

A Conceptual Framework to Develop Long-Term Ecological Research and Management Objectives in the Wider Caribbean Region

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The Caribbean Sea and its watersheds show signs of environmental degradation. These fragile coastal ecosystems are susceptible to environmental impacts, in part because of their oligotrophic conditions and their critical support of economic development. Tourism is one of the major sources of income in the Caribbean, making the region one of the most ecotourism dependent in the world. Yet there are few explicit, long-term, comprehensive studies describing the structure and function of Caribbean ecosystems. We propose a conceptual framework using the environmental signature hypothesis of tropical coastal settings to develop a series of research questions for the reef–sea–grass–wetland seascape. We applied this approach across 13 sites throughout the region, including ecosystems in a variety of coastal settings with different vulnerabilities to environmental impacts. This approach follows the strategy developed by the Long Term Ecological Research program of the National Science Foundation to establish ecological research questions best studied over decades and large spatial areas.

Keywords: Caribbean, eutrophication, LTER (long-term ecological research), coastal settings, human influence

Recent reviews describing human impacts on coastal and marine ecosystems in the Caribbean emphasize two major problems. First is the lack of information about processes controlling the productivity of diverse coastal ecosystems. Second is the potential long-term negative impact of human disturbances on the goods and services these ecosystems provide (Richards and Bohnsack 1990, Ogden 1997). The Caribbean Sea has been diagnosed as an ecosystem showing “signs of environmental stress” (Richards

and Bohnsack 1990), representing a global trend in which human impacts on marine ecosystems are more the rule than the exception. A current debate in environmental resource management concerns how best to understand the magnitude of ecosystem change associated with human impacts and to designate the global regions that are more susceptible to human activities (Vitousek et al. 1997). In the Caribbean Sea and its watersheds, degradation of water and land resources is related to major declines in biodiversity

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Figure 1. Location of study sites in the wider Caribbean region: 1, Everglades, Florida; 2, Puerto Rico (wet); 3, Puerto Rico (dry); 4, San Juan, Venezuela; 5, Morrocoy National Park, Venezuela; 6, Los Roques, Venezuela; 7, Ciénaga Grande, Colombia; 8, Bocas del Toro, Panama; 9, Twin Cays, Belize; 10, northern Belize wetland complex; 11, Sian Ka'an, Mexico; 12, Celestun Lagoon, Mexico; 13, Terminos lagoon, Mexico.

(Solow 1995), species extinction (Brooks and Smith 2001), mass mortality of organisms (Lessios 1988, Harvell et al. 1999), and reduction of marine resource productivity (Jackson et al. 2001). Furthermore, watersheds of the Caribbean Sea are one of the top five hotspots of marine and terrestrial biodiversity identified around the world, representing an area with an exceptional concentration of endemic species. Caribbean watersheds are undergoing an exceptional loss of habitat; only about 10% of their primary terrestrial vegetation remains (Myers et al. 2000, Brooks and Smith 2001).

The Caribbean Sea consists of fragile coastal ecosystems that are susceptible to environmental impacts, in part because of their oligotrophic conditions (Richards and Bohnsack 1990, Lapointe 1997) and their critical support of economic development. The wider Caribbean region includes 36 to 40 countries, with a total population of 38 million (figure 1; CIA 2003). Travel and tourism are major sources of income in the Caribbean, making the region one of the most ecotourism

dependent in the world. The Caribbean travel industry had gross earnings of \$17 billion in 1999, which provided about 900,000 direct and indirect jobs and contributed about a quarter of the region's foreign exchange profits. Travel and tourism were expected to generate \$34.6 billion of economic activity in 2003, and this amount will grow to \$78.4 billion by 2013 (WTTC 2003). Employment in the travel industry in 2003 was estimated at 1,857,000 jobs, or 12% of total employment (1 in every 8 jobs) in the region. Approximately 100 million tourists visit the Caribbean annually, contributing about 43% of the combined gross national product and one-third of the export earnings for the region (including the Dominican Republic, Puerto Rico, Jamaica, the Bahamas, Cuba, Barbados, Aruba, Bermuda, Trinidad and Tobago, and Curaçao; WTTC 2003). In addition to supporting intense tourism activities, the Caribbean Sea is one of the most heavily traversed seas worldwide. Shipping activities in the region include the transport of oil, which generates pollution in the

form of bilge water and garbage dumped into the ocean (Atwood et al. 1987). In addition, there is a significant amount of pollution from nonpoint sources within the region, including contaminants such as sewage, solid-waste leachates from landfills, industrial and agricultural runoff, and petroleum products (Atwood et al. 1987).

These impacts threaten the biodiversity and environmental quality of coastal ecosystems in the region. The extent of the loss of biological diversity is still poorly known (Loreau et al. 2001), particularly in the Caribbean, where species extinction occurs at an accelerated rate. However, we know that of the 197 endemic mammals and birds across the Lesser and Greater Antilles, at least 43 have become extinct over the last 500 years (Myers et al. 2000). It is estimated that in the last 150 years eight species of vertebrates have become extinct in Jamaica alone, and more than 100 plant species indigenous to Trinidad and Tobago may be threatened by extinction. Despite much more widely publicized support for biodiversity conservation, the lack of regional governmental and institutional support for research suggests that trends of declining biological diversity in the Caribbean will continue over the next several decades (Myers et al. 2000, Brooks and Smith 2001). This trend is ongoing despite the presence of 22 Ramsar Convention sites and 20 coastal biosphere reserves located throughout the Caribbean region (table 1).

There are few comprehensive, long-term research programs aimed at understanding the ecosystem services of coastal settings in the Caribbean, despite the strong ecological and economic importance of coastal ecosystems to the region. Regional research projects initiated in the 1970s and 1980s, such as CARICOMP (Caribbean Coastal Marine Productivity) and CARIPOL (Caribbean Petroleum Pollution Monitoring Project), have provided useful information about changes in the distribution, structure, and productivity of coral reef, sea grass, and mangrove ecosystems as influenced by petroleum pollution. Similarly, the Association of Island Marine Laboratories of the Caribbean, or AIMLC, has played an important role in assisting and initiating collaborative research among its members (Ogden 1987). More recently, the TEAM (Tropical Ecology, Assessment, and Monitoring) Initiative at Conservation International (www.conservation.org/xp/CIWEB/home) has developed the first early-warning system for global biodiversity, which will provide much-

Table 1. Locations of selected Ramsar sites and biosphere reserves around the wider Caribbean Sea.

Country or territory	Ecosystem	Ramsar site ^a	Biosphere reserve ^b
Guatemala	Maya		•
	Sierra de las Minas		•
Honduras	Rio Plátano		•
Nicaragua	Cayos Miskitos and coastal zone	•	
	Wetlands, Bluefield Bay	•	
	San Juan River	•	
Costa Rica	Northeast wetlands	•	
	Gandoca-Manzanillo	•	
	Cordillera Volcánica Central		•
	La Amistad		•
Panama	Darién		•
	La Amistad		•
Colombia	Ciénaga Grande de Santa Marta lagoon	•	•
	San Andres Seaflower		•
Venezuela	Los Olivitos lagoon	•	
	Cuare	•	
	Los Roques	•	
	Restinga lagoon	•	
	Tacarigua Lagoon	•	
Aruba and Netherlands Antilles		•	
Saint Lucia		•	
Guadeloupe		•	
British Virgin Islands		•	
Puerto Rico	Guánica Commonwealth Forest		•
	Luquillo Experimental Forest		•
North, Middle, and East Caico Islands		•	
Cayman Islands		•	
Jamaica	Black River	•	
Cuba	Zapata lagoon	•	•
	Baconao		•
	Buenavista		•
	Cuchillas del Toa		•
	Península de Guanahacabibes		•
	Sierra del Rosario		•
Mexico	Ria Lagartos	•	
	Dzilam	•	
	Sian Ka'an		•
	Calakmul		•
Florida (United States)	Everglades and Dry Tortugas	•	•

a. See www.wetlands.org/RDB/neotropics/Caribbean.html.

b. See www.unesco.org/mab.

needed knowledge about tropical ecosystems. This program is designed to supply information necessary for assessing the overall effectiveness of conservation efforts.

We have developed a conceptual framework to analyze the diverse ecological properties of coastal settings in the Caribbean region and evaluate the ecological vulnerability of these ecosystems to a variety of human and natural disturbances. In creating this framework, we emphasized the biogeochemical properties and primary productivity of the ecosystems that form the reef–sea-grass–wetland seascape. Our approach follows the strategy developed by the Long Term Ecological Research (LTER) program of the National Science Foundation to establish research questions that are

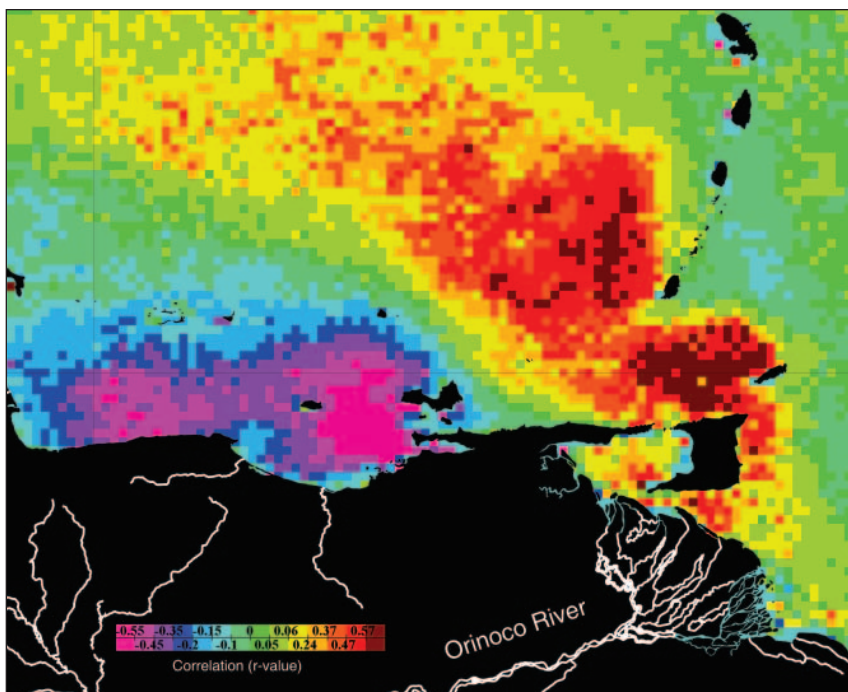


Figure 2. Spatially mapped correlation coefficients between the monthly climate of Orinoco River (Venezuela) discharge and the ocean color (reciprocal of monthly averaged water-leaving radiance at 412 nanometers, from SeaWiFS [Sea-viewing Wide Field-of-view Sensor] data) between November 1997 and October 2002. The region of high positive correlation shows that the hydrological regime of the Orinoco is in phase with the ocean color field, suggesting a vast region of fluvial influence of the Orinoco's highly colored waters. The adjacent region of negative correlation west of the plume is an area where upwelling-induced phytoplankton blooms tend to be out of phase with the Orinoco discharge.

best studied over decadal time periods and large spatial areas (Kaiser 2001, Hobbie et al. 2003). The sites described in this article are national reserves, parks, or research areas from the Caribbean region that are described as vulnerable or heavily influenced by human activities. Ecological research at some of these sites has been performed on a regular basis since the 1970s. However, the long-term records of selected ecological processes for these sites are inadequate to quantitatively define the magnitude and direction of ecosystem change, which limits the development of appropriate coastal management plans.

The ocean ecosystem of the wider Caribbean region

The Caribbean Sea is considered the smallest ocean basin and classified as the second largest sea in the world (2,512,950 square kilometers [km²]) (figure 1; Dillon et al. 1987). Located in the Western Hemisphere between North and South America, the Caribbean Sea is bordered on the north and east by the West Indies archipelago, on the south by South America, and on the west by the Central American isthmus and the Yucatán Peninsula. All Central American countries except El Salvador have extensive coastal areas along the Caribbean Sea. Several oceanic islands are a major feature of the

Caribbean seascape, including Dominica, Martinique, and the Barbados on the eastern boundary; Cuba and Hispaniola (Haiti and the Dominican Republic) to the north; and Jamaica and the Cayman Islands to the northwest. Although south Florida is not geologically part of the Caribbean Sea, it is considered part of the region because of the strong oceanic connection downstream through east-west water circulation. The wider Caribbean region thus includes coastal regions in the Caribbean Sea proper and upstream areas in south Florida and the Yucatán Peninsula (including the Usumacinta–Terminos lagoon complex).

The Caribbean Sea includes four major basins, with approximately half of the water deeper than 3600 meters (m) (Richards and Bohnsack 1990). Many areas exceed 4000 m in depth, with the deepest region—in the Cayman Trench, located between Cuba and Jamaica—ranging from 7535 to 7686 m. Because of the active semi-independent movement of the Caribbean plate, there are earthquakes and volcanic activity throughout the region (Dillon et al. 1987). Seasonal variation in temperature is small, ranging from 25 degrees Celsius (°C) in the winter to 28°C in the summer. Ocean circulation in the region is strongly influenced by the trade winds that form westward patterns, causing upwelling along the South American continent. Water flows into the Caribbean Sea

mostly through the Grenada, St. Vincent, and St. Lucia passages in the southeast. The water continues westward as the Caribbean Current, the main surface circulation in the Caribbean Sea. The flow turns westward as it crosses the Cayman Basin, and it enters the Gulf of Mexico as a narrow boundary current through the Yucatán Straits, where it forms both the loop current in the Gulf of Mexico and the Gulf Stream south of Florida (Fratantoni 2001). The average flow of these currents is 24 million m³ per second, with near-surface velocities approaching 80 to 150 centimeters per second in the Yucatán Current (Coats 1992). This water circulation results in high connectivity among the different basins.

Vast regions of the Caribbean are influenced by river discharge. Mean discharge to the region that includes the coastal areas of Venezuela, Trinidad and Tobago, and Grenada (figure 2) is more than 2100 km³ per year (Fekete et al. 2002), but a significant volume of Amazon water is also delivered to the Caribbean via the North Brazilian Current (Hellweger and Gordon 2002). The two largest rivers of the region, the Orinoco (1103 km³ per year; figure 2) and the Magdalena (228 km³ per year; figure 3) (Restrepo and Kjerfve 2000), account for well over 60% of the fresh water discharged directly into

the Caribbean. The influence of the Orinoco River plume on the ecology and biogeochemistry of the western Caribbean extends to areas close to Puerto Rico and the Dominican Republic, again demonstrating the degree of connectivity in the Caribbean basin (Salisbury et al. 2001). These rivers represent point sources for large fluxes of dissolved and particulate constituents (figures 2, 3). These river constituents typically have dramatic effects on the primary productivity of coastal waters. Turbid conditions limiting productivity, with a zone of high productivity at the distal end of turbid plumes, have been reported by several investigators (Demaster et al. 1996).

Coastal ecosystems of the wider Caribbean region

Geomorphic features and geophysical energies of coastal settings (Thom 1982), along with regional climate, have been identified as environmental signatures that constrain the structure and function of tropical coastal ecosystems (Thom 1982, Twilley 1995). These environmental signatures have been used to generalize patterns across coastal geomorphological types, including reefs, lagoons, estuaries (drowned river valleys), and deltas (Downing et al. 1999). The vulnerability of different coastal ecosystems to human disturbance can be associated with these environmental signatures. The combination of geophysical processes (e.g., river discharge, wind, and water residence time) and biogeochemical properties of a coastal setting provides a way to summarize how stressors limit the structure and function of coastal ecosystems. For example, changes in light availability and nutrients are two key factors that determine both the type and the rate of primary production among four geomorphological types of coastal settings (figure 4).

Our approach provides a conceptual framework to generalize the impacts of land-use changes on ecosystem health across different coastal settings in the Caribbean basin. Ecosystem health is the condition in which “an ecosystem is active and maintains organization and autonomy over time and is resilient to stress” (Costanza 1992). To characterize environmental signatures, we considered 10 categories, including regional climate, geomorphological type, and anthropogenic characteristics (table 2). These categories have been recognized as forcing functions that regulate the structure and function of coastal ecosystems (Thom 1982, Twilley 1995). Values for each category are represented in nominal and ordinal scales, since information is lacking across most coastal settings (e.g., nutrient loading rates, sea-level rise). The ordinal scales are ranges of values using established classification systems. Another characteristic of each site is the

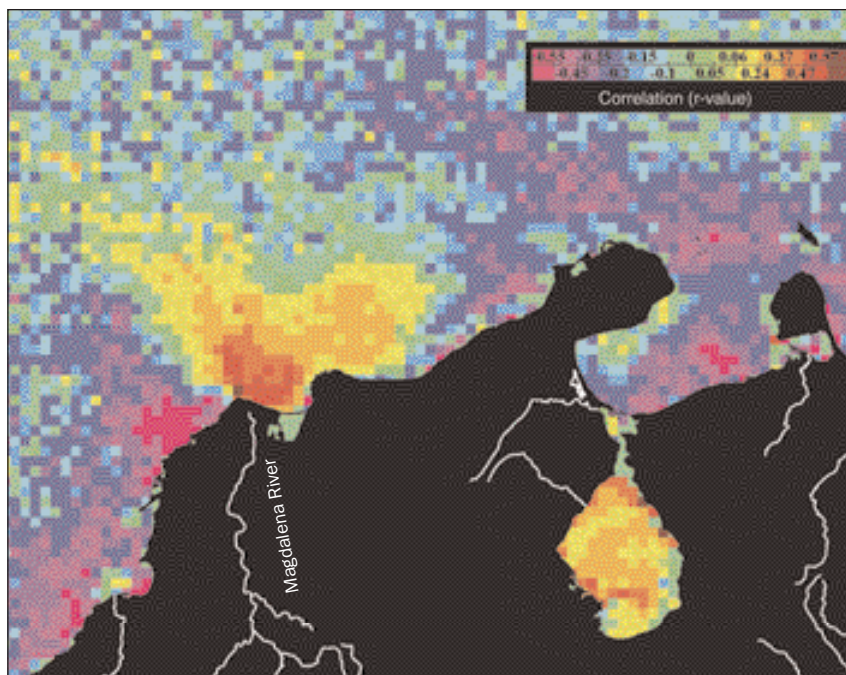


Figure 3. Spatially mapped correlation coefficients between the monthly climatology of Magdalena River (Caribbean coast of Colombia) discharge and the ocean color (monthly averaged water-leaving radiance at 555 nanometers (nm), from SeaWiFS [Sea-viewing Wide Field-of-view Sensor] data) between November 1997 and October 2002. The 555-nm band has been used as a proxy for light scattering by particles (sediment and detritus). The region of high positive correlation suggests that the Magdalena River is the source of a large sediment plume.

initial effort to establish long-term ecological research. The selected sites were grouped along this continuum of environmental signatures based on geomorphological type (figure 4; Twilley 1995, Downing et al. 1999). The main assumption of this framework is that the susceptibility of tropical coastal settings to eutrophication will vary along this continuum of environmental signatures.

Availability of nutrient and light resources, along with water residence time, defines environmental signatures from marine to river-dominated coastal settings (figure 4). The dual resource gradient (light and nutrients), along with the variance in salinity, determines the diversity of ecosystems in the coastal setting. The coastal seascape consists of reef, sea grass, and wetland ecosystems distributed across longitudinal and topographic gradients of any coastal setting. The longitudinal gradient in salinity occurs from tidal freshwater to euhaline environments. Within each of these salinity regimes, there are topographic gradients from submerged (subtidal) to emergent (intertidal and floodplain) zones. Emergent zones include fringe (edge of intertidal) to interior (supratidal) and floodplain regions. Reefs and sea grasses colonize the submerged zone, and wetlands (mangrove, marshes, and forested wetlands) colonize the fringe, interior, and floodplain regions of the emergent zone.

Table 2. Characteristics of the study sites.

Ecosystem	Freshwater inflow	Topographic relief	Nutrient flux	Mineralogy	Type of landscape	Precipitation-to-evapotranspiration ratio	Mean tidal range	Disturbance (hurricanes)	Susceptibility to sea-level rise	Landscape management
Everglades, Florida	Low to medium	Low	Low	Karstic	Continental	Medium	0.5	Medium	Medium	Restoration
Puerto Rico/wet	Medium (river)	High	Medium	Nonkarstic	Oceanic	Medium	0.5	High	Medium	
Puerto Rico/dry	Low	High	Low	Nonkarstic	Oceanic	Low	0.5	Medium	High	
San Juan, Venezuela	High (river)	Medium	High	Nonkarstic	Continental	High	3	Low	Low	
Morrocroy National Park, Venezuela	Low	Low	Low	Karstic	Continental	Medium	0.5	Low	High	Rehabilitation
Los Roques, Venezuela	Low	Low	Low	Karstic	Oceanic	Low	0.5	Low	High	
Ciénaga Grande, Colombia	High (river)	High	High	Nonkarstic	Continental	Low	0.5	Low	Medium	Rehabilitation
Bocas del Toro, Panama	Low	High	Low	Nonkarstic	Continental	High	0.25	Low ^a	Medium	
Twin Cays, Belize	Low	Low	Low	Karstic	Oceanic	Low	0.25	Medium	High	
Northern Belize wetland complex	Low to medium	Low	Low	Karstic	Continental	Medium	–	Medium	High	
Sian Ka'an, Mexico	High to medium	Low	Medium	Karstic	Continental	Low	0.5	Low	Low	
Celestun Lagoon, Mexico	Medium to high	Low	Low	Karstic	Continental	Medium	0.5	Medium	High	
Terminos lagoon	Medium to high	Low	High	Nonkarstic	Continental	Medium	0.5	Low	Medium	

a. Volcanic activity.

The coastal seascape can be described by the ratio of emergent to submerged area (wetland-to-water ratio). The relative distribution of reef–sea–grass–wetland ecosystems across a coastal seascape varies with the four geomorphological types used in this classification of coastal settings, which can be linked to specific combinations of geophysical energies. Reefs and lagoons are marine-dominated coastal settings, with coral reef and sea grass communities dominating the coastal seascape. In these coastal settings, the emergent zone is limited to the intertidal area, with a reduced wetland-to-water ratio. Light is plentiful in the submerged zone of this coastal setting, yet nutrients are low, resulting in oligotrophic conditions. In river-dominated coastal settings, coral reefs and sea grasses are less abundant in the submerged zone, and wetlands dominate the more extensive emergent zone. Depending on the degree of freshwater input and tidal range, the ratio of emergent to submerged zone increases in these coastal settings, as in a delta, for example.

Many of the sites we reviewed have more than one geomorphological type, with multiple gradients resulting in diverse combinations of coastal ecosystems (figure 4). For example, Terminos lagoon, in Mexico, is a delta-lagoon complex that has extensive marshes and mangroves in its river-dominated seascapes, in contrast with the extensive sea grasses in its marine-dominated regions. The environmental signature concept describes how each of these ecosystems in a coastal seascape has a characteristic structure and function that can be related to available resources (e.g., nutrients), regulators (e.g., salinity), and hydrologic gradients unique to a coastal setting.

Environmental signature of selected coastal settings

The environmental signature of a coastal (regional) setting is a combination of geomorphological type, geophysical energies, and levels of disturbance. There are conspicuous differences in topographic relief throughout the entire Caribbean region. Areas with average altitudes from 2000 to 3000 m above mean sea level (msl), associated with volcanic activity, can be found in Honduras, El Salvador, Costa Rica, Panama (e.g., Bocas del Toro; table 2), and the Lesser Antilles. The highest altitude adjacent to the coastal zone in the Caribbean, located in the Ciénaga Grande de Santa Marta deltaic region of Colombia, is 5775 m above msl. In contrast, lower altitudes (less than 500 m above msl) are geologically associated with extensive karstic topography, as in the Yucatán Peninsula (Celestun, Sian Ka'an), Belize (Twin Cays), and south Florida (the Everglades; table 2). Topographic relief classes were assigned to each site: low (e.g., the Everglades), medium (e.g., San Juan River), or high (e.g., Ciénaga Grande), depending on the major regional geological features. Four of the 13 sites are oceanic islands; two sites are on high islands and two on low islands.

The combination of regional climate and topographic features influences the amount of freshwater input at each site. Although the Caribbean coast of Colombia is arid, the Ciénaga Grande has a deltaic geomorphology because of the

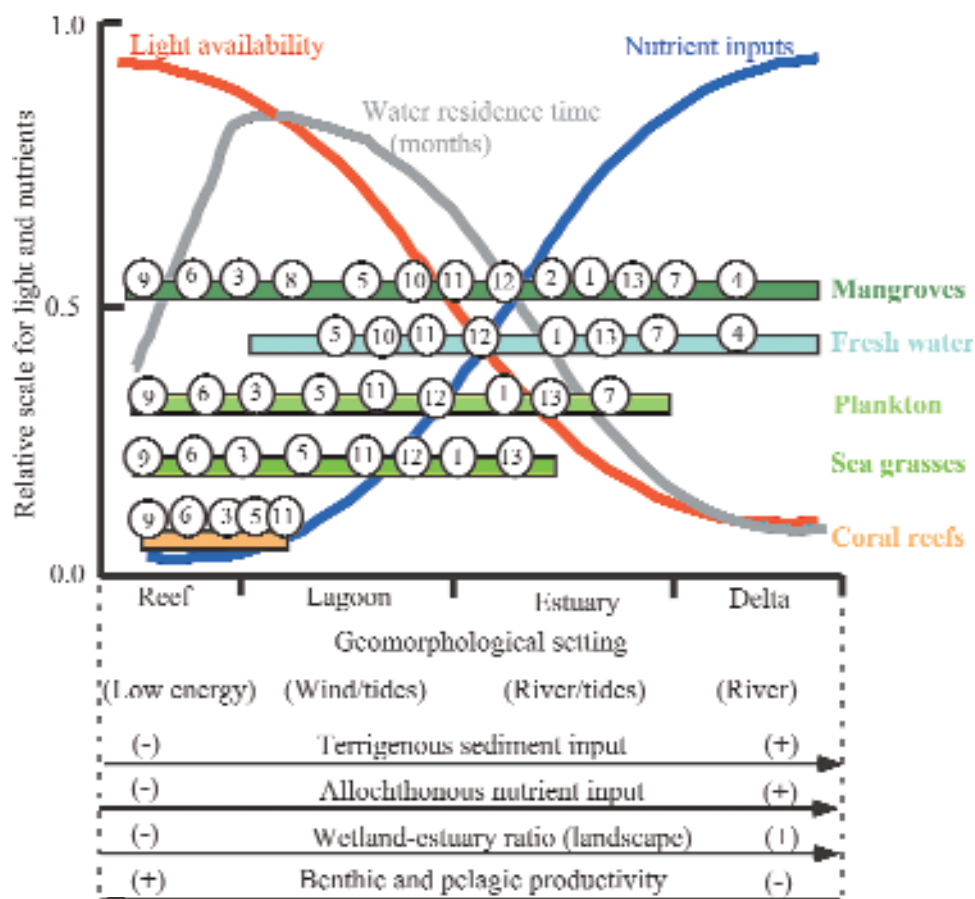


Figure 4. Conceptual framework of the interaction between the amount of light, nutrient inputs, and water residence time across different types of estuaries, based on geomorphology from carbonate reefs to river-dominated deltas. The horizontal arrows indicate an increase or decrease of sediment and nutrient inputs, wetland-to-estuary ratio, and benthic and pelagic productivity. The presence or absence of mangroves, sea grasses, and coral reefs in each coastal setting is indicated by the bars, as are the influences of fresh water and plankton productivity. Numbers representing study sites were placed along the bars depending on the dominant ecosystem found at each site: 1, Everglades, Florida; 2, Puerto Rico (wet); 3, Puerto Rico (dry); 4, San Juan, Venezuela; 5, Morrocoy National Park, Venezuela; 6, Los Roques, Venezuela; 7, Ciénaga Grande, Colombia; 8, Bocas del Toro, Panama; 9, Twin Cays, Belize; 10, northern Belize wetland complex; 11, Sian Ka'an, Mexico; 12, Celestun Lagoon, Mexico; 13, Terminos lagoon, Mexico. Modified from Downing and colleagues (1999).

Magdalena River, a large freshwater subsidy to the region. Arid regions of the Yucatán Peninsula receive extensive groundwater flow in the Sian Ka'an and Celestun Lagoons (Herrera-Silveira and Comin 2000). More moist regions include the San Juan River estuary in Venezuela, Bocas del Toro in Panama, Terminos lagoon in Mexico, and the Everglades watershed in Florida (table 2). Puerto Rico is a high island with extreme differences in precipitation, representing arid and moist sites at similar geographical locations. Although the tidal regime across sites is small (0.2–0.5 m, except in San Juan River estuary; table 2), water residence time differs among the sites depending on the magnitude of river discharge, as in the

Ciénaga Grande de Santa Marta, Colombia (7–11 days), and Celestun Lagoon, Mexico (25 days). We define a fertility gradient across these geomorphological types as associated with nutrient input, residence time, and light regime.

The frequency and magnitude of disturbance, both natural and human, are also important considerations in the environmental signature of a coastal setting. Hurricanes have a strong effect on the ecological conditions of the Caribbean region. Although hurricane impacts are generally greater in oceanic (e.g., Puerto Rico, Twin Cays, Belize) than in continental seascapes (e.g., San Juan, Venezuela; Sian Ka'an, Mexico; table 2), the latter can also receive considerable damage.

For example, Hurricane Andrew hit southern Florida in 1992, affecting extensive urban areas and mangrove wetlands (Smith et al. 1994). Hurricane Mitch, in 1998, was a category 5 storm when it hit coral reefs, mangrove forests, and urban centers in Honduras, Nicaragua, and Guatemala. Forecasting the condition of ecosystem functions, ecosystem services, and natural resource capital in the Caribbean region requires knowledge of large disturbances such as El Niño–Southern Oscillation (ENSO) events and hurricanes. These forcing functions have spatially specific effects on coastal settings, increasing the diversity in ecosystem structure and function across the coastal seascape. Since the 1970s, ENSO events have occurred more frequently and persisted longer (Trenberth and Hoar 1997). Temporal patterns in precipitation are strongly modulated by episodic events such as hurricanes and ENSO. Because these global phenomena are controlled by climate change, the frequent occurrence of extreme climate events in the Caribbean could be more relevant than the fluctuations of the mean climate (Stenseth et al. 2002).

Impacts of sea-level rise on coastal settings are better assessed using regional values rather than global averages (Church 2001). Most intertidal wetlands in south Florida and the Caribbean can survive the present regional rates of sea-level rise, which range from 1.2 to 2.3 millimeters per year. The sustainability of these intertidal wetlands relies on migrating inland to areas of decreasing tidal inundation along undeveloped shores. However, activities associated with urbanization, such as tourism, infrastructure, and agriculture, can remove supratidal regions, restricting the migration of intertidal wetlands in response to climate change. An increase in sea level alone would not be enough to “drown” coral reefs (Kleypas et al. 2001), but the combination of sea-level rise and decreased water quality (e.g., increase in nutrient enrichment and turbidity) would result in flooded coastlines that could affect many coral reefs and change reef distribution at local and regional scales. Thus, sea-level rise in combination with eutrophication and increasing sea surface temperatures has the potential to modify reef distribution not only in the Caribbean region but globally (Kleypas et al. 2001). Caribbean countries, like other small island and coastal areas, face difficult decisions in confronting the adverse effects of global climate change and associated sea-level rise. Consequently, the vulnerability of coastal resources and infrastructure to sea-level rise increases constantly, highlighting the urgent need for an integrated framework for coastal management (Twilley et al. 2001).

Ecological vulnerability across environmental signatures

The 13 sites in this overview illustrate the ecological vulnerability of the coral reef–sea-grass–wetland seascape across different environmental signatures in coastal settings. Areas with different levels of disturbance need to be included in ecosystem assessment to advance our understanding of the trajectories that ecosystems follow after major changes attributable to human effects, natural causes, and their

interaction (Vitousek et al. 1997). Our selected sites across the wider Caribbean include different degrees of human impact on the structure and function of ecosystems in diverse environmental signatures. The management variable (table 2) refers to projects that have been implemented to rehabilitate and restore coastal ecosystems at the coastal seascape level.

Coral reefs are one of the most conspicuous coastal ecosystems in the Caribbean Sea, where the second longest barrier reef in the world and largest in the Northern Hemisphere is located off the coast of Belize (Hughes 1994). Recent evaluations of the global decline in reef area describe the western Atlantic Ocean and the Caribbean Sea as the regions where the most serious losses are occurring (Gardner et al. 2003). The reefs of the Caribbean and adjacent coastal waters constitute about 12% of the global total and are major indicators of the environmental stress in the region (Wilkinson 2000). Degradation and destruction of reefs are caused by sedimentation, destructive fishing, poorly regulated mining and construction, and anthropogenic nutrient inputs (Szmant 2002). Current estimates indicate that 29% of the Caribbean reef areas are considered at high risk because of increased runoff and sedimentation caused by deforestation, nutrient contributions from hotel and shipping wastes, coastal construction, and mining.

Studies in the selected sites and throughout the Caribbean region have focused on monitoring changes in reef extension, in species composition, and in the frequency of events such as bleaching, herbivory, and invasion by fleshy macroalgae (Aronson et al. 2002). The sites with large areas of coral reef cover are Everglades National Park, Florida; Morrocoy National Park (Parque Nacional Morrocoy) and Los Roques, Venezuela; Bocas del Toro, Panama; Twin Cays, Belize; Celestun Lagoon, Mexico; and Sian Ka’an, Mexico (table 2).

Considerable efforts in the wider Caribbean have been dedicated to evaluating the damage caused by coral diseases such as white band, and by coral bleaching due to an increase of 1°C to 2°C in sea surface temperatures above mean monthly summer values (Skirving and Guinott 2001). A current paradigm suggests that a fixed bleaching temperature threshold of 1°C to 2°C above the present average sea temperature needs to be reevaluated, since a broad spectrum of responses indicates that the temperature threshold changes over time as a result of acclimation and evolution (Hughes et al. 2003). Current reports suggest a massive regionwide decline of corals across the Caribbean basin, with the “average hard coral cover on reefs being reduced by 80%, from about 50% to 10% cover, in three decades” (Gardner et al. 2003). Yet it is still not clear what the relative roles of climatic and local human factors are, and how they interact in determining the long-term trajectories of reef decline (Buddemeier et al. 2003).

Recent studies on species turnover in the Belize Barrier Reef have shown a significant shift of coral reef species over hundreds of square kilometers in less than a decade (Aronson et al. 2002). These results confirm the short temporal scale on which human activities affect coral reef habitats. For

example, Hughes (1994) discussed the role of overfishing and reduced herbivory as the main factors inducing dramatic shifts from coral-dominated to algae-dominated systems in Jamaica. According to new surveys, all of the classic reef zonation patterns found in Jamaica in the 1950s have disappeared. Documented structural and functional changes in Jamaican reefs illustrate how overfishing, herbivory, and large physical disturbances (e.g., hurricanes) interact to modify reef communities in the Caribbean region at the coastal seascape level. More recently, Lapointe (1997) argued that in addition to these causes, studies of macroalgal blooms need to evaluate how excess nutrient concentrations in water columns deteriorate reef areas. Documentation of nutrient enhancement in the Caribbean is scarce, despite the environmental stress caused by eutrophication (Aronson and Precht 2000). Because of the lack of long-term data on nutrient enrichment in coral reef habitats, controversies remain about the relative importance of eutrophication and herbivory in promoting macroalgae blooms in coral reefs (Hughes et al. 1999, Lapointe 1999, McCook 1999, Aronson and Precht 2000, Szmant 2002).

The shallow-water communities of Morrocoy National Park, Venezuela, provide a good example of the complexity involved in assessing the interaction of large-scale disturbances (human and natural), overfishing, herbivory, and eutrophication on coral reef habitats in the wider Caribbean (table 2). The 320-km² park consists of semienclosed, interconnected embayments (Bone et al. 1998). Early in 1996, mass mortalities were recorded for coral reefs (60%–90%), gastropods, sipunculans, polychaetes, and sponges, following unusually low temperatures apparently caused by upwelling of cold water along the Venezuelan coast (Laboy-Nieves et al. 2001). Evaluation of coral recovery 3 years after the disturbance shows that there are still large extensions of dead reefs and of reefs covered by algae and sand (Villamizar 2000).

The disturbance of reef communities associated with this upwelling event along the Venezuelan coast occurred along with increased human impacts in the region. These included urban and industrial development around the park, sewage inputs from tourism facilities, unregulated recreational and commercial fishing, and coral bleaching and other diseases (Villamizar 2000). These impacts, along with the large inputs of sediments, nutrients, and organic matter transported by rivers during the rainy season, all slowed the recovery of coral reefs. Sea temperature was probably the trigger that initiated the massive mortalities (Laboy-Nieves et al. 2001), but lower temperatures increased the chance of mortality for already stressed coral reef habitats and associated communities. Additional die-offs were observed at the end of 1996, when the highest precipitation in 28 years was registered. Low salinity and hypoxic conditions triggered mass mortalities of fishes, holothurians, sea urchins, and sea stars, along with a significant reduction in the area of sea grass (Laboy-Nieves et al. 2001). The high precipitation was apparently associated with the 1995–1996 ENSO, an event that further

confounded the identification of causes for the massive coral mortality in this park system.

Sea grasses are also affected by excessive nutrient inputs (Duarte 1995). Regional differences in nutrient availability determine the distribution of different sea grass species along salinity gradients (Fourqurean et al. 2001). High nutrient loading causes algal blooms, which increase turbidity and reduce the photosynthetic efficiency and growth of sea grasses. The excess nutrients also result in greater growth and production of epiphytes, to the extent of accelerating sea grass dieback. Phosphorus (P) has been identified as a limiting nutrient in karstic substrates, so an increase in this nutrient will certainly increase sea grass biomass in the short term (Jensen et al. 1998).

Some sea grass species have a narrow tolerance for salinity changes, which can trigger major shifts in species composition (Lirman and Cropper 2003). Organisms are affected more by extreme salinities during major disturbances than by values observed under average environmental conditions. Salinity in association with nutrient enrichment can also become a stressor when freshwater inputs are drastically reduced. For example, the mass mortality of sea grasses in Florida Bay has been attributed to long-term salinity stress caused by reduced freshwater flow. Moreover, studies show that salinity stress can exacerbate susceptibility to other factors (e.g., pathogens, temperature), leading to extensive die-offs. Studies in Florida Bay have been critical in understanding how changes in salinity and P limitation affect species composition and productivity patterns (Fourqurean et al. 1995). Florida Bay studies have also evaluated the physiological response of sea grasses to stress resulting from iron deficiency, low oxygen concentrations, and drastic reductions in salinity. Computer simulation models for sea grasses are being developed for Florida Bay; they incorporate different hierarchical levels, from physiological to spatially explicit seascape processes (Fong et al. 1997).

The high biological diversity found in the coral reefs of the Caribbean Sea is strongly influenced by the presence of mangrove forests and sea grasses. These three ecosystems form strongly coupled habitat complexes, which are not completely understood, along the coastal seascape (Twilley et al. 1998, Koch and Madden 2001, McKee et al. 2002). There is a continuum across these ecosystems in which complex nutrient exchanges define the spatial and temporal distribution of mangroves, sea grasses, and coral reefs. Nutrient availability is highly controlled by nutrient recycling in mangrove forests and sea grasses (Duarte 1995, Rivera-Monroy and Twilley 1996, Feller et al. 2003a). The resulting high rates of primary production and organic material production sustain complex trophic food chains. Therefore, negative impacts in one ecosystem can cascade across the coastal seascape, affecting other areas. For example, mangrove deforestation in the coastal zone can significantly reduce the productivity of sea grasses and coral reefs by causing excessive sediment loads that increase turbidity.

The total mangrove area for the wider Caribbean region is estimated at 25,882 km² (Spalding et al. 1997), representing about 50% of the total mangrove area in the Neotropics. The physiognomy of mangrove forests in the Caribbean region is diverse, from scrub forests (less than 1.5 m tall) in the interior of islands to well-developed forests (more than 30 m tall) in river-dominated coastal seascapes. These gradients provide insights into the multiple stressors that can affect mangrove forest growth. Mangrove forests growing under nutrient-limited conditions respond quickly to fertilization. Recent studies in karstic environments in the Caribbean (Twin Cays, Belize; table 2) have found that nitrogen (N) and P are not uniformly distributed within mangrove ecosystems (Feller et al. 2003b). At Twin Cays, both N and P enrichment significantly increased productivity along a tidal gradient; trees were generally P limited in the interior zones of the forest but N limited in the fringe. This response is associated with low P availability in carbonate-rich sediments. Nutrient-enrichment field experiments, like the one performed in Belize, are limited in the Caribbean, although it appears that mangrove forests in Bocas del Toro, Panama, are also prone to P limitation (Lovelock et al. 2004). Chen and Twilley (1999) showed how patterns of forest development in Shark River, Florida, differ along a fertility gradient defined by total P concentration. This fertility gradient is apparently caused by greater inputs of mineral material (enriched with P) at the mouth of the estuary, where mangrove trees grow significantly larger (more than 10 m tall) than at the head of the estuary (less than 5 m tall). The fact that the main P source at this site originates at the mouth of the estuary underscores the importance of nutrient sources for mangrove development.

Rehabilitation of ecosystems in the wider Caribbean region

A rehabilitation project in the Ciénaga Grande de Santa Marta, Colombia, and a restoration project in the Florida coastal Everglades are the largest such projects in the coastal Neotropics (table 2). The degradation of water quality, alteration of hydrological regime, and loss of species and habitat in both coastal regions are the main conditions that prompted the planning, development, and financial support of these projects. The Ciénaga Grande region provides a dramatic example of negative anthropogenic effects; the loss of an extensive mangrove area (about 350 km²) and the reduction or disappearance of important commercial fish stocks have increased the region's poverty and social unrest. Hydrological alteration in the Ciénaga Grande was the result of the construction of roads and levees in the 1950s to improve transportation and ranch farming. In the Everglades, an extensive canal system was developed in the 1940s to optimize water management for agriculture practices, urban development, and flood protection (Davis et al. 1994). Negative environmental impacts in the Everglades include massive sea grass die-offs, coral reef mortality, low water quality, noxious algae blooms, habitat fragmentation, and major changes in

vegetation distribution and diversity that have altered the density and spatial dispersion of wild and commercial animal species (Davis et al. 1994). Freshwater redirection is the main restoration measure in both the Ciénaga Grande and the Everglades, but the geomorphological differences between the two sites (figure 4) make the outcome of both projects comparatively uncertain. Because there have been no previous long-term projects of this type, it is unclear what the actual ecological response, and the effectiveness of restoration measures, will be.

The overall objective of the Ciénaga Grande rehabilitation project was to reduce soil salinity by reconnecting the floodplain to the Magdalena River through five dredged channels in areas of historical distributaries (Botero and Salzwedel 1999). All five planned channels were dredged by 1998, and mangrove recovery was apparent after the practical salinity level dropped from more than 100 to 40–50, a range normally observed in mangrove forests (Rivera-Monroy et al. 2004). In the Everglades, restoration aims to divert fresh water to allow a more natural overland flow (sheet flow) through the freshwater marshes of Taylor and Shark River sloughs to the estuaries and coastal zone. The full Everglades restoration plan will be completed over the next 10 to 30 years; some hydrologic structures have already been removed, and freshwater flow has been restored in some regions.

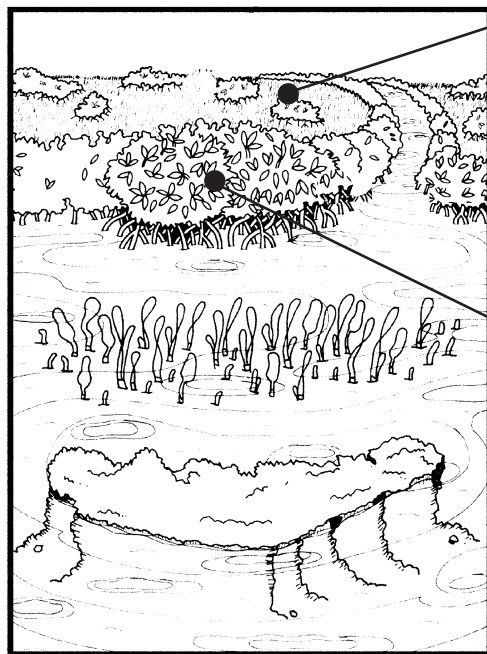
Research questions to test the environmental signature hypothesis

We propose a series of questions describing the vulnerability of coastal ecosystems to human and natural disturbance across the coral reef–sea-grass–wetland coastal seascape, based on findings at each of our research sites (figure 5). The vulnerability of this coastal seascape depends on the environmental signatures of tropical coastal settings. These questions follow our main hypothesis that the susceptibility of tropical coastal systems to disturbance will vary the environmental signature of coastal settings. The questions are grouped by ecosystem to facilitate their location in our conceptual framework, but ecosystems should be viewed as closely interconnected to each other in a seascape. Figure 5 indicates the location of the ecosystems and illustrates their hydrologic connectivity. For example, sea grasses are absent on deltaic systems because of high sediment loads (figure 4). As mentioned above, the study sites listed in table 2 represent discrete points across the range of coastal settings, allowing an intersite comparison of factors that control nutrient cycling and primary productivity. Thus, multiple questions could be tested simultaneously at multiple sites, which represent a combination of environmental factors. Rather than trying to establish an exhaustive list of questions, we focused on the research problems that integrate different ecological processes at different temporal scales along an environmental signature, from uplands to oligotrophic coastal waters.

The general research questions that encompass the environmental signature concept are as follows:

- How do long-term changes in freshwater flow control the magnitude of nutrient and organic-matter inputs to the estuarine zone?
- How will human-induced changes in nutrient enrichment, together with these changes in hydrology, affect patterns and magnitudes of primary and secondary production in diverse types of coastal settings?
- How will these direct impacts by cultural eutrophication interact with long-term changes in climate drivers (sea-level rise, hurricanes, fires) to modify ecological patterns and processes across different coastal settings?

Any application of the approach and research agenda proposed here to carry on long-term ecological studies in the Caribbean will need to take into consideration the financial requirements of the study and the strong cultural and political differences among all nations forming the wider Caribbean region. One of the major impediments to reducing environmental degradation of the Caribbean Sea is the complex process needed to establish a regional management plan for marine resources. Richards and Bohnsack (1990) pointed out more than a decade ago that the real problem was the lack of coordinated support among the 36 to 40 Caribbean nations and territories for monitoring the rich and diverse ecosystems in the region. Some of the major impediments to such coordination are the wide

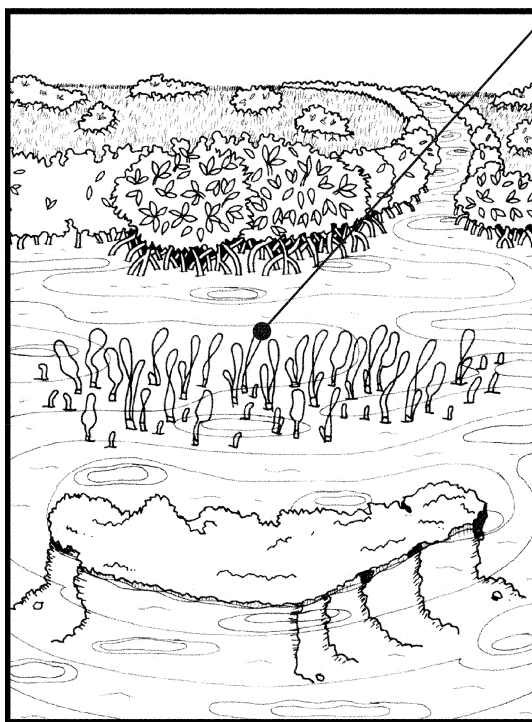


Freshwater and brackish marshes

1. How do differences in freshwater flow modify the spatial distribution of wetlands in the upper regions of the watershed?
2. What is the nutrient (phosphorus and nitrogen) removal capacity of wetlands around agricultural and urban areas?
3. What changes in species community composition and productivity occur in response to an increase in nutrient loads?
4. How does the quality and quantity of organic matter change along a hydrological gradient from freshwater marshes to mangrove forests?

Mangroves

1. Does aboveground (wood, litterfall) and belowground productivity change in response to differential nutrient enrichment (phosphorus versus nitrogen)?
2. Are mangrove species-specific growth rates modified by changes in hydroperiod and along salinity gradients, and what physiological mechanisms are developed or optimized to maintain these growth rates?
3. How fast are productivity and nutrient flux patterns within mangrove forests reestablished after major human (e.g., freshwater diversions) and natural (e.g., hurricanes) disturbances?
4. Does the relative importance of organic matter exported from mangrove forests as a major food source to sustain secondary production vary across geomorphological settings?
5. How do accretion and elevation rates in mangrove forests vary in response to change in sea-level rise across the Caribbean?



Sea grasses

1. What is the minimum nutrient loading rate that triggers the replacement of sea grass-dominated systems with phytoplankton-dominated systems? Is the magnitude of this rate similar across different geomorphological settings?
2. How are the growth and reproduction rates of sea grass modified as nutrient availability increases? Are species-specific responses related to site-specific hydrological and salinity regimes?
3. What is the role of the interaction between sediment oxygen concentrations and nutrient availability in controlling the spatial distribution and mortality of sea grass?
4. How are the growth rate and spatial distribution of sea grass affected when mangrove forests are removed?
5. How fast do sea grasses recover after major natural (hurricanes) and human (nutrient enrichment) disturbances?

cultural, educational, and economic differences among these countries. Of particular importance are the diverse management policies (or complete lack thereof) that each country has developed, based on economic priorities that do not embrace sustainable development.

One of the major priorities for sustainable management of the rich diversity of ecosystems in the wider Caribbean is to develop cost-effective research programs addressing common management issues in different locations. Cross-domain approaches and collaborations could foster the development of analytical and experimental tools to address common environmental problems in the region. The approach and research agenda

Figure 5. Proposed research questions along an upstream-downstream salinity gradient encompassing marshes, mangroves, sea grasses, and coral reefs.
(continued on next page)

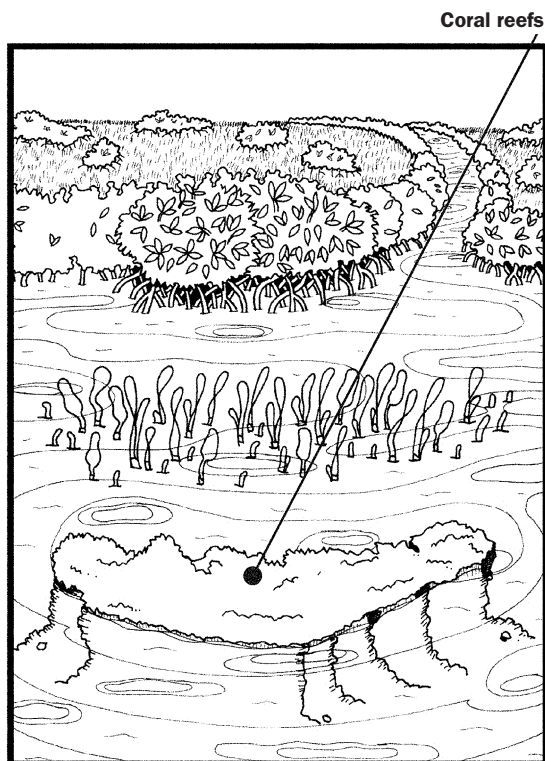


Figure 5. (continued)

presented in this article aim to strengthen research initiatives already present in the region, such as CARICOMP. We envision our research questions as a template to organize and synthesize current ecological information and design system-level ecological research in the long term. Accomplishing these tasks will require the active involvement of organizations such as the International Long Term Ecological Research (ILTER) network. The ILTER network can help to consolidate and organize regional research efforts with collaboration and support from the US LTER program, in addition to other international organizations (e.g., UNESCO's MAB [Man and the Biosphere] Programme or the LOICZ [Land-Ocean Interactions in the Coastal Zone] Project).

Future strategies to advance research on the coastal and oceanic resources of the Caribbean region will need the active participation of scientists, not only in posing ecologically relevant questions but also in designing multi- and interdisciplinary studies in which political and social issues are major components (Balmford et al. 2002). This is particularly true given the diverse geopolitical borders and economic importance of the region. We believe that because of the economic value, large-scale interconnectivity, and complexity of the ecological processes in the wider Caribbean region, finding solutions to the area's environmental problems within the next 10 to 15 years represents a major challenge to estuarine and coastal science.

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1. Can a significant increase in nutrient (phosphorus and nitrogen) loading into coastal areas with extensive coral reefs lead to coral mortality because of excessive macroalgal growth?
2. What is the interactive role of nutrient flux increases (phosphorus and nitrogen) and herbivory in maintaining coral reef areas and reducing macroalgal colonization?
3. What is the effect of high sediment load in controlling herbivory and macroalgal abundance in coral reefs?
4. How fast can coral reefs recover from large-scale (e.g., hurricanes, sedimentation) and local (e.g., coral bleaching) disturbances? And how do human impacts affect the rate of recovery?
5. Are there significant long-term differences in nutrient loading in coral reef areas across the Caribbean?

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References cited

- Aronson RB, Precht WF. 2000. Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. *Limnology and Oceanography* 45: 251–255.
- Aronson RB, Macintyre IG, Precht WF, Murdoch TJT, Wapnick CM. 2002. The expanding scale of species turnover events on coral reefs in Belize. *Ecological Monographs* 72: 233–249.

- Atwood DK, Burton FJ, Corredor JE, Harvey GR, Mata-Jimenez AJ, Vasquez-Botello A, Wade BA. 1987. Cooperative coastal ecology at Caribbean Marine Laboratories. *Oceanus* 30: 25–32.
- Balmford A, et al. 2002. Economic reasons for conserving wild nature. *Science* 297: 950–953.
- Bone D, Perez D, Villamizar A, Penchaszadeh PE. 1998. Parque Nacional Morrocoy, Venezuela. Pages 151–159 in B. Kjerfve, ed. CARICOMP—Caribbean Coral Reef, Seagrass and Mangrove Sites. Paris: United Nations Educational, Scientific and Cultural Organization.
- Botero L, Salzwedel H. 1999. Rehabilitation of the Ciénaga Grande de Santa Marta, a mangrove-estuarine system in the Caribbean coast of Colombia. *Ocean and Coastal Management* 42: 243–256.
- Brooks T, Smith ML. 2001. Caribbean catastrophes. *Science* 294: 1469–1471.
- Buddemeier RW, Ware JR, Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR. 2003. Coral reef decline in the Caribbean. *Science* 302: 391–393.
- Chen R, Twilley RR. 1999. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida. *Estuaries* 22: 955–970.
- Church JA. 2001. Climate change: How fast are sea levels rising? *Science* 294: 802–803.
- [CIA] US Central Intelligence Agency. 2004. The World Factbook. (25 July 2004; www.cia.gov/cia/publications/factbook/)
- Coats DA. 1992. The Loop Current. Chapter 6 in Milliman JD, Imamura E, eds. *Physical Oceanography of the U.S. Atlantic and Eastern Gulf of Mexico*. Herndon (VA): US Department of the Interior.
- Costanza R. 1992. Toward an operational definition of ecosystem health. Pages 239–256 in Costanza R, Norton BG, Haskell BD, eds. *Ecosystem Health: New Goals for Environmental Management*. Washington (DC): Island Press.
- Davis SM, Gunderson LH, Park WA, Richardson JR, Mattson JE. 1994. Landscape dimension, composition, and function in a changing Everglades ecosystem. Pages 419–444 in Davis SM, Ogdin JC, eds. *Everglades: The Ecosystem and Its Restoration*. Delray Beach (FL): St. Lucie Press.
- Demaster DJ, Smith WOJ, Nelson DM, Aller JY. 1996. Biogeochemical processes in Amazon shelf waters: Chemical distributions and uptake rates of silicon, carbon and nitrogen. *Continental Shelf Research* 16: 617–628.
- Dillon WP, Edgar NT, Scanlon KM, Klitgord KD. 1987. Geology of the Caribbean. *Oceanus* 30: 42–52.
- Downing JA, et al. 1999. The impact of accelerating land-use change on the N-cycle of tropical aquatic ecosystems: Current conditions and projected changes. *Biogeochemistry* 46: 109–148.
- Duarte CM. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41: 87–112.
- Fekete BM, Vörösmarty CJ, Grabs W. 2002. High-resolution fields of global runoff combining observed river discharge and simulated water balances. *Global Biogeochemical Cycles* 16 (3): 1042.
- Feller IC, Whigham DF, McKee KL, Lovelock CE. 2003a. Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. *Oecologia* 134: 405–414.
- Feller IC, McKee KL, Whigham DF, O'Neill JP. 2003b. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry* 62: 145–175.
- Fong P, Jacobson ME, Mescher MC, Lirman D, Harwell MC. 1997. Investigating the management potential of a seagrass model through sensitivity analysis and experiments. *Ecological Applications* 7: 300–315.
- Fourqurean JW, Powell GVN, Kenworthy WJ, Zieman JC. 1995. The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos* 72: 349–358.
- Fourqurean JW, Willis A, Rose CD, Rutten LM. 2001. Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Marine Biology* 138: 341–354.
- Fratantoni DM. 2001. North Atlantic surface circulation during the 1990's observed with satellite-tracked drifters. *Journal of Geophysical Research* 106: 22067–22093.
- Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR. 2003. Long-term region-wide declines in Caribbean corals. *Science* 301: 958–960.
- Harvell CD, et al. 1999. Emerging marine diseases—climate links and anthropogenic factors. *Science* 285: 1505–1510.
- Hellweger FL, Gordon AL. 2002. Tracing Amazon River water into the Caribbean Sea. *Journal of Marine Research* 60: 537–549.
- Herrera-Silveira JA, Comin FA. 2000. An introductory account of the types of aquatic ecosystems of Yucatán Peninsula (SE Mexico). Pages 213–227 in Munawar M, Lawrence SG, Munawar IF, Malley DF, eds. *Aquatic Ecosystems of Mexico: Status and Scope*. Leiden (The Netherlands): Backhuys.
- Hobbie JE, Carpenter SE, Grimm NB, Gosz JR, Seastedt TR. 2003. The US Long Term Ecological Research program. *BioScience* 53: 21–32.
- Hughes T, Szmant AM, Steneck R, Carpenter R, Miller S. 1999. Algal blooms on coral reefs: What are the causes? *Limnology and Oceanography* 44: 1583–1586.
- Hughes TP. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547–1551.
- Hughes TP, et al. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 15: 929–933.
- Jackson JBC, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293: 629–638.
- Jensen HS, McGlathery KJ, Marino R, Howarth RW. 1998. Forms and availability of sediment phosphorus in carbonate sand of Bermuda seagrass beds. *Limnology and Oceanography* 43: 799–810.
- Kaiser J. 2001. An experiment for all seasons. *Science* 293: 624–627.
- Kleypas JA, Buddemeier RW, Gattuso JP. 2001. The future of coral reefs in an age of global change. *International Journal of Earth Sciences* 90: 426–437.
- Koch MS, Madden CJ. 2001. Patterns of primary production and nutrient availability in a Bahamas lagoon with fringing mangroves. *Marine Ecology Progress Series* 219: 109–119.
- Laboy-Nieves EN, Klein E, Conde JE, Losada F, Cruz JJ, Bone D. 2001. Mass mortality of tropical marine communities in Morrocoy, Venezuela. *Bulletin of Marine Science* 68: 163–179.
- Lapointe BE. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography* 42: 1119–1131.
- . 1999. Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs. *Limnology and Oceanography* 44: 1586–1592.
- Lessios HA. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annual Review of Ecology and Systematics* 19: 371–393.
- Lirman D, Cropper WP. 2003. The influence of salinity on seagrass growth, survivorship, and distribution within Biscayne Bay, Florida: Field, experimental, and modeling studies. *Estuaries* 26: 131–141.
- Loreau M, et al. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294: 804–808.
- Lovelock CE, Feller IC, McKee KL, Engelbrecht BMJ, Ball MC. 2004. The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. *Functional Ecology* 18: 25–33.
- McCook LJ. 1999. Macroalgae, nutrients and phase shifts on coral reefs: Scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18: 357–367.
- McKee KL, Feller IC, Popp M, Wanek W. 2002. Mangrove isotopic ($\delta N-15$ and $\delta C-13$) fractionation across a nitrogen vs. phosphorus limitation gradient. *Ecology* 83: 1065–1075.
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Ogdin JC. 1987. Cooperative coastal ecology at Caribbean marine laboratories. *Oceanus* 30: 9–15.
- . 1997. Marine managers look upstream for connections. *Science* 278: 1414–1415.
- Restrepo J, Kjerfve B. 2000. Magdalena River: Interannual variability (1975–1995) and revised water discharge and sediment load estimates. *Journal of Hydrology* 235: 137–149.

- Richards WJ, Bohnsack JA. 1990. The Caribbean Sea: A large marine ecosystem in crisis. Pages 44–53 in Sherman K, Alexander LM, Gold BD, eds. *Large Marine Ecosystems: Patterns, Processes, and Yields*. Washington (DC): American Association for the Advancement of Science.
- Rivera-Monroy VH, Twilley RR. 1996. The relative role of denitrification and immobilization in the fate of inorganic nitrogen in mangrove sediments. *Limnology and Oceanography* 41: 284–296.
- Rivera-Monroy VH, Twilley R, Medina E, Moser EB, Botero L, Francisco AM, Bullard E. 2004. Spatial variability of soil nutrients in disturbed riverine mangrove forests at different stages of regeneration in the San Juan River estuary, Venezuela. *Estuaries* 27: 44–57.
- Salisbury JE, Campbell JW, Meeker LD, Vörösmarty C. 2001. Ocean color and river data reveal fluvial influence in coastal waters. *Eos, Transactions of the American Geophysical Union* 82: 221–224.
- Skirving W, Guinott J. 2001. The sea surface temperature story on the Great Barrier Reef during the coral bleaching event of 1998. Page 350 in Wolanski E, ed. *Oceanographic Processes of Coral Reefs: Physical and Biological Links in the Great Barrier Reef*. Boca Raton (FL): CRC Press.
- Smith TJ III, Robblee MB, Wanless HR, Doyle TW. 1994. Mangroves, hurricanes, and lightning strikes. *BioScience* 44: 256–262.
- Solow AR. 1995. Estimating biodiversity: Calculating unseen richness. *Oceanus* 38 (2): 9–10.
- Spalding M, Blasco F, Field C. 1997. *World Mangrove Atlas*. Okinawa (Japan): International Society for Mangrove Ecosystems.
- Stenseth NC, Mysterud A, Ottersen C, Hurrell JW, Chan KS, Lima M. 2002. Ecological effects of climate fluctuations. *Science* 297: 1292–1296.
- Szmant AM. 2002. Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? *Estuaries* 25: 743–766.
- Thom BG. 1982. Mangrove ecology: A geomorphological perspective. Pages 3–17 in Clough BF, ed. *Mangrove Ecosystems in Australia: Structure, Function, and Management*. Canberra: Australian National University Press.
- Trenberth KE, Hoar TJ. 1997. El Niño and climate change. *Geophysical Research Letters* 24: 3057–3060.
- Twilley RR. 1995. Properties of mangrove ecosystems and their relation to the energy signature of coastal environments. Pages 43–62 in Hall CAS, ed. *Maximum Power*. Boulder: University Press of Colorado.
- Twilley RR, Rivera-Monroy VH, Chen R, Botero L. 1998. Adapting an ecological mangrove model to simulate trajectories in restoration ecology. *Marine Pollution Bulletin* 37: 404–419.
- Twilley R, Barron EJ, Gholtz HL, Harwell MA, Miller RL, Reed DJ, Roser JB, Siemann EH, Wetzel RG, Zimmerman RJ. 2001. *Confronting Climate Change in the Gulf Coast Region*. Cambridge (MA): Union of Concerned Scientists.
- Villamizar E. 2000. Estructura de una comunidad arrecifal en Falcon, Venezuela, antes y despues de una mortalidad masiva. *Revista de Biología Tropical* 47: 19–30.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997. Human domination of Earth's ecosystems. *Science* 277: 494–499.
- Wilkinson C. 2000. *Status of Coral Reefs of the World: 2000*. Townsville (Australia): Australian Institute of Marine Science.
- [WTTC] World Travel and Tourism Council. 2003. *Caribbean Travel and Tourism: A World of Opportunity*. London: WTTC.