SLA	0.28
N_{mass}=0.31+0.49×A_{mass}	0.68	N_{mass}=0.65+0.23×A_{mass}	0.09	N_{mass}=0.87+0.18×A_{mass}	0.13
G_s=1.65+0.44×A_{mass}	0.30	G_s=1.11+0.62×A_{mass}	0.26	G_s=1.63+0.31×A_{mass}	0.04
G_s=2.05+0.35×N_{mass}	0.07	G_s=1.81+0.30×N_{mass}	0.02	G_s=1.06+0.98×N_{mass}	0.12

Reich et al. (1999) also performed a principal components analysis (PCA) to determine if species from different functional groups (forbs, shrubs, deciduous broad-leaved trees, evergreen broad-leaved trees, coniferous needle-leaved trees) clustered together in multivariate space. After re-entering the data from Table 2 of Reich et al. (1999), I performed a PCA on those data to recover their trait loadings and species ordination. I used those loadings to predict where the "composite mangroves" would be expected to occur in multivariate space if the leaf-trait relationships observed for upland species by Reich et al. (1999) were the same for mangroves. I then performed a PCA on all the data (Reich et al.'s and the "composite mangroves") combined to see if the results would differ if mangroves were included in the overall analysis. Only the nine mangrove species for which I had values for all five leaf traits in Table 1 were used in the PCA.

Principal axis scores for the predicted mangroves were compared with those observed in the combined analysis using a matched-pairs *t*-test. PCAs were done using S-Plus on untransformed data that were first standardized into standard deviation units [(observation – mean) / SD]. Because Shipley and Lechowicz (2000) did

not provide leaf lifespan data, their wetland herb dataset was not used in the PCA.

Correlations among mangrove leaf traits were similar in direction to those observed by Reich et al. (1999), but differed in magnitude (slopes of the regressions) (Table 2, Fig. 5). With respect to leaf lifespan, G_s declined 48% faster, but N_{mass}, A_{mass}, and SLA declined 64%, 85%, and 91% slower for mangroves than were predicted by Reich et al.'s (1999) general leaf-trait equations. Similarly, with respect to SLA of mangroves, G_s increased 109% faster while N_{mass} increased 88% slower than predicted, but A_{mass} was nearly identical to that predicted. Across the observed range of mangrove A_{mass} rates, G_s increased 41% faster while N_{mass} decreased 53% faster than predicted. G_s also increased 14% faster with N_{mass} than predicted (Table 2, Fig. 5). Fits of the regression lines for mangroves were generally poorer than those for upland biomes, principally because of the small sample size (n=9).

Leaf trait relationships among SLA, N_{mass}, A_{mass}, and G_s of wetland herbs (Shipley and Lechowicz 2000) differed from those observed both for upland biomes and mangroves (Table 2, Fig. 5). As for mangroves, slopes of
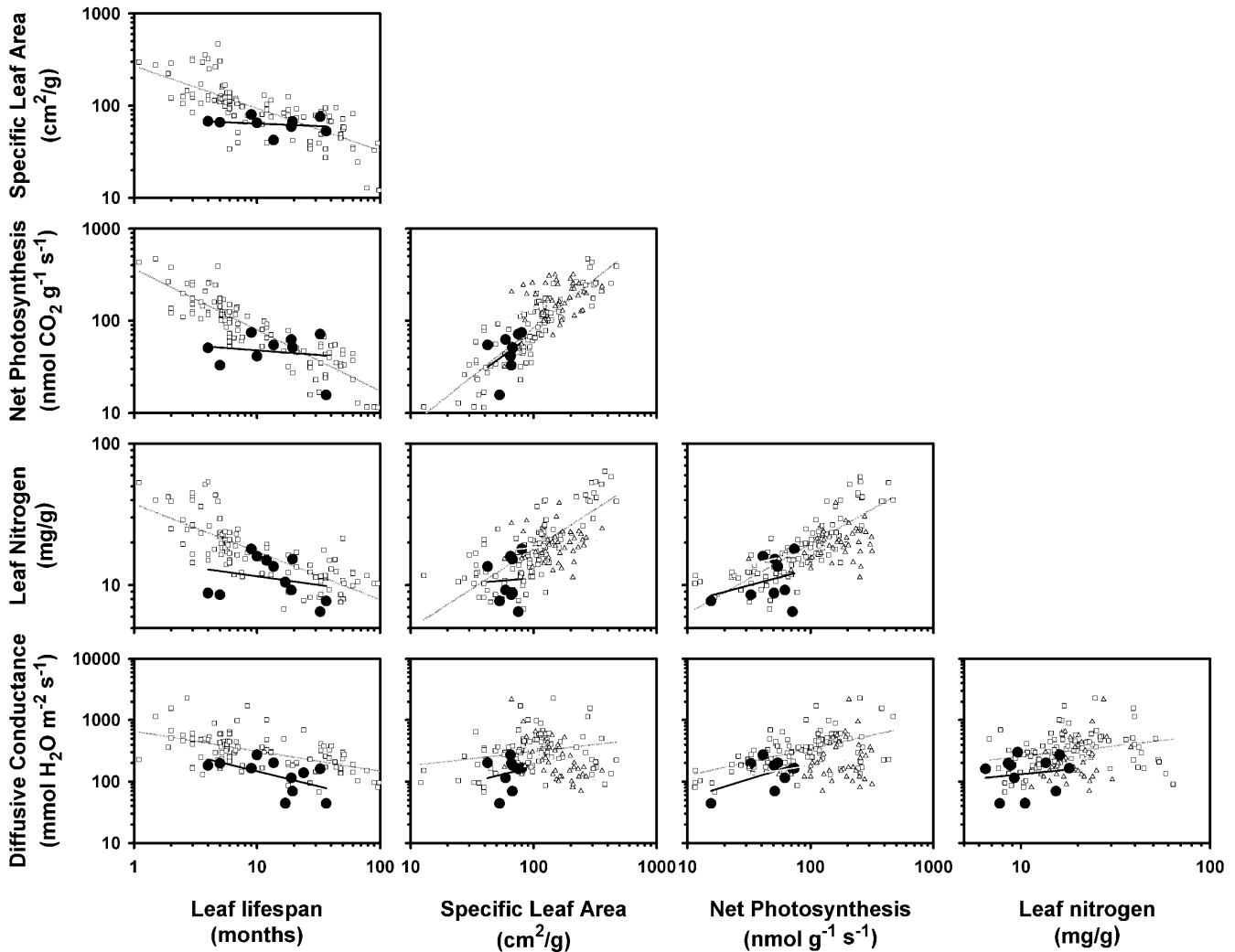
Fig. 5 Scatterplot matrix of the relationship among five leaf traits: leaf lifespan, diffusive conductance, nitrogen content, photosynthetic rate, and specific leaf area. *Small open squares* and *dark grey regression* lines are data from Reich et al. (1999) for 105 species from six upland biomes. *Small open triangles* and light *grey regression lines* are data from Shipley and Lechowicz (2000) for 40 species of wetland herbs. No data on leaf lifespan are provided in Shipley and Lechowicz (2000). *Large black symbols* and *black regression lines* are data for the "composite mangroves" in Table 2

the regression lines relating leaf traits of wetland herbs were lower than those for upland plants. In general, the slopes of the regression lines relating leaf traits of the wetland herbs were also lower than those for mangroves, but intercepts were higher. Thus wetland herbs, with their relatively small ranges of SLA, N_{mass}, A_{mass}, and G_s fell within the cluster of points representing upland plants in Fig. 5 (with the exception of the relationship between N_{mass} and G_s which is more similar to that of mangroves). The regression lines of the wetland herbs also fit the data relatively poorly, despite somewhat larger sample sizes ($n=40$) than was available for the mangroves.

Applying the loadings of the PCA of Reich et al. (1999) to the nine "composite mangrove" species for

which complete data were available predicted that mangroves would not form a natural grouping, and would not be distinguishable from the non-mangrove species (Fig. 6, predicted mangrove plot). However, the PCA that included not only the non-mangrove species but also the "composite mangroves" did not qualitatively re-shape the arrangement of non-mangrove species in multivariate space, but did cluster together the "composite mangroves" more tightly (Fig. 6, observed mangrove plot). In the latter PCA, the "composite mangroves" clustered closely with evergreen (tropical) broadleaved trees of tropical and subtropical forests. The scores of the nine mangrove taxa on principal axis 1 differed slightly ($P=0.08$) between those predicted by the first PCA and those observed in the second PCA. No difference ($P=0.27$) was observed between predicted and observed locations on principal axis 2. Loadings on each axis did not differ by more than a few percent in magnitude, and were similar in direction between the two PCAs (Table 3). In both PCAs, principal axis 1 primarily reflected (left to right) increasing leaf lifespan and decreasing leaf SLA and A_{mass}. Principal axis 2 reflected (bottom to top) primarily decreasing G_s and N_{mass}.

Table 3 Loadings of the five variables on the two principal axes shown in Fig. 6 for the Reich et al. (1999) data set alone, and for that dataset together with the "composite mangroves". Variable names as in Table 1; PCAs were conducted on variables standardized to standard deviation units

Variable	Biomes of the Americas		Biomes of the Americas plus "composite mangroves"	
	PC-1	PC-2	PC-1	PC-2
Leaf lifespan	0.473	0.092	0.464	0.049
SLA	−0.528	0.267	−0.531	0.220
N_{mass}	0.318	−0.593	0.302	−0.694
A_{mass}	−0.553	−0.109	−0.557	−0.137
G_s	−0.303	−0.746	−0.318	−0.694
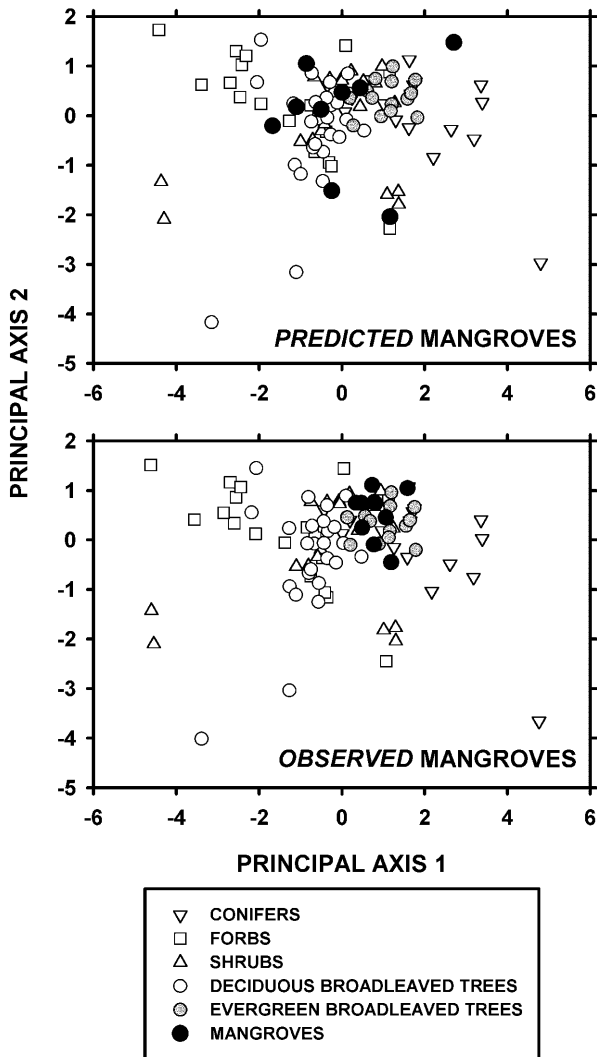
Fig. 6 Principal components analysis (PCA) of leaf traits of mangrove and of 96 species from six upland biomes. The "predicted mangroves" plot (*top*) illustrates the placement of the 9 "composite mangrove" species expected from the ordination of the 96 upland species. The "observed mangroves" plot (*bottom*) illustrates the placement of the mangrove species when they are included in the PCA along with the upland species

Are mangroves really different?

The macroecological analysis of mangrove leaf traits suggests that for pairwise relationships (Fig. 5), mangroves respond differently from upland plants to environmental stressors. Mangroves have thicker leaves that live longer, photosynthesize more slowly, and have lower nitrogen content than upland species. Because of the generally higher *y*-intercepts for the leaf-trait relationships of wetland herbs (except for the G_s vs N_{mass} relationship), differences between mangroves and wetland herbs appear to be in the same direction as between mangroves and upland plants (Fig. 5). The qualitative conclusion from Fig. 5 is that in terms of leaf traits and their relationships, freshwater wetland herbs are more like upland plants than they are like mangroves. This interpretation argues for the relatively large importance of salinity in determining mangrove leaf traits (Ball 1988, 1996). This appears to be a convergent property among mangroves, not a species- (or genus-) specific (Table 1) characteristic. Mangroves cluster together in multivariate ecophysiological space, a result not predicted by leaf-trait relationships of upland plants (Fig. 6), but not unexpected given the restriction of these diverse taxa to a habitat with a common set of severe environmental stressors. In multivariate leaf-trait space (Fig. 6), mangroves are most similar to evergreen trees of tropical wet forests (cf. Ball 1996).

The results for these woody halophytes need to be taken with a large grain of salt, however. Reich et al. (1999) and Shipley and Lechowicz (2000) measured all leaf traits simultaneously on single plants. Therefore, in their data there is a true link between, for example, leaf N content and net photosynthetic rate because these values were measured on the same leaf. In contrast, the mangrove leaf trait data are from "composite" plants; for example, leaf N data and photosynthetic rates for *Bruguiera gymnorrhiza* come from different plants and different studies, albeit in the same country. True tests of the hypotheses suggested in Figs. 5 and 6, that mangroves have unique sets of leaf-trait relationships, require long-term data collection on individual leaves of individual plants. Further, the large dataset of Reich et al. (1999) has broad taxonomic diversity and the results are supported even after phylogenetic relationships have been accounted for (Ackerly and Reich 1999). I did not apply phylogenetically independent contrasts to the "composite mangroves" because the sample size for which complete data were available was only nine species, five of which are in the Rhizophoraceae (Table 1). However, the large number of mangrove species, and their representation in many plant families would allow for independent contrast analysis, once more data were amassed.

A research agenda for mangrove macroecology

The two examples presented illustrate that for fundamental questions in mangrove ecology – determinants of diversity and its relationship to ecophysiology – that there is much yet to be done, and much to be learned from the macroecological approach. In presenting a research "agenda" for mangrove macroecology, I suggest only the first steps and the list is not meant be exhaustive.

Documenting zonation

Although there now are comprehensive regional lists of "true" (sensu Tomlinson 1986) mangrove species (e.g. Spalding et al. 1997), data on within-swamp distributions (i.e. zonation) are surprisingly unreliable. Most publications report only dominant species, and describe zones without quantifying them. The minimum data required to assess zonation (or gradients) are:

- A complete list of species in a given forest;
- A measure of the abundance of each species where it occurs;
- Measurements of edaphic parameters and topographic relief wherever composition and abundance data are taken;
- Ideally, data should be taken in contiguous quadrats along transects (Dale 1999).

Quantitative analyses of zonation should begin with testing the null hypothesis of no zonation, and then precede to describe zonation only if the null hypothesis is rejected (cf. Ellison et al. 2000). The analysis should also include an assessment of why available species in the regional species pool do not occur at the study site. Explicit consideration of dispersal probabilities (local current regimes) and biotic factors (especially pre- and post-dispersal propagule predation, competition, facilitation) would improve significantly our understanding of the interplay of local and regional processes in determining within-forest patterns of distribution and abundance.

Global diversity of mangrove ecosystems

Even fewer data are available or organized on the distribution and abundance of mangrove associates, including plants, animals, and microorganisms. Ellison et al. (1999) illustrated that collation and analysis of published data of a single faunal group associated closely with mangroves – littorinid snails – led to stronger inferences about processes leading to global diversification of mangroves. I expect similar increases in our understanding of these forests to come from detailed analysis of distribution patterns of other tight associates, notably vascular epiphytes (Gomez and Winkler 1991; Ellison and Farnsworth 2001), macroalgae (Littler 1989), sessile invertebrates (Rützler 1969; Farnsworth and Ellison 1996), insects (Murphy 1990), crabs (Jones 1984), fish

(Krishnamurthy et al. 1984), and fungi (Kohlmeyer 1984; Hyde and Lee 1995). The long-standing debate on the importance of mangroves as nursery grounds for fish (reviewed in Ellison and Farnsworth 2001) could be clarified if we had a more complete global assessment of the diversity of fish associated with mangroves. If nothing else, a comprehensive assessment of the diversity of mangroves would illustrate the importance of these threatened forests as ecosystems of high diversity, in contrast to their current perception as ecological deserts.

Initially, existing data should be collated to identify geographical gaps in coverage and to determine common methods for subsequent collections. As for analyses of zonation, analyses of global diversity patterns require both distribution and abundance data. Ideally, collection of such diversity data also should include size measurements of associated trees and determination of key ecosystem properties (e.g. salinity, water and soil temperatures, litterfall, so that the data could be used to associate measurements of mangrove productivity (Saenger and Snedaker 1993) with heterotrophic diversity.

Functional traits and ecosystem dynamics

Renewed interest in the relationship between plant functional traits and ecosystem dynamics has been spurred by the recognition that traits that are easily measured, such as SLA, are well-correlated with traits that are more difficult to measure, including rates of photosynthesis and diffusive conductance (Reich et al. 1992, 1997, 1999; Shipley and Lechowicz 2000). Scaling relationships that appear to be independent of species identity (Enquist et al. 1999, 2000; Enquist and Niklas 2001; Niklas and Enquist 2001) should allow these leaf-level traits to be used to develop robust predictions of the responses by mangrove ecosystems to increases in global temperature and sea level. The existing data for mangroves, however, are weak. Only four *Rhizophora* spp. are included in the dataset (Cannell 1981) analyzed by Niklas and Enquist (2001), and the data I culled from the literature (Table 1) to compare with those of Reich et al. (1999) and Shipley and Lechowicz (2000) are "composites".

Besides needing better, replicated data on correlated leaf traits of individual mangrove trees, more data on measurements of mangrove stand productivity are needed. Saenger and Snedaker (1993) compiled existing data (through 1992) on standing biomass and litterfall of mangroves throughout the world. Their salient result, that the litterfall of individual species increases with plant height and towards the equator, cannot be scaled easily to either mixed-species stands or whole forests. In particular, general allometric theory predicts that overall ecosystem productivity should be independent of plant size (Enquist et al. 2000; Enquist and Niklas 2001; Niklas and Enquist 2001). This theory, like that of Reich et al. (1992, 1997, 1999) on the scaling of leaf traits could be tested independently using data from mangroves. This would be a major contribution to general

ecological theory, and would also let us really decide whether mangroves are different from other biomes in their ecosystem properties. I suspect that they are not, and an integration of "mangrove ecology" into "ecology" would help advance both.

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Different Kinds of Mangrove Forests Provide Different Goods and Services

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Different kinds of mangrove forests provide different goods and services

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Abstract. The goods and services that mangrove forests provide to society are widely understood but may be too generally stated to serve as useful guidelines in decision-making. Understanding the differences between fringe, riverine, and basin forests may help to focus these guidelines and to determine the best use of a particular forest. Fringe mangroves are important primarily for shoreline protection. Riverine forests, which are likely to be the most productive of the three types of forests, are particularly important to animal and plant productivity, perhaps because of high nutrient concentrations associated with sediment trapping. Basin forests serve as nutrient sinks for both natural and anthropogenically enhanced ecosystem processes and are often important sources of wood products. Exploitation of a forest for one particular reason may make it incapable of providing other goods and services.

Key words. Mangrove forests, flood protection, nutrients, wastewater recycling, timber harvesting, shrimp ponds.

INTRODUCTION

Mangrove forests are widely recognized as providing a wide variety of goods and services to people, including protection from floods, provision of a variety of plant and animal products, sediment trapping, and nutrient uptake and transformation (FAO, 1994). Destruction of these forests continues, however, in spite of this understanding of their importance. Although these wetlands are abundant along many protected shorelines around the world, the life-sustaining but still poorly documented benefits they can provide, such as support to offshore fisheries, are likely to be diminishing.

The lack of a direct, easily observed relationship between a mangrove forest and the benefits it provides (and sometimes the lack of sufficient research to document it) may be one reason for continued exploitation, and often loss, of these wetlands. Another reason may be the generality that cloaks many discussions of the importance of these wetlands. In fact, not all mangrove forests provide all the goods and services attributed to them. There are significant differences in the characteristics of mangrove habitats, not only between continents and regions but within individual stands of mangroves as well. Using a simple rationale for classifying a given mangrove stand may assist land-use managers in determining its likely value to society and subsequently in using it more wisely. The purpose of this paper is to develop a simple functional classification of mangrove forests and to identify which goods and services are likely to derive from which kinds of forests.

DIFFERENCES WITHIN AND AMONG MANGROVE FORESTS

Efforts to understand mangrove forests focused for many years on the significance to tree species distributions of spatial differences in soil water characteristics (Macnae, 1968), short-term differences in propagule dispersal and survival (Rabinowitz, 1978; Smith, 1987), competition among species (Clarke & Hannon, 1971), and geomorphological history or characterization of estuaries (Thom, Wright &

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Coleman, 1975). Some studies have de-emphasized tree species zonation because of the large number of exceptions to simple patterns (e.g. West, 1977). High and low intertidal zones are likely to differ as a result of gradients in frequency of inundation, soil porewater salinity, and soil waterlogging, that are usually interrelated and often difficult to predict in the absence of information about both regional hydrology and animal activity. No consistent pattern or cause of mangrove zonation has yet to be derived (Smith, 1992).

Two systems that may be particularly useful to land managers have been proposed for classifying mangrove forests. Six different kinds of mangrove forests are commonly distinguished in the Neotropics, where many are underlain by a carbonate limestone base: overwash, fringe, riverine, basin, scrub, and hammock (Lugo & Snedaker, 1974, Cintrón, Lugo & Martinez, 1986). A more general system has been proposed for Old World mangroves, which are more likely to develop on accreting sediments deposited by rivers and tides (Woodroffe, 1992). This system distinguishes three extremes, based on dominant physical processes: river-dominated, tide-dominated, and interior mangrove forests. Intermediate kinds of forests, including the six New World types, can be located within this framework (Fig. 1a).

In this paper, we adopt a hybrid of these systems, combining the familiarity of Lugo & Snedaker's terms with the flexibility of Woodroffe's system. We refer to tide-dominated mangroves as fringe mangroves, river-dominated mangroves as riverine mangroves, and interior mangroves as basin mangroves (Fig. 1b). Basin mangroves are likely to contain the most variation within a region, including low and high intertidal zones as well as small forests far inland, fed only occasionally by storm tides. Others have used the same system already for more local descriptions (e.g. Florida: Odum & McIvor, 1990). We suggest that this framework can be used to define the extremes among mangrove forests within any region without having to determine how fringe mangrove forests (for instance) in one part of the world are related to fringe mangrove forests in another.

The three extremes are easily described. Fringe mangroves receive the brunt of the tides, which are often full-strength seawater. Prop roots, buttresses, and pneumatophores are common among trees in this part of a forest. Riverine mangroves are flooded by river water as well as by tides, so that salinity is moderate.

Trees in this zone are likely to be among the most productive in a forest (Twilley, Lugo & Patterson-Zucca, 1986). Basin mangroves generally cover large areas behind fringe and riverine mangroves, and only occasionally do tides inundate an entire basin forest. Soil salinity may be very high at higher elevations where evapotranspiration causes salts to accumulate. In small forests that are frequently flooded, or where rainfall is high and/or groundwater flow is substantial, a basin mangrove forest can be of moderate or even low salinity (e.g. Cintrón *et al.*, 1978; Semeniuk, 1983; Ewel *et al.*, 1998a). Clearly, there may be substantial differences in hydrology, nutrient cycling, and productivity between these three types of forests (Twilley, 1995). Productivity (generally measured by litterfall alone in these forests) is closely related to water turnover, with riverine >fringe >basin (Pool, Lugo & Snedaker, 1975), because higher turnover is likely to mean: (i) an increased supply of nutrients, silts, and clays; (ii) less accumulation of toxic substances in porewater; and (iii) greater aeration of the soil matrix.

Distinct boundaries between the three hydro-geomorphic types of mangrove forest in the same stand may be difficult to define. Some characteristics of each, such as inundation time and porewater salinity, may vary from region to region, and there is likely to be no single measure that enables one kind of forest to be unambiguously assigned to one zone or another. Nevertheless, recognizing these broad groupings should assist in formulating generalizations that may be particularly helpful in establishing appropriate management policies (e.g. Bacon, 1994).

GOODS AND SERVICES PROVIDED BY MANGROVE FORESTS

In this paper, we consider a range of goods and services provided by mangrove forests (Table 1). Some, such as sediment trapping, nutrient processing, and providing food and habitat for animals, are essential for preserving ecosystem integrity and regional biodiversity. Others are not obtained without considerable human intervention, such as harvesting mangrove trees. The magnitude and quality of each of these goods and services are likely to vary among the three hydrogeomorphic zones, and no zone can be designated as 'most' or 'least' important overall.
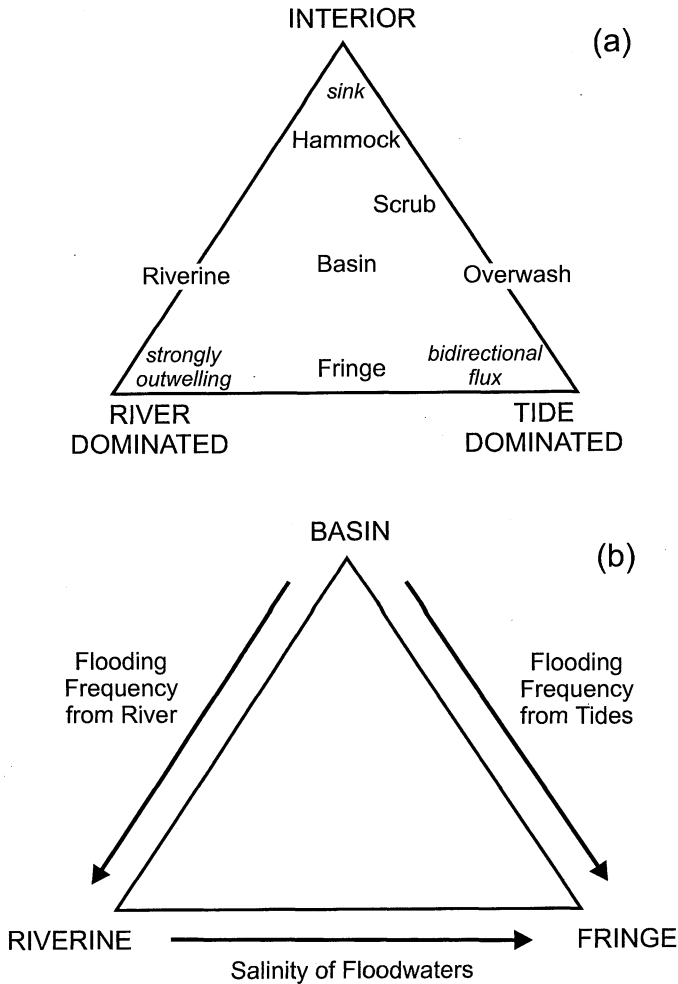
Fig. I. (a) The relationships among three functional types of mangrove forests (river-dominated, tide-dominated, and interior), dominant physical processes (in italics), and six types of mangrove forests described for the Neotropics (Woodroffe, 1992). (b) Proposed relationship among three functional types of mangrove swamps that can be distinguished within any given region (original).

Sediment trapping

Entire mangrove forests can trap and retain sediments generated in the uplands by virtue of their position in the landscape (Lynch *et al.*, 1989; Parkinson, DeLaune & White, 1994). Riverine forests are likely to be particularly important in this respect, because river waters usually carry a heavier sediment load than ocean tides. Sediments deposited in fringe forests can be riverine in origin, however, having been recirculated within the nearshore waters (Wolanski, Mazda & Ridd,

1992). Basin swamps also trap sediments, receiving the finest particles that are carried past riverine and fringe forests by floods and tides. They may also trap sediments deposited by runoff from uplands along the landward edge of the swamp.

Simply leaving mangrove forests intact avails society of the service of sediment trapping, because removal of the forest, particularly along the banks of fringe and riverine mangrove forests, opens up vulnerable soils to erosion and offshore sediment deposition. Mangrove forests can also be exploited for this service

Table 1. Relative importance of different types of mangrove forests in providing goods and services. 1 = most important

Role	Riverine	Basin	Fringe
Trap sediments	1	2	3
Process nutrients and organic matter			
Provide a source of detritus to nearshore waters	1	3	2
Serve as a sink for nutrients and carbon			
C, N	2	1	3
P	1	3	2
Improve water quality	2	1	3
Provide food and habitat for animals	1	3	2
Provide aesthetically pleasing environments	1	3	2
Protect shorelines	2	3	1
Provide plant products	2	1	3

when excess sediments generated by anthropogenic activities such as road construction and upland forest clearing are prevented from washing out to offshore seagrass beds and coral reefs. Riverine forests are most important in this respect, but basin forests often perform this service also, as well as narrow fringe forests that directly abut against uplands (Nixon *et al.*, 1984). The ability of mangrove forests to receive sediments is limited, however, because trees are killed when lenticels on pneumatophores, prop roots, and young stems are buried. The second largest cause of mangrove loss on the Pacific island of Pohnpei, Federated States of Micronesia, over a 10-year period, was road construction, due to both clearing the road bed and the death of adjacent and downstream trees from excess sedimentation (W. Raynor, The Nature Conservancy, pers. comm.).

The prospect of sea level rise brings a new dimension to the importance of sediment trapping. It is possible that thoughtful manipulation of sediment delivery to a mangrove forest could ensure continued existence of the forest even in the face of rising tides. An understanding of the balance between sediment accretion and compaction as well as of potential vegetation and hydrodynamic changes due to associated climate change would also be required, however.

Processing of organic matter and nutrients

The exchanges of nutrients and detritus between mangroves and near-shore waters in areas of different geomorphology and hydrodynamics are widely accepted as important but complex and difficult to quantify (Boto & Bunt, 1981; Twilley, 1985; Gong & Ong, 1990; Wattayakorn, Wolanski & Kjerfve, 1990). Measurements of the net flux of different forms of nutrients and organic matter are required in order to understand the role and relative importance of mangrove forests to biogeochemistry and productivity of coastal waters (Boto & Wellington, 1988; Rivera-Monroy *et al.*, 1995). As observed for salt marshes, there may be a net flux of inorganic nutrients into mangroves from coastal waters and a net export of organic nutrients associated with particulate and dissolved organic matter export (Twilley *et al.*, 1997). Even though there are still few studies of these processes, highlighting important differences between fringe, riverine, and basin mangroves may transcend much of this complexity.

Organic matter export

Estimates of carbon export to offshore waters range across two orders of magnitude; the average rate is about $210\,\text{gC m}^{-2}\,\text{yr}^{-1}$, with greatest export values coming from fringe mangroves (Table 2). In Rookery Bay, Florida, for instance, fringe mangrove forests export twice as much organic matter per hectare as basin forests (but taking the area of each type of wetland into account results in equal loading rates of detritus between them; Twilley, 1982). The presence of crabs that consume litter (28–79% of annual leaf fall; Robertson, 1986, 1988; Robertson & Daniel, 1989; Twilley *et al.*, 1997) may increase the tightness of nutrient cycles in the mangrove forest and decrease the amount of outwelling, particularly from interior portions of basin forests and especially in Old World sites, where crabs are more common (Jones, 1984). High productivity and relatively short residence times

Table 2. Export of organic carbon from mangrove forests (after Twilley *et al.*, 1992).

Swamp type	Export ($gC\ m^{-2}\ yr^{-1}$)	Location	Reference
Fringe	2	Hong Kong	Lee (1989)
Basin	64	Florida, USA	Twilley (1985)
Basin	91	Florida, USA	Lugo & Snedaker (1974)
Swamp*	110	New Zealand	Woodroffe (1985)
Fringe	186	Florida, USA	Heald (1969)
Fringe	292	Florida, USA	Odum & Heald (1972)
Swamp*	340	Hinchinbrook, Australia	Robertson (1986)
Fringe	401	Puerto Rica, USA	Golley, Odum & Wilson (1962)
Swamp*	420	Hinchinbrook, Australia	Boto & Bunt (1981)
Average	210		

* Because flux measurements were made at the mouth of a tidal creek, exchange represents the combined export from both fringe and basin mangroves and therefore the entire swamp.

of litter in riverine and fringe mangroves, both associated with higher frequency of inundation, make them particularly important, except where basin zones are much larger.

Nutrient sink

Basin mangrove forests may rank lower in organic matter export because of lower flooding frequency, but they may have higher rates of organic matter and nutrient accumulation. Soil redox potential is a particularly important measure of the soil environment for determining characteristics of nutrient cycles because of its control over oxidation states of P, N, S, Mn, Fe, and many other elements. It should be lowest where hydroperiods are longest, although the presence of pneumatophores and prop roots (McKee, Mendelssohn & Hester, 1988) and the absence of strong differences in water turnover rates between the zones (Ewel *et al.*, 1998a) may mitigate this. Basin mangrove forests are more likely to serve as a sink for inorganic N because of the likelihood of denitrification in an anaerobic environment, but in fact both denitrification and nitrogen fixation rates in mangrove swamps are slow (e.g. Rivera-Monroy & Twilley, 1996). Denitrification can be significant, even in a fringe mangrove forest, under sewage enrichment, however (Corredor & Morell, 1994). Formation of H_2S and CH_4 should be particularly common in basin mangrove forests, but oxygen transport via prop roots (e.g. McKee *et al.*, 1988) may slow the formation and release of these gases.

Water quality improvement

The service of nutrient processing has often been exploited for water quality improvement. Mangrove forests, like wetlands in general around the world, often inadvertently receive untreated wastewater of both human and animal origin. Basin mangrove forests may be particularly useful for transforming nutrients, particularly N, and immobilizing microbes and chemicals such as pesticides (Clough, Boto & Attiwill, 1983). Denitrification effectively removed nitrate from a heavy wastewater load in a Puerto Rican basin mangrove forest, for instance (Corredor & Morell, 1994). However, the full implications of disposal of wastewater into mangrove forests are seldom considered. To safeguard human health, effluent should be retained in an area free from contact with humans or commonly eaten fish and shellfish, i.e. as far back in a basin forest as possible. Although increased productivity of an ecosystem was once considered as a useful by-product of this kind of enrichment, the changes in a habitat that can follow such dramatic changes in ecosystem function, both on-site and downstream, are now regarded as potentially harmful (Ewel, 1997). Nevertheless, when the expense of constructing a wastewater treatment plant is considered, wetlands are still commonly selected as receiving areas for effluent.

Retrofitting mangrove forests for wastewater treatment is preferable to destruction, and wastewater disposal may even be considered as a tool in mangrove restoration. Directing secondarily treated wastewater

through a complex of coastal ecosystems on a Caribbean island resulted in both 'mangrove rejuvenation' and increased use by water birds and other wildlife (Bacon & Morgan, 1996). Although care must still be taken to meet acceptable public health standards, the 'constructed wetland' model used widely now in the USA (Ewel, 1997) may be appropriate for coastal wetlands in many tropical countries.

Animal habitat

Mangrove forests support animal populations both within the forest and in offshore areas. Some of these animals spend only part of their life cycle in mangrove forests, either during a particular stage of their maturation or as migrants (Yáñez-Arancibia *et al.*, 1988; Yáñez-Arancibia, Lara-Domínguez & Day, 1993). Where mangroves are a dominant source of carbon, they are important to estuarine consumers (Rodelli *et al.*, 1984). Crabs are among the characteristic invertebrate fauna of mangrove forests that are particularly important in human food chains. Densities of crabs are especially likely to be highest on unvegetated mudbanks adjacent to mangroves, with lower numbers along fringe mangroves; their densities are often low inside mangrove forests, however, perhaps because of low food quality as a result of high concentrations of tannins (Alongi & Sasekumar, 1992). There, they are more common at high intertidal locations than at lower zones, perhaps because feeding times are longer (McIvor & Smith, 1995).

Some species of crabs process detritus, as described earlier, and some feed on propagules (and thereby directly affect forest structure; Smith, 1987). They are clearly important in maintaining ecosystem processes in mangrove forests, and many provide food, both directly and indirectly, to people. Culturing mangrove crabs (specifically *Scylla serrata* (Forsk.)) has been proposed, but this would have to be done without clearing the forest or impeding water flows in order to maintain suitable habitat. Crab production might be increased by augmenting food supply, such as with kitchen scraps, but because mangrove crabs are territorial and can be cannibalistic (T. J. Smith III, US Geological Survey, Biological Resources Division, pers. comm.), this is not likely to be sustainable on a commercial scale.

Juvenile shrimp (e.g. penaeid prawns) are also important components of the invertebrate fauna. Shrimp are more common in fringe and riverine mangroves as well as in more frequently inundated

portions of basin mangroves (Robertson & Blaber, 1992). Conflicting data indicate that shrimp obtain carbon from plankton and possibly epiphytic algae rather than from mangroves (Primavera, 1996) and that mangrove-derived carbon fuels bacteria production that is subsequently found in higher trophic levels (Cifuentes *et al.*, 1996). It is possible that the roles of mangrove detritus and *in situ* primary productivity in supporting higher trophic levels vary among different types of estuary.

The use of land where mangrove forests once grew to culture shrimp (prawns) has a long tradition in Asia. Mariculture and shrimp farming expanded more recently into Ecuador, where, by the late 1980s, there were more shrimp produced than anywhere else in the world (Twilley, Bodero & Robadue, 1993). The intensity of use ranges from trapping shrimp within mangrove forests and holding them there until harvest, usually for a lunar cycle, to more intense systems where mangrove trees coexist with pond and shrimp, as in the traditional 'tambak' of Indonesia. Much more intensive culture techniques have been introduced recently, primarily in basin mangroves, where mangrove trees are totally cleared and ponds are dug to a depth of 1–2 m. Much of this started in the Philippines, initially for the culture of milkfish (*Chanos chanos* Forsskal.). The system depended on the natural fertility of the ponds, which decreased in productivity very quickly, and required the clearing and construction of new ponds in a system of shifting aquaculture. Most of the mangroves in the Philippines had been degraded when shrimp culture (*Penaeus monodon* Fabricius) took hold. By the early 1990s, 50% of the mangrove forests in Thailand (Spalding, Blasco & Field, 1997) and 21% of the mangroves in Ecuador (CLIRSEN, 1992) had been lost, mostly due to construction of shrimp ponds.

Overall, approximately 24% of shrimp ponds in Thailand have been abandoned because of diseases (which have also affected ponds in India, the Philippines, Taiwan, and Indonesia) (Stevenson & Burbridge, 1997). Also, many mangrove soils, particularly in the Old World tropics, are potentially acid sulphate soils, and sulphuric acid will form (reducing water pH to around 3) if the soil is oxidized (as when water circulation begins after the ponds are built). This can be overcome by heavy liming and extensive flushing (which is not only expensive but reduces water quality in the neighbouring estuary). Mangrove forests are still being used because mangrove land is grossly undervalued and often belongs to the state. There is thus an urgent need to establish the real

value of mangrove land not only in economic terms but also in terms of its ecological and sociological value.

There is no clear explanation for the high densities of fish that have been reported in and around mangrove forests, although they are often associated with *Rhizophora* forests, where well-developed prop roots may provide safety from predation (Robertson & Blaber, 1992). Habitat availability for juvenile and adult fish is likely to be greater in fringe and riverine forests, as well as in those portions of basin forests where tidal channels provide access.

Many higher vertebrates also use mangrove forests. Few amphibians are found in mangroves (although, for example, ranid frogs occur in mangroves in SE Asia and the Philippines), but several reptiles, including crocodiles, snakes, and lizards, use mangrove forests (Macnae, 1968; Hutchings & Recher, 1983). Some sea turtles feed on mangrove roots and leaves and appear to use mangrove estuaries as nursery areas (Odum, McIvor & Smith, 1982).

Large numbers of birds use mangroves for feeding and/or nesting in many parts of the world. For example, 181 species are reported from Florida mangroves, but very few are heavily dependent on these forests alone. Those most closely associated with mangrove forests feed primarily in the canopy and are especially common in fringe and riverine forests (Odum *et al.*, 1982). Fringe and riverine mangroves are especially important to migrating birds (Ogden, 1994). More than 200 species of birds have also been reported from Australian mangrove forests, including some endemic species (e.g. the mangrove heron, *Butorides striatus* (L.)) (Hutchings & Recher, 1983).

Many mammals also use mangrove forests, most of them in addition to other terrestrial or aquatic ecosystems. There are a few endemic mammal species in mangroves, e.g. a crab-eating rat (*Xeromys myoides* Thomas) in Australia (Hutchings & Recher, 1983), the leaf monkey (*Presbytis cristatus* (Raffles)) in Malaysia, and the proboscis monkey (*Nasalis larvatus* (Wurmb.)) in Borneo (Macnae, 1968). Mangroves are particularly important to a few large mammals, such as large cats (e.g. the Royal Bengal tiger, *Panthera tigris* Linnaeus, in the Sundarbans, between India and Bangladesh), as well as a variety of deer and otters (Odum *et al.*, 1982; Dugan, 1993; FAO, 1994).

Aesthetically pleasing environment

Large, undisturbed stands of mangrove forests are attractive to tourists (Hamilton & Snedaker, 1984).

Boardwalks and canoe trails, particularly along stately riverine corridors and the edges of fringe mangrove forests, provide an opportunity for obtaining income from otherwise undeveloped land as well as for educating laypeople on the functions and values of wetlands.

Healthy stands of fringe and riverine mangroves, however, are not always appreciated. In the USA, the State of Florida recently passed legislation that permits homeowners to prune mangroves along the shoreline to allow an unobstructed view, in spite of the fact that one of the most common species, *Rhizophora mangle* L., does not retain the ability to regenerate after cutting (Gill & Tomlinson, 1969; Snedaker *et al.*, 1992). The 'Ding' Darling National Wildlife Refuge, also in Florida, cuts 'windows' in the stands of mangroves that grow up along dikes to allow easier viewing of wildlife, particularly alligators and wading birds that use the ditches on the other side.

Protection from floods

Protection of human infrastructure from storm surges, tidal waves, and floods is one of the most widely touted services provided by wetlands. This is because (1) the boundaries of a wetland indicate the extent of normal flooding and therefore the zone where human development should cease, and (2) wetland vegetation decreases the rate at which water passes over land, slowing the destructive force of floodwaters as they approach the uplands. Like many other ecosystem services, in spite of the general recognition it receives, the value of shoreline protection (or flood protection in general) provided by a wetland lies in the cost that society does not have to pay until that service is lost (Goulder & Kennedy, 1997).

Mangroves develop only along low-energy or protected coasts, where sediments are retained and mangrove seedlings can become established. Only where high energy events such as major storm surges and tidal waves are episodic are mangrove forests likely to be important in protecting human structures. In such places, fringe mangrove forests are believed to be particularly important, but this is a difficult hypothesis to prove, and anecdotal evidence is not always convincing (Clough, 1993). Perhaps the most widely cited observation is Fosberg's (1971) suggestion that the loss of more than 100,000 lives in Bangladesh in 1970 following a hurricane and tidal wave might have been reduced had large areas of mangroves not been replaced by rice paddies. Other anecdotes are

accumulating. Erosion along a coastal road behind mangroves on St. John, US Virgin Islands, after a hurricane in fall 1995 was least where the mangroves were thickest (T.J. Smith III, pers. comm.). Loss of mangroves following diversion of a river on the Pacific island of Kosrae, Federated States of Micronesia, has been correlated with increased wear on the coastal road and nearby structures by storm tides (K.C. Ewel and R. R. Twilley, pers. obs.). Instances in which storm surges have affected vegetation on the landward side of mangrove forests while mangrove remained unscathed (e.g. Steers, 1977) do not prove that the disturbed area would have suffered further destruction had the mangroves not been there. In the absence of more definitive data, however, it seems apparent that zoning regulations that protect a wetland to its landward limit, recognized as the normal upper limit of flooding, should enable it in turn to protect homes, roads, and other infrastructure from flood damage.

Pacific Islanders in the western Carolines recognize the importance of the characteristically drooping branches along the edge of fringe mangrove forests for breaking the force of storm tides (K.C. Ewel, pers. obs.). The roots of mangrove trees in both fringe and riverine forests play an important role in binding surface soils tightly (e.g. Scoffin, 1970). Both fringe and riverine mangroves are therefore particularly important for preventing shorelines from eroding, thereby not only affording shoreline protection but protecting offshore seagrass beds and coral reefs from sediment deposition as well.

Basin mangrove forests may assist in protection from episodic floods as well, both by reducing water velocity and by adding flood storage capacity behind fringe and riverine forests. The amount of forest necessary for adequate protection in a particular area depends on the geomorphology of an individual shoreline as well as on the frequency and magnitude of possible storms.

Plant products

An impressive diversity of plant products is harvested from mangrove trees, including tannins, honey, medicinal products, and thatch (Hamilton & Snedaker, 1984). Some of these can be obtained with little impact on the forest; harvesting for firewood and timber probably has the greatest effect.

Net primary productivity of mangrove forests, as measured by litterfall, is often high relative to upland forests at the same latitude (Saenger & Snedaker, 1993),

but tree growth rates vary considerably from site to site, generally decreasing with latitude (Twilley et al., 1996). Mangrove forests appear to be most productive where there is no distinct dry season, and biomass can exceed 250 Mg/ha (Ong et al., 1979), reaching 350–400 Mg/ha in protected areas of Malaysia (Putz & Chan, 1986). The best growth of mangrove trees is generally believed to occur in riverine forests, where floods deposit sediments periodically (e.g. Lacerda et al., 1993; Hussain, 1995), but harvesting is often most common in basin forests where large monospecific stands and less frequent flooding may make extraction more economical.

Different species of mangrove timber have different physical properties (FAO, 1994) but there is no information on how variations within and among species may be related to the physical forces that affect different kinds of forests. Some species, like *Avicennia,* are widespread ecologically; they are very soft and have little commercial use. *Rhizophora,* which is also found in a variety of different environments and often in extensive, almost monospecific stands, has many uses and is the most widely exploited commercial genus. The wood is very hard and dense but tends to split very readily. It is not suitable for furniture but is often used for firewood and charcoal and is ideal for conversion to rayon. It is also often used for poles and, because it is extremely resistant to rot under anaerobic conditions, is very suitable as piling material. A number of less widely spread genera like *Xylocarpus* and *Heritiera* are found primarily in basin or riverine mangrove forests; they are excellent furniture grade timber but are seldom exploited for that purpose because they tend to occur in low numbers. *Xylocarpus* is used extensively in Micronesia for carving.

In most of the tropics, mangrove timber has traditionally been used mainly as fuelwood (either directly as firewood or after conversion to charcoal), as fishing stakes, and as building materials (pilings, poles, and timber for buildings and boats). Here, mangrove use is not a matter of choice but rather of survival, and intensity of use depends on ease of access and population pressures.

Commercial production is common primarily in Asia, where large stands of *Rhizophora* are harvested for poles (including pilings), charcoal and, more recently, woodchips (for conversion into rayon). Where the net productivity of mangroves is high, it is possible to harvest timber on a sustainable basis. A simple rule of thumb—clearfelling small patches and thinning around 15 years and again around 20 years—was developed

in the early part of this century in Malaysia by British foresters (Watson, 1928). The classic success case is in the Matang Mangrove Forest in Malaysia where *Rhizophora apiculata* BL. has been harvested sustainably (annual coupe of about 1000 ha) since the early part of this century (Ong, 1995). Here the timber is used as poles for piling as well as for the production of charcoal (for export). Yet, in the same country, pristine mangroves (e.g. the mangrove forest of the Rajang Delta in Sarawak) have been badly degraded as a result of harvesting for woodchips (annual coupe of about 600 ha). This operation started in the late 1960s and ran out of mangrove timber after about 25 years. A minimum girth system of management was practiced but appears to have failed. A similar operation in the neighbouring State of Sabah was closed down earlier.

The mangrove woodchip industry is now very active in some of the best mangrove forests (in Kalimantan, Sumatra and Irian Jaya) in Indonesia, where it operates almost unnoticed in remote, sparsely populated, or unpopulated areas, where some of the world's best pristine mangrove forests (*Rhizophora*-dominated) have been targeted. These operations generally last for about 25 years and then are moved to another site. It is not known if the Indonesian operations can be sustained as they are presently run, but a sustained-yield management system has not been implemented elsewhere (Ong, 1995).

MAKING DECISIONS BASED ON GOODS AND SERVICES

The usefulness of mangrove forests can be attributed to both the diversity among forests and the diversity of goods and services that they supply. A synopsis of the relative importance of fringe, riverine, and basin mangrove forests indicates that all three may be considered critical in at least one respect (Table 1). Riverine forests, with their nutrient inflows and moderate salinities are important interfaces between the more expansive basin forests and the fresh and salt water inflows. Basin forests, on the other hand, with their more restricted water flows, are often the sites of greatest human activity. Fringe mangrove forests, subject to the greatest water movement and consistently high salinity, are critical as a protective barrier for the rest of the forest and, occasionally, for human structures as well.

Understanding the importance and best use of different parts of a forest may help in formulating management policies that enable the continued supply of essential goods and services. For instance, a basin forest from which crabs are harvested should not be used for wastewater treatment, and timber harvest should be restricted or even prohibited in riverine and fringe forests, which are more subject to erosion than basin forests. All three kinds of forests can be aesthetically pleasing and are important in production of animals and nutrient processing, although in very different ways.

Exploiting a mangrove forest for one product or service can reduce its ability to provide others. Timber harvest, water quality improvement, and shrimp ponds are all concentrated in basin forests, where they are likely to reduce a forest's potential for creating an aesthetically pleasing environment, change the nature of its nutrient cycles, and alter habitat for animal populations. However, with regional planning it should be possible to determine where conflicting goods and services could be obtained from different zones within the same forest, perhaps as mitigation for preserving a similar forest in an area where habitat value or recreation benefits may be higher. For instance, some of the concern about unregulated growth of shrimp ponds centres around the loss of water quality in neighbouring coastal ecosystems. Distributing effluent from shrimp ponds into nearby basin mangrove forests would not only limit negative impacts on water quality in coastal ecosystems (Robertson & Phillips, 1995), but it could also increase mangrove tree growth rates, thereby reducing intensity of harvesting in more pristine stands.

We do not yet understand all the consequences of disturbances to mangrove forests. For instance, does removal of large volumes of timber from basin mangrove forests lead to sediment compaction as dead roots decay, in turn leading to lower redox levels and changes in habitat value for both plants and animals? Lower redox but no apparent subsequent changes in species composition in small basin-zone gaps in high-rainfall forests have been recorded (Ewel *et al.*, 1998b), and these effects might be accentuated in more arid regions. Lower redox values could also increase release of N_2, H_2S, and perhaps CH_4 to the atmosphere to the extent that they affect regional or even global climate. However, we cannot yet define acceptable limits that can be used to formulate management policies in different parts of the world.

Acknowledging and understanding the diversity that exists within mangrove forests should provide a broader

perspective for judging all the implications of the uses of this important form of wetland. Aggregating this diversity around simplifying concepts such as the distinctions among fringe, riverine, and basin zones in mangrove forests may assist local natural resource managers in restricting uses of these wetlands to the kind of forest where they are most likely to be tolerated and even sustained. Boundaries among these zones may be difficult to define, and particular zones in one area may not be directly comparable to the same zone in another area. A conservative approach, until more definitive guidelines can be obtained, may be to define Best Management Practices that limit potentially destructive management practices, such as harvesting, within the first 50 or 100 m (or some multiple of the normal tidal range) of a fringe or riverine forest. Being able to restrict development by means of easily understood guidelines may be the first step not only toward reducing the loss of mangrove forests in a region but also to reducing the rate of loss of their goods and services.

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Identifying ecosystem services using multiple methods: Lessons from the mangrove wetlands of Yucatan, Mexico

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Abstract. The failure to properly account for the total value of environmental and natural resources results in socially undesirable overexploitation and degradation of complex ecosystems such as mangrove wetlands. However, most ecosystem valuation research too often focuses on the question of "what *is* the value" and not enough on "*what* people value." Nonmarket valuation practitioners have used qualitative approaches in their work for some time. Yet, the relative strengths and weaknesses of different qualitative methods have been more the subject of speculation than systematic research. The statistical examination of focus group and individual interview data on ecosystem services illustrates that the two methods generate important but different ecosystem service data. Further, the data show that the use of multiple data collection methods offers a more robust understanding of what people value.

Introduction

The failure to properly account for the total value of environmental and natural resources results in socially undesirable overexploitation and degradation of complex ecosystems such as mangrove wetlands (Clark, 1996; Farnsworth and Ellison, 1997; Hamilton et al., 1989; Spaninks and van Beukering, 1997). Complex environmental and natural resources, such as the Yucatán's mangrove wetlands, represent substantial sources of cultural, intergenerational, environmental, and economic wealth (Aylward and Barbier, 1992; Bann, 1997; Barbier, 1994; Barbier et al., 1997; Carson, 1998; Perrings, 1995). However, most ecosystem valuation research is "too focused on the question of 'what *is* the value' and not enough on *what*, in particular, people value" (Swallow et al., 1998). There is a need for resource valuation research to identify the range and relative importance of the components of ecosystem value rather than merely estimate some value for a particular ecosystem service.

Despite this need for understanding the components of ecosystem value, it is prohibitively expensive and unrealistic to conduct detailed empirical nonmarket valuation studies of each ecosystem. The need for ecosystem valuation information is especially great for those public good services of ecosystems that are not well-captured in markets (Aylward and Barbier, 1992; Barbier et al., 1997; Carson, 1998; Mitsch and Gosselink, 1993). In particular, the value of wetland ecosystems may be especially great in developing countries where efficient markets for wetland services do not exist (Aylward and Barbier, 1992; Barbier et al., 1997; Carson, 1998). However, the availability of valuation methods for estimating wetland economic values does not necessarily mean that the pertinent resources services are identified and included in wetland ecosystem valuation studies and policy decisions.

The reported research examines two relatively inexpensive research methods for helping researchers identify relevant ecosystem services associated with a mangrove wetland. Using focus groups and individual interviews, the researcher explored what local resource beneficiaries associate with the mangrove wetland of Chelém Lagoon. The study identifies the particular mangrove wetland services important and relevant to the inhabitants of two communities along the coastal fringe west of Progresso, Mexico. The study demonstrates that the use of both focus groups and in-depth individual interviews can lead to a more robust understanding of what people value about a shared ecosystem. Furthermore, the study addresses a gap in the resource valuation literature by using an empirical

method to compare the outcomes of group discussions with individual interviews concerning ecosystem services (Chilton and Hutchinson, 1999).

First, the paper reviews some of the natural resource services attributed to mangrove ecosystems. Next, the paper describes how valuation research has used qualitative research methods in some valuation studies of natural resources. The paper then describes the research design and method that was used to test the hypothesis that focus groups and individual interviews help researchers identify substantially similar ecosystem services associated with a mangrove wetland. The research results are presented before discussing the implications of the findings on the usefulness of multiple methods, ways to improve valuation studies, and the ability of statistical analysis to shed light on the significance of qualitative data.

Background

Mangrove wetland values

The term mangrove refers to a number of tree species capable of living in saltwater or salty soils. Mangroves and their ecosystems are found in intertidal areas of sheltered coastlines called lagoons and estuaries. Ecologically, mangrove wetlands maintain high levels of biological productivity; export nutrients to outside waters; and provide habitat for valuable plant and animal species (Clark, 1996). Mangrove ecosystems are also important to the subsistence livelihood of tropical coastal communities (Hamilton et al., 1989; Hamilton and Snedaker, 1984). Mangrove ecosystems potentially provide an array of important indirect services – prevention of storm damage, flood and water control, support of fisheries, waste absorption, recreation, and transport (Barbier, 1994; Barbier et al., 1997). Mangrove ecosystems may be directly exploited by extracting goods such as fish, agriculture, wildlife, wood, and fresh water (Bann, 1997; Bennet and Reynolds, 1993; Farnsworth and Ellison, 1997; Hirsch and Mauser, 1992; Kunstadter et al., 1985; Ruitenbeek, 1992). Additionally, mangrove wetlands have also been said to be significant sources of nonuse benefits that do not flow from direct use of the ecosystem (Aylward and Barbier, 1992; Barbier, 1994; Barbier et al., 1997).

Mangrove ecosystems, like other complex environmental and natural resources, are potential sources of an array of use and nonuse values (Barbier, 1994; Barbier et al., 1997; Carson, 1998; Hamilton et al., 1989). While not dependant upon entry directly into markets, use values require that some *in situ* activity takes place that benefits individuals (Freeman,

1993). Examples of natural resource use values include camping, hunting, wood collection, fishing, farming, as well as such things as breathing clean air. Values independent of *in situ* activities have been called passive use or nonuse values. Examples of nonuse values include the value of knowing the resource simply exists, the value some people attribute to some potential use of the resource, and the value of knowing that future generations will have the resource (Freeman, 1993). In order to properly account for the total value of ecosystems in their decision-making, policymakers should understand the extent and magnitude of use and nonuse values associated with the resource.

Qualitative methods and valuation studies

Social scientists in diverse fields of study regularly use qualitative methods as comprehensive research tools and as important components in designing and implementing reliable research studies (Krueger, 1994; Morgan, 1997; Schwarz, 1997; Sudman et al., 1996; Weiss, 1994). Studies for estimating the economic value of environmental and natural resources range from market or behavior-based methods to direct methods such as contingent valuation (CV) studies.[1] For some time, resource valuation researchers have been advised to consider using focus group interviews as well as individual interviews for questionnaire pretesting and development (Mitchell and Carson, 1989). Despite some initial skepticism of the utility of qualitative methods for designing nonmarket valuation studies (e.g., Arrow et al., 1993), focus groups have been increasingly recognized and relied upon as important aspects of resource valuation questionnaire design and evaluation (Carson and Mitchell, 1993; Schkade and Payne, 1994; Chilton and Hutchinson, 1999; Hutchinson et al., 1995). Individual interviews have also been reported to provide efficient means for collecting information on beneficiaries' use and understanding of mangrove ecosystems at the local level (Kovacs, 1999).

Work by cognitive psychologists and survey method researchers underscore the value of qualitative research methods for questionnaire design (Schwarz, 1997; Sudman et al., 1996). These same researchers point out that one qualitative research method alone may be insufficient to learn about respondents' resource use and understanding. Some researchers suggest that focus groups and individual interviews may lead to the discovery of different information (De Jong and Schellens, 1998; Kitzinger, 1994a, 1994b). Other researchers assert that focus group research should be combined with other types of research, including individual interviews, to triangu-

late or corroborate research findings (Bryman, 1988; Morgan, 1996). Multiple qualitative methods such as focus groups and one-on-one interviews may be useful for revealing a wide range of local beneficiaries' ideas about and conception of complex environmental and natural resources (e.g., Carson et al., 1994; Chilton et al., 1998; Hutchinson et al., 1995). Thus there is a need for research that compares the outcomes of focus group and individual interviews regarding the respondents' understanding of complex ecosystems (Chilton and Hutchinson, 1999).

Research design and method

Research question

The relative strength and weakness of particular qualitative research methods "has been more the subject of speculation than systematic research" (Morgan, 1997: 13). A few researchers have explored differences in focus group and individual interview information (De Jong and Schellens, 1998; Kitzinger, 1994a, 1994b). Qualitative methods may be used successfully to learn from local beneficiaries how they use, perceive, and value environmental and natural resources (Mandondo, 1997). Studies also show that resource beneficiaries' ideas about natural resources may differ from those of scientists and so-called experts (Talawar and Rhoades, 1998). This reported research examines the research hypothesis that focus groups and individual interviews, all else being equal, reveal similar sets of information about a shared mangrove ecosystem.

Participants

The communities of Chelém and Chuburná, Mexico are located along a 15-kilometer stretch of coastal fringe that borders the Gulf of Mexico on one side and Chelém Lagoon on the other. These villages are comprised of families that have traditionally relied upon the natural resources of the region, including the mangrove wetland, for their subsistence and livelihood. Focus group interviews and individual in-depth interviews were conducted with residents of these communities as part of a study evaluating the importance of mangrove wetlands in Yucatán, Mexico. Chelém and Chuburná share similar socio-economic characteristics and have roughly 475 and 215 households respectively (Instituto Nacional de Estadística Geografía e Informática (INEGI), 1992). A total of 97 year-round residents from the two communities were interviewed in one of 12 focus groups[2] or 19 individual in-depth interviews.[3]

Design and procedure

The research design allowed for examination of the collected data across interview type, gender, and community (see Figure 1). Research assistants canvassed randomly selected sections of the target communities at staggered times of day to recruit participants. The focus groups were comprised of between four and seven individuals of the same gender from the same village. No respondent or their family members participated in more than one focus group or interview. The focus groups and individual interviews were designed and implemented following the generally accepted practices of Morgan[4] (1996, 1997, 1998) and Weiss[5] (1994) respectively. A Mexican professional moderator using a specially prepared discussion guide conducted the focus groups and individual interviews. All focus group and individual interviews were tape-recorded and subsequently transcribed.

Qualitative analysis

The qualitative data analysis allowed the researchers to (1) discover themes, (2) consider the choice and meanings of words, (3) consider the context(s) of data collection, and (4) consider the consistency of responses (Krueger, 1994). Although work remains in developing uniform guidelines and rules for the qualitative coding and analysis process (Fredricks and Miller, 1997), the researcher attempted to systematically reveal elements of respondents' experience and perceptions. The qualitative analysis did not produce simple counts of things, but rather "fractured" the data and rearrange it into categories that facilitated understanding the data and comparing the data within and between categories (Maxwell, 1996; Strauss and Corbin, 1990). After the transcripts were read, the analyst used memos (researcher's notes and observations), categorizing strategies (coding and thematic analysis), and contextualizing strategies (narrative analysis and individual case studies).

The 12 focus group and 19 individual interview transcripts resulted in more than 500 pages of text. An iterative, grounded theory approach (Strauss and Corbin, 1990) was used to code the transcripts. First, almost every word of a randomly selected subset of transcripts was coded (open coding). Next a set of thematic or summary codes was developed (axial coding). When no new open codes were necessary to code additional transcripts, all of the study's transcripts were axial coded. The final iteration of coding the text, selective coding, focused on organizing the data into 36 categories relevant to respondents' resource use, value, understanding, perception, and control of the ecosystem. The reported research is one means for
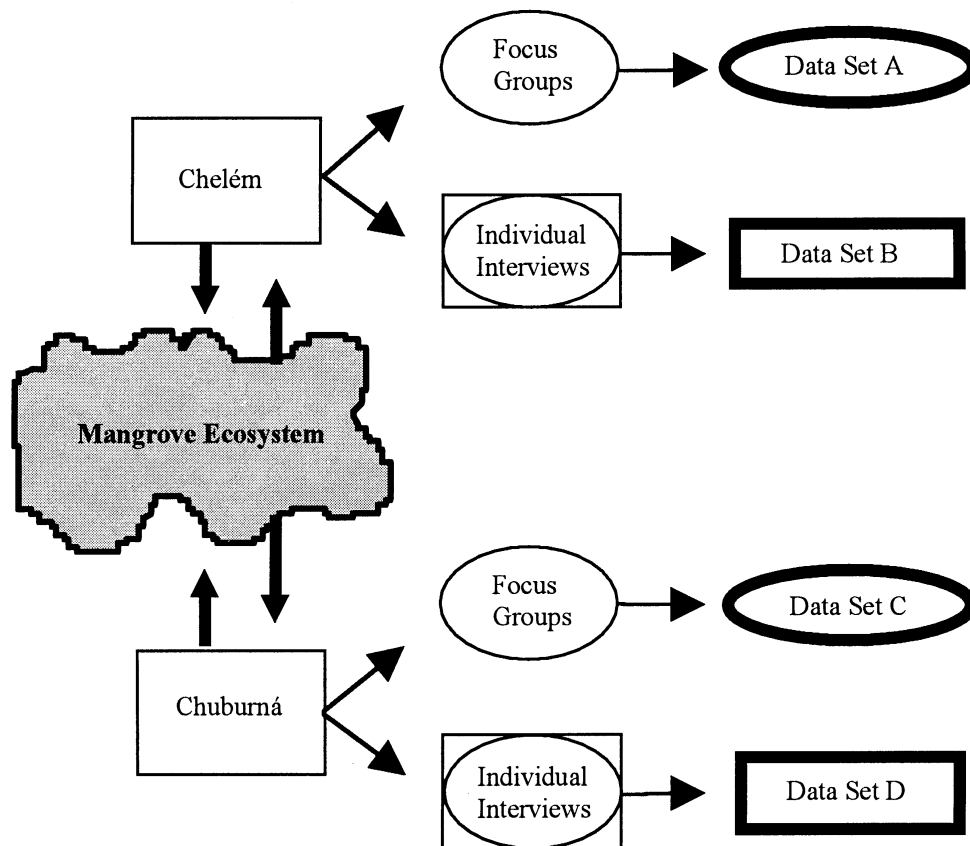
Figure 1. Research design.

trying to understand the significance of what the qualitative research revealed about local beneficiaries' use, perception, and understanding of Chelém Lagoon.

Operationalizing hypothesis test

If focus groups and individual interviews concerning respondents' relationships with a local mangrove ecosystem yield similar data on beneficiaries' perceptions and appreciation of ecosystem services, one would expect, all else being equal, that transcripts of those sessions would evidence a similar set of data on such services. That is, it would be reasonable to expect that a uniform process of coding the focus group and individual interview transcripts would result in similar distributions of codes that capture use and nonuse services associated with the mangrove ecosystem. Likewise, if there were particular use and nonuse services of importance to resource beneficiaries, one might expect that systematic analysis of the focus group and individual interview data would evidence a higher frequency of such codes. This paper focuses on testing the hypothesis that focus groups and individual interviews reveal substantially similar information concerning resource services associated with a mangrove ecosystem. Presentation of research findings

concerning resource beneficiaries' social conflicts and discussion of socially sensitive topics may be found elsewhere (Kaplowitz, 1998, 1999; Kaplowitz and Hoehn, 1998).

While for some qualitative researchers, summary discursive reports of their findings (e.g., consumer preferences among brands of a product) are sufficient, other researchers rigorously test their research hypotheses with a statistical analysis of collected qualitative data (e.g., De Jong and Schellens, 1998; Krippendorff, 1980). The statistical analysis of qualitative data has been found to be both possible and helpful (De Jong and Schellens, 1998; Krippendorff, 1980; Weber, 1990). Differences in focus group and individual interview data of text evaluation exercises have been tested using code frequencies, t-tests, and analysis of variance (De Jong and Schellens, 1998). Similarly, the analysis of manifest attributes of text and accompanying inferential attributes has been performed using various counts, percentages, and statistical measures (Gray and Denstein, 1998). In their recent analysis of focus group data collected in anticipation of a contingent valuation studies, Chilton and Hutchinson (1999) "quasi-quantified" qualitative data to test divergence of respondent and researchers definitions of goods.

Table 1. Ecosystem service variables.

Topic variable	Example	% sessions rasing topic	
		Focus groups interviews	Individual
Beauty	Wetland is beautiful; a pretty place to see; enjoy the views	100	11
Chivita	*Melongena melongena*; small shellfish collected; as food and in commerce	100	95
Crab	Collected as bait; frozen for use during 2 month octopus season	92	42
Lagoon fishing	We fish in lagoon; people come to fish in wetland; there are nets day and night at lagoon entrance	92	90
Salt extraction	Used to be salt here; salt ponds once lucrative; construction destroyed salt business	92	37
Shrimp	Seawater brings shrimp; when shrimp here, all fish for them; not as many shrimp as in past	75	16
Nongame species	Flamingoes; crocodiles; heron; turtles; seagulls	67	42
Ducks	Ducks sometimes here; few locals benefit; need permit to hunt ducks	42	42
Recreation	Take guests for ride there; sometimes picnic there; celebrate Mass there annually	42	32
Storm protection	Can protect boats from storm; helps if water rises;	42	16
Wood	Some collect wood for fires; not much wood collection lately	17	5

The research reported here created and used discrete variables grounded in economic theory that were derived from the iterative reading, analysis, and coding of the transcripts. These discrete variables recorded those instances that focus group discussions and individual interviews raised topics concerning wetland ecosystem services associated with Chelém Lagoon. For example, the variable Lagoon fishing, recorded discussion of fishing for corvina, mullet, or other species in the lagoon. Such variables accommodated wide-ranges of discussion topics as well as allowed the coded transcript data to be subsequently analyzed using statistical software. The research question was operationalized to statistically test the null hypothesis that respondents' discussions of the wetland ecosystem raised the same wetland services equally during focus groups and individual interview sessions.

Results

The focus group and individual interview transcript data were transformed into 12 summary variables to test the research hypothesis. One summary variable, Interview type, records the type of interview (e.g., focus group or individual interview) associated with each case of coded data. The other 11 summary variables capture those wetland ecosystem services raised by respondents during the focus groups and individual interviews. Table 1 illustrates the 11 ecosystem service variables that resulted from the coding and variable transformation process of the focus group and individual interview data. Table 1 also presents some examples of representative references and the percentage of focus group and individual interview sessions that raised each topic. As can be seen, most of the services discussed by participants are extractive or consumptive use services (e.g., crab, shrimp, and wood collection). Some of the services discussed are nonconsumptive uses (e.g., recreation, storm protection). A few ecosystem discussed by participants appear to be noncunsumptive uses but arguably may evidence some nonuse value (e.g., beauty, nongame species).

Table 2 illustrates the relative ranking of frequencies for the ecosystem services variables for the focus group and individual interview data. It illustrates, for example, that wetland beauty was raised during every focus group discussion (rank 1), but was only the seventh most frequent service topic raised during individual interviews (rank 7). While perhaps a similar range of ecosystem services were discussed in the focus groups and in the individual interviews, not every individual interview or focus group raised the entire range of mangrove services. However, apparent differences in aggregate frequencies alone however are insufficient to support or reject the null hypothesis.

Table 2. Rank of service frequencies.

Rank	Focus groups	Individual interview
1	Beauty Chivita	Chivita
2	Crab Lagoon fishing Salt extraction	Lagoon fishing
3	Shrimp	Crab Ducks Nongame species
4	Nongame species	Salt extraction
5	Ducks Recreation Storm protection	Recreation
6	Wood	Shrimp Storm protection
7		Beauty
8		Wood

Table 3. Focus group and individual interview data associations.

Topic		Interview type		χ^2	P	Odds ratio
		Group	Indiv.			
Beauty	Yes	12	2	23.77[a]	0.001	9.50
	No	0	17			
Chivita	Yes	12	18		n.s.	
	No	0	1			
Crab	Yes	11	8	7.62[a]	0.006	15.12
	No	1	11			
Fishing	Yes	11	17		n.s.	
	No	1	2			
Salt extract	Yes	11	7	9.08[a]	0.003	18.86
	No	1	12			
Shrimp	Yes	9	3	10.87[a]	0.001	16.00
	No	3	16			
Nongame	Yes	8	8		n.s.	
	No	4	11			
Ducks	Yes	5	8		n.s.	
	No	7	11			
Recreation	Yes	5	6		n.s.	
	No	7	13			
Storm protection	Yes	5	3		n.s.	
	No	7	16			
Wood	Yes	2	1		n.s.	
	No	10	18		n.s.	

[a] d.f. = 1, $N = 31$

Absolute differences may be statistically insignificant when sample size, proportions, expected frequencies, and distributions are taken into account.

As a result, crosstabulation analysis of each ecosystem service variable with the interview type variable was generated to test the null hypothesis that, in the sample population, the same percentage of focus groups and individual interviews raised each wetland service for discussion (see Table 3). Table 3 illustrates the Pearson chi-square test of the distribution of observed instances that focus groups and individual interviews raised each ecosystem service topic against the null hypothesis that each interview type results in the same frequency of the topic being raised. The null hypothesis was rejected for four variables – Beauty ($P < 0.001$), Crab ($P < 0.006$), Salt Extraction ($P < 0.003$), and Shrimp ($P < 0.001$). To examine the strength of the association of interview type with respondents' raising the particular ecosystem service in discussion, odds ratios were computed. Table 3 shows, it is about 9 times more likely that a focus group of local resource beneficiaries raises the topic of the mangrove ecosystem's beauty than an individual interview. The topics of crab collection, salt extraction, and fishing for shrimp are respectively 15, 19, and 16 times more likely to be raised in focus groups than raised by individual during one-on-one interviews.

To further appreciate the significant differences observed in the frequencies of discussion of ecosystem services by focus group and individual interview data, it should be remembered that 4 times as many people participated in focus groups (78) than in individual interviews (19). All else being equal, if there are differences in focus group and individual interview data that are a linear function of number of people, the expected odds ratios should be closer to 4. However, the observed odds ratios are two to four times that. This suggests that more than the larger numbers of participants in focus groups is responsible for the increased frequency that certain topics were raised by focus groups.

Four of the six most frequently mentioned topics differed significantly in the frequency in which focus groups and individual interviews raised them in discussions. Therefore, the research findings support the rejection of the null hypothesis. The data show that focus groups and individual interviews revealed significantly different ecosystem service information.

Discussion

The two methods, focus groups and individual interviews, do not reveal equal sets of information nor do they rank ecosystem services comparably. While the data illustrate that resource beneficiaries associate a variety of ecosystem services with complex ecosystems, most of the services discussed tended to be extractive uses of the ecosystem. The focus groups and individual interviews were dominated by discussion of lagoon fishing of one type or another. Although wetland beauty was raised in all of the focus groups, the low frequency of its discussion by individual interviews seems to more accurately reflect individual beneficiaries' relative appreciation for nonconsumptive and nonuse values of the ecosystem. This is no surprise given the economic difficulties facing the communities and Mexico as a whole. The focus groups and individual interviews were replete with discussions of the difficulty for providing for one's family. Increasing commercial fishing pressure in the Gulf of Mexico has decimated the once rich coastal fishing resource. Local beneficiaries increasingly rely upon the lagoon and its mangrove ecosystem for subsistence. Therefore, it is no surprise that consumptive use services predominate conversations about the ecosystem.

Only 4 of the 11 wetland services discussed by participants were non-extractive in nature – Beauty, Nongame species, Recreation, and Storm Protection. The relatively low frequencies associated with the use services of storm protection and recreation in both focus groups and individual interviews support the notion that these services are not particularly significant to most residents. The other two non-extractive services, Beauty and Nongame species, arguably capture some respondents' recognition and appreciation of nonuse ecosystem services. While wetland beauty and the presence of nongame species in the ecosystem may be classified by some as use values because of the benefits derived from *in situ* enjoyment of these services, these variables also capture participants' expressed sentiments that wetland beauty and diversity should be preserved for future generations.

Value of multiple methods

It appears important that wetland beauty was ranked first by groups and seventh by individuals. The statistically significant difference in the frequency that focus group and individual interview discussions raised wetland beauty comports favorably with the findings of De Jong and Schellens (1998) concerning focus group and individual interview data. The mangrove ecosystem focus groups did lead researchers to discover different information about ecosystem services than the individual interviews. Had only focus group information been collected and relied upon, it would haven been reasonable to believe that wetland beauty was extremely important to local beneficiaries (perhaps on a par with lagoon fishing). Conversely, had researchers only relied upon individual interview data, wetland beauty and nonuse values might have easily been dismissed as unimportant or beyond the apprehension of respondents. However, using both individual interview and focus group data revealed that wetland beauty was significant to individuals but only accessible after a dynamic exchange of information. The focus groups seem to have provided a dynamic that allowed respondents to identify and discuss nonconsumptive and, at times, nonuse ecosystem services such as wetland beauty. This finding is in line with the recent work by cognitive psychologists that shows that increased interaction and exchange of information improves respondents' understanding of complex ideas (Schwarz, 1997; Schwarz and Sudman, 1995; Sudman et al., 1996). This result, researchers learning of different and complimentary ecosystem services using focus groups and individual interviews, clearly supports the desirability of using multiple methods to corroborate qualitative research findings in future ecosystem valuation work (Bryman, 1988; Morgan, 1996).

Implications for valuation research

The results also underscore the difficulty of designing studies and instruments for estimating the total economic value of a complex ecosystem. Valuing nonmarket and nonuse services associated with natural resources, especially in developing countries, seems to require extra care. While the study supports the notion that nonconsumptive and nonuse values may be significant for wetland ecosystems in developing countries (Aylward and Barbier, 1992), the data reveal the potential import of using multiple qualitative methods for identifying potential values to be measured.

In the case at hand, local resource beneficiaries seemed better able to identify and appreciate nonconsumptive and nonuse values in focus group discussions rather than in individual interviews. Since valuation methods such as contingent valuation or contingent ranking rely upon individuals, not in groups, making trade-off choices to reveal nonuse and total economic values, the findings suggest the import of designing better valuation survey instruments. The results seem to suggest the value of researchers using groups to learn about the array of services that matter to beneficiaries before using individual interviews to validate such findings. Likewise, it seems important to use

sequential qualitative methods to evaluate how best to communicate and increase information exchange concerning ecosystem services in value elicitation instruments.

Researchers' perceptions and beneficiaries' understanding

The literature is full of lists of use and nonuse services that in some but not all cases can be associated with mangrove ecosystems (e.g., Barbier, 1994; Barbier et al., 1997; Janssen and Padilla, 1996; Spaninks and van Beukering, 1997). These mangrove services include on-site fisheries, fuelwood collection, timber harvests, off-site fishery support, aquaculture, carbon sequestration, growing of medicinal plants, biodiversity, recreation, transportation, meat production, flood control, storm protection, option values, existence values, and bequest values. A daunting set of services to have to include in a particular valuation effort. However, the findings show that by using qualitative methods, beneficiaries can help researchers narrow the set ecological services to those most relevant for study.

In Chelém, the focus groups and individual interviews left no doubt that lagoon fishing (especially for "chivita", crab, and shrimp) is of utmost importance to local people. A few nonconsumptive uses and possible nonuse values were articulated by respondents (nongame species and the beauty of the ecosystem) while the relative insignificance of ecosystem storm protection services and wood collection was also made apparent. Furthermore, the small role that mangrove wood and wood collection plays in the lives of local beneficiaries in Chelém Lagoon contrasts with the findings of Kovacs (1999). Together, the use of focus groups and individual interviews allowed the researcher to identify those service most relevant to local beneficiaries and to further investigation.

Significance of differences

The most frequent and least frequent ecosystem services raised using the two methods were not statistically different across methods. This seems to imply that, regardless of method, participants recall and articulate common wetland ecosystem uses equally at the extremes of usage or importance in focus groups and individual interviews. For example, the collection of chivita (*Melongena melongena*) from the muddy bottom of Chelém Lagoon has become the predominant subsistence strategy for the regions' communities.[6] Chivita collection has replaced more conventional lagoon fishing and collection of crab as the most important ecosystem service. Therefore, it is no surprise that more than 90% of both the focus

groups and individual interviews raised chivita collection and lagoon fishing in discussions. Conversely, the ecosystem services that only occupy a minor or cursory place in the communities' appreciation of wetland services do not differ significantly in their frequency of discussion in focus groups and individual interviews.

However, the frequency that several ecosystem services raised in focus groups and individual interviews did differ significantly. The extractive ecosystem services that differed significantly may be thought of as sub-components of the more general mangrove ecosystem "fishing" service. The difference in these frequencies may be a function of the difference in the dynamics of a focus group discussion and a one-on-one depth-interview. For example, shrimp collection (mentioned in 75% of focus groups and 16% of individual interviews) happens to be an occasional and contentious phenomenon in the lagoon. The recent construction of a duck habitat restoration dike by Ducks Unlimited and activities of the Mexican Navy, according to participants, have resulted in drastic curtailment of the once annual or biannual inundation of shrimp in the lagoon. The data show that it is 16 times more likely that shrimp collection be raised in focus groups than individual interviews. The lower frequency that individual interviews raised the topic of shrimp collection may well reflect the decreased role of shrimp collection in beneficiaries' use of the mangrove lagoon. The topic's high frequency of discussion in focus groups may reflect a collective need or desire of individuals to process or air feelings associated with the loss of this service.

Similarly, a statistically significant divergence between focus group and individual interview data was observed in salt extraction data. At one time, individuals in the region could construct salt ponds, flood them with seawater, allow the water to evaporate, and then collect and sell crystallized sea salt. However, the area's lucrative salt mining business has been defunct for years. The change followed the flooding and ipso facto enlarging of Chelém Lagoon that resulting when the Mexican government dredged and constructed a safe harbor and naval station in the lagoon in the late 1960s and early 1970s (Paré and Fraga, 1994). Like the shrimp collection data, individual interviews raised salt extraction as an ecosystem service significantly less often than focus groups. It is about 19 times more likely that a focus group raise salt extraction than an individual interview raise that same topic. People's discussion of the lagoon in groups seemed to trigger discussion of the loss of ecosystem services, like salt extraction.

Apparently, focus group data can leave researchers with an impression about the significance of a resource

service that substantially differs from the impression left by individual interview data. The differences observed in the frequencies of the discussions of crab collection, salt extraction, and shrimp fishing activities illustrate that specific components of inclusive use values (e.g., Lagoon Fishing) are more likely to be raised in focus groups rather than individual interviews.

Better understanding from qualitative methods

There was not obvious difference in the frequency that groups and individuals raise chivita collection or the broader discussion topic of lagoon fishing. It seems that virtually every family in the two communities, at one time or another has adopted chivita collection as part of their subsistence survival strategy. Furthermore, it is common for almost everyone in the area to refer to himself or herself as a "pescador" (fisherman). This despite the fact that many of these individuals provide for themselves and their families by working in nearby factories or doing construction work. Not only do individuals perceive themselves as fisherpeople, it was learned throughout the groups and interviews that respondents include chivita collection, crab and shrimp collection together with line and net fishing for other species when speaking about lagoon fishing. What makes this especially important, is that local researchers from nearby Mérida working on coastal zone management in the region were surprised to learn of the extent to which the respondents relied upon chivita collection. It was their belief that chivita was a minor component of residents' subsistence strategy and that near-shore fishing in the gulf was the predominant occupation in the area.

The researcher learned that unfortunately as one respondent put it,

> We used to make a living fishing in the sea ... Now you can't make a profit more than 2–3 months from fishing in the sea ... The same problem is also happening in the estuary, it used to be that you could take all the crab you wanted. Now only the small ones are around ... While some try to work elsewhere, people sustain their families with chivita from the wetland (Transcript 18).

The individual interview data and the focus group data about beneficiaries' uses and perceptions of Chelém Lagoon services appear to be complimentary. While both methods revealed information about ecosystem services, the relative weight that each of the services received differed by method. For example, ecosystem beauty was raised in every focus group. However, only 11 percent of individual interviewees raised ecosystem beauty. This contrast indi-

cates that the notion of a nonconsumptive or nonuse ecosystem service may be difficult for individuals to conceptualize and associate with an ecosystem without the benefit of a dynamic exchange of information (e.g., informational priming in a survey instrument). The use of multiple qualitative methods would seem valuable to researchers charged with the task of designing a study or instrument addressing beneficiaries' stated preferences or values for nonconsumptive use services and nonuse services associated with complex ecosystems.

Conclusion

This study demonstrates that use of multiple qualitative methods can help researchers develop a more complete understanding of beneficiaries' natural resource values. Reliance upon one qualitative method, focus groups or individual interviews, would have provided researchers with a less than complete understanding of beneficiaries' uses, perceptions, and values associated with their shared mangrove ecosystem. This study shows the two qualitative research methods to be complementary, not substitute, methods for learning about ecosystem services.

The study demonstrates the value of using individual interviews in addition to focus groups in the economic valuation study design process. Such interviews can be used to evaluate the effectiveness of the instrument at communicating complex information as well as to judge respondents' ability to meaningfully undertake the requisite valuation tasks. Incorporating both focus groups and individual interviews into the conceptualization and design phase of valuation studies seems capable of shaping ecosystem valuation research so that it is more concerned with "*what* people value."

The incorporation of statistical examination of focus group and individual interview data on ecosystem services illustrates that the two methods generate different ecosystem service data. The findings suggest that focus group ecosystem service data reflect differences that may be attributable to dynamic processing of information. This finding is in line with others' research that shows increased interaction and exchange of information improves respondents' understanding of complex ideas (Schwarz, 1997; Schwarz and Sudman, 1995; Sudman et al., 1996). The systematic statistical analysis of individual interview and focus group data can provide an empirical basis for better understanding of ecosystem services and their value to respondents.

Notes

1. Contingent valuation (CV) studies elicit economic values for environmental amenities and natural resources using carefully designed and administered surveys. CV studies are one type of stated-preference approach researchers use to reveal how individuals value environmnetal and natural resources.

2. Focus groups are carefully planned discussions designed to learn about subjects' perceptions on a defined area of interest in a permissive, nonthreatening environment. They are conducted by a skilled moderator who follows a discussion guide and involve as few to as many as 12 informants.

3. Individual interviews (also called unstructured, exploratory, intensive, in-depth, and depth interviews) are guided conversations whose goal is to elicit from interviewees (also called informants) rich, detailed materials that can be used in qualitative analysis. The interviewer used the same discussion guide as used in focus groups to guide the one-on-one conversations.

4. Dr. David Morgan is a highly regarded and widely published focus group researcher. He is a Professor in the Institute on Aging and the Department of Urban Studies and Planning at Portland State University. His works include such classics as *Focus Groups as Qualitative Research* (1988) and *The Focus Group Kit* (1998).

5. Dr. Robert Weiss is Director of the Work and Family Research Unit and Professor at the University of Massachusetts. Weiss is renown as a qualitative researcher and the author of *Learning from Strangers: The Art and Method of Qualitative Interview Studies* (1994).

6. Chivita (*Melongena melongena*) is a small mollusk found in the mud flats on estuaries. It is also known as a West Indian Crown Conch.

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Mangrove Conservation and Coastal Management in Southeast Asia: What Impact on Fishery Resources?

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This paper focuses on relationships between mangroves and coastal fish resources. A review of the literature highlights the lack of quantified relationships. We show that mangroves can be considered as a particular case of an estuarine environment, and then address the broader issue of the relationships between tropical estuaries and fishery resources. An estuarine fish community is composed of three main assemblages, respectively from continental, strictly estuarine or marine origin. The major characteristics of these assemblages are defined. On this basis we detail the different and sometimes opposite impacts of major rehabilitation actions on each assemblage. The biological approach is then widened by a critical overview of current approaches in economic valuation of mangrove-related fish resources. This provides a rational and scientific foundation for economic analysis of resources and for coastal management decisions, and allows us to define priorities for further scientific and policy research in these areas. © 1999 Elsevier Science Ltd. All rights reserved

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Introduction

One of the often stated reasons for rehabilitating mangrove ecosystems is the importance of these systems to coastal fisheries (e.g. Pauly, 1985; Twilley *et al.*, 1996). This paper reviews current knowledge about relationships between mangrove extent and coastal harvests, focusing on Southeast Asia. Quantified information on this topic is very scarce, but ecological studies show that mangroves and their special features can be considered as a particular case of an estuarine environment. As coastal resources are linked more broadly to coastal environments and estuaries it appeared necessary to set the problem at a larger scale (McHugh, 1985).

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Given the need for practical guidelines in the field of coastal management (SEAFDEC, 1997), we propose a biology-based conceptual framework for the rehabilitation of estuarine and coastal fish resources. Integrating economics into such a framework is essential if it is to be useful for sustainable management (Day *et al.*, 1997).

This integrated approach has highlighted gaps in the information available to managers, and allows us to suggest priority fields for coastal management research, in biology as well as in economics.

Quantified Relationships between Mangroves and Coastal Resources

To our knowledge, only Yañez-Arancibia *et al.* (1985), in the Gulf of Mexico, have shown a clear positive correlation between commercial finfish catches and the total area of coastal vegetation – mostly mangroves (Table 1). They also demonstrated that one of the factors exhibiting the strongest correlation with fish catches was river discharge, as previously mentioned by several authors in temperate regions (e.g. Chapman, 1966; Sutcliffe, 1972, 1973). De Graaf and Xuan (1997) showed a correlation between finfish catches and mangrove, but the issues were complicated by significant changes in fishing effort. Gilbert and Janssen (1997) reported a rather weak relationship between commercial fisheries production and mangrove in the Philippines.

This lack of published material on quantified relationships between mangroves and finfish resources led us to examine relationships between mangroves and the other major coastal fisheries resource, shrimps. In this field, four studies quantifying this relationship have been published. Turner (1977) found a positive correlation between shrimp catches and the vegetated surface area of estuaries in the Gulf of Mexico. In Louisiana, the percentage of brown shrimps in total shrimp catches was correlated with the area of adjacent mangrove (Table 1). However, Chansang (1979) noted several biases which might make these results questionable.

TABLE 1
Quantified relationships between mangroves and coastal resources.

Reference	Formula	X	Y	R^2	n
Yañez-Arancibia et al. (1985)	$\mathrm{Ln}\,Y = 0.496\,\mathrm{Ln}\,X + 6.070$	Coastal marshes (km²)	Fish capture (tons)	0.48	10
Turner (1977)	$Y = 1.96\,X - 4.39$	Percentage of saline vegetation in an hydrological unit	Percentage of brown shrimps	0.92	7
Martosubroto and Naamin (1977)	*No equation given* $Y = 0.1128\,X + 5.473$	Hectares of vegetated estuary Mangrove area (×10 000 ha)	Annual shrimp yield Shrimp production (×1000 tons)	0.69 0.79	5, 8
Paw and Chua (1989)	$Y = 0.8648\,X + 0.0991$	Log_{10} of mangrove area	Log_{10} of penaeid shrimp catch (tons)	0.66	17
Staples et al. (1985)	$Y = 1.074\,X + 218.3$	Mangrove shoreline (km)	Banana prawn catch (tons)	0.58	6
Pauly and Ingles (1986)	$\mathrm{Log}_{10}\mathrm{MSY} = 0.4875$ $\log_{10}\mathrm{AM} - 0.0212L + 2.41$	MSY = Maximum Sustainable Yield of penaeids AM = area of mangroves L = degrees of latitude			

Martosubroto and Naamin (1977), working in Indonesia, showed a positive correlation between annual catch of prawns and area of mangrove (Table 1). Chansang (1979) noted that in this case the relationship was not linear and that there was a negative correlation between the area of tidal forest and the shrimp yield *per unit area*, i.e. its productivity. This implies that a certain minimum mangrove area is necessary for a high production, a point also noted by Pauly and Ingles (1986) who suggest that the impact of destruction of a mangrove area might be greater if this area is small and residual.

Paw and Chua (1989) found in the Philippines a positive correlation between mangrove area and penaeid shrimp catch whilst Staples et al. (1985) in Australia found a positive correlation between the total length of mangrove lined rivers and the annual catch of banana prawn (Table 1). Lastly, Pauly and Ingles (1986) showed that most of the variance of the MSY of penaeids could be explained by a combination of area of mangrove habitats and latitude.

Robertson and Blaber (1992) concluded that in spite of evidence of a correlation between mangrove and commercial fisheries, a causal link had not been established. Indeed all of these studies suffer from problems of auto-correlation. Where regressions or correlations are based on geographical variations in catch and mangrove cover, it is unclear as to whether mangrove is the causal factor, or the many other factors related to mangrove cover, such as extensive shallow seas, intertidal area, tidal creeks, organic matter, or simply length of coastline. Where historic data are used, the parallel decline in fisheries production and mangrove area may be related to a wide variety of other factors (e.g. Twilley, 1988; Von Post and Ahman, 1997). Such correlations are therefore dangerous without a thorough assessment of a wide variety of contextual factors.

Estuarine Environment and Coastal Fish Resources

Mangroves are often considered as an ecosystem *per se*, due to their strong specificities (e.g. Snedaker and Snedaker, 1984; Field and Dartnall, 1987; Twilley et al., 1996) but they belong to intermittently brackish tidal zones and can be seen as a part of tropical estuarine systems.

In this section we detail the major features of the estuarine environment, and see why mangroves are a particular case of this environment. A review of literature demonstrating the dependence of fish harvests on estuarine environments shows the importance of these systems in terms of sustainable management of the coastal resource. Therefore mangrove conservation needs to be included within the framework of estuarine management and rehabilitation.

Major features of the estuarine environment

The ecological features of estuaries are detailed elsewhere (e.g. Day, 1981; Yañez-Arancibia, 1985; Baran, in press). Dozens of studies show that estuaries play a nursery role for several coastal fish species. In most cases adults spawn at sea and larvae come to estuaries by active swimming and passive tidal transport. Three major factors can explain this nursery role: trophic resources, water turbidity, and structural diversity.

First, the concentration of nutrients due to freshwater inflow, nutrient trapping, tidal mixing and environmental modulation (Knox 1986) results in a high primary productivity. This is the base of a food web where zooplankton, mysids and shrimps provide abundant and diversified trophic resources to fish post-larvae and juveniles.

Second, turbidity reduces the perception distance of predators and increases the escape rate, and thus the survival of young fishes (Kneib, 1987).

Third, diversity, structural complexity and shallowness of estuarine habitats provide multiple spatial and trophic niches favourable to juveniles.

Recent definitions of estuaries explicitly include adjacent coastal waters, particularly in the tropical zone (Rodriguez, 1975; McHugh, 1985; Day *et al.*, 1989). In Southeast Asia, the wide extent of estuarine waters and their associated fish fauna has been well documented (Hardenberg, 1949; Blaber, 1981; Ong and Sasekumar, 1984; Chullasorn and Martosubroto, 1986; Chong *et al.*, 1990) and illustrates the notion of the "coastal estuary" (Longhurst and Pauly, 1987; Baran, 1995). This notion simply states that in the wet tropics, the upper boundary of an estuarine zone is the limit of tidal influence in a river, and the lower boundary is the limit of the turbid or brackish zone on the continental shelf, in the rainy season. Although this concept is relatively obvious, it has scarcely been applied in fish biology, as proven by the paucity of comparative studies between estuarine and coastal environment, although recent papers insist on a global system functioning approach (Robertson and Blaber, 1992; Day *et al.*, 1997).

Mangroves as a particular case of an estuarine environment

Mangroves grow in littoral tropical zones characterised by the alternation of tidal floods (intertidal areas) and the presence of freshwater, at least temporarily (Blasco, 1982; Tomlinson, 1986). The same two factors are used by Fairbridge (1980) to define an estuarine zone. Combined with a minimal temperature of 16°C, these factors delineate the classical tropical mangrove belt (see Chapman, 1977). Southeast Asia belongs to this belt, and mangrove is the dominant coastal biotope in this region (Table 2).

From a fish biology point of view, mangroves are located in estuarine zones and play the nursery role of estuaries in general, as attested by more than thirty papers (see Day, 1981; Day *et al.*, 1989; Laegdsgaard

TABLE 2

Length of coastline and surface of mangrove for the countries of Southeast Asia.

Country	Coastline (km)[a]	Surface of mangrove (km^2)
Brunei	161	171[b]
Cambodia	443	601[c]
Indonesia	54 716	45 421[c]
Malaysia	4 675	6 424[c]
Philippine	36 289	2321[b]
Singapore	193	56[b]
Thailand	3 219	2 641[c]
Vietnam	3 444	2 723[c]

[a] CIA World fact book (http://www.odci.gov/cia/publications/nsolo/wfb-all.htm).
[b] WCMC: Coral reefs and mangroves of the world http://www.wcmc.org.uk/marine/data/coral_mangrove/index.html.
[c] Spalding M.D. Blasco F., Field C.D. 1996 World Mangrove Atlas. International Society for Mangrove Ecosystems, Okinawa, Japan.

and Johnson, 1995; Baran *et al.*, in press). However they exhibit particular features including an exceptional productivity and an enhanced role of protection for juveniles against predation.

Their productivity is expressed in terms of mangal leaf litter, as first stated by Odum and Heald (1972, 1975), supplemented by the activity of benthic cyanobacteria, diatoms and microalgae (Alongi, 1988, 1989) and by the production of epiphytic algae fixed on mangrove roots (Rodriguez and Stoner, 1990). This overall production allows the development of a particularly dense zooplanktonic, then micro, meio and macrobenthic fauna (Alongi 1989, 1990).

Compared to estuaries, the role of protection against predation is amplified by the dense web of mangal pneumatophores and prop-roots where numerous post-larvae and juveniles can escape or hide (Krishnamurthy and Prince Jeyaseelan, 1981; Robertson and Duke, 1987; Thayer *et al.*, 1987). It also results from the shadow created by leaf cover which reduces contrasts and thus reduces the distance from which predators can see their prey. This enhances the survival rate of juvenile fish (Helfman, 1981).

The dependence of coastal resources on estuarine and mangrove environment

Studies in the Gulf of Mexico provide clear evidence that the fish resource is dependant on the estuarine environment. According to McHugh (1976) for instance, in 1961, 97% of the fish biomass harvested by the US in this zone was of species living a part of their life in estuaries; Lindall and Saloman (1977) considered that between 1961 and 1971, 90% of the fish biomass harvested in the Gulf of Mexico was estuarine-dependant. On a wider scale, Houde and Rutherford (1993) calculated that estuarine-dependant resources made up 50% of the total US commercial landings in 1990.

This relationship between estuaries and commercial fisheries is also seen in Australia (see Blaber, 1997) and in South Africa, where Whitfield (1990) showed that

43% of fish taxa utilised estuarine systems as nurseries and/or foraging areas. Lenanton and Potter (1987) suggested that the estuarine environment allows a higher growth rate of fish. Moreover Nixon (1982) has shown that the fish harvest in estuaries and lagoons is proportional to the primary productivity of these zones.

Despite these studies, the estuarine-dependence of fisheries remains controversial. For instance, Lenanton and Potter (1987) noted that between 1976 and 1984 estuarine fisheries contributed 20.3% of the biomass and 2.4% of the value of total Australian fisheries, and that most species were estuarine opportunists, and not estuarine dependents.

In an overview, Blaber et al. (1989) concluded that the multiple studies focusing on the degree to which various inshore marine fishes in the Indo-West Pacific were dependant on estuaries, particularly as nurseries, had produced no clear-cut conclusions.

Although environmental conditions prevailing in mangroves are likely to be highly favourable to the fish fauna harvested near shore, the ecological dependance of coastal fish on mangroves remains poorly quantified. In Malaysia Ong and Sasekumar (1984) and Gearing et al. (1984) have shown the importance of mangrove-derived detrital food sources for coastal resources. Chong et al. (1990) demonstrated that mangroves were a feeding ground for juveniles of commercially important fish species, and Sasekumar et al. (1992) concluded that Malaysian mangroves supported fisheries by providing habitat and food to both fish and prawns. De Sylva and Michel (1975) compared the ichthyofauna in a normal and a defoliated estuary in Vietnam and found that the trophic system was far more simple and unstable where the mangal had been removed (see also Hong and San, 1993). However comparative studies between mangrove and littoral zones exhibit contradictory results: Blaber et al. (1985) and Robertson and Duke (1987) concluded that the mangroves they studied did not play a significant nursery role for species of high commercial value, while in other studies or sites, different conclusions have been reached (Blaber et al., 1989; Robertson and Duke, 1990).

Lastly, Quinn and Kojis (1985); Thollot (1992) and Laroche et al. (1997) concluded that the relationships between mangroves and reef ichthyofaunas were limited. It has also been suggested that littoral surf zones and creeks may provide alternative habitats for juvenile fishes (Beckley, 1985; Bennett, 1989, Whitfield, 1989; Blaber and Milton, 1990).

In conclusion, several studies support the hypothesis that coastal fish resources are closely linked to estuaries and mangroves, even if controversy remains about their degree of dependence.

Estuarine Fish Ecology and Rehabilitation

The estuarine fish resource (sensu lato) is composed of three different assemblages of continental, estuarine and marine origin, which have different life history traits. A given rehabilitation action will have different and sometimes opposite impacts on these assemblages depending on their ecology. The economic impact of rehabilitation will also depend on the assemblage favoured. In this section, after a synthetic overview of the respective ecology of the different estuarine fish assemblages, we predict the consequences of three major types of rehabilitation actions on these assemblages.

Following several syntheses (Albaret, 1994; Albaret and Diouf, 1994; Baran 1995; Diouf 1996; Blaber, 1997), the main features of estuarine fish communities in tropical environments similar to those of Southeast Asia can be summarised as follows.

1. *The assemblage of continental origin* occupies the upper part of the estuary during the flood, but does not go into the brackish zone. Fish do not reproduce in the estuarine zone, but wetlands contiguous to the river play an important nursery role for these species.

2. *The estuarine assemblage* is particularly tolerant to environmental variations. Species of this group breed and grow within the estuary; adults of certain species feed inside the limits of the geographical estuary and adults of other species partly feed outside, along the coastal estuary. Among them are poorly studied but quantitatively important species (blenniids, gobiids) whose larvae might be an important source of food to juveniles of other species (Little et al., 1988; Pandaré and Tamoïkine, 1993; Tito de Morais and Tito de Morais, 1994).

3. *The coastal assemblage* is made of species only caught at the mouth of the estuary, at different stages; however they are mostly met along the coast, always in brackish waters. Dominant representatives are pelagic plankton-feeders. This assemblage also consists of species caught in the estuary once in their life history, but not breeding in it.

The different types of rehabilitation actions have been summarised below under the following headings: coastal rehabilitation, modification of river hydrology, and pollution mitigation.

Coastal rehabilitation

Here we consider three possible impacts of coastal rehabilitation: mangrove reforestation, decrease of water turbidity (for instance by stopping dredging) and a widened mouth of the estuary (through removal of harbour dykes).

Following conclusions of the previous sections, one can expect mangrove reforestation to have a positive impact both on estuarine and coastal assemblages, through an increase of organic inputs to the coastal zone, a higher primary productivity and a gain of

nursery habitats. No impact is expected on the continental assemblage which does not use the mangroves.

Several works have demonstrated the importance of turbidity to juvenile fishes (e.g. Cyrus and Blaber, 1987a,b). Therefore a decrease of mineral turbidity due to stoppage of dredging may be negative both for coastal and estuarine juvenile assemblages although reduced destructive disturbance of the benthos may have a positive impact. The affinity of the continental assemblage for clear waters apparently has to be determined case by case.

Lastly, experience from West African estuaries indicates that in similar hydrological conditions, the larger the mouth of the estuary (in size and depth), the more coastal and marine fishes within the estuary, particularly big predators of higher economic value.

Modification of river hydrology

First, in the case of a dam rehabilitation (removal) for instance, switching back to a larger *annual average outflow* would involve an increase of nutrients input in the estuarine system. This would have a positive impact on the primary production, and consequently on the whole estuarine and coastal fish production ("outwelling hypothesis", Darnell, 1967; Odum *et al.*, 1974). Furthermore, the habitat of the strictly estuarine assemblage would be extended. The continental assemblage in the estuarine zone should not be affected.

Second, switching back to increased *hydrological variability* of the river can be expected to have three main consequences.

1. An intensification of the seasonal flush-out, which is a major event in the functioning of any estuary (Day *et al.*, 1989). In the freshwater part of the river the continental assemblage could be positively influenced as the flood is often a signal for reproduction (Lowe-McConnell, 1987; Wootton, 1990). In the estuarine part of the river, where this assemblage does not breed, the impact would above all be expressed in terms of better catches of adult freshwater fishes during the rainy season. The strictly estuarine assemblage could be adversely affected by a flush-out of trophic elements outside the estuarine zone, meanwhile this export of nutrients as well as of energy would clearly favour the group of coastal fishes.

2. A more mobile estuarine front would have a positive impact on the assemblage of continental origin: an intensified flood could improve the access to adjacent wetlands playing a nursery role for its juveniles. It can be expected to have a positive impact on the estuarine assemblage, through a seasonal increase of the surface of brackish and turbid waters. In contrast it is likely to have a negative impact on the coastal assemblage (reduction of the zone under marine influence, which can lead to a decrease of the catch of marine fishes (e.g.

sharks) within the limits of the estuarine zone (Baran, 1995; Baran *et al.*, in press).

3. The increased variation of the estuarine front will also be expressed in terms of higher physico-chemical variability. The assemblage of continental origin is sensitive to environmental variations, and seems to structure slowly in a rather stable environment within the estuarine zone (Albaret and Ecoutin, 1990; Baran, 1995), therefore is should be adversely impacted.

Pollution mitigation

Pollution mitigation would have a global positive impact on any assemblage; however one must distinguish mineral and organic pollution, the latter being sometimes considered as an enrichment of the estuarine and coastal system (De Sylva and Michel, 1975; Soule and Soule, 1981).

In conclusion, a given modification has different impacts on each assemblage of the estuarine and coastal community. This indicates the importance, in terms of economics and management, of a functional approach to the fish resource at the assemblage level. It also shows that the problem of estuarine and coastal rehabilitation must be set in clear terms: is the concern about commercially important species (approach of Lenanton and Potter, 1987; Chong *et al.*, 1990) or with all species, i.e. with biodiversity?

Economic Significance of Changes in the Fishery Assemblages

Global estimates

The economic value of the fisheries function of mangrove has been discussed by Christensen (1982); Hamilton and Snedaker (1984); Dixon (1989); Ruitenbeek (1991); Gren and Soderqqvist (1994); Hambrey (1996a); Gilbert and Janssen (1997), Barbier *et al.* (1997) and Costanza *et al.* (1997). The values estimated by these authors for the annual fisheries related income from 1 ha of mangrove range from US$66 to almost US$3000/ha.

There are three important questions relating to these estimates. The first relates to their validity. Most are derived simply by multiplying the commercial landed value of the fish or shrimp catch by the area based yield estimates discussed above in the section on quantified relationships. The problems associated with these yield estimates apply equally to any valuation based on them. Furthermore, several of the value estimations are based on the total commercial fisheries yield, rather than that component which depends specifically on mangrove. They are therefore likely to be over-estimates of the real value.

The second relates to the practical value of these estimates for decision making and resource management in the coastal zone. These estimates are "global"; in other words they aggregate commercial fishery

production on the one hand, and they assume uniformity of mangrove, in terms of any nursery function, on the other. As discussed by Hambrey (1996a,b) the nursery function of mangrove is likely to be highly variable, with some areas being of far greater value, and others of far lower value than the global estimates would suggest. For this reason the use of such figures for decision making related to specific areas of mangrove is likely to be misleading.

Estimates based on specific assemblages

The foregoing analysis suggests that it may be useful, as a first step, to disaggregate the fisheries function as it relates to the three major assemblages of continental, estuarine and coastal species. The total commercial value of each of these assemblages should be relatively easy to assess, and the economic value of gross environmental changes can then be assessed in accordance with the framework provided in Fig. 1. Although in most circumstances it will be impossible to put a single accurate figure on the cost or value associated with any environmental change, such an approach should allow for the estimation of a much more concise range of values, related to specific commercial interests, than those derived from the global estimates discussed above. More accurate figures, and ones related to particular species, will depend on improved understanding of the ecology of each assemblage and its component species. Thus the relative importance of turbidity, nutrients,

organic matter, shade or physical diversity to particular species or species groups, or to prey species, will need to be estimated in order to assess the impact of specific environmental changes such as mangrove loss.

Valuation of biodiversity

Some aspects of biodiversity, such as abundance or variety of prey of commercial species, may have a direct impact on traded fishery production, and can be estimated relatively easily, given sufficiently accurate ecological relationships.

However, where biodiversity is not related to a specific traded or marketed fishery commodity, valuation is far more difficult. There are a variety of approaches to the valuation of non-traded goods and services, most of which are based on the creation of a hypothetical market, in which people's willingness to pay (WTP) or willingness to accept (WTA) is estimated using interview or questionnaire techniques (e.g., Pearce and Turner, 1990; Costanza *et al.*, 1997). However, there are serious limitations associated with the approach, and the values generated should be used with caution. As a result, several authors have suggested alternatives to valuation as a basis for decision making. These include the estimation of trade-offs with alternative activities which can be valued (for example what would be the *opportunity cost* of conserving bio-diversity rather than commercial exploitation (Hambrey, 1996a), and damage schedule approaches (Knetsch, 1994; Chuenpagdee, 1996). The
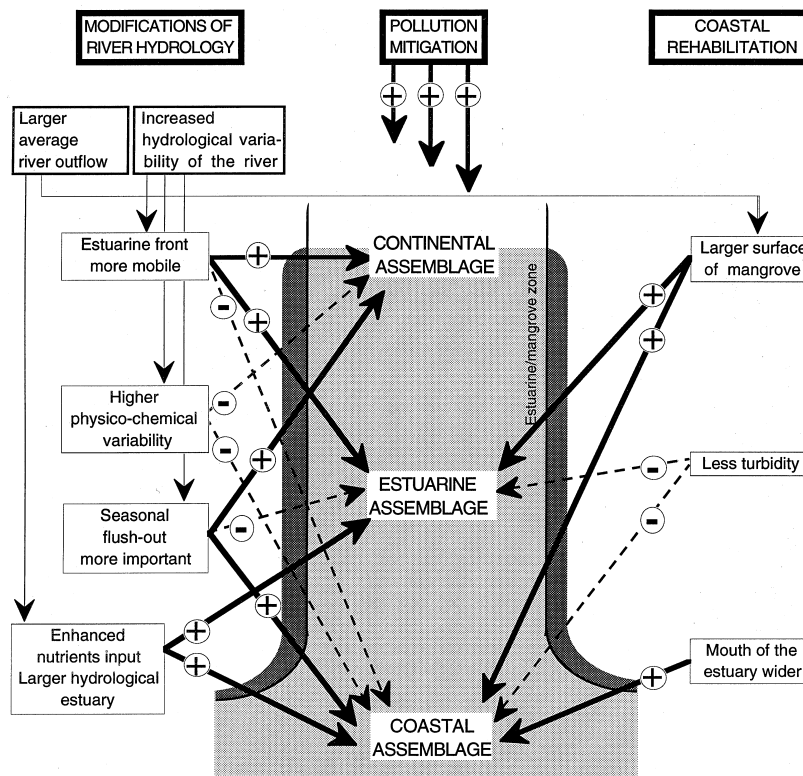

Fig. 1 Summary of the impacts of different rehabilitation actions on the three basic components of an estuarine fish resource. Bolded lines: positive impact, Dotted lines: negative impact.

latter depend upon expert or community estimates of *relative* (rather than cash) values of different resources, or damage to those resources. Community involvement is a key feature of all these approaches.

Conclusions and Definition of Priority Fields of Study

This study indicates the lack of well established quantified relationships between fish yields and area of mangrove. This concern could be addressed in Southeast Asia by a detailed analysis of capture data as a function of mangrove area in different countries, taking full account of the spatial and historic variations in fishing effort. This seems to be possible thanks to current fisheries data such as that of FAO and ICLARM, or data from national Departments of Fisheries, and recent remote sensing data on mangrove surfaces such as those of Spalding *et al.* (1996).

In addition, it is essential to determine, for a given local fishery, the real dependency of fish resources on estuarine environment by answering the following questions: (1) is the estuarine zone essential for a given species? (2) are there alternative areas for its development? (3) which parameters are critical in its life-history? (4) what are its trophic relationships with other species? Studies in Thailand and Africa (Ikenoue *et al.*, 1990; Baran, 1995; Diouf, 1996; Laroche *et al.*, 1997) show that a statistical multivariate approach could efficiently address these issues. Useful and low-cost additional information can be obtained by questioning traditional fishermen (Poizat and Baran, 1997).

A major conclusion of this study is that mangroves can be considered as a particular case of an estuarine environment, and that the continuity and interdependence of riverine, estuarine and marine environments is a biological reality for coastal fish resources. Therefore, the management of their resources has to be integrated, going beyond the frequent division of responsibilities between inland and marine/coastal fisheries management bodies (e.g. for Southeast Asia: World Bank, 1991).

Biologically, such a global approach can be dealt with using a compartmental model, in which each compartment interacts with others. We propose that each biotic compartment of the model be defined in terms of functional biology (a given group corresponds to a set of species having similar response to environmental modifications). This kind of model, initially focusing on fish resources, can evolve to integrate increasing knowledge on the functioning of the system, and can also integrate economic parameters.

Estimates of the economic value associated with estuarine and mangrove resources, and the changes in value associated with specific environmental changes, depend largely on an understanding of the underlying physical and ecological relationships, and their quantification as far as possible. In practice these values will vary greatly according to the local physical, ecological, economic and social context. A case study approach to economic valuation, using the compartmental framework discussed above, and undertaken prior to, and in parallel with more detailed physical and ecological studies, is therefore required for the purposes of coastal management.

This integration of economic and physical/ecological studies is essential for several reasons. Firstly, preliminary economic analysis, based on existing information, is a powerful tool for evaluating the likely value of new information or improved understanding. It serves to focus physical and ecological studies on key issues or processes. At its simplest for example, it may suggest the desirability of focusing on a particular fish assemblage with high commercial value. Secondly, it is essential that economists understand the nature of, and limitations of, physical or ecological relationships and models, so that suitable explanations, and where appropriate cautions, can be presented alongside any aggregated economic values presented to decision makers.

The difficulties associated with the (contingent) valuation of biodiversity have been noted above. It is therefore highly desirable that the indirect, but commercial value of biodiversity – in terms of food and prey for commercially valuable species, or in terms of total ecosystem function – be assessed and modelled as far as possible. This is ambitious, and will require a sophisticated understanding of physical and ecological processes and relationships. It is essential that economists be brought into this area of research from the outset; the product will have far more long term legitimacy than contingent valuation approaches. Associations of ecologists and economists to tackle issues of this kind have been surprisingly rare, and the broad similarities between economic and ecological modelling unrecognized for too long.

In parallel with these broader studies, we need to undertake more localized studies, based as much on local knowledge as on biological surveys, to identify "fish nursery hot spots". Accurate valuation of these areas once identified is likely to be relatively straightforward in economic terms, providing a sound basis for management decisions.

Finally, it should be remembered that economic analysis is designed to facilitate decision making, and should not become an end in itself. Economic analysis should therefore be kept as simple, transparent and accessible as possible. Where of necessity it becomes complex, its assumptions and its inaccuracies must be clearly communicated to all decision makers.

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ELSEVIER

The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries

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Abstract

Visual census surveys were used to study the distribution of coral reef fishes that are associated with seagrass beds and mangroves in their juvenile phase, on various coral reef sites along the coast of the Caribbean island of Curaçao (Netherlands Antilles). The hypothesis tested was that various reef fish species occur in higher densities on coral reefs adjacent to nursery habitats than on reefs located at some distance to these habitats. Of 17 coral reef fish species that are known to use bays with seagrass beds and mangroves as nurseries (nursery species), 15 were observed in quadrats on the reef. Four nursery species, *Haemulon sciurus*, *Lutjanus apodus*, *Ocyurus chrysurus* and *Scarus coeruleus* occurred in significantly higher densities on coral reefs adjacent to bays with seagrass beds and mangroves. *Lutjanus analis*, *Lutjanus mahogoni* and *Sphyraena barracuda* also had their highest densities on reefs adjacent to these bays, although differences between the distinguished reef categories were not always significant. It is suggested that these seven species are highly dependent on the presence of bays with seagrass beds and mangroves as nurseries on an island scale. Eight other species that are known to use seagrass beds and mangroves as nurseries did not have their highest densities on reefs adjacent to bays with seagrass beds and mangroves. For six of these species, juveniles were also observed on the reef. It is suggested that these species are able to use the reef as an alternative nursery and do not depend strictly on the presence of bays with seagrass beds and mangroves as nurseries.
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Keywords: nursery grounds; mangrove swamps; seagrasses; coral reef fishes; migration; juveniles

1. Introduction

In various parts of the world, shallow coastal areas containing mangroves and seagrass beds are considered important nurseries for juvenile fish (Pollard, 1984; Parrish, 1989; Baelde, 1990; Robertson and Blaber, 1992). Pelagic fish larvae settle into these habitats, and grow from juveniles to subadults or adults that leave these habitats by means of post-settlement migrations (Jones, 1991; Blaber, 2000). In the Caribbean, shallow waters with mangroves and seagrass beds are characterised by the presence of high densities of juveniles of several coral reef species that are assumed to migrate to the coral reef on reaching the (sub)adult stage (Austin, 1971; Louis and Guyard, 1982; Nagelkerken et al.,

2000a; Cocheret de la Morinière et al., 2002; Adams and Ebersole, 2002; Nagelkerken and van der Velde, 2002). On the island of Curaçao (Netherlands Antilles), Nagelkerken et al. (2000b) showed that an inland marine bay with seagrass beds and mangroves served as a nursery habitat for at least 17 coral reef species (indicated below as nursery species). It has been shown on various islands that a reduced density of several of these nursery species on the coral reef is related to the absence of seagrass beds and mangroves (Nagelkerken et al., 2002). This suggests that these nursery species depend on the presence of seagrass beds and mangroves as a nursery habitat. If this is the case, coral reefs adjacent to mangrove and seagrass nursery areas might be expected to harbour higher densities of adults of these nursery species than reefs located at greater distance to these nursery areas, assuming that adult migration along the coast between reefs is limited.

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The island of Curaçao provides an opportunity to test this hypothesis along the coast of a single island. The occurrence of both seagrass beds and mangroves is restricted to several shallow inland marine bays situated at the southwestern part of the island, allowing a clear distinction to be made between reefs adjacent to bays with seagrass beds and mangroves, reefs adjacent to bays without seagrass beds and mangroves, and reefs located at some distance from bays. In a pilot study, Nagelkerken et al. (2000b) already observed reduced densities of six nursery species on the reef at an increasing distance from a single bay with nursery habitats. However, their study focused on only a few species and a small part of the reef, and did not consider the possible relation with fish size.

While subadult or adult bay-to-reef migrations are likely to supply coral reefs adjacent to bays with nursery species, reefs at some distance from these habitats can be colonised either by fish dispersal on reefs along the coast or by small populations of juvenile fish larvae that settle and survive on these reefs. Several studies (Tulevech and Recksiek, 1994; Macpherson, 1998; Zeller, 1998) suggest that it is predominantly the larger individuals that undertake migrations along the reef over larger distances. Whereas the population of nursery species on coral reefs adjacent to bays with seagrass beds and mangroves is represented by older juveniles, subadults and adults (Nagelkerken et al., 2000b; Cocheret de la Morinière et al., 2002; Nagelkerken and van der Velde, 2002), it might be expected that the population of nursery species on coral reefs at great distances to bays with seagrass beds and mangroves would consist predominantly of adults.

The present study tested the hypothesis that juveniles and adults of nursery species occur in higher densities on coral reefs adjacent to nursery habitats than on reefs located at some distance to these habitats. In accordance with this, reduced densities of adults and the absence of juveniles on coral reefs away from these bays, are expected. The degree to which nursery species might utilise the coral reef as an alternative juvenile habitat instead of seagrass and mangrove habitats was also investigated.

2. Materials and methods

2.1. Study area

The present study was carried out on the coral reef at the leeward southwestern coast of the Caribbean island of Curaçao, Netherlands Antilles (Fig. 1). The coast on this side of the island is characterised by the presence of a continuous fringing coral reef that consists of a small surf zone and a reef flat that gradually slopes down to a 'drop-off' at 7—12 m (Bak, 1975). At the drop-off, the reef slopes off steeply and ends in a sandy plain at depths

of 80—90 m. The southwestern coast features eight large inland bays (Fig. 1), which are dominated by mangroves, seagrass beds and a muddy/sandy seabed (Table 1). Rocky substratum, in the form of boulders and erosional notches, is present to some degree only in Spanish Water Bay. Notches are formed at and under the water line through biochemical solution of the fossil reef terrace along the shoreline (de Buisonjé and Zonneveld, 1960). Fringing mangroves grow in stands along the sandy shoreline of the bays and consist of *Rhizophora mangle* (see Nagelkerken et al., 2000b and Nagelkerken et al., 2001 for a detailed description of these habitats). Seagrass beds in Spanish Water Bay and Fuik Bay consist of *Thalassia testudinum* whereas those in Piscadera Bay consist of *Syringodium filiforme*. All bays have a narrow entrance from the open sea. The water of Zakito Bay is polluted with heavy metals from a desalination plant and has an elevated temperature and salinity (Nagelkerken, unpubl. data). The average daily tidal range in Curaçao is about 30 cm (de Haan and Zaneveld, 1959), and the bays are not subject to strong tidal currents.

2.2. Study design

The distribution of the 17 nursery species (listed in Table 2) was studied at 11 coral reef sites in a gradient along the southwestern coast at varying distances from two types of bays. The 11 reef sites were subdivided into four 'reef categories' (Fig. 1): (1) three coral reef sites adjacent to bays featuring major seagrass beds and mangrove habitats, indicated below as sg—mg bays (distance to the bay <1 km); (2) three coral reef sites adjacent to bays dominated by bare sediment without marine vegetation (distance to the bay <1 km), but situated at some distance to sg—mg bays, indicated below as mud/sand bays (distance to nearest sg—mg bay between 3.2 and 25.6 km); (3) two coral reef sites situated between sg—mg bays (distance to nearest sg—mg bay between 3.1 and 3.5 km, and to nearest mud/sand bay between 8.0 and 15.5 km); and (4) three coral reef sites located at greater distance to sg—mg bays (distance to nearest sg—mg bay between 11.6 and 38.5 km, and to nearest mud/sand bay between 4.7 and 13.4 km). The reef at Holiday Beach was located close to a bay (St. Anna Bay), but was nevertheless defined as a reef situated between sg—mg bays (Fig. 1). Due to industrial activities in St. Anna Bay (involving the presence of a large harbour, oil refinery and shipyards), all natural marine vegetation and muddy/sandy habitats have been destroyed, and the water is highly polluted (van den Hoek et al., 1972). Therefore, the ecological function of this bay cannot be considered typical for a mud/sand bay, and the reef close to this bay cannot be considered typical for a reef adjacent to an unpolluted mud/sand bay.
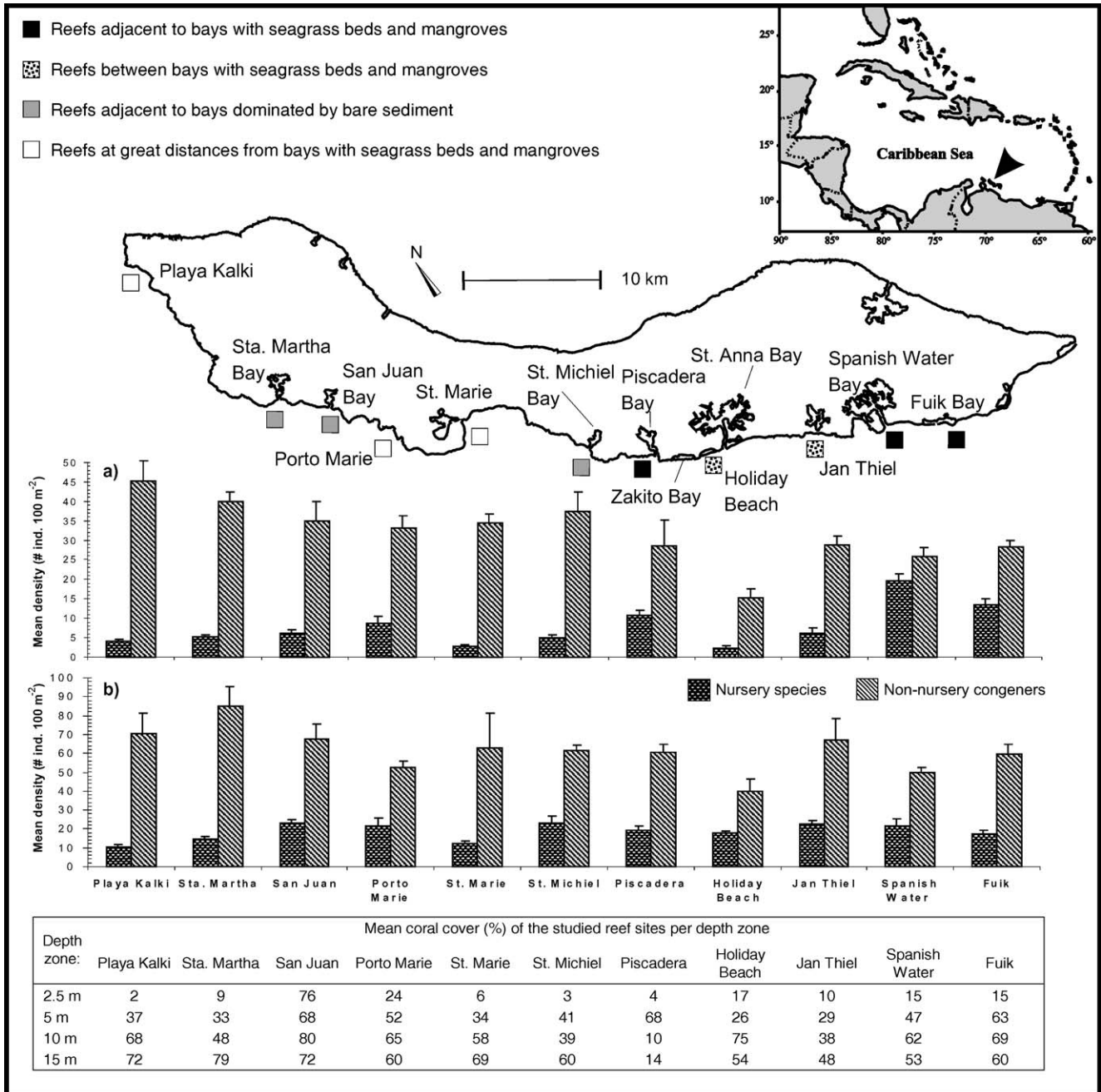
Fig. 1. Locations of the eight largest bays and 11 reef sites sampled on the island of Curaçao (latitude 12′ N, longitude 68′ W). The density pattern of nursery species and their non-nursery congeners along the gradient of reef sites is shown below the map of Curaçao. Separate patterns are shown (a) for pooled densities of the seven nursery species that had their highest densities at reef sites adjacent to bays with seagrass beds and mangroves (see Table 1) and their congeners, and (b) for pooled densities of the eight nursery species that did not have higher densities at reef sites adjacent to bays with seagrass beds and mangroves (see Table 1) and their congeners. Error bars indicate SEM. The table shows the mean coral cover (%) of each depth zone.

Besides the 17 nursery species, the densities of nine common non-nursery congeners of the nursery species were also determined on the reef sites: *Acanthurus bahianus*, *Acanthurus coeruleus*, *Chaetodon striatus*, *Haemulon carbonarium*, *Haemulon chrysargyreum*, *Scarus taeniopterus*, *Scarus vetula*, *Sparisoma aurofrenatum* and *Sparisoma viride*. Based on Nagelkerken et al. (2000b) it is assumed that juveniles of these congeners do not use seagrass and mangrove habitats as a nursery.

Data on the reef fish community structure were collected by visual census in quadrats using SCUBA and a stationary point-count method (Polunin and Roberts, 1993) by two independent observers. Square quadrats of 10 × 10 m were surveyed at four depth zones: shallow

Table 1
Main shallow-water habitats of the eight largest bays along the southwestern coastline of Curaçao, and the abundance of nursery species

	Total bay area (m²)	Bay area covered by seagrass beds (%)	Bay area consisting of muddy/sandy seabeds (%)	Length of inundated mangroves along shoreline (m)	Value as nursery	Lutjanus analis	Lutjanus apodus	Lutjanus griseus	Lutjanus mahogoni	Gerres cinereus	Chaetodon capistratus	Haemulon flavolineatum	Haemulon sciurus	Haemulon parra	Ocyurus chrysurus	Scarus iserti	Sparisoma chrysopterum	Sphyraena barracuda
Sta. Martha Bay	569,238	—	100	—	Low	**	*	*	—	***	—	—	—	—	*	—	—	***
San Juan Bay	159,060	—	100	60	Low	*	*	*	—	**	—	—	—	—	—	—	—	—
St. Michiel Bay	193,640	—	100	—	Very low	—	*	—	—	***	—	—	—	—	—	—	—	*
Piscadera Bay	726,168	2	98	3964	High	***	***	***	—	**	*	***	**	—	*	***	***	***
Zakito Bay	140,151	—	100	2267	Very low	—	—	—	—	*	—	—	—	—	—	—	—	—
St. Anna Bay	4,190,000	—	100	—	Very low	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Spanish Water Bay	2,846,511	15	82	8702	High	—[a]	*	*	—[a]	*	***	***	***	—[a]	***	—[a]	—[a]	***
Fuik Bay	687,556	3	97	3200	High	*	*	—	***	*	**	*	*	—	*	*	*	*

The presence of 13 nursery species is based on Nagelkerken et al. (2001) and unpublished data (Nagelkerken) for which the bays were sampled using a beach seine net. Based on estimated total standing stocks of juveniles on seagrass beds and muddy/sandy seabeds, presence of species is expressed as absent (−), low (*), high (**) or very high (***). Classes are distinguished per species by dividing the highest total standing stock by three. Based on mean abundance and mean species richness of nursery species in the main nursery habitats of the bays, Nagelkerken (unpubl. data) classified the nursery function of the bays as high, low or very low. No data are available for St. Anna Bay, but its nursery function is assumed to be very low (see text). nd, no data.

[a] Presence in seagrass/mangrove habitats demonstrated by means of visual census (Nagelkerken et al., 2000b).

Table 2

Size classes (cm) used to define juveniles for each nursery species, based upon half the length of the smallest maturation sizes obtained from FishBase World Wide Web (Froese and Pauly, 2002) and Munro (1983) (for *Lutjanus analis*, the maturation size of *Ocyurus chrysurus* was used to distinguish the juveniles (see text))

Species	Juveniles	Species	Juveniles
Acanthurus chirurgus	0–10	*Lutjanus griseus*	0–10
Chaetodon capistratus	0–5	*Lutjanus mahogoni*	0–12.5
Gerres cinereus	0–10	*Ocyurus chrysurus*	0–12.5
Haemulon flavolineatum	0–5	*Scarus coeruleus*	0–15
Haemulon parra	0–12.5	*Scarus guacamaia*	no data
Haemulon plumieri	0–10	*Scarus iserti*	0–10
Haemulon sciurus	0–10	*Sparisoma chrysopterum*	0–12.5
Lutjanus analis	0–12.5	*Sphyraena barracuda*	0–30
Lutjanus apodus	0–12.5		

reef flat (2.5 m), reef flat (5 m), drop-off (10 m) and reef slope (15 m). A single 10 m line was used as a reference for the size of a complete quadrat. At each site, ten quadrats (placed in a direction parallel to the coastline) per depth zone were surveyed, to a total of 40 quadrats per site. These 40 quadrats were surveyed during three visual census rounds: 16 quadrats at each site in December 1999, 16 quadrats in January 2000 and 8 quadrats in February 2000. After placing the quadrat line, the observer waited for 5 min to minimise fish disturbance. All nursery species within or passing through the quadrat were then counted over a period of 10 min. During fish counting the observer was at the edge of the quadrat for 8 min. After 8 min, the observer moved through the quadrats to search for and/or estimate sizes of possible small juvenile fish hiding behind or between coral boulders. Care was taken to ensure that fishes that regularly moved in and out of the quadrat were not counted twice. Fishes were classified into size classes of 2.5 cm. Each reef site was visited by the two observers simultaneously and each observer collected a total number of 20 quadrats. The location on the reef, within a reef site, where an observer would place the quadrats was randomly allocated to each of the observers during each census round, making sure not to recount the same area of reef. Species identification and quantification were first thoroughly and simultaneously practised by the two observers. Estimation of size classes was trained by repeatedly estimating the sizes of 40 pieces of electrical wires of known length (range 2.5–50 cm, in classes of 2.5 cm) under water. Training was continued until differences in size-estimation were minimal (maximum difference of one size class of 2.5 cm for wire sizes <15 cm and two size classes for sizes >15 cm) between the two observers. Training in fish species identification was continued until it was the same between the observers. The training procedure started two weeks before the census and was repeated before each census round (three census rounds over a period of three months).

For each species, data were also analysed separately for juveniles, based upon their maturation size (Table 2). Maturation sizes were obtained from FishBase World Wide Web (Froese and Pauly, 2002) and Munro (1983). If this database gave maturation size as a range, the smallest observed maturation size was used. Juveniles were defined as individuals smaller than half the maturation size (i.e., maturation size divided by two) to be able to distinguish them from larger subadults. Maturation size for *Lutjanus analis* was 37.5 cm, which is much larger than that of the other Lutjanidae studied (i.e., 17.5–22.5 cm). This value was based on only one study (quoted in FishBase World Wide Web), and may therefore not be very reliable. The same maturation size for *L. analis* as for *Ocyurus chrysurus* was therefore used. This was based on the fact that *O. chrysurus* and *L. analis* have almost the same maximum length, and because for *O. chrysurus* a large number of studies have determined the maturation size (quoted in FishBase World Wide Web).

Since fish densities are often correlated to the degree of coral cover (Luckhurst and Luckhurst, 1978; Hixon and Beets, 1993; Grigg, 1994) the total hard coral cover (both living and dead corals) at each site for each depth zone was visually quantified. To estimate coral cover of the quadrat, the 10×10 m quadrat was divided into four quarters of 5×5 m. For each quarter, coral cover was estimated separately and was averaged for the whole quadrat afterwards. The 10 m quadrat line was marked with a red label in the middle to visually estimate the size of each quarter. Because the number of quadrats for which the cover was estimated was not constant for each site (between 6 and 10 estimations per depth zone per site), cover was averaged for quadrats and expressed as mean hard coral cover per depth zone per site.

2.3. Statistical analysis

Principal Component Analysis (PCA) was used to study the spatial distribution pattern of nursery species along the gradient of reef sites. PCA was carried out on log^{10}-transformed mean fish densities (with all size classes pooled) per reef site, using the Canoco 4.0 ordination program (ter Braak and Smilauer, 1998). Default options were used for the analysis: scaling was focused on inter-species correlations (to focus more on the relationships between species), species scores were divided by the standard deviation (to reduce the influence of species with a large variance in density), and the data were centred by species (used for ordinary PCA, where each species is weighted by its variance).

To test the influence of coral cover on fish density, separate linear regressions were run for each species at each depth zone. Since *Haemulon parra* occurred only at one reef site, no regression analysis could be performed

for this species. For each species, mean fish density (with all size classes pooled) at each site ($N = 11$) was used as the dependent variable and mean hard coral cover was used as the regression. Regression analyses were performed using SPSS version 11.5.

The influence of the presence of a bay nursery habitat on the occurrence of nursery species on the reef was tested using generalized linear models. Because the data consisted of counts, a model based on a Poisson distribution was used. For each quadrat, visual census counts of all size classes were pooled. Because the 10 quadrats of a depth zone were laid out in a line parallel to those in other depth zones, counts of quadrats distributed over the four depth zones were pooled to one count. Therefore, data for each site consisted of 10 counts (i.e., each a sum of counts over four depth zones). These fish counts were used as the dependent variable in the model. The factor 'reef category' was used as a fixed factor. Because data were collected during three time periods (visual census rounds), a three-level block was added to the model, each level being one visual census round. The log link function and type 3 analysis were used in the model. Post-hoc comparisons between reef categories were made by calculating differences of least squares means. Statistics were performed using the SAS system for Windows V8.

3. Results

3.1. Total fish density

In the present study, 15 of the 17 known nursery species were observed in the quadrats on the reef. *Haemulon plumieri* and *Scarus guacamaia* were not observed.

Of the 56 linear regressions between fish density and coral cover, only three were significant: *Haemulon sciurus* in the 15 m zone ($P < 0.01$; $R^2 = 0.63$; $Y = 0.91 - 1.20X$), *Scarus coeruleus* in the 5 m zone ($P < 0.01$; $R^2 = 0.65$; $Y = 0.60 + 1.57X$) and *Lutjanus mahogoni* in the 5 m zone ($P < 0.05$; $R^2 = 0.37$; $Y = -2.63 + 11.08X$).

PCA allowed the reef sites to be divided into four clusters (Fig. 2). One cluster was formed by the three reef sites adjacent to sg–mg bays and was characterised by nine nursery species. Compared with the other reef sites, the mean densities of seven of these species were highest on reefs adjacent to sg–mg bays (Table 3). A second cluster was formed by the reefs between sg–mg bays and was characterised by high densities of *Chaetodon capistratus*. A third cluster was formed by two reefs adjacent to mud/sand bays and one reef at great distance from sg–mg bays, and harboured five species. Two reefs located at great distance from sg–mg bays and one reef adjacent to a mud/sand bay formed

a fourth cluster, in which none of the species had their highest densities.

Generalized linear models were significant for 14 species (Table 3). Post-hoc comparisons showed significantly higher counts of *Ocyurus chrysurus*, *Lutjanus apodus*, *Haemulon sciurus* and *Scarus coeruleus* in the category reefs adjacent to sg–mg bays than in the other three categories (Fig. 3a, Table 3). *Ocyurus chrysurus* had decreasing counts on reefs located at increasing distances from sg–mg bays. *Lutjanus mahogoni* and *Lutjanus analis* also had their highest densities in the category reefs adjacent to sg–mg bays (Fig. 3a). For these two species, fish counts in the category reefs adjacent to sg–mg bays differed significantly from those in the categories reefs between sg–mg bays and reefs adjacent to mud/sand bays, but not from reefs at great distance from sg–mg bays. *Sphyraena barracuda* had its highest density in the category reefs adjacent to sg–mg bays, but a significant difference between counts was only found between reefs adjacent to sg–mg bays and reefs at great distance from sg–mg bays.

Of the other eight nursery species, two had their highest density in the category reefs between sg–mg bays (*Chaetodon capistratus* and *Sparisoma chrysopterum*) and two in the category reefs adjacent to mud/sand bays (*Haemulon flavolineatum* and *Scarus iserti*) (Table 3). Three species had their highest densities in the category reefs at great distance from sg–mg bays (*Gerres cinereus*, *Lutjanus griseus*, and *Haemulon parra*). Densities of *Acanthurus chirurgus* were highest on reefs adjacent to sg–mg bays and on reefs adjacent to mud/sand bays.

Pooled densities of the seven nursery species occurring in higher densities on reefs adjacent to sg–mg bays were higher at all reef sites adjacent to sg–mg bays than at other reef sites (Fig. 1a). This pattern was not found for the other eight nursery species observed on the reef (Fig. 1b). Non-nursery congeners of species with higher densities on reefs adjacent to sg–mg bays, had their highest densities on reef sites in the southwestern part of the gradient along the coast of the island, at great distance from bays with sg–mg (Fig. 1a). Non-nursery congeners of species without higher densities on reefs adjacent to sg–mg bays did not show higher densities in any particular part of the gradient of reef sites examined (Fig. 1b).

3.2. Juvenile fish density

For the seven nursery species which had their highest densities (for the entire size range) on reefs adjacent to sg–mg bays, juveniles were also observed on the coral reef (Fig. 3b). An exception was *Lutjanus analis*, for which only adults were observed on the reef. Juveniles of *Haemulon sciurus* were only observed on reefs adjacent to sg–mg bays, and those of *Sphyraena barracuda* only
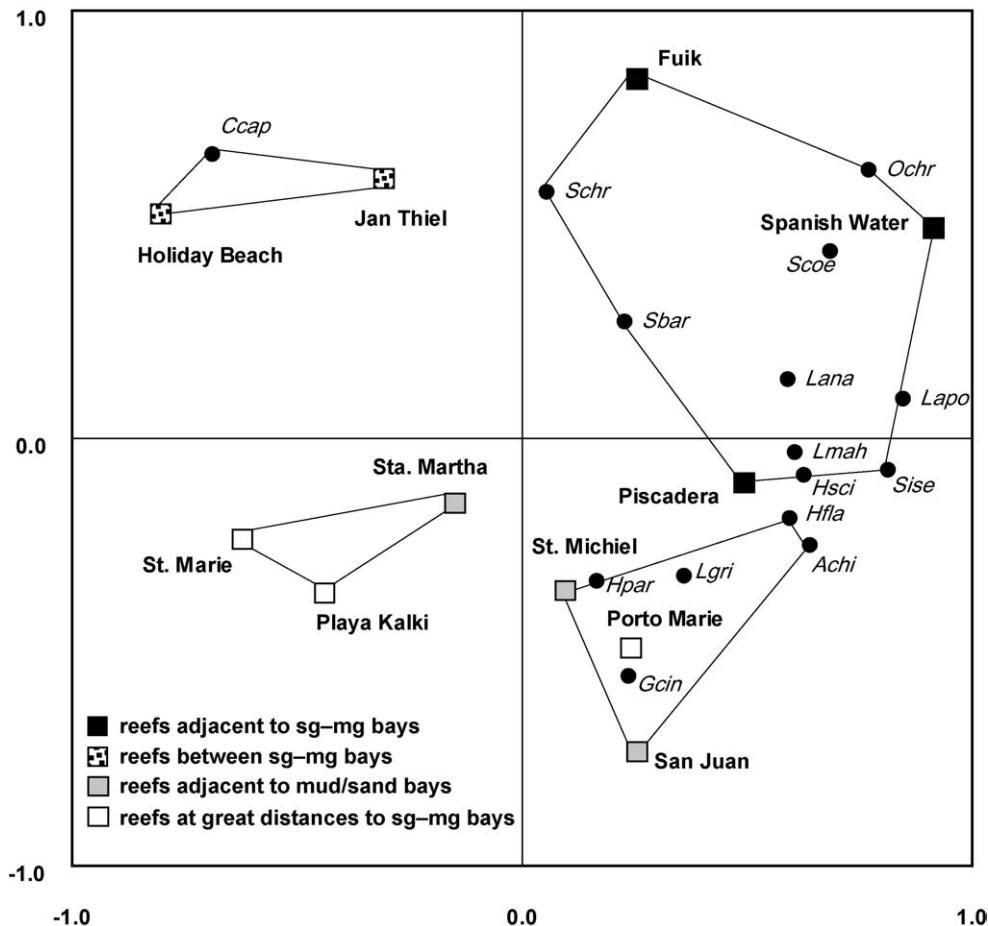
Fig. 2. Principal Component Analysis (PCA) of mean densities of the 15 nursery species at various reef sites. The horizontal axis represents the first PCA axis, the vertical axis the second PCA axis. The first two axes accounted for 67.9% of the total variance. Abbreviations: sg–mg bays: bays with seagrass beds and mangroves; mud/sand bays: bays dominated by muddy/sandy seabeds; *Achi*: *Acanthurus chirurgus*; *Ccap*: *Chaetodon capistratus*; *Gcin*: *Gerres cinereus*; *Hfla*: *Haemulon flavolineatum*; *Hpar*: *Haemulon parra*; *Hsci*: *Haemulon sciurus*; *Lana*: *Lutjanus analis*; *Lapo*: *Lutjanus apodus*; *Lgri*: *Lutjanus griseus*; *Lmah*: *Lutjanus mahogoni*; *Ochr*: *Ocyurus chrysurus*; *Scoer*: *Scarus coeruleus*; *Sise*: *Scarus iserti*; *Schr*: *Sparisoma chrysopterum*; *Sbar*: *Sphyraena barracuda*. On the basis of sites and species which showed the highest similarity in composition and density distribution (using PCA), four clusters of sites and species were identified and bordered by lines.

on reefs between sg–mg bays. Despite the presence of juveniles of six of these seven nursery species on the coral reef, densities of their juveniles were much higher in seagrass beds and mangroves than on the reef (Fig. 3b). An exception was *Scarus coeruleus*, for which juvenile densities on the coral reef and those in seagrass beds in Spanish Water Bay were similar.

For the eight nursery species which did not show highest densities (for the entire size range) on reefs adjacent to sg–mg bays, juveniles were also found on the coral reef, except *Lutjanus griseus* and *Haemulon parra* (Fig. 4a). The eight species can be divided into two groups. Densities of juveniles of *Chaetodon capistratus*, *Haemulon flavolineatum*, *Gerres cinereus*, *L. griseus*, and *H. parra* were considerably higher in seagrass beds or mangroves in Spanish Water Bay than on the reef (Fig. 4a) whereas juveniles of *Sparisoma chrysopterum*, *Scarus iserti*, and *Acanthurus chirurgus* showed similar

densities in seagrass/mangrove habitats and in reef habitats (Fig. 4b).

4. Discussion

The present study showed significantly higher densities of four nursery species on reefs adjacent to sg–mg bays than in all three other reef categories, whereas three other nursery species showed significantly higher densities at reefs adjacent to sg–mg bays than in two of the three other reef categories. This is probably caused by the very high densities in the bays (summarised in Table 1) of juveniles, which migrate to the adjacent reef when reaching adulthood. This connectivity between nursery habitats in a bay and the reef adjacent to a bay has been indicated before for Spanish Water Bay (Nagelkerken et al., 2000b; Nagelkerken and van der Velde, 2002;

Table 3
Results of the generalized linear models with reef category as fixed factor and survey time as random block

	Model		Block		Mean density per reef category (# ind. 100 m^{-2})				P-values of post-hoc comparisons					
	X^2	P	X^2	P	1	2	3	4	1–2	1–3	1–4	2–3	2–4	3–4
Species with highest density for reef category 1														
Ocyurus chrysurus	654.50	<0.001	0.95	ns	**6.2**	1.9	1.3	0.5	<0.001	<0.001	<0.001	0.009	<0.001	<0.001
Lutjanus apodus	245.36	<0.001	1.20	ns	**4.0**	0.7	1.5	1.7	<0.001	<0.001	<0.001	<0.001	<0.001	ns
Haemulon sciurus	54.66	<0.001	9.39	0.009	**0.7**	0.1	0.4	0.1	<0.001	0.006	<0.001	0.005	ns	0.001
Scarus coeruleus	55.69	<0.001	13.25	0.001	**0.4**	0.0	0.2	–	0.001	0.026		0.020		
Lutjanus mahogoni	23.13	<0.001	58.76	<0.001	**2.3**	1.8	1.3	1.9	0.041	<0.001	ns	0.026	ns	0.004
Lutjanus analis	11.87	0.009	5.94	ns	**0.2**	0.0	0.0	0.1	0.033	0.011	ns	ns	ns	ns
Sphyraena barracuda	10.47	0.015	9.13	0.010	**0.2**	**0.2**	0.1	0.1	ns	ns	0.006	ns	0.045	ns
Other species														
Chaetodon capistratus	501.77	<0.001	3.20	ns	1.8	**7.3**	1.1	2.2	<0.001	<0.001	0.027	<0.001	<0.001	<0.001
Sparisoma chrysopterum	106.78	<0.001	3.36	ns	1.0	**1.7**	0.9	0.2	<0.001	ns	<0.001	<0.001	<0.001	<0.001
Haemulon flavolineatum	53.40	<0.001	3.08	ns	6.3	4.7	**7.6**	5.8	<0.001	0.001	ns	<0.001	0.003	<0.001
Scarus iserti	210.51	<0.001	84.45	<0.001	9.3	6.0	**9.9**	5.0	<0.001	ns	<0.001	<0.001	0.012	<0.001
Gerres cinereus	31.08	<0.001	0.90	ns	0.2	0.2	0.5	**0.6**	ns	0.006	<0.001	0.002	<0.001	ns
Lutjanus griseus	22.52	<0.001	5.25	ns	0.1	–	0.1	**0.2**		ns	ns			ns
Haemulon parra	np				–	–	–	**0.1**						
Acanthurus chirurgus	28.00	<0.001	91.24	<0.001	**1.5**	0.9	**1.5**	0.8	0.001	ns	<0.001	0.002	ns	<0.001
Haemulon plumieri	np				–	–	–	–						
Scarus guacamaia	np				–	–	–	–						

P-values of post-hoc comparisons (differences of least mean squares) between the four types of reef categories are shown. Fish counts were converted into mean fish densities per reef category; highest mean density is printed in bold. Abbreviations and symbols: np: not enough counts to perform the test; ns: non-significant (P > 0.05); –: not observed; 1: reefs in front of bays with seagrass beds and mangroves; 2: reefs between bays with seagrass beds and mangroves; 3: reefs in front of bays dominated by bare sediment; 4: reefs at great distances from bays with seagrass beds and mangroves.

Cocheret de la Morinière et al., 2002). The present study suggests that all sg–mg bays along the southwestern coast of the island of Curaçao show this type of connectivity for certain coral reef fish species. A direct interlinkage between these habitats by fish life-cycle migration is difficult to show, but studies using otolith microchemistry (Gillanders, 2002; Gillanders and Kingsford, 1996) have confirmed the existence of these life-cycle migrations between juvenile habitats and adult habitats in temperate marine fish species.

Regarding these seven species with the highest densities on reefs adjacent to sg–mg bays, Nagelkerken et al. (2002) found that densities of *Haemulon sciurus*, *Lutjanus apodus* and *Ocyurus chrysurus* were greatly reduced on coral reefs of islands lacking seagrass and mangrove habitats relative to islands where these habitats were present, indicating that these species are highly dependent on these nursery habitats. For *Lutjanus analis*, *Sphyraena barracuda* and *Scarus coeruleus*, Nagelkerken et al. (2002) found a possible dependence on mangrove and/or seagrass nurseries. The present study suggests that the presence of sg–mg bays strongly influences the distribution pattern of these six species on the coral reef along the coast of a single island. Since mud/sand bays that lack seagrass and mangrove habitats have a limited nursery function (Nagelkerken et al., 2001; Table 1), sg–mg bays are likely to function as the main, and for some species the only, source of

new individuals on the reef, resulting in high densities on reefs adjacent to these bays.

An exception was *Lutjanus mahogoni*, for which density differences between reefs adjacent to sg–mg bays and the other types of reef categories were not as large as those for the other six species. A possible explanation may be found in the ability of this species to spend its juvenile phase on the reef. Based on observations of juveniles on the reef in the present study and by Wilson (2001) and Nagelkerken et al. (2000a), "local recruitment" on the reef may be an important source of new individuals. The higher densities on reefs adjacent to sg–mg bays might be a result of an additional input of individuals from these habitats onto the reef. Comparisons of densities of this species between islands with and without seagrass beds and mangroves did not reveal any differences (Nagelkerken et al., 2002) and are consistent with this hypothesis.

If sg–mg bays function as the main source of new individuals on the reef, the presence of these six species on reefs not adjacent to sg–mg bays may partly result from fish dispersal along the coast. This may explain why the three types of reef located at great distance from sg–mg bays showed much lower densities for six of these nursery species. Studies have shown that fishes are able to migrate along reefs over distances ranging from hundreds of metres to several kilometres (Tulevech and Recksiek, 1994; Kanashiro, 1998; Mazeroll and
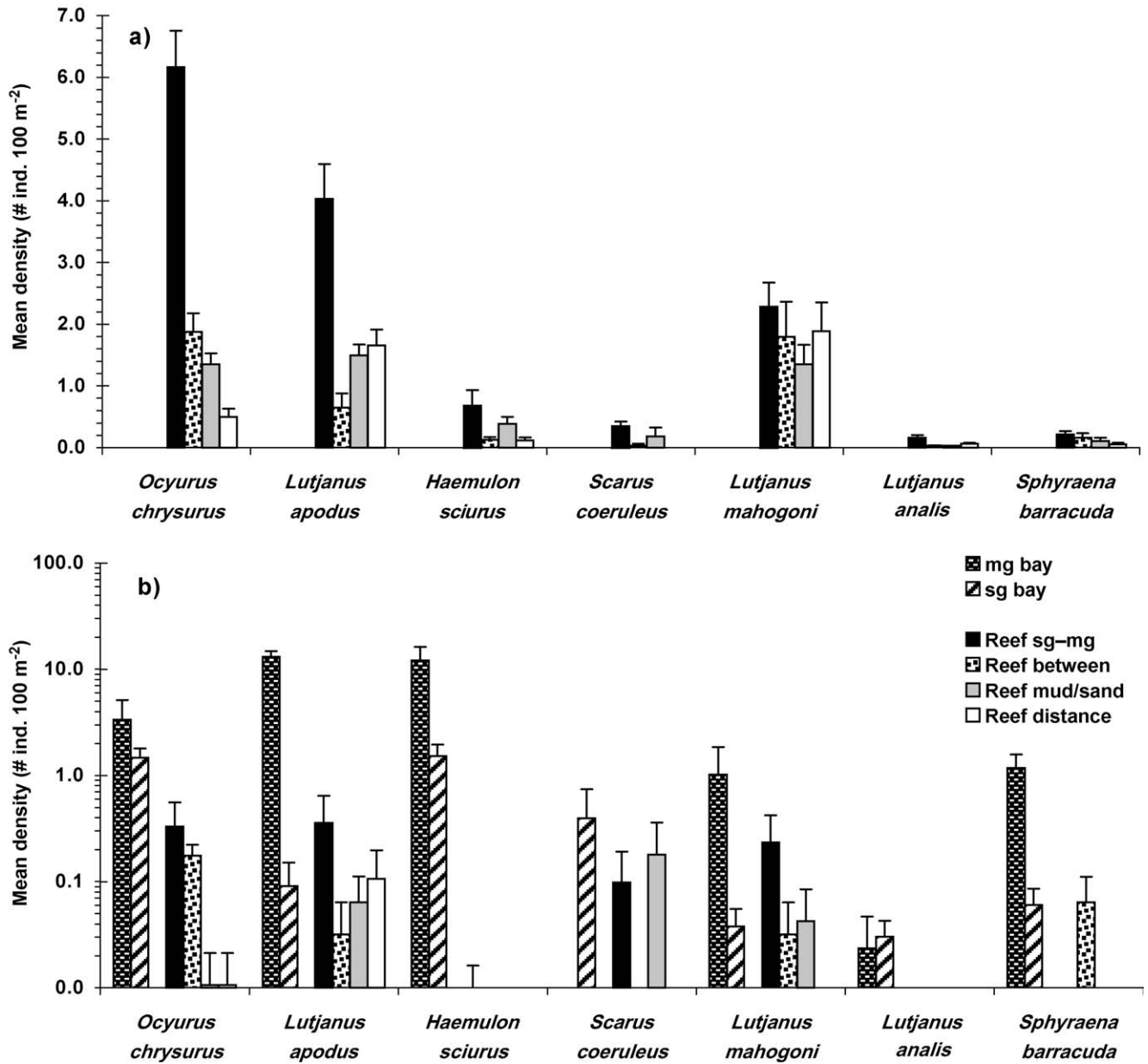
Fig. 3. Mean densities of (a) the entire size range and (b) juveniles of the seven nursery species that had higher densities on reefs adjacent to bays with seagrass beds and mangroves than at other locations (see Table 3). (b) Also shows densities of juveniles in mangroves and seagrass beds in Spanish Water Bay (data recalculated from Nagelkerken and van der Velde, 2002), to allow comparison with densities on the reef. Note that the *Y*-axis of (b) is on a log[10]-scale. Error bars indicate SEM. mg bay: mangrove habitat in Spanish Water Bay; sg bay: seagrass habitat in Spanish Water Bay; Reef sg–mg: reefs adjacent to bays with seagrass beds and mangroves; Reef between: reefs between bays with seagrass beds and mangroves; Reef mud/sand: reefs adjacent to bays dominated by bare sediment; Reef distance: reefs at great distances to bays with seagrass beds and mangroves.

Montgomery, 1998; Zeller, 1998; Chapman and Kramer, 2000). Long-distance dispersal of *Haemulon sciurus*, *Lutjanus analis*, *Lutjanus apodus*, *Ocyurus chrysurus*, and *Sphyraena barracuda* may have contributed to the presence of small fish populations on reefs located at some distance from their main nursery habitats.

The presence of adults of species that had their highest densities on reefs adjacent to sg–mg bays in the other reef categories may also be explained by the survival of juveniles that have settled and grown up directly on these reefs, rather than in seagrass or mangrove habitats. Although it has been shown, for example, that predation pressure results in low survival of Haemulidae on reefs (Beets, 1997), some individuals may survive and contribute to small populations on reefs at some distance from seagrass and mangrove habitats (Shulman and Ogden, 1987). In the specific case of *Scarus coeruleus*, which showed its highest densities on reefs adjacent to sg–mg bays, local recruitment can play a major role because juvenile densities on the reef were comparable to
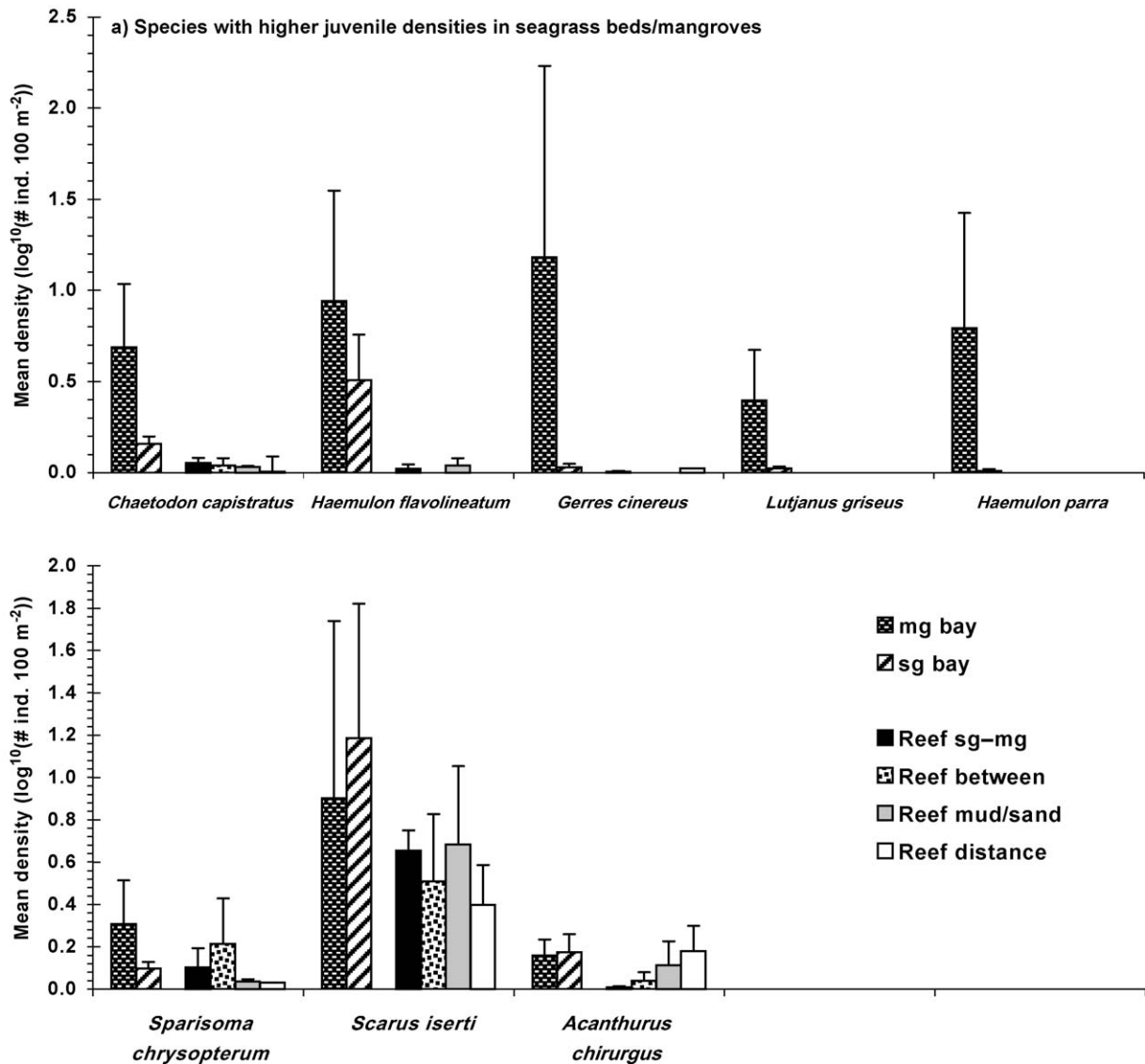
Fig. 4. Mean densities of juveniles of the eight nursery species that did not have higher densities on reefs adjacent to bays with seagrass beds and mangroves than at other locations. Densities are shown on a $\log^{10}$-scale for the coral reef (this study) and for the mangroves and seagrass beds of Spanish Water Bay (data recalculated from Nagelkerken and van der Velde, 2002). Species with higher juvenile densities in seagrass beds/mangroves than on the reef (a) are distinguished from species with similar densities in seagrass beds/mangroves and on the reef (b). Error bars indicate SEM. For abbreviations see the legend to Fig. 3.

those in seagrass beds. Other studies have also observed juveniles of *S. coeruleus* on patch reefs (Overholtzer and Motta, 1999). These observations suggest that this species can also use the coral reef as a nursery.

One problem with the interpretation of the present results is that all reefs in front of bays with seagrass bed and mangrove nurseries were located on the southeastern part of the coast, whereas all reefs in front of mud/sand bays and reefs at great distances from bays with mangroves and seagrass beds were located on the northwestern part of the island. Factors other than absence/presence of bays with mangrove and seagrass beds may therefore also influence the reef fish communities at these reef categories. It is argued that even if such factors play

a role, the influence of the presence/absence of nursery bays on the fish community structure of various reef fish species is greater than these other factors. Firstly, and most importantly, if other factors were primarily responsible, then non-nursery congeners of the nursery species would also show significantly elevated densities at reefs in front of nursery bays. This was not the case. Secondly, coral cover at 2, 5, and 10 m depth and overall coral cover did not differ significantly between the southeastern and northwestern reefs ($P > 0.213$, t-test). Only at 15 m depth was the coral cover significantly higher at the latter reefs than at the former ($p = 0.047$, t-test), but the data indicated that with the exception of one fish species no high positive correlation was present

between coral cover and fish densities. Thirdly, *Ocyurus chrysurus*, *Lutjanus apodus* and *Haemulon sciurus* which showed the highest difference in density between the reefs in front of the bays with nursery habitats and the other three reef categories, were three of the four nursery species for which Nagelkerken et al. (2002) indicated that they showed a very high dependence of mangrove/seagrass nurseries at various islands throughout the Caribbean. Environmental factors such as water temperature, salinity and turbidity do not vary in a systematic way at the two parts of the island, partly due to the ocean currents which run straight along the entire southwestern coast of the island. The island does not have any fishing reserves, and fishing takes place along the entire sheltered southwestern coast. It is therefore concluded that the presence of nursery bays is in this case the best possible explanation for the elevated densities of seven nursery species on reefs in front of sg–mg bays.

Among the eight nursery species that did not occur in higher densities as mainly adults on reefs adjacent to sg–mg bays, two groups were distinguished: one including species with higher juvenile densities in seagrass beds/mangroves than on the coral reef, and one including species with similar juvenile densities in seagrass beds/mangroves and on the reef. The first group includes two species (*Chaetodon capistratus* and *Haemulon flavolineatum*) for which local recruitment is probably the main source of adults, because juveniles were found on the entire reef while no higher total density was observed on reefs adjacent to sg–mg bays. Nagelkerken et al. (2000a) also found juveniles of both species on the reef. Nagelkerken et al. (2001) showed a major nursery function of mud/sand bays for *Gerres cinereus* (see Table 1). And since mud/sand bays are present over a large part of the coast, the observations of juveniles of this species at the various reef sites at great distance from sg–mg bays might be explained by the presence of these bays. Juveniles of *Lutjanus griseus* and *Haemulon parra* were predominantly observed in sg–mg bays (Table 1) and not on the coral reef. The presence of these species on reefs at some distance to sg–mg bays might therefore be explained by dispersal along the coast.

For the second group, local recruitment is thought to be the main source of adults on reef sites other than reefs adjacent to sg–mg bays. Nagelkerken et al. (2002) described both *Acanthurus chirurgus* and *Sparisoma chrysopterum* as species that do not depend on mangroves or seagrass beds as nurseries. However, the same study indicated that *Scarus iserti* depends heavily on the presence of seagrass beds and mangroves as nurseries. The results of the present study suggest that around Curaçao, the species is well capable of using the reef as an alternative nursery and is therefore not restricted to seagrass beds and mangroves as nurseries. Small juveniles (0–5 cm) were also frequently observed on most

reef sites. Ontogenetic migrations from sg–mg bays to reefs located much farther away are therefore not likely.

Various studies have demonstrated a close correlation between habitat complexity and total fish density (Luckhurst and Luckhurst, 1978; Bell and Galzin, 1984; Grigg, 1994). In the present study, however, the relation between coral cover and fish density was only evident for *Scarus coeruleus*, suggesting that this species favours reefs with a high coral cover. For the two other species which showed a significant relation between density and coral cover, the relation was only significant in one depth zone, and was negative for *Haemulon sciurus*, whereas for *Lutjanus mahogoni* the degree of variation explained by the regression line was very low. Furthermore, the non-nursery congeners of the nursery species showed different distribution patterns among the reef sites than the nursery species. It is therefore likely that in this study coral complexity did not influence the distribution of the sampled nursery species along the coast.

The results of the present study indicate that the distribution of *Haemulon sciurus*, *Lutjanus apodus*, *Ocyurus chrysurus* and *Scarus coeruleus* on the coral reef along the coast of a single island is significantly related to the presence of sg–mg bays. *Lutjanus analis*, *Lutjanus mahogoni* and *Sphyraena barracuda* showed a similar trend but densities at reefs adjacent to sg–mg bays were only significantly higher than those at two of the three reef categories. Six of these seven nursery species showed much higher juvenile densities in seagrass/mangrove habitats than on the reef, but were nevertheless also found as adults on reef locations at some distance from these nursery habitats, suggesting dispersal along the reef. *Acanthurus chirurgus*, *Scarus iserti* and *Sparisoma chrysopterum* showed comparable juvenile densities in seagrass/mangrove habitats and reef habitats, and were also found as adults at various reef sites, suggesting that they can complete their entire life cycle on the reef and are not highly dependent on seagrass beds and mangroves.

Acknowledgements

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AMERICAN CROCODILE
Crocodylus acutus

American crocodiles are primitive-looking reptiles native to the United States, Mexico, Central America, northern South America, and a number of islands in the Caribbean. This species of crocodile (there are 23 species of crocodilians around the world) primarily inhabits mangrove swamps, brackish creeks, and coastal canals. In the U.S., crocodiles only occur in salt and brackish water habitats in the southern tip of the Florida mainland and around the Florida Keys. American crocodiles are often confused with American alligators; both species can occur in the same habitats in South Florida, so differentiation between the two may be necessary. Fortunately, there are some noticeable differences between the two species. Crocodiles have longer, thinner snouts than alligators. Alligators are dark gray or black as adults, whereas crocodiles are a light gray or tan. Also, if you observe a basking animal and wonder which species it is, check out the teeth (from a distance, of course!). Crocodiles have a very noticeable tooth (the 4th tooth on each side of the lower jaw) that is visible even when the mouth is closed. The lower 4th tooth of alligators is not visible because they are hidden in grooves in the jaw.

Although crocodiles over 20 feet long have been recorded in Central and South America, individuals reaching 12-13 feet long in the U.S. are considered very large. Crocodiles are accomplished predators that feed on fish, crabs, birds, and small mammals. "Crocs" pose no real danger to humans unless provoked or molested; they should only be observed from a distance, and never be approached or fed. Female American "crocs" lay 20 - 70 eggs in either a hole or a mound nest. They do not guard the nest as aggressively as alligators but may stay near the nest until the babies hatch up to 100 days later. The mother "croc" may even dig out the hatchlings and carry them to the water in her mouth. The hatchlings face many predator species like raccoons, birds, fish, and other crocodiles — most are eaten before they reach adult size. American crocodiles are endangered in all parts of their range. Habitat destruction and overcollecting for the skin trade have reduced the number of crocodiles. Unlike American alligators, which have made a comeback in much of their range, crocodiles have not faired as well. Careful management of habitat, scientific research, and public education are essential if we want these magnificent animals to survive.

Baby crocodiles!

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