



Impacts of Hurricane Mitch on Seagrass Beds and Associated Shallow Reef Communities along the Caribbean Coast of Honduras and Guatemala

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Executive Summary

Seagrass meadows and shallow reef communities in the Caribbean Sea were evaluated to assess impacts from Hurricane Mitch (October 26 - November 5, 1998). Sites in Honduras and Guatemala were established along an impact gradient (high, medium, and low) for each of two disturbance types (wind and sediment). At each of the six sites, two transects were established perpendicular to the shoreline to determine vegetation cover and community composition. Duplicate cores were collected along each transect to determine sediment stratigraphy and aboveground and belowground biomass. In addition, short shoots of *Thalassia testudinum*, the dominant seagrass species at all sites, were collected, and the distance between leaf scars (plastochrone interval, or PI) was measured to reconstruct the growth history and shoot chronology at each site.

Study sites were selected based on initial aerial and ground surveys conducted in December 1998, July 1999, and December 1999. Factors considered in site selection included geographical proximity to known storm track and associated areas of high winds, rainfall, and runoff; presence of seagrass beds; and observed damages to adjacent mangrove or other forested communities. The six sites and their associated predicted impact types and levels were distributed as follows: Guanaja, Honduras, north shore (wind, high impact); Roatan, Honduras, north shore (wind, intermediate impact); Roatan, Honduras, south shore (wind, low impact); Punta Manabique, Guatemala (sediment, high impact); Cayos Cochinos, Honduras (sediment, intermediate impact); and Bahia la Graciosa (sediment, low impact). Collection of field data for the six sites occurred in January 2001 and August 2001.

Transects and sediment stratigraphy did not show evidence of seagrass burial or large-scale destruction as a result of hurricane passage, although there was evidence of deposition at the sediment high-impact site, Punta Manabique. *Thalassia testudinum* was the dominant seagrass species on all transects with coverage greater than 50% at the wind-impacted sites. Other species present included two additional seagrass species, five macroalgae and numerous hard corals and soft corals. *Thalassia* biomass and presence of other species in the bottom community, especially at the island sites, was fairly typical for Caribbean seagrass meadows. Of the 10 response variables that we measured at the 6 sites, none precisely followed patterns that we predicted based on hurricane impacts, though some differences observed might have been hurricane-related. In general, seagrass beds and bottom communities were largely buffered from significant storm impacts by the water column.

Guanaja, the site that was impacted by the strongest winds from Mitch and where mangrove communities were completely destroyed by the storm, had high species richness and high to average abundance of *Thalassia testudinum*. Guanaja was also the only site that showed an increase in growth in the year immediately following Mitch, but the growth rate had been higher three years before the hurricane. Punta Manabique, the site that we predicted to have a high degree of sediment impact from Mitch, had only a patchy distribution of *Thalassia* and low species richness, but belowground biomass there was higher than at other sites. Seagrasses at Punta Manabique appeared to be subjected to substrate movements and frequent burial by sandy sediments. This was the only site to show a steady increase in growth rate over four years, but there was no change from the year immediately preceding to the year immediately following Mitch. The high growth rate and belowground biomass for this site, therefore, may be the result of frequent partial burial of leaf-producing rhizomes, but this is probably an ongoing phenomenon and may not be associated with Hurricane Mitch.

From our general observations, we noted other evidence of changes that may be associated with Hurricane Mitch, but most of the changes appeared to have been relatively small. At the site in Guanaja, Honduras, an area approximately 3 m from the adjacent mangrove forest appeared to have been scoured, as evidenced by increased water depth and a lack of seagrasses. On the northern shoreline of Roatan, Honduras, a thin layer of calcareous algae (*Halimeda* spp.) plates may have been deposited by the storm. In eastern Guatemala, the shoreline on the western end of Punta Manabique was reported to have eroded approximately 30 m landward because of the storm. At Cayos Cochinos, Honduras, 3-4 m of beach also appeared to have eroded recently, perhaps during Mitch; at this location, the opportunistic seagrass *Halodule wrightii* had recently become established. In general, the seagrass communities that were examined appeared healthy and to have received little significant alteration because of Hurricane Mitch.

Background

Seagrasses are highly productive flowering plants that often form vast meadows over shallow, unconsolidated sediments in coastal areas. As one of the most important aquatic biotopes (Vicente, 1992; Connolly, 1994; Heck and others, 1997; Michot, 1997; Arrivillaga and Baltz, 1999a; Michot, 2000), seagrasses influence coastal processes and are of great importance to humans. They significantly modify the physical, chemical, and sediment properties of coastal areas and provide nursery habitats that sustain coastal fishery resources. Additionally, seagrass meadows serve as habitat for numerous marine invertebrates and as foraging grounds for fishes, birds, and endangered marine mammals.

The high rates of primary productivity and growth of seagrasses are comparable and/or often exceed that of terrestrial agricultural crops. Moreover, because of their high standing crop and the fact that few organisms feed directly on them, seagrasses produce large amounts of dissolved and particulate detritus, which plays a major role in coastal trophic dynamics. The surface of seagrass leaves and their erect shoots allow for the attachment of epibiotic organisms. They also stabilize their habitat by slowing water currents, promoting sedimentation, and reducing resuspension of both inorganic and organic materials. The structurally complex water column, which is provided by their dense leaf baffle, forms shelter for an extremely diverse fauna of all trophic levels. Additionally, the leaf baffle generates and entrains autochthonous as well as allochthonous organic material, creating an active environment for decomposition and nutrient cycling (Phillips, 1992).

The effects of hurricanes on seagrass meadows have not been widely studied. The general effects of perturbation to seagrass meadows were discussed by Clarke and Kirkman (1989) and Short and Neckles (1999). Hurricanes can affect seagrass beds in several ways. Increased turbulence associated with waves and currents generated by hurricane-force winds can result in physical tearing, stripping, and breakage of plant leaves and shoots. Scouring of bottom sediments and removal of the associated seagrasses and other organisms can occur, especially near reefs, shorelines, or other elevational features. Sediments in the water column can be redistributed by the storm and then deposited on top of seagrass beds, resulting in partial or complete burial. Additional sediments eroded from adjacent beaches and other landforms can be washed into the seagrass meadow and cause burial and changes in substrate quality, as shown in Chandeleur Sound, Louisiana, by Michot and others (1999). And lastly, increased overland precipitation associated with hurricanes cause flooding and increased runoff, resulting in the

deposition of huge amounts of riverine sediments into bays, estuaries, and adjacent marine systems.

Following Hurricane Gilbert (September 1988), Marba and others (1994) studied its effects on the *Thalassia* meadows of the Caribbean coast of Yucatan, Mexico. They found differences in internodal lengths (plastochrone interval, or PI) that were attributable to the storm's impact on the seagrass beds in terms of increased sediment deposition. Cabello-Pasini and others (2002) found that *Zostera marina* (eelgrass) meadows on the Pacific coast of Mexico were significantly reduced by light limitation that resulted from storm-induced resuspension of bottom sediments. Hurricane impacts to seagrass beds have also been shown to have occurred in Guadeloupe and Puerto Rico (Bouchon and others, 1991; Rodriguez and others, 1994; Salazar-Vallejo, 2002). By contrast, Posey and Alphin (2002) found that sedimentation from three hurricanes had little effect on offshore benthic communities on the Atlantic coast of North Carolina's Outer Banks.

Extensive beds of *Thalassia testudinum* (turtlegrass) and *Syringodium filiforme* (manateegrass) (family Hydrocharitaceae) exist along the Caribbean coast of Central America, especially along the Bay Islands of Honduras and the Bahia de Amatique of Guatemala (Hanlon and Voss, 1975; Arrivillaga and Baltz, 1999; Heyman and Kjerfve, 2001). In order to maintain their many functions, it is critical that seagrass beds remain healthy (Shrader-Frechette, 1994) and maintain desirable vital signs in order to handle environmental stress and restore equilibrium following perturbations. Techniques for the evaluation of seagrass growth dynamics and age structure (Zieman, 1974; Duarte, 1994; Durako, 1994) can be used to evaluate turtlegrass (*Thalassia testudinum*) ecology, its responses to perturbations, and its population's status and trends. Also, analysis of the age structure of a seagrass population, through the examination of plastochrone intervals (Arrivillaga and Baltz, 1999b), can be used to determine whether the population is expanding, declining, or in equilibrium.

The objective of our study was to evaluate the effects of Hurricane Mitch (October-November 1998) on shallow water, live-bottom marine communities. To accomplish this, we measured species distribution, abundance, biomass and demography of selected seagrass beds along the Caribbean coast of Honduras and Guatemala. We used data from transects, biomass cores, and sediment cores. Also, shoots of *Thalassia testudinum* were collected and analyzed in the laboratory for shoot age by plastochrone interval (PI) measurement.

Methodology

Site Selection

Potential study sites were selected during initial air and ground surveys conducted in December 1998, July 1999, and December 1999. Based on these initial surveys, we hypothesized that damages to bottom communities from Hurricane Mitch may result from disturbance caused by hurricane-force winds above the water surface or from sedimentation effects within the water column. Sites within the path of the hurricane and near the eye would experience high winds and the associated storm surge, increased wave energy, and perhaps movement and redistribution of bottom sediments. Sites that may have been too far from the storm's path to experience high winds could still be affected by the redistribution of sediments in the water column from the high precipitation on the mainland and its associated flooding, increased river stages, and increased runoff into the sea. We devised a sampling scheme that called for establishment of sites in areas subjected to high winds or high sediment loads from

Mitch. For each high impact site we would select a nearby reference site that should have had very little impact from winds or sediments, as well as a third site subjected to intermediate impact levels. Thus our plan was to select six sites in areas known to have had seagrass meadows prior to the storm. Three sites would represent high, medium, and low impacts from winds, and three would represent high, medium, and low impacts from sediments. We selected sites in conjunction with our colleagues studying storm effects to mangrove communities (see Cahoon and Hensel, 2002; Cahoon and others, 2002; Hensel and Profitt, 2002; McKee and McGinnis, 2002).

Wind-effect sites were selected based on known storm path and wind data and on the level of damage observed to mangrove communities adjacent to seagrass beds. Hurricane Mitch was strongest and had its highest winds (in excess of 290 km/h (180 mph)) when the eye was located about 119 km northeast of the island of Guanaja, Honduras (fig. 1), on 27 October 1998. We estimated (Doyle and others 2002) that winds on the island of Guanaja peaked at 255 km/h (159 mph) during Mitch's passage over the island. Our initial survey revealed several mangrove stands on Guanaja in which all trees were killed. We selected a site near the village of Mangrove Bight, on the north shoreline of the island (plate 1), where winds and waves from the counterclockwise rotation associated with Hurricane Mitch would have been strongest and from the north. A narrow, low-lying portion of the island of Roatan about 50 km west of Guanaja (fig. 1) was selected as a reference site for Guanaja. The north side of Roatan, subjected to higher winds and waves from Mitch's northerly winds, had some dead mangroves but most trees survived the storm (plate 2); this site was selected as our intermediate wind-impacted site. The south side of Roatan, largely protected from Mitch's northerly winds, had very few dead mangroves (plate 2); we used this site as our low-impact reference site. The three wind-impacted sites were sampled in January of the year 2000.

Sedimentation-effect sites were selected based on proximity to riverine sediment sources and on our initial examination of shoreline sediment deposits, vegetation, and mangrove communities. Punta Manabique, Guatemala (fig. 1), was selected as the high-impact sediment site. This site represented the closest seagrass bed to the Caribbean shoreline for the entire north coast of Guatemala and Honduras. Extremely high amounts of precipitation on the mainland of Honduras and Guatemala (>60 cm in some locations during Hurricane Mitch) resulted in record sediment loads being deposited into the Caribbean from all rivers along the northern shoreline of those two countries. We know of no extant seagrass beds along the north-facing shoreline, probably due to the high turbidity and wave energy. Seagrass meadows and coral reefs were reported to have occurred at Punta Sal, Honduras (Heyman and Kjerfve, 2001), but we learned from local biologists that these communities disappeared prior to Hurricane Mitch. During our aerial surveys we observed areas of dark substrate in shallow water along the north-facing shoreline of Punta Manabique, Guatemala. When we investigated from the ground, however, we were unable to verify the presence of seagrasses, and we concluded that what we had seen from the air were probably algal beds. At Punta Manabique we were able to find patchy seagrass beds just a few hundred meters from the northern shoreline, but in an area that was somewhat protected by a peninsula (plate 3). Our initial inspection of those seagrass beds revealed partial burial at the base of the plants (plate 4). Bahia la Graciosa (fig. 1; plate 5) is a protected bay located about 10 km from Punta Manabique; we selected this bay as our low-impact reference site for Punta Manabique. Cayos Cochinos, Honduras (fig. 1; plates 6 and 7), was selected as the intermediate-impact site for sediment effects because it represented the closest seagrass beds to the Honduras coast and thus could potentially have been affected by sediment plumes carried

from the mainland just 25 km to the south (Ogden and Ogden, 1998). The three sediment-impacted sites were sampled in August of the year 2000.

Transect Establishment

At each of the six study sites, two seagrass transects were used to evaluate distribution and abundance of seagrasses and other organisms within each study site. They were in line with the landward research plots established by a mangrove research team; our seagrass transect numbers correspond to mangrove transect numbers (Cahoon and Hensel, 2002; Cahoon and others, 2002; Hensel and Profitt, 2002; McKee and McGinnis, 2002). Since there were three mangrove transects, and only two seagrass transects, per study site, our transect numbers were not always numbered consecutively. Our transects were oriented perpendicular to the shoreline.

Species Distribution and Abundance

Sample stations were spaced along the transect at 1-m intervals from the shoreline to 10 m out, then at 10-meter intervals until 50 m out from the shoreline. Beyond 50 m from shore, samples were taken at 50 m, 100 m, or 200 m as appropriate to obtain an adequate representation of samples along the length of the transect (table 1). A global positioning system device (GPS) was used to record the beginning and end point of each transect and to measure distances between sample stations. At each sample station, time, water depth, distance from shoreline, species present, and cover class (per m²) for each species was recorded (plate 7). Water depth was measured with a flexible tape, weighted with an approximately 5 kg steel reinforcing rod or with a bamboo pole marked with centimeter intervals. Depth was measured from the water surface and adjusted for tides, to give all depths from mean sea level (MSL). Water depths were measured to the nearest centimeter every 3 m until 50 m from shore, then every 50 m seaward to the fringing reefs. At Punta Manabique, the transects ended at 80 m, as depth increased rapidly after 80 m from shore. At Bahia la Graciosa, turbidity prevented visual estimates of bottom communities more than 100 m from shore; one transect was continued across the bay to record depths.

Percent cover by seagrasses and soft bottom communities (algae and soft corals), occurring in a 1 m² area surrounding the point of depth measurement, was estimated visually along each transect. Estimates of cover were rated as Class 1 (1-10%), Class 2 (15-40%), Class 3 (45 - 70%), or Class 4 (75-100%) for each organism noted within the m².

Coring Stations

Sediment and vegetation cores to sample biomass, sediment stratigraphy, and plastochrone intervals were taken along each transect (plate 8). We typically took four cores, two at 10 m and two at 50 m from the shoreline (table 1). We attempted to collect a minimum of 20 intact samples (short shoots) of the seagrass community. They were taken from within 5 m of the transect at each core sample station for analysis of shoot growth chronology.

Sediment and Vegetation Cores

Cores were taken from each transect with a 10 cm (4 inch) core sampler. The device was made with a 4-inch inside diameter PVC pipe with a cutting edge beveled on the outside surface of one end of the pipe. A cap was cemented onto the opposite end and a hole approximately 1.50 cm diameter was drilled into the center of the cap.

Specimens were obtained by forcing the beveled end of the core sampler through the seagrass community and as far as possible into the sediment, usually to approximately 40 cm beneath the substrate surface (Gallegos and others, 1993). A rubber stopper was then placed in the hole in the cap to prevent water from entering the core sampler when it was removed from the sediment. The core sampler and core were then pulled from the sediment and the stopper was removed, allowing the water to drain out. The intact sediment core, with associated seagrass community, was removed from the coring device and placed on a flat surface where photographs were taken and sediment characteristics were recorded (plate 9).

After sediment descriptions were completed, each core was then washed in a sieve bucket to separate sediment from plant material. Vegetation was thoroughly washed to remove sediment and detritus and then individually bagged. The bags of vegetation were transported back to the laboratory for additional analysis

Biomass

Seagrass samples were separated by species and then by plant components. Each sample was separated into aboveground (leaves) and belowground (horizontal and vertical rhizomes, roots, and leaf sheaths from beneath the surface) vegetation. The plant components collected at the Roatan-south, Roatan-north, and Guanaja study sites were processed for biomass at the field camp. Biomass was estimated by displacement volume. Each sample was placed and submerged in a 100 ml graduated cylinder containing a known volume of water. The total volume of water and plant components was determined, then the original volume of water was subtracted to determine the volume of the plant component. Plant volumes were subsequently converted to grams dry mass using a regression equation developed in another study using *Thalassia* specimens from Chandeleur Islands, Louisiana, USA (Michot and Rafferty, unpublished data, 2000). Short shoots were placed in 70% ethyl alcohol in a plastic bag, and retained for PI measurements; other plants parts were discarded.

Plant components collected from Punta Manabique and Bahia la Graciosa, Guatemala, and Cayos Cochinos, Honduras, were transported on ice from the field camp to the laboratory at the National Wetlands Research Center (NWRC), Lafayette, Louisiana, for further processing. The samples were placed into a drying oven at 60°C and dried to a constant mass.

Sediment Stratigraphy

The length of each core was measured to the nearest cm and photographed. Strata within each core were identified and described, and the depth (thickness) of each stratum was measured. Descriptions of strata included color and visual estimates of major substrate components. The major substrate components were: 1) organics -- partly decomposed peat-like remnants of vegetation; this material ranged from nearly intact mangrove roots to small fragments of vascular tissue; 2) sand -- quartz (siliceous, mineral) grains that appeared to be fine sands (0.10 mm - 0.25 mm; Carlisle and Collins, 2000); 3) carbonate -- fine, marl-like particles of calcium carbonate; 4) shell fragments -- pieces of broken calcium carbonate mollusk shells; 5) algal skeletons -- calcium carbonate precipitated by algae, mostly plate-like structures produced by *Halimeda* spp.

Shoot Growth Chronology

We attempted to collect a minimum of 15 intact short shoots (vertical, leaf producing rhizomes) of *Thalassia testudinum* at each coring station for chronological analysis. Samples were returned to the NWRC for enumeration of leaf scars and measurement of plastochrone intervals (PI = distance between leaf scars; plate 10) to determine age and growth rate (Duarte

and others, 1994). To ensure accurate age estimation, only shoots with an intact apex were used in the analysis. PI distances were measured using a scanning-power light microscope mounted on a Henson's stage device with a graduated crank. The device was linked with an optical encoder for measuring linear distances to the nearest 0.01mm (10 μ m). Digital readings from the device were automatically transferred to a desktop computer integrated with a program for data storage and real-time display. This technique, originally developed for use in tree-ring studies (Doyle and Gorham, 1996), accurately measures the linear interval between adjoining leaf scars (PIs). The shoot to be measured was placed on the stage of the microscope with the shoot apex centered in the ocular crosshairs. The microscope stage (with its shoot) was slowly moved to the right by means of a screw attached to the graduated crank. At the end of each PI (i.e., when the next leaf scar was centered in the ocular crosshairs), the operator pushed a button, at which time the total distance for that PI was digitally transferred to the computer, and the distance was reset to zero. This process was repeated for each PI. The program simultaneously displayed a graphical output of the data for that shoot on the computer monitor as data were entered. At the end of each shoot, the file was saved and a new file was set up for the next shoot.

Statistical Analysis

Distribution, Abundance and Biomass

To estimate percent cover for each species, we assigned numeric values to each of the four cover classes based on the midpoint for its range, as follows: Class 1 (1-10%), midpoint = 0.055%; Class 2 (15-40%), midpoint = 0.275%; Class 3 (45-70%), midpoint = 0.575%; Class 4 (75-100%), midpoint = 0.875%. For each site, we then calculated mean percent cover by summing over all stations and all transects, by species, and dividing by the total number of stations. We used Student's *t* to test each mean for significant difference from zero. To estimate frequency of occurrence for each species we divided the number of stations where that species was present by the total number of stations for the transect. We used a categorical model to test for frequency differences among sites.

To evaluate differences among sites in percent cover (several species) and biomass (*Thalassia* only), we used a two-way analysis of variance (ANOVA), with model elements being impact type (sediment or wind), impact level (high, medium, or low), and the two-way interaction. We used the *F*-statistic to test for significant model effects ($\alpha = 0.05$). For pairwise comparisons of means we used Duncan's test for significant main effects and *t*-test (with Bonferroni adjustment to reduce Type I error) for significant interactions.

Shoot Growth Chronology

We used the growth rate value of 21 leaf scars per year (Duarte and others, 1994; Arrivillaga and Baltz, 1999b) to develop a time scale for each *Thalassia* shoot. Time intervals were hindcast from collection date so that plastochrone intervals (PI) could be placed in classes based on time relative to Hurricane Mitch. The classes used for data analysis were in 1-year increments from 3 years prior to Hurricane Mitch to 2 years following. The wind-impacted and sediment-impacted sites were sampled at different times (January and August 2001, respectively) and thus had different time classes (Wind: 3 years pre-Hurricane Mitch to 1 year post-Hurricane Mitch [4 classes]; Sediment: 2 years pre-Hurricane Mitch to 2 years post-Hurricane Mitch [4 classes]). Therefore, we ran separate two-way ANOVAs for wind-impacted and sediment-impacted sites to assess differences in mean PI intervals among sites and among time classes within sites. In addition to the PI analysis we estimated shoot age (years) for each shoot by

dividing the number of PIs by 21 (PIs per shoot, average from literature). We then used ANOVA to assess variation among sites in mean shoot age. Although our shoot age estimates may be biased due to our tendency to select longer shoots for laboratory measurements, we assume that any such bias would be consistent among study sites.

Results

Species Distribution and Abundance

Seagrasses

Thalassia testudinum was the dominant seagrass species on all transects in terms of frequency of occurrence as well as percent cover (table 2). The mean percent coverage of *Thalassia* on all transects, except the Punta Manabique (sediment, high impact) site, was significantly ($P < 0.002$) different from zero. The seagrass meadow at Punta Manabique was extremely patchy and did not differ from zero ($P = 0.11$). *Thalassia* coverage was significantly higher at the wind-impacted sites than at the sediment-impacted sites (fig. 2). Among the wind-impacted sites, percent coverage of *Thalassia* did not differ ($P > 0.05$) and averaged 70-100%; frequencies also did not differ ($P > 0.05$) and ranged from 87-100% (table 2). Among sediment-impacted sites, *Thalassia* coverage ranged from 5-43% with frequencies from 8-70% (table 2); cover and frequency at Punta Manabique (sediment, high impact) were significantly lower than at the other two sites (fig. 2).

Syringodium filiforme was found in low densities on all three wind-impacted sites (table 2). The mean percent cover for these sites were significantly ($P < 0.002$) different from zero. *Syringodium* was not found at any of the three sediment-impacted sites. Trace amounts showed up in vegetation core samples. We found significant ($P < 0.0001$) differences in cover among the three wind-impacted sites. Percent coverage and frequency were greatest (11% cover, 64% frequency) at Roatan-north; intermediate (50% cover, 46% frequency) at Guanaja; and lowest (<1% cover, 17% frequency) at Roatan-south (table 2).

Halodule wrightii was found at only one site, Cayos Cochinos (sediment, intermediate impact) and only in the shallow water within 5 m of the shoreline (table 2). The mean percent coverage at that site was not significantly different from zero ($P=0.07$).

Macro-algae

Two species of a calcareous alga, *Halimeda*, were present and fairly common throughout the four Honduras study sites (table 2). Calcareous deposits of *Halimeda* were a major component of the marle sediment at those sites. *Udotea* sp. was scattered throughout the Honduras sediment cores in low densities, as were two species of *Penicillus*. Macro-algae were sparse at the two mainland sites in Guatemala, and were absent from our transects there. We found *Halimeda opuntia* to be significantly ($P < 0.0007$) higher in percent cover on Roatan-north and Roatan-south than on Guanaja or Cayos Cochinos.

Soft corals and miscellaneous organisms

Gorgonia (sea fans) were uncommon but scattered throughout, mostly on or near the reefs. Other taxa identified on the transects were *Porites* (reef corals), Actiniaria (sea anenomes), Porifera (sponges), Echinodermata (urchins [*Diadema*], brittle stars, sea stars), Gastropoda (snails), and Bryozoa (moss animals). Summary descriptions of organisms found

along each transect and their abundance, along with graphical displays of transect cover types depth profiles, is presented in a later section (see Sediment and Vegetation Overview by Site: Substrates, Biotic Community, and Disturbance).

Biomass

All biomass cores contained *Thalassia* and some cores also contained trace amounts of other species (e.g., *Syringodium*); only *Thalassia* was used for biomass analysis. We found considerable variation in the aboveground and belowground biomass of *Thalassia* taken from the core samples. Mean total plant biomass pooled over all sites for *Thalassia* was 1068 g dry mass m⁻² (346 g m⁻² aboveground and 722 g m⁻² belowground). All samples had a greater biomass in the belowground portion than aboveground, thus resulting in root:shoot ratios of greater than 1 (table 3). Because of extreme variability among samples, however, only at the two medium-impact sites did that value significantly ($P < 0.05$) differ from one.

Mean aboveground biomass of *Thalassia* from the six sites ranged from 93 g m⁻² at Bahia la Graciosa (sediment, low impact) to 527 g m⁻² at Roatan north (wind, intermediate impact; table 3). The wind-impacted sites had higher ($P < 0.05$) aboveground biomass values than the sediment-impacted sites, and the low-impact sites had lower ($P < 0.05$) levels than the medium-impact sites; means for the medium- and high-impact sites did not differ ($P > 0.05$; fig. 3).

Mean belowground biomass of *Thalassia* from the six sites ranged from 262 g m⁻² at Bahia la Graciosa (sediment, low impact) to 1269 g m⁻² at Punta Manabique (sediment, high impact; Table 3). The means from those two sites were significantly different ($P < 0.05$) from each other, but means from the three wind-impacted sites did not differ ($P > 0.05$; fig. 3).

Thalassia biomass tended to decrease somewhat with distance from shore (table 4), but the relationship was weak and inconsistent. At our sites, water depth generally increased with distance from shore only to a point (approximately midway or more between the shoreline and the fringing reef), and then became shallower as distance to the reef decreased (see depth profiles in a later section, Sediment and Vegetation Overview by Site). We plotted biomass against water depth (fig. 4) and found a negative correlation that was significant ($P < 0.004$) but weak ($r^2 = 0.1744$ for belowground and 0.2270 for aboveground samples). Several of the belowground samples from Punta Manabique (sediment, high impact) were outliers in that they had much greater biomass than would be predicted by water depth (fig. 4); this could be indicative of higher than normal rhizome growth at this site, perhaps due to the high sedimentation rate (see Shoot Growth Chronology, below).

Shoot Growth Chronology

Plastochrone intervals (PI) for all samples were quite variable, with a range of 50-7400 um (table 5). Mean PIs for all six sites were significantly ($P < 0.0001$) different from one another (fig. 5). The two Guatemala sites, Punta Manabique and Bahia la Graciosa, had PI values that were almost twice as high as the PI values for the four Honduras sites.

When we looked at PI means among time classes for each site, we found a significant ($P < 0.0001$) interaction between impact level (low, medium, or high) and time class within both the wind and the sediment impact site groups. Among the wind-impacted sites, Guanaja (wind, high impact) was the only site to show a significant ($P > 0.05$) change in mean PI from 1 year pre-Mitch to 1 year post-Mitch time classes; the medium- and low-impact sites showed no such change (fig. 6). All three sites had an earlier year in which the mean PI was significantly ($P > 0.05$) greater than the years immediately before or after Mitch (2 year pre-Mitch for Roatan-north, and 3 year pre-Mitch for the other two sites). None of the sediment-impacted sites showed

a significant change from immediate pre-Mitch to immediate post-Mitch years (fig. 7). Cayos Cochinos (sediment, medium impact) showed no significant change at all among years. The two Guatemala sites showed gradual changes over the four-year time period, but in opposite directions, and neither showed a change from 1 year pre-Mitch to 1 year post-Mitch.

Thalassia shoot age among all samples ranged from 0.19 y to 10.33 y (table 6). We found no significant difference ($P > 0.05$) among the three wind-impacted sites (fig. 8). Among the sediment-impacted sites, shoots at Cayos Cochinos (medium impact) were significantly older than shoots from the other two sites. The two Guatemala sites, by contrast, had the youngest shoots.

Sediment Stratigraphy

We found marl (calcium carbonate mud) to be the predominant soil type at four Honduras study sites. The marl was mostly homogeneous along the length of the cores, although some stratification was noted according to particle size (fine, medium, or coarse marl) and presence or absence of other materials. Shell and *Halimeda* fragments were usually present throughout core samples with *Thalassia* roots extending 12-30 cm down from the surface. We noted no sediment horizons in the subtidal zone that appeared to have been deposited from Hurricane Mitch. Mangrove peat deposits and branch fragments were found in the deepest zone of cores from Roatan-north and Bahia la Graciosa. The two Guatemala (sediment-impacted) sites had substrates consisting of mostly sand (Punta Manabique) or sand, silt, and shells (Bahia la Graciosa). Detailed descriptions of sediment cores at each site are presented in a later section (see Sediment and Vegetation Overview by Site: Detailed Description of Sediment Cores).

Sediment and Vegetation Overview by Site

Substrates, Biotic Community, and Disturbance

Roatan-south, Honduras (wind, low impact)

Substrates. Substrates in the area were generally homogeneous and made of fine carbonate mud (marl) with *Halimeda* plates, some shells, and invertebrates, suggesting little transport by currents or tides. Several invertebrates were noted. On the leeward side of the fringing reef, the substrate was coarse shell, other skeletal calcium carbonate fragments, and sand; this community apparently receives much wave energy from the seaward side of the reef. Calcareous, coenocytic algae were common components of the bottom community in depths greater than 0.5 m.

Biotic community. The seagrass community (figs. 9 and 10) was dominated by *Thalassia testudinum* from the mangrove shoreline seaward to the fringing reefs. *Thalassia* produced 75 - 100% cover seaward to approximately 550 m, and approximately 40 - 75% cover from 550 m seaward to the fringing reef (740-800 m). Mangroves along the shoreline were dense and dominated by *Rhizophora*. Dead but intact leaves were common in the *Thalassia* community, making up nearly 50% of the canopy in much of the shallow-water community.

Syringodium filiforme was found but was not a common part (<10% cover) of the deeper water seagrass community >100 m from the mangrove shoreline. *Syringodium* appeared to be more common on the seaward-facing bottom slopes.

Disturbance noted. The seagrasses near the shoreline were robust, dense, and appeared to have received little or no trauma from high winds during Hurricane Mitch.

Roatan-north, Honduras (wind, intermediate impact)

Substrates. Substrates were mostly fine carbonate mud (marl) with *Halimeda* plates and gravel. Organic materials were mixed with the carbonate several decimeters beneath the substrate surface. Mangrove peat was evident 30-40 cm beneath the surface of several sample cores. Substrates immediately landward of the reef were limestone, coarse coral rubble and boulder corals, with soft corals common among the boulder corals. Also, several invertebrates were noted. A layer of coarse sediment at the surface of two cores may indicate recent sediment deposition.

Biotic community. The seagrass community (figs. 11 and 12), dominated by *Thalassia testudinum*, covered 75-100% in most areas from the mangrove shoreline to the fringing reef (1000 m). *Syringodium filiforme* occurred nearly throughout, usually forming <50%. The calcareous algae *Halimeda opuntia* and *Halimeda incrassata* were common throughout, usually forming <50% cover and were most common on a seaward-facing slope about 200 m from the shoreline. The mangrove community was predominately *Rhizophora mangle*.

Disturbance noted. This area appeared to have received little or no disturbance from high winds. Seagrasses near the shoreline were robust and dense and appeared to have received little or no trauma from Hurricane Mitch. During sampling, the fringing reef (approximately 1 km from the mangrove shoreline) appeared to receive much wave energy from the prevailing northwesterly winds. Conditions were windy and rough landward of the reef but did not appear to affect the seagrass community.

Guanaja, Honduras (wind, high impact)

Substrates. Substrates in this area were mostly fine to medium calcium carbonate mud (marl). Coarse mud and fine shell fragments 15-20 cm were found beneath the fine mud in the areas 50 m from the shoreline. *Thalassia* rhizomes and roots occurred to approximately 20 cm beneath the substrate surface.

Biotic community. *Thalassia* dominated the bottom community from the shoreline to the fringing reef (figs. 13 and 14). *Syringodium filiforme* was present but not dominant, from approximately 100 m from the mangrove shoreline to the reef on one transect and was only present near the shoreline on the other. Much of the seagrass community near the mangrove (*Rhizophora mangle*) shoreline was close to the water surface and appeared stressed by continuous wave action. However, *Thalassia* growth beneath the substrate surface in the near-shore areas appeared to be dense.

Disturbance noted. The predominately red mangrove (*Rhizophora mangle*) community adjacent to the sample areas was severely altered by Hurricane Mitch with few living trees noted. Adjacent to the mangrove shoreline was an area approximately 2 m wide without seagrasses and with substrate to approximately 0.5 m deeper than the adjacent seagrass community. This area appeared to have been scoured and may have been a part of the seagrass community extending to the mangrove edge prior to Hurricane Mitch. Also, this area appears to have been beneath the mangrove canopy that previously dominated the shoreline. Canopy shade may have affected seagrass vigor, making it more vulnerable to storm damage resulting in the erosion and associated sedimentation. Small *Udotea* colonies were common in this area.

Bahia la Graciosa, Guatemala (sediment, low impact)

Substrates. The shoreline had a narrow (approximately 20 m) fringe of mangrove forest with other trees dominant farther back from the shoreline (see Mangrove Forest Structure report). Substrates in this area were fine sand, carbonate mud, and organic material. Near the mangrove shoreline, the organic material was finer than that found farther from the shoreline (>20 m) and was subtended by fine sand. One core contained much woody debris below 30 cm from the substrate surface. *Thalassia* roots were found approximately 10 cm beneath the substrate surface in another sample (10 m from the mangrove shoreline). About 50 m from the mangrove shoreline, the surface substrates were similar. Sand and shell fragments were found below about 10 cm beneath the substrate surface. No woody debris was noted in the samples taken 50 m from the shoreline.

Biotic community. *Thalassia testudinum* dominated the seagrass community from the mangrove shoreline seaward to the fringing reefs (figs. 15 and 16). *Thalassia* produced 75-100% cover seaward for at least 100 m from the mangrove shoreline. Further than approximately 100 m from the mangrove shoreline, the seagrass community could not be seen due water turbidity, and no cover estimates were recorded. We extended one transect (B1; fig.15) across the bay to the southern mangrove shoreline on the opposite side. Although turbidity prevented us from surveying the bottom community at depths > 2 m, we did document that seagrasses were present near the south shoreline at shallower depths. It appears from our survey that seagrasses occupy the photic zone around the bay to about 500-1000 m from the shoreline.

Disturbance noted. This area appeared to have received little or no disturbance from high winds or from sedimentation, though water clarity was lower than at any of the other sites. The seagrasses near the shoreline were robust and dense, though farther out they were more sparse than most of the other sites, and biomass decreased considerably from 10 to 50 m out (see table 4). It is doubtful, however, that patterns observed were related to Hurricane Mitch; rather, they may represent chronic conditions at the bay.

Cayos Cochinos, Honduras (sediment, intermediate impact)

Substrates. The shoreline community was mostly open beach with associated strand; coconut palm stumps seaward of the shoreline indicated that the shoreline had eroded 3-5 m at some time in the past. Substrates were largely calcium carbonate skeletal materials (shell fragments, coral rubble, and *Halimeda* plates) mixed with sand and calcium carbonate mud (marl). Cores taken more than 50 m from the shoreline contained less sand and were mostly large skeletal fragments.

Biotic community. The seagrass community, dominated by *Thalassia testudinum*, formed an incomplete and patchy canopy with about 50% cover (figs. 17 and 18). The *Thalassia* community occurred mainly in shallow, rocky substrates and appeared stressed from wave energy and tidal exposure. Calcareous algae, such as *Halimeda incrassata* and *Penicillus dumetosus*, occurred with the *Thalassia*, and soft corals were common in deeper water near the fringing reef. *Halodule wrightii* was noted along the recently eroded shoreline.

Disturbance noted. Much of this area is shallow and rocky and appears to receive nearly continuous wave action, suggesting continuous disturbance. The shoreline seems to have eroded as evidenced from the palm stumps, but this may have occurred before Hurricane Mitch. At a transect point 50 m from the shoreline we found a distinct layer of fine sediment, 1 cm wide, about 25 cm beneath the substrate surface. This layer was too deep to have been from Hurricane Mitch but could have been deposited during Hurricane Fifi in 1974. In the *Thalassia* dominated meadows, areas of scoured sandy substrate were noted. A matrix of rhizomes and roots was

observed in the margins of these areas 10-15 cm beneath the surface and often extending two to three times deeper into the substrate. These areas were common and appeared to be naturally occurring; their association with storm events is not clear.

Punta Manabique, Guatemala (sediment, high impact)

Substrates. Substrates throughout this area were fine sands with few shell fragments, much like the shoreline sand. The substrate was light brown to about 10 cm and dark to medium gray beneath, which may indicate oxidation near the surface and anoxia beneath the brown surface sediment. In one core, the gray sand was mixed with small areas of brown sand. The brown coloration may have resulted from the transporting of oxygen into the anoxic layer by seagrass roots or other organisms. The substrate surface was rippled in most areas, and appeared to be covering the bases and lower parts of most *Thalassia* leaves, suggesting that this sand may be part of recent or contemporary fluvial deposition (Yamataki, H., oral communication, 2001).

Biotic community. Seagrasses in this area occurred mostly in patches ca. 40 – 80 m from the shoreline; only *Thalassia testudinum* was observed (figs. 19 and 20). Much of the *Thalassia* community was sparse and no macro-algae or macro-invertebrates were noted. The plants in these communities appeared to be stressed, and the short shoots and leaf bases appeared to be covered with sand. Also, the beach and associated nearshore substrates appeared to be consistent with substrates commonly found on high wave or tidal energy shorelines.

Disturbance noted. The shoreline community was mostly open beach with associated strand. Much of the shoreline (to 50 m shoreward) was eroded during Hurricane Mitch, so that the sampling sites may have been located 10 m and 50 m from the former shoreline (i.e., similar to the 10 m and 50 m locations on the other transects). No observations of bottom communities were completed where water depth was greater than 2.5 m due to turbidity. In general, the substrate had the appearance of having been deposited recently, so that substrates here may be unstable and could be covering seagrasses in some areas; however, none of our cores revealed buried seagrass beds.

Detailed Description of Sediment Cores

Roatan-south, Honduras: wind, low impact (fig. 21).

R2-2 Two cores (a and b), 60 m from the shoreline, surface to 20 and 25 cm beneath the substrate. Both were homogeneous throughout, made up of fine carbonate mud (marl) with <10% *Halimeda* plates.

R2-3 Two cores (a and b), 90 m from shoreline, depth into substrate not recorded (estimated at 30 cm). The substrate was homogeneous throughout, made up of fine carbonate mud (marl) with shell fragments.

R3-1 One core, 800 m from shoreline, immediately shoreward from the fringing reef, surface to 32 cm beneath the substrate. Coarse calcium carbonate and shell fragments throughout.

Roatan-north, Honduras: wind, intermediate impact (fig. 22).

R4-1 One core, 15 m from shoreline, surface to 32 cm beneath the substrate surface. The substrate was homogeneous throughout, made up of fine to medium marl (carbonate mud).

R5-1 Two cores (a and b) 10 m from shoreline, surface to 40 cm and 42 cm below sediment. From the sediment surface to 18-30 cm beneath the surface the substrate was fine,

medium, or coarse shelly marl (carbonate mud). Below to 40 to 42 cm the marl was mixed ca. 50% with organic material and mangrove peat.

R5-2 Two cores (a and b) 50 m from shoreline, surface to 42 and 44 cm beneath the substrate surface. From the surface to 25 and 27 cm the substrate was coarse or fine carbonate mud (marl). Below those depths the CaCO₃ mud was mixed approximately 50% with organic (mangrove and *Thalassia*) peat.

Guanaja, Honduras: wind, high impact (Figure 23).

G1-1 Two cores (a and b), 10 m from the shoreline, surface to 50 cm and 53 cm beneath the substrate surface. Both cores were made up of fine to medium carbonate mud (marl), one with approximately 20 cm of coarse carbonate sediment at the surface; this 20 cm of coarse sediment contained several *Thalassia* rhizomes. The other core contained many *Thalassia* roots in the sediment to ca. 30 cm beneath the substrate.

G1-2 Two cores (a and b), 50 m from the shoreline, surface to 37 and 50 cm beneath the substrate. Both cores were made up of medium carbonate sediment from the surface to 12-15 cm beneath the surface; *Thalassia* rhizomes were evident in this layer of one core. Beneath the medium sized sediment layer was coarse sediment.

G3-1 Two cores (a and b), 10 m from the shoreline, surface to 41 and 44 cm beneath the substrate. Both cores were composed of medium to fine carbonate mud (marl), with *Thalassia* rhizomes evident in the 10-11 cm beneath the substrate surface.

G3-2 Two cores (a and b), 50 m from the shoreline, surface to 40 and 48 cm beneath the substrate. One was made up mostly of medium carbonate mud (marl) with about 2 cm coarse sediment (*Halimeda* plates) at the surface; *Thalassia* rhizomes were evident to about 19 cm below the sediment surface. The second core was composed of medium carbonate mud (marl) to about 19 cm beneath the surface, subtended by coarse mud; *Thalassia* rhizomes were evident to approximately 9 cm beneath the substrate surface.

Bahia la Graciosa, Guatemala: sediment, low impact (Figure 24):

B1-1 Two cores (a and b), 10 m from the shoreline, surface to 42 and 45 cm beneath the substrate. The substrates making up both cores was composed on the surface of dark gray fine sand, organic material, and carbonate mud (organic ooze) to 10-12 cm beneath the substrate surface. Sandy silt occurred beneath the surface layer to 20-27 cm; this was subtended by silty fine sand.

B1-2 Two cores (a and b), 50 m from the shoreline, surface to 48 and 35 cm beneath the substrate surface. The surface to 8-12 cm beneath the substrate surface was dark sandy silt. Silty sand with shells subtended the surface layer.

B2-1 Two cores (a and b), 10 m from the shoreline, surface to 48 and 50 cm beneath the substrate surface. The surface to 8-12 cm beneath the substrate surface was sandy silt to 15-17 cm; *Thalassia* roots were evident to approximately 10 cm beneath the substrate surface. Silty sand made up the substrate to 38-40 cm, with < 50% woody debris mixed with the sand below 30 cm; the bottom 10 cm of the longer sediment core was almost entirely woody debris.

B2-2 One core (a), 50 m from the shoreline, surface to 50 cm beneath the substrate surface. The substrate surface was sandy silt with shells to 8 cm, subtended by silty sand with 10-20% shell fragments.

Cayos Cochinos, Honduras: sediment, intermediate impact (fig. 25):

C1-1 Two cores (a and b), 10 m from the shoreline, surface to 22 and 18 cm beneath the substrate surface. The surface to 4 cm beneath the surface was dark gray sand (70%) with small shell fragments (30%). Beneath the surface layer to 13-16 cm was light gray with equal parts sand, fine shell fragments, and calcium carbonate mud (marl); beneath this to the bottoms of the samples was equal parts of sand and fine shell fragments with a small amount of carbonate mud. A few *Thalassia* roots occurred throughout the samples, and rhizomes and short shoots occurred to 14 cm below the substrate surface in one sample.

C1-2 Two cores (a and b), 50 m from the shoreline, surface to 24 and 15 cm beneath the substrate surface. The sediment surface to 4-7 cm beneath the surface was dark gray and made up mostly of shell fragments (about 80%) with sand and some calcium carbonate mud (marl). Beneath the surface layer to 10-15 cm was small coral rubble and large shell fragments with variable amounts of sand and carbonate mud. The bottom 11-24 cm of the longer core was mostly (90%) shell fragments with sand and carbonate mud; the bottom 2 cm of this also had small coral rubble mixed with the shells. *Thalassia* rhizomes and roots occurred 8-15 cm beneath the substrate surface in one sample.

C2-1 Two cores (a and b), 10m from the shoreline, surface to 23 and 29 cm beneath the substrate surface. The sediment surface to 3-6 cm beneath the surface was gray calcium carbonate mud (marl) with *Halimeda* plate fragments (30%). Beneath this layer to 10-17 cm was mostly *Halimeda* plates (50-70%) light gray carbonate mud; subtending this layer were equal parts of fine *Halimeda* plate fragments and gray carbonate mud. *Thalassia* roots and rhizomes occurred in one sample from 4-10 cm beneath the substrate surface.

C2-2 Two cores (a and b), 50 m from the shoreline, surface to 30 and 39 cm beneath the substrate surface. The sediment surface to 5-11 cm beneath the surface was small coral rubble and *Halimeda* plates. Beneath the surface layer to 30 and 32 cm was mostly small *Halimeda* plate fragments and small coral rubble with carbonate mud (to 20%). This layer was interrupted (at 24 cm and 26 cm beneath the surface of each core respectively) with 1 cm of fine carbonate mud (marl) with *Halimeda* plate fragments. The longer core had *Halimeda* plate fragments from 32-39 cm, and *Thalassia* rhizomes, roots, and shoots in the surface layer (0-11 cm).

Punta Manabique, Guatemala: sediment, high impact (fig. 26):

P1-1 Two cores (a and b), 40 m from the shoreline, surface to 48 cm beneath the substrate surface. The substrates of both cores were mostly sand. The sand at the substrate surface to 4-8 cm beneath the surface was light brown; beneath this, the sand was dark gray and grading to a medium gray near the bottoms of the cores.

P1-2 Two cores (a and b), 70 m from the shoreline, surface to 50 cm each beneath the substrate surface. The substrates of both cores were mostly sand. The sand at the substrate surface to 9-10 cm beneath the surface was light brown; beneath this, the sand was dark gray and grading to a light gray near the bottoms of the cores. The gray sand of one core contained some brown mottling (or striping).

Discussion

Quantitative Site Comparisons

None of the 10 response variables precisely followed patterns that we predicted based on hurricane impacts, though some differences observed might have been hurricane-related (table 7). Guanaja, the site that experienced the highest winds from Mitch, also had the highest species richness (two seagrass species, five macroalgae, and hard and soft corals were present). Guanaja also had slightly lower percent cover and percent frequency of *Thalassia* than the two Roatan sites, though the differences were not significant. We have no prehurricane data, but if we can assume that the three sites were similar before the storm, then we could hypothesize that the wave action generated by Hurricane Mitch resulted in tissue damage, mortality, and/or uprooting of individual *Thalassia* (and possibly *Syringodium*) plants. The subsequent loss of plant cover would have resulted in an increase in available substrate (and lack of competition and shading) for colonizing macroalgae, which would explain the greater species richness at Guanaja. This hypothesis, however, is weak given the lack of significant differences in *Thalassia* abundance among sites. In addition, we found no significant differences in aboveground or belowground biomass for *Thalassia*, nor in root:shoot ratios, among the three wind-impacted sites.

Syringodium was more abundant at Guanaja than at Roatan-south, but it was more abundant at Roatan-north than at either of the other two sites, so the differences were probably not hurricane-related. Also, though Guanaja had higher species richness, the two Roatan sites had greater abundance for the two species of *Halimeda* that were present at all three sites.

The lack of differences in shoot age among the three wind-impacted sites also downplays the role of hurricane impacts. Analysis of PIs by years before and after Mitch was inconclusive. Guanaja did show a significant increase in growth rate (PI) in 1999, the year following Mitch, but growth at that site had been even greater three years prior to Mitch (1996), so other forces besides Mitch are apparently at play here. There was no hurricane in the Caribbean that would have influenced Guanaja in 1996 (Heyman and Kjerfve, 2001; Doyle and others, 2002). Roatan-south also showed its highest growth rate in 1996, but Roatan-north showed its highest growth in 1997. We would like to note that some individual shoots showed what appeared to be a significant PI change after Mitch, but our analysis of PI by year, pooled over all shoots, is inconclusive. Accordingly, we plan to conduct a separate analysis, looking at PI change by individual shoot, to see if a more pronounced hurricane effect can be shown.

Among the sediment-impacted sites, the two mainland sites in Guatemala (Punta Manabique and Bahia la Graciosa) showed similarities to each other, whereas the Cayos Cochinos site was more similar to the other insular sites at Roatan and Guanaja, especially in terms of species richness (table 7) and sediments. Differences in substrates and long-term turbidity probably had a greater effect on observed site differences than did Hurricane Mitch. Punta Manabique did seem to be subjected to a high sedimentation rate, but this may be a chronic condition, independent of hurricane effects. Bahia la Graciosa, though it was undoubtedly well protected from hurricane effects by its geographical position, was similar to Punta Manabique in that it had low species richness, low shoot age, and a high growth rate (table 7). Biomass was also lowest at Bahia la Graciosa, apparently due to factors that are not associated with Hurricane Mitch (we would predict biomass to be higher at the low-impact site). Cover and frequency of *Thalassia* at Punta Manabique were lower than at any other site, a further indication of the harsh growing conditions there due to sedimentation. It is possible that *Thalassia* was more widespread at this site prior to Mitch, but we can only speculate on this

point due to lack of pre-hurricane data. Shoots at Punta Manabique were among the youngest, but also the fastest growing, and had the highest belowground biomass; aboveground biomass was average. These factors are indicative of plants whose vertical growth must keep pace with the sedimentary rate. Gallegos and others (1993) found a similar response (i.e., increased growth rate) associated with increased sedimentation after Hurricane Gilbert in *Thalassia* shoots from the Yucatan of Mexico.

Shoots at Punta Manabique did show an increase in growth rate (PI) over time, but there was no increase immediately following Hurricane Mitch. Growth rate there was lowest two years pre-Mitch (1997), then increased in 1998 (the year immediately prior to Mitch), remained steady in 1999 (one year post-Mitch), then increased again in 2000 (two years post-Mitch). If our chronology is correct, then these increases in growth rate cannot be attributed to Mitch. Bahia la Graciosa, on the other hand, showed a steady decrease in growth rates over the same time period and followed the same pattern as Punta Manabique, but in the opposite direction. According to our predictions, growth rates at Bahia la Graciosa should have remained steady over time. Clearly the patterns shown at the two Guatemalan sites do not indicate a strong hurricane impact. Growth rates of shoots collected at Cayos Cochinos did not change over the four-year period; this indicates a stable environment and thus very little impact from Mitch.

General Observations

Coastal communities

Shoreline communities in most locations were mangrove forests. The mangroves most commonly found on the shorelines were red mangroves (*Rhizophora mangle*), a common dominant on the seaward margins of intertidal forests in the Caribbean area (Tomlinson, 1986). Though seagrass beds may have been buffered somewhat from the increased water column depth resulting from the storm surge, the mangroves at Guanaja were severely damaged during Hurricane Mitch, so that almost no living trees were noted in the intertidal forest. Damage to the mangrove forest was also noted on the northern shore of Roatan, Honduras, but changes to the forest did not appear to be extensive; little or no change was noted to the mangroves on the shoreline adjacent to the seagrass community. At Punta Manabique, Guatemala, and Cayos Cochinos, Honduras, the shorelines were open sandy beaches, dominated by coastal strand and occasional coconut palms (*Cocos nucifera*). Erosion and concomitant shoreline migration occurred at the sites with open beach and strand communities.

Shoreline migration occurred because of Hurricane Mitch in one, possibly two of our study sites. At Punta de Manabique, the open beach shoreline was reported by local inhabitants to have eroded about 30 m. This was partly confirmed, as we found *Thalassia* communities occurring no less than 40 m from shore. At Cayo Grande, Cayos Cochinos, Honduras, the shoreline appears to have eroded at some time in the past. Seaward of the open beach community at this site was an area approximately 10 m wide that was an open, sandy substrate, but that we did not notice as exposed at low tide; seaward of this area the *Thalassia* community was nearly continuous to the fringing reef. Within the cleared area were *Cocos nucifera* stumps that had been recently cut, and *Halodule wrightii*, an early seagrass colonizer, grew sparsely throughout, suggesting that this area may have become exposed within the previous months.

At the study site on Guanaja, no seagrasses occurred in the first 2-3 m of the transects. This area was nearly devoid of vegetation and was about 0.5 m deeper than the adjacent mangrove and seaward seagrass communities. This margin landward of the seagrass community appeared to have been scoured by wave action that accompanied the storm. This area also

appeared to have been the approximate limit of canopy and attendant shade that had been cast by the former mangrove forest. If this area had been shaded before the storm, growth of seagrasses may have been limited and thus less resistant to scour by storm waves. *Udotea flabellum* was common but not dominant in this cleared area and was attached to shells or other stable surfaces.

Seagrass communities

Bottom communities were dominated by seagrasses, most commonly turtlegrass (*Thalassia testudinum*). Seagrass communities at most locations were nearly continuous from the shallow water adjacent to shorelines to fringing reefs. Turtlegrass dominated and provided nearly all the canopy for these communities. Manateegrass (*Syringodium filiforme*) was common, but not dominant among the turtlegrass in many areas; manateegrass was not commonly found in shallow water where disturbance by waves, or tidal exposure, appeared to occur regularly. Shoalgrass (*Halodule wrightii*) was noted at one study site (Cayos Cochinos; see above: Coastal Communities). At 50% of the study sites (Roatan north, Guanaja, and Cayos Cochinos), the seagrass communities within approximately 30 m of the shoreline were exposed during low tides; the turtlegrass that dominated these areas formed dense mats of sub-surface rhizomes and rosettes of short leaves. These areas appeared to have diverse invertebrate assemblages. In deeper waters, these communities appeared to have well-developed *Syringodium* populations as common components with the turtlegrass.

At the study sites that appeared to be the most protected from winds and associated disturbances (Roatan south, Roatan north near shore, and Bahia la Graciosa), seagrasses were robust with long leaves. In much of the area adjacent to these study sites and other protected areas, turtlegrass formed dense communities with few other species evident. In water more than 1 m deep, calcareous algae were common to codominant. The bottom community at Bahia la Graciosa was an exception to this, as few organisms other than *Thalassia* were noted. This area is part of an estuarine bay system and the salinity of the bay water at the time of sampling was lower than normal seawater; changes in salinity may not allow dense establishment of organisms, including *Thalassia*. Growth of *Thalassia* in water greater than approximately 1 m deep was sparse.

At Guanaja and Punta Manabique, storm-related disturbances from wind and sedimentation, respectively, were greatest. At the study site on Guanaja, no seagrasses occurred in the first 2-3 m of the transect. This area was nearly cleared of vegetation and was approximately 0.5 m deeper than the adjacent mangrove and seaward seagrass communities. This margin landward of the seagrass community appeared to have been scoured by wave action that accompanied the storm. This area also appeared to have been the approximate limit of canopy and attendant shade that had been cast by the former mangrove forest. If this area had been shaded before the storm, growth of seagrasses may have been limited, and thus less resistant to scour by storm waves. *Udotea flabellum* was common but not dominant in this cleared area and was attached to shells or other stable surfaces.

At Punta Manabique, currents that parallel the shoreline appear to dominate the offshore waters. Estuarine fresh water mixing also appears to occur in this area (water salinity was lower than normal seawater). Heavy rains that occurred at the time of field operations may have caused freshwater input by way of groundwater seepage, and flow through the estuarine mangrove community may have contributed to this mixing. These are factors that cause continuous changes to the system, so that establishment of well-defined communities has not occurred. Turtlegrass was common in this area but not abundant, and areas in which it clearly formed established

communities were patchy and discontinuous. The substrate was sand that appeared to be sorted by the fluid activity of water, so that sand grains about the same size appeared to have accumulated throughout the study area. The substrate appeared to be moving and continuously relocated along the offshore area. This was supported by the nature of the seagrasses growing in these substrates. Much of the seagrass community here consisted of widely spaced turtlegrass ramets; many of these leaf shoots and associated leaves appeared to be partly buried, so that the substrate was above the shoot apex and leaf bases.

Algal and invertebrate communities

Calcareous, coenocytic macroalgae (mostly *Halimeda* spp.) were common to co-dominant with the seagrasses and appeared to be most common in areas that were protected from disturbances from waves or tidal currents. Two species of *Halimeda* were present and fairly common throughout the Honduras study sites. Calcareous skeletal plates from these algae were a major component of the carbonate mud sediment. *Udotea flabellum* and *Penicillus* spp were also noted in low densities at many sample locations. These species are typical of Caribbean water bottoms (Ogden, 1998; Ogden and Ogden, 1998; Wysor, 2002).

Invertebrates were noted at most sample locations. *Gorgonia* (sea fans) were uncommon but scattered throughout, and were mostly on or near fringing reefs. Finger coral (*Porites porites*), Anenomes, Porifera (sponges), Echinoderms (urchins [*Diadema*], brittle stars, sea stars), Gastropods, and Bryozoans were noted primarily in shallow water seagrass communities with occasional disturbances from waves or occasional tidal exposure.

Substrates

Our examination of sediment cores failed to show any sediment layer or burial of seagrass beds that could be attributable to Hurricane Mitch. At Cayos Cochinos, Honduras, 50 m from shoreline, a 1 cm sediment layer approximately 25 cm beneath the substrate surface was distinct and noted in two sediment cores. We hypothesize that this may have been deposited during a previous storm event, possibly Hurricane Fifi approximately 26 years previous (Ogden and Ogden, 1998). Because of the depth in the sediment layer (25 cm), this is a plausible hypothesis since Fifi, with sustained winds up to 95 mph, passed between the Bay Islands and the Honduras mainland in 1974 (Doyle and others 2002). Four additional hurricanes passed near that part of the Caribbean in 1960, 1961, 1969, and 1978 (Heyman and Kjerfve, 2001).

Substrates were mostly shells or other calcium carbonate skeletal fragments, including coral rubble in most locations. These carbonate particles were usually fine, forming a carbonate mud with an appearance similar to fresh water marl (Yamataki, oral communication, 2001), in areas that appeared to be protected from frequent wave or tidal disturbances. *Halimeda* spp. plates were commonly mixed with the fine sediments, suggesting that these fragile algal skeletons may be part of the material that forms the fine carbonate mud substrate. In areas of high wave activity, such as immediately landward of fringing reefs, coarse coral rubble and shells, similar to substrates described by Gallegos and others (1993) were common substrate components. These substrates appeared to be continuously moved by currents and waves.

Sand was also common in the substrates, especially at Bahia la Graciosa and Punta Manabique, Guatemala. At Bahia la Graciosa, the sediments were a mixture of sand, organic material, and relatively little calcium carbonate material. This bay appears to be partly dominated by fresh water, so that marine organisms that precipitate calcium carbonate may not be well established in that area. Some shells were noted in the sediments, but few or no skeleton-

producing organisms were noted at this site. At Punta Manabique, the substrate was almost all fine sand and appeared to be continuously moved by the strong, long-shore currents that prevailed in this area. The sandy substrate was continuous with the shoreline beach. Also in this area, some shells were noted in the sediments, but few or no skeleton-producing organisms were noted at this site.

Peat layers were noted in some of the sediment samples from Roatan-north and Bahia la Graciosa. In most cases, this peat appeared to have been derived from mangroves and may indicate a change in the shoreline communities. The peat layers may represent a mangrove forest that occurred previously at these locations, suggesting that the shorelines have moved 50 m or more since the deposition of substrate.

Comparisons with Other Studies

The assemblages of seagrasses, algae, and corals found at our study sites were typical for Caribbean systems, and comparison of our results with recent studies (Arrivillaga and Baltz, 1999a; Ogden, 1998; Ogden and Ogden, 1998) revealed that the bottom communities had not changed appreciably over time. *Thalassia* biomass values from our study were equal to or greater than values reported in the literature from Louisiana (Michot and Chadwick, 1994), Florida (Gidden, 1965; Iverson and Bittaker, 1986), Texas (Onuf, 1996), Mexico (Gallegos and others, 1993), and Guatemala (Arrivillaga and Baltz, 1999b). Though belowground biomass of *Thalassia* was greater than aboveground biomass (i.e., root:shoot ratio > 1) for all of our sites, the variation among samples was such that the ratio was significantly different from one in only two sites, Roatan-north and Cayos Cochinos, and we found no significant difference among sites. Our sites had a high proportion of aboveground biomass compared to other studies. Gallegos and others (1993) cited two studies in which both leaf and rhizome biomasses were measured; in those studies, root:shoot ratios were 5.25 in the Virgin Islands and 9.0 in Florida. Fourqurean and Zieman (1991) also found a root:shoot ratio of 5.25, and Lee and Dunton (1996) indicated that root:shoot ratio was 4.88 in Corpus Christi Bay, Texas.

At Bahia la Graciosa, turtlegrass biomass (aboveground and belowground) was the lowest among our sites; this was especially true for samples from deeper (>1.5 m) water. Turbidity at this site was high, and as an estuarine community, may be high much of the time, so that water clarity and sunlight transmissivity are low. Because of reduced light levels, reduced production of turtlegrass may occur in deeper, turbid water (Fourqurean and Zieman, 1991). Czerny and Dunton (1995) found that turtlegrass growing in reduced light conditions were eliminated or their numbers were reduced in shaded areas. We found the greatest total biomass of turtlegrass at the site on the northern shore of Roatan, a site protected by a well-established fringing reef, but a site that likely received intermediate wind impacts. At Punta Manabique, the site with the highest belowground biomass, sediments appeared to be shifting nearly continuously, so that nearly all of the *Thalassia* ramets appeared to be partly buried by moving sediment. Rhizomes within the sediment may be required to increase internode lengths to keep leaves above sediments as they are deposited, thus producing much biomass in these parts. Leaves of the turtlegrass plants noted at this site appeared small, but healthy. The small size of the leaves in this area may be partly caused by stress from sedimentation. Williams (1988) found that *Thalassia* plants produced smaller leaves when stressed by predatory activity on leaves. This stress is different from partial burial by sediments but is similar in causing a change (increase) in resource allocation for leaf production. This may also partly account for reduced leaf canopies in shallow, tidally exposed turtlegrass communities that were found at three of the study sites.

Using the PI technique, researchers have been able to age seagrass shoots in the Mexican Caribbean up to 18 years old (Marba and others, 1994b); shoot age in our study ranged from less than 1 year to 10 years. PI variation in *Thalassia* shoots has been linked to disease or stress, such as the seagrass dieback phenomena in Florida Bay (Durako, 1994). The catastrophic mortality of turtlegrass has occurred in Florida Bay since 1987 and has been attributed to environmental stress, which increases susceptibility to disease (Carlson and others, 1994; Durako and Kuss, 1994; Thayer and others, 1994). Healthy seagrass populations include shoots of varying ages (demographic heterogeneity) with a substantial number of older shoots. In contrast, reductions in shoot size and an age-structure shift to younger ages are characteristics of unhealthy seagrass beds (Durako, 1994). All seagrass beds in our study showed great variation in PI and in shoot age, which would indicate a lack of stress in those beds; however, further analysis of age distribution in our samples is warranted.

Conclusions

We studied seagrass beds and bottom communities at six Caribbean sites in Honduras and Guatemala to assess potential damage from Hurricane Mitch. We used data from transects, core samples, and laboratory analysis to assess damage. None of the 10 response variables precisely followed patterns that we predicted based on hurricane impacts, though some differences observed might have been hurricane-related. In general, seagrass beds and bottom communities were largely buffered from significant storm impacts by the water column. Guanaja, the site that was impacted by the strongest winds from Mitch and where mangrove communities were completely destroyed by the storm, had high species richness and high to average abundance of *Thalassia testudinum*, the dominant seagrass species at all sites. Guanaja was also the only site that showed an increase in growth in the year immediately following Mitch, but the growth rate had been higher three years before the hurricane. Punta Manabique, the site that we predicted to have a high degree of sediment impact from Mitch, had only a patchy distribution of *Thalassia* and low species richness, but belowground biomass there was higher than at other sites. Seagrasses at Punta Manabique appeared to be subjected to substrate movements and frequent burial by sandy sediments. This was the only site to show a steady increase in growth rate over four years, but there was no change from the year immediately preceding to the year immediately following Mitch. The high growth rate and belowground biomass for this site, therefore, may be the result of frequent partial burial of leaf-producing rhizomes, but this is probably an ongoing phenomenon and may not be associated with Hurricane Mitch.

From our general observations, we noted other evidence of changes that may be associated with Hurricane Mitch, but most of the changes appeared to have been relatively small. At the site in Guanaja, Honduras, an area 3 m from the adjacent mangrove forest appeared to have been scoured, as evidenced by increased water depth and a lack of seagrasses. On the northern shoreline of Roatan, Honduras, a thin layer of calcareous algae (*Halimeda* spp.) plates may have been deposited by the storm. In eastern Guatemala, the shoreline on the western end of Punta Manabique was reported to have eroded approximately 30 m landward because of the storm. At Cayos Cochinos, Honduras, 3-4 m of beach also appeared to have eroded recently, perhaps during Mitch; at this location, the opportunistic seagrass *Halodule wrightii* had recently

become established. In general, the seagrass communities that were examined appeared healthy and to have received little significant alteration because of Hurricane Mitch.

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Table 1. Summary of seagrass transects by site, including general information on location, length, depth and sampling scheme, Hurricane Mitch study, Honduras and Guatemala.

Study Site	Transect No.	Length (shoreline to reef) and depth Latitude Longitude	No. Visual Cover Stations (interval)	No. Cores (distance from shore)
Wind Disturbance Low Impact (Roatan - south)	R-2	L: 740 m D: 0.5 – 3.7 m 16° 25.243N 86° 04.356W	40 (3 m) 6 (100 m)	2 (30 m) 2 (60 m) 2 (90 m) 2 (120 m)
	R-3	L: 800 m D: 0.8 – 6.4 m 16° 25.225N 86° 14.145W	7 (70-200 m)	2 (800 m)
Wind Disturbance Medium Impact (Roatan - north)	R-4	L:1100 m D: 0.3 – 4.3+ m 16° 25.561N 86° 13.746W	13 (100 m)	1 (15 m)
	R-5	L: 1000 m D: 0.2 – 4.3+ m 16° 25.634N 86° 13.805W	12 (3 – 5 m) 19 (100 m)	2 (10 m) 2 (50 m)
Wind Disturbance High Impact (Guanaja)	G-1	L: 800 m D: 0.3 – 4.5+ m 16° 30.576N 85° 51.978W	7 (1-2 m) 4 (10 m) 15 (50 m)	2 (10 m) 2 (50 m)
	G-3	L: 750 m D: 0.1 – 3.5 m 16° 30.607N 85° 51.938W	5 (1-5 m) 15 (50 m)	2 (10 m) 2 (50 m)
Sediment Disturbance Low Impact (Bahia la Graciosa)	B-1	L: 3800 m D: 0.90 – 6.40m 15°52.55N 88° 31.85 W	10 (1 m) 5 (10 m) 12 (50 m) 4 (100 m) 5 (500 m) 3 (50 m)	2 (10 m) 2 (50 m)
	B-2	L: 600 m D: 0.78 – 5.20 m 15°52.34N 88°31.30W	10 (1 m) 5 (10 m) 6(100 m)	2 (10 m) 2 (50 m)
Sediment Disturbance Medium Impact (Cayos Cochinos)	C-1	L: 100 m D: 0.13 – 1.69 m 15°58.35N 86°28.26W	10 (1 m) 11 (10 m) 1 (40 m)	4(10 m) 4 (50 m)
	C-2	L: 150 m D: 0 - 15.15 m 15°58.30N 86°28.30W	11 (1 m) 9 (10 m) 1(20 m) 1(30m)	4 (10 m) 4 (50 m)
Sediment Disturbance High Impact (Punta Manabique)	P-1	L: 200 m D: 0.79 – 4.87 m 15°57.23N 88°37.18W	11 (10 m) 1 (40 m) 3 (10 m) 1 (20 m)	2 (40 m) 2 (70 m)

	P-2	L: 200 m D: 0 – 7.54 m 15°57.29N 88°37.18W	11 (1 m) 8 (10 m) 2 (50 m)	2 (80 m)
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Table 2. Mean percent cover and percent frequency (in parenthesis) for all species of seagrass, algae, and coral, by site and transect, for Honduras and Guatemala (THAL = *Thalassia testudinum*, SYRI = *Syringodium filiforme*, HALO = *Halodule wrightii*, HOPU = *Halimeda opuntia*, HINC = *Halimeda incrassata*, UDOT = *Udotea* sp., PDUM = *Penicillus dumetosus*, CAUL = *Caulerpa mexicana*).

Site	Transect	No. of Stations	Seagrass			Algae					Coral	
			THAL	SYRI	HALO	HOPU	HINC	UDOT	PDUM	CAUL	Hard	Soft
Wind Disturbance												
Roatan-south (Low)	R2	46	85 (100)	1 (17)	0	13 (41)	1 (9)	0	0	0	<1 (2)	<1 (2)
	R3	7	79 (100)	1 (14)	0	5 (29)	5 (29)	0	0	0	2 (14)	0
	Total	53	84 (100)	<1 (17)	0	12 (40)	2 (11)	0	0	0	1 (4)	<1 (2)
Roatan-north (Med.)	R4	13	78 (100)	22 (92)	0	7 (31)	5 (31)	0	<1 (8)	0	2 (8)	3 (23)
	R5	31	72 (100)	6 (52)	0	14 (42)	4 (52)	0	1 (23)	0	<1 (3)	<1 (6)
	Total	44	74 (100)	11 (64)	0	12 (39)	4 (45)	0	1 (18)	0	<1 (5)	1 (11)
Guanaja (High)	G1	26	66 (85)	5 (46)	0	3 (19)	4 (38)	<1 (8)	1 (12)	0	3 (15)	<1 (8)
	G3	20	77 (90)	5 (45)	0	1 (5)	2 (25)	0	3 (5)	0	1 (5)	<1 (5)
	Total	46	71 (87)	5 (46)	0	2 (13)	3 (33)	<1 (8)	2 (9)	<1 (5)	2 (11)	<1 (7)
Sediment Disturbance												
Bahia la Graciosa (Low)	B1	39	22 (54)	0	0	0	0	0	0	0	0	0
	B2	21	55 (71)	0	0	0	0	0	0	0	0	0
	Total	60	33 (60)	0	0	0	0	0	0	0	0	0
Cayos Cochinos (Med.)	C1	22	42 (68)	0	3 (23)	1 (23)	1 (23)	0	1 (14)	1 (9)	6 (23)	0
	C2	22	45 (73)	0	0	4 (45)	0	0	0	0	4 (14)	0
	Total	44	43 (70)	0	2 (11)	2 (34)	<1 (11)	0	<1 (7)	<1 (5)	5 (18)	0
Punta Manabique (High)	P1	16	11 (19)	0	0	0	0	0	0	0	0	0
	P2	21	0	0	0	0	0	0	0	0	0	0
	Total	37	5 (8)	0	0	0	0	0	0	0	0	0

Table 3. Mean and SE values for *Thalassia testudinum* aboveground and belowground biomass (grams dry mass m⁻²) and root:shoot ratio, based on core samples from transects in Honduras and Guatemala.

Site	N	Aboveground			Belowground			Root:Shoot Ratio		
		Mean	SE	Signif.*	Mean	SE	Signif.*	Ratio	SE	Signif.*
Wind Disturbance										
Roatan-south (Low)	8	379.88	92.97	A	631.01	119.91	AB	2.41	0.6405	A
Roatan-north (Med.)	5	527.07	96.06	B	1201.61	301.61	AB	2.35	0.3757	A ¹
Guanaja (High)	8	442.45	66.62	AB	652.54	87.45	AB	1.64	0.3061	A
Sediment Disturbance										
Bahia la Graciosa (Low)	8	92.85	38.06	C	262.48	108.14	A	5.65	2.6628	A
Cayos Cochinos (Med.)	8	361.43	99.20	D	631.72	157.17	AB	1.89	0.2713	A ¹
Punta Manabique (High)	6	323.72	88.24	CD	1268.68	420.52	B	3.09	0.9393	A

*Means with the same letter are not significantly different (alpha = 0.05) among sites within aboveground, belowground, or root:shoot categories.

¹ The mean root:shoot ratio is significantly different from one.

Table 4. *Thalassia testudinum* estimated aboveground and belowground biomass (grams dry mass m⁻²) for all transects by site and distance from shore, Hurricane Mitch study, Honduras and Guatemala.

Transect Study Site	Number of cores (Distance from Shore)	Estimated Aboveground Biomass (g/m ²)	Estimated Belowground Biomass (g/m ²)
Wind Disturbance Low Impact (Roatan - south)	2 (30 m)		
	2 (60 m)	472.3	1083.0
	2 (90 m)	567.6	451.7
	2 (120 m)	90.9	336.9
	2 (800 m)	388.8	652.5
Wind Disturbance Medium Impact (Roatan - north)	1 (15 m)	269.6	776.9
	2 (10 m)	597.5	1752.6
	2 (50 m)	603.3	863.0
Wind Disturbance High Impact (Guanaja)	4 (10 m)	412.7	547.3
	4 (50 m)	422.3	757.8
Sediment Disturbance Low Impact (Bahia la Graciosa)	4 (10 m)	166.9	428.8
	4 (50 m)	18.8	96.1
Sediment Disturbance Medium Impact (Cayos Cochinos)	4(10 m)	542.0	905.9
	4 (50 m)	180.5	357.6
Sediment Disturbance High Impact (Punta Manabique)	2 (40 m)	426.5	1626.0
	4 (70-80m)	272.5	1090.0

Table 5. Summary of mean and SE values for *Thalassia testudinum* plastochrone intervals (: m) with minimum and maximum values for Hurricane Mitch study sites in Honduras and Guatemala.

Site	N	Mean	SE	Min	Max	Signif.*
Wind Disturbance						
Roatan-south (Low)	1537	631.14	8.86	90	2660	A
Roatan-north (Med.)	3669	505.84	4.26	50	2590	B
Guanaja (High)	3653	569.01	5.43	50	4100	C
Sediment Disturbance						
Bahia la Graciosa (Low)	2167	939.42	12.3	70	5530	D
Cayos Cochinos (Med.)	4663	419.30	2.46	80	2540	E
Punta Manabique (High)	1554	1042.73	21.23	130	7400	F

*Means with the same letter are not significantly different (alpha = 0.05) among sites.

Table 6. Summary of mean and SE values for shoot age (years) of *Thalassia testudinum* with minimum and maximum for each site.

Site	N	Mean	SE	Min	Max	Signif.*
Wind Disturbance						
Roatan-south (Low)	19	3.24	0.51	0.43	10.33	BC
Roatan-north (Med.)	61	2.46	0.24	0.24	10.10	C
Guanaja (High)	62	2.32	0.22	0.33	8.24	C
Sediment Disturbance						
Bahia la Graciosa (Low)	83	1.39	0.10	0.19	4.29	A
Cayos Cochinos (Med.)	69	3.39	0.25	0.52	8.19	B
Punta Manabique (High)	60	1.46	0.13	0.38	4.90	A

*Means with the same letter are not significantly different (alpha = 0.05) among sites.

Table 7. Disturbance types, degrees of disturbance expected and observed by site, Hurricane Mitch study, Honduras and Guatemala. For the 10 response variables studied, each site is classified as either Low (L), Medium (M), or High (H) relative to the other sites or to expected hurricane impacts (see previous figures and tables for actual values).

Site	Disturbance Expected		# Taxa Present	<i>Thalassia</i>		<i>Thalassia</i> Biomass			Plastochrone Intervals		Shoot Age	Stratigraphy (Disturbance Noted)
	Type	Level		Cover	Frequency	BG	AG	BG / AG Ratio	Mean	Year		
Roatan-south	Wind	L	6	H	H	M	M	L	M	L	M	L
Roatan-north		M	7	H	H	M	H	M	M	L	M	L
Guanaja		H	9	H	M	M	M	L	M	M	M	L
Bahia la Graciosa	Sediment	L	1	M	M	L	L	L	H	L	L	L
Cayos Cochinos		M	7	M	M	M	M	M	M	L	H	L
Punta Manabique		H	1	L	L	H	M	L	H	M	L	L



Figure 1. Maps of the Caribbean coast of eastern Guatemala and northern Honduras showing the six seagrass and soft coral study sites for Hurricane Mitch: (1) Punta Manabique, (2) Bahía La Graciosa, (3) Cayos Cochinos, (4) Roatan-north, (5) Roatan-south, (6) Guanaja.

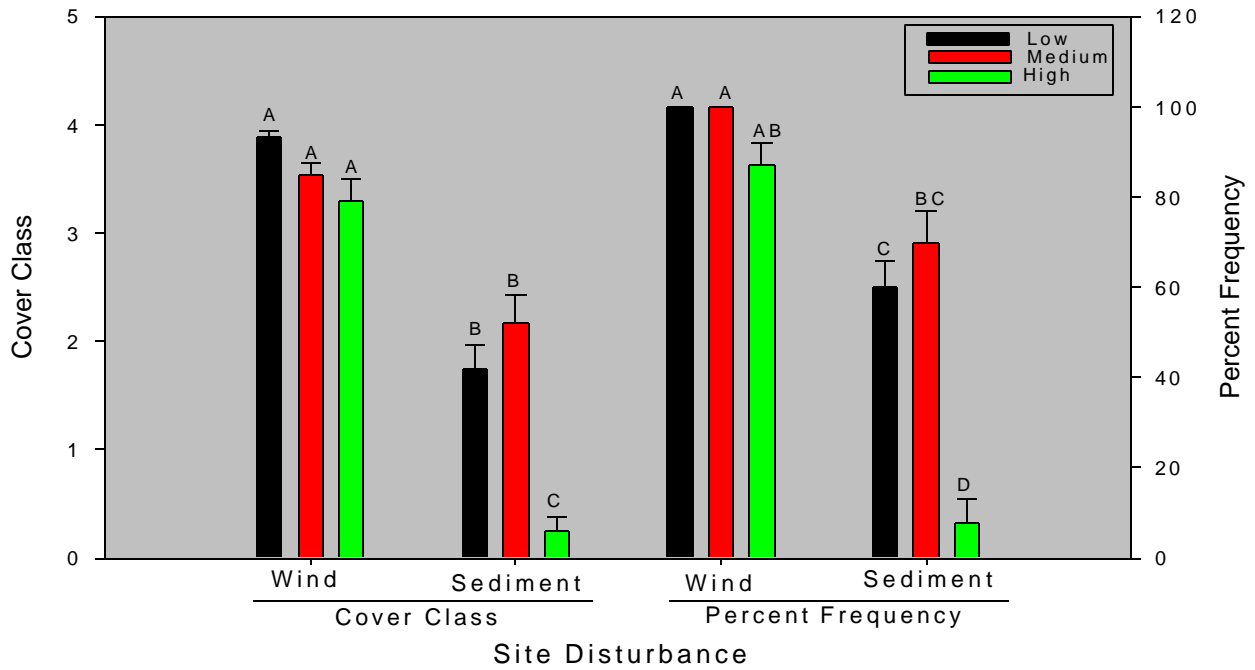


Figure 2. Mean cover class and percent frequency of occurrence of *Thalassia testudinum* along transects, by site, Hurricane Mitch study, Honduras and Guatemala. Bars with the same letter are not significantly different ($P > 0.05$).

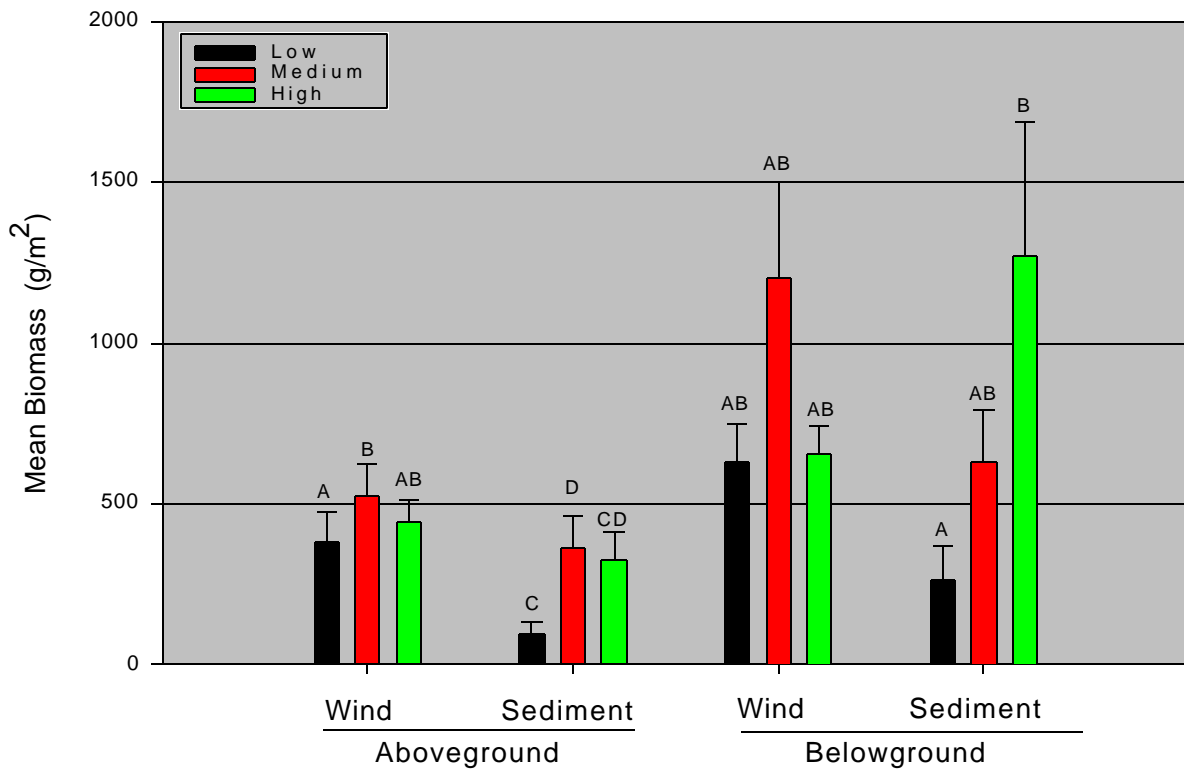


Figure 3. *Thalassia testudinum* aboveground and belowground biomass (g dry mass m²) by site, Hurricane Mitch study, Honduras and Guatemala. Bars with the same letter are not significantly different ($P > 0.05$).

Biomass of *Thalassia testudinum* Above and Beneath the Substrate
Surface and Depth of Seagrass Communities

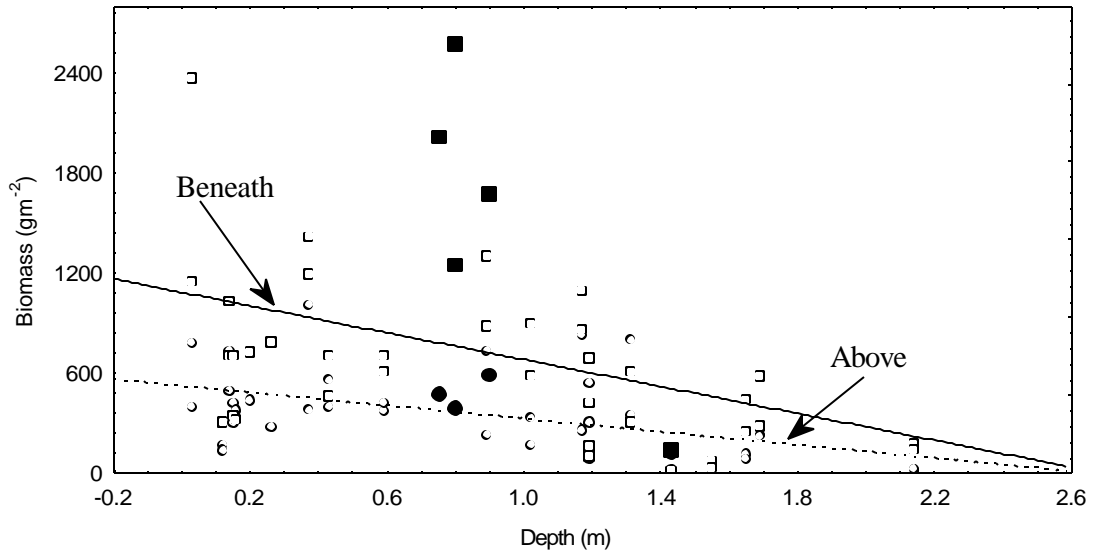


Figure 4. Biomass of *Thalassia testudinum* above and beneath the substrate surface, and depth of seagrass communities in northern Honduras and eastern Guatemala. Squares are below-substrate biomass estimates, and they represent mostly horizontal and vertical rhizomes and roots; circles are above-substrate biomass estimates and represent mostly leaves. Filled symbols represent estimates from Punta Manabique, Guatemala, where disturbance from sedimentation may have promoted rhizome growth.

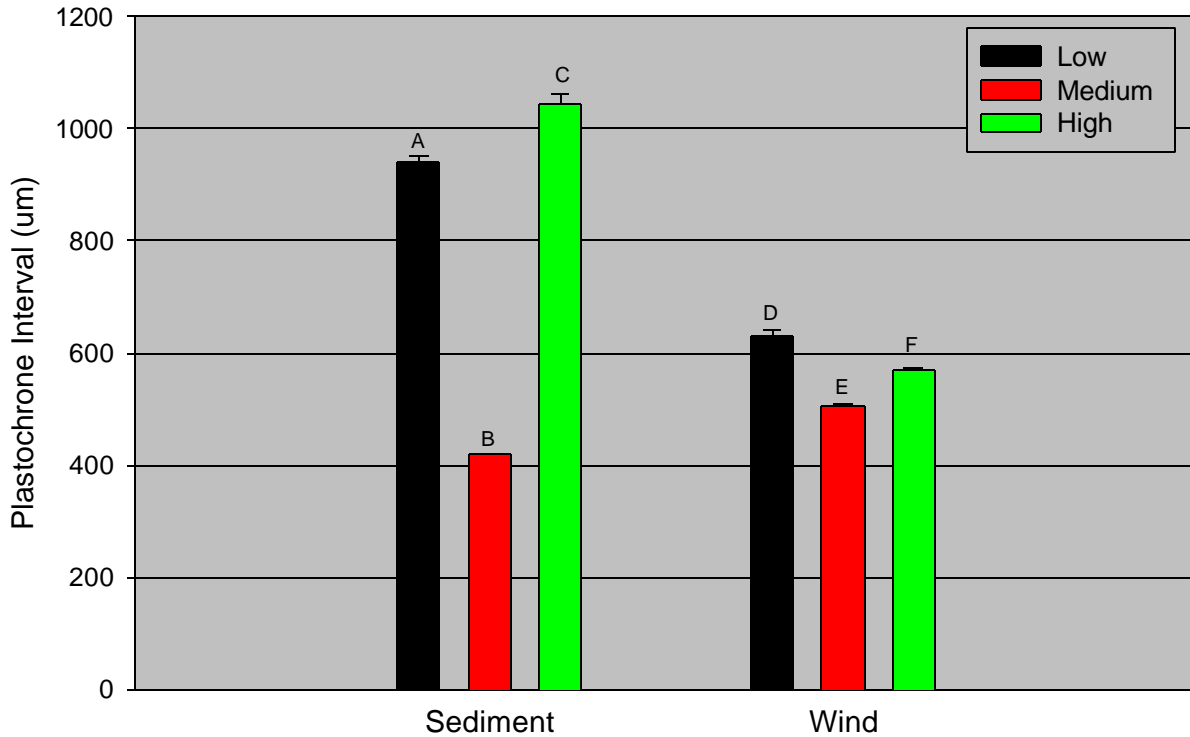


Figure 5. Mean plastochrone intervals (um) for shoots of *Thalassia testudinum* in sediment and wind impacted sites of Honduras and Guatemala; bars with the same letter are not significantly different ($P > 0.05$).

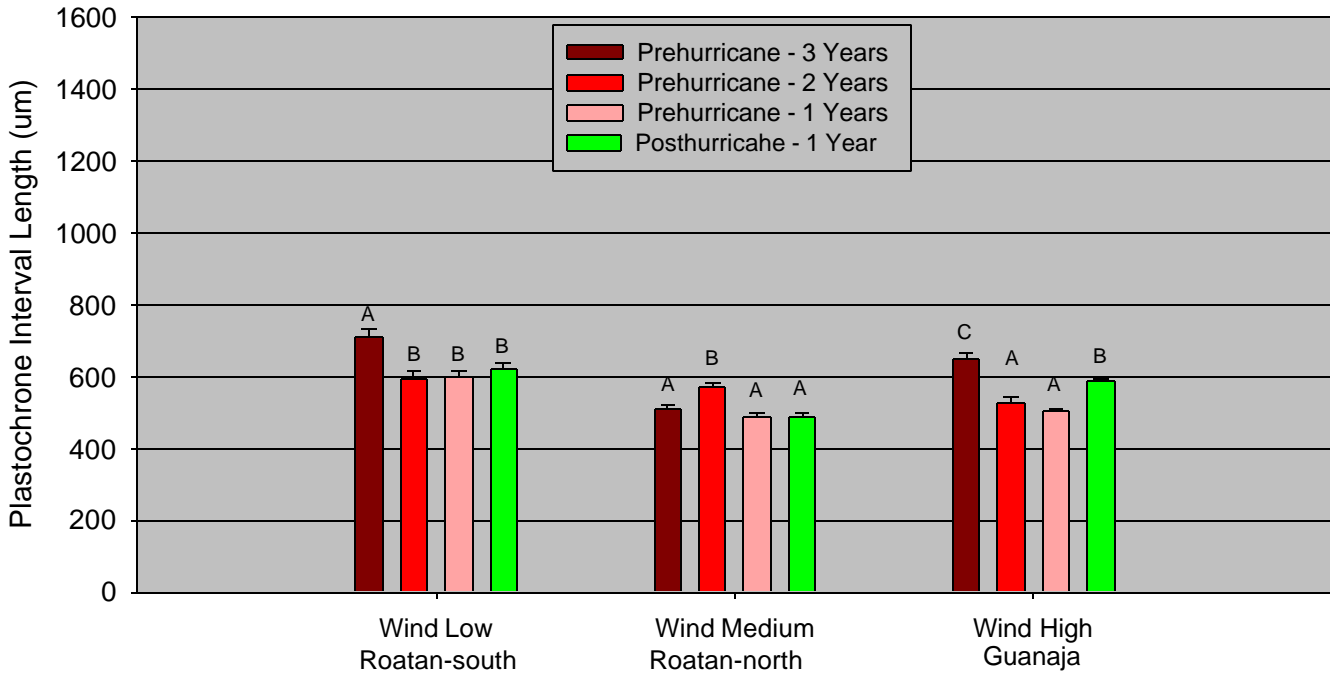


Figure 6. Mean plastochochone interval length (um) for shoots of *Thalassia testudinum* in wind impacted sites of Honduras and Guatemala for time periods relative to Hurricane Mitch (October 1998); Bars with the same letter are not significantly different ($P>0.05$) within sites.

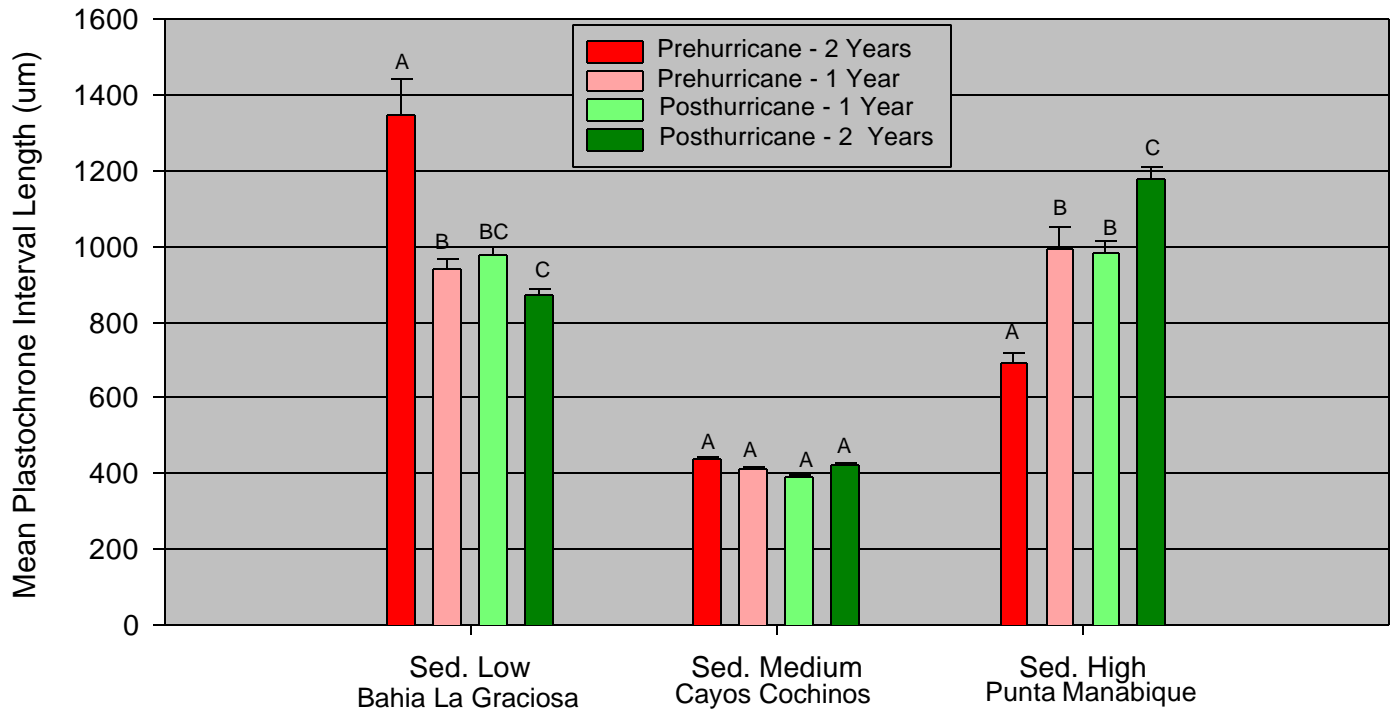


Figure 7. Mean plastochochone interval length (um) for shoots of *Thalassia testudinum* in sediment impacted sites of Honduras and Guatemala, for time periods relative to Hurricane Mitch (October 1998); Bars with the same letter are not significantly different ($P>0.05$) within sites.

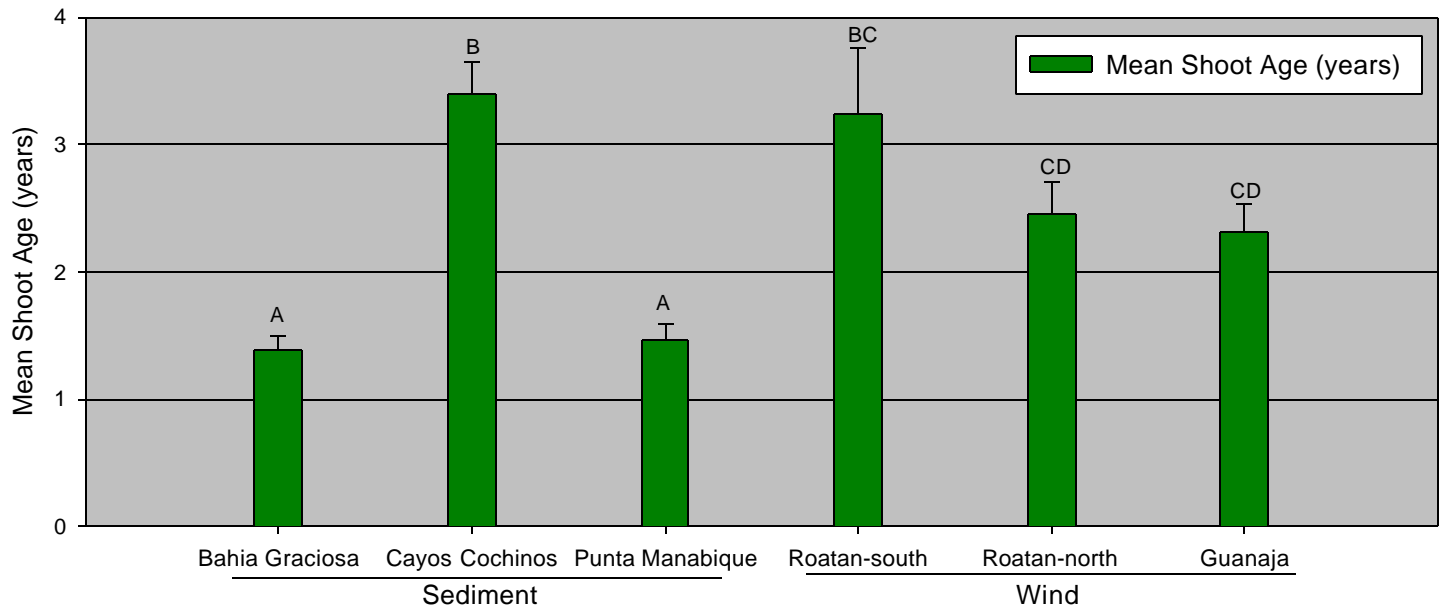


Figure 8. Mean Shoot age of *Thalassia testudinum* by site, Hurricane Mitch study, Honduras and Guatemala; Bars with the same letter are not significantly different ($P>0.05$) among sites.

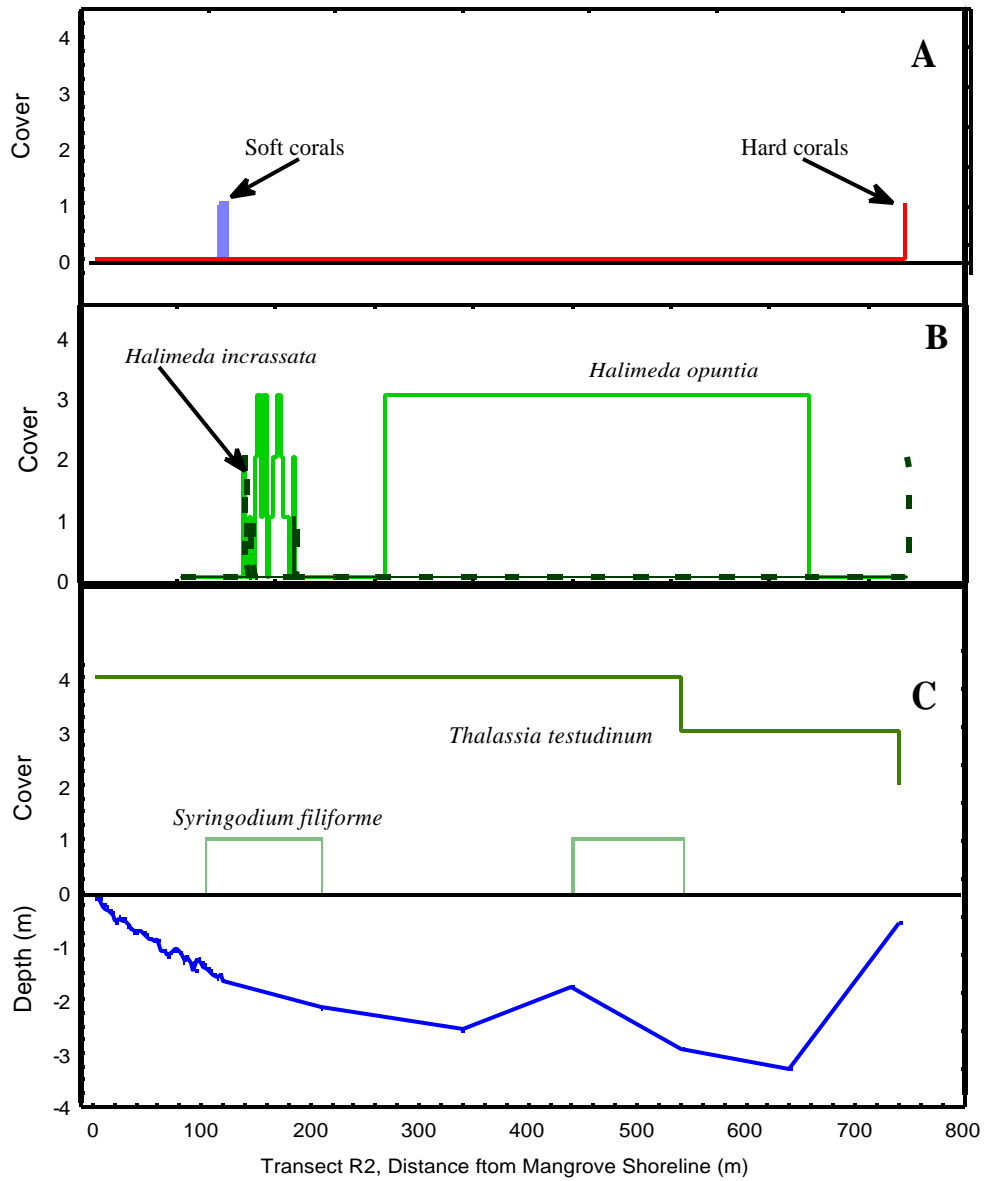


Figure 9. Transect R2, Roatan-south, Honduras. Leeward side of the island with low disturbance from winds expected. Depth and bottom communities: Depth (bottom graph) and Cover estimates are indicated at distances from the mangrove shoreline (beginning of transect) offshore. Cover values are visual estimates of bottom coverage by bottom community components: 0- no cover noted, 1- 1% to 15% cover, 2- 16% to 45% cover, 3- 46% to 75% cover, 4- 76% to 100% cover. **A:** hard corals and soft corals; **B:** calcareous algae; **C:** seagrasses.

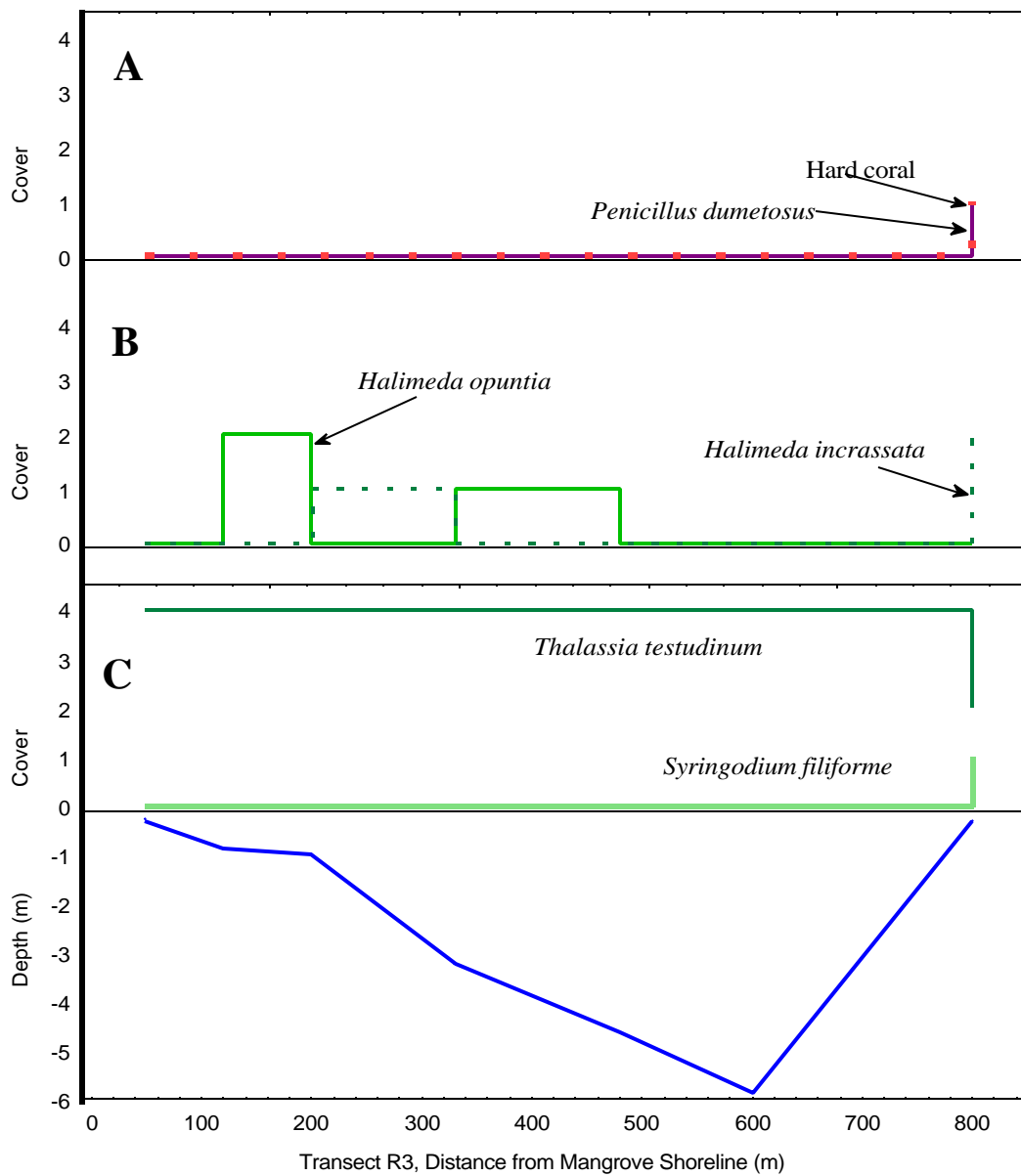


Figure 10. Transect R3, Roatan-south, Honduras. Leeward side of the island with low disturbance from winds expected. Depth and bottom communities: Depth (bottom graph) and Cover estimates are indicated at distances from the mangrove shoreline (beginning of transect) offshore. Cover values are visual estimates of bottom coverage by bottom community components: 0- no cover noted, 1- 1% to 15% cover, 2- 16% to 45% cover, 3- 46% to 75% cover, 4- 76% to 100% cover. **A**: hard coral and calcareous alga *Penicillus dumetosus*; **B**: calcareous algae; **C**: seagrasses.

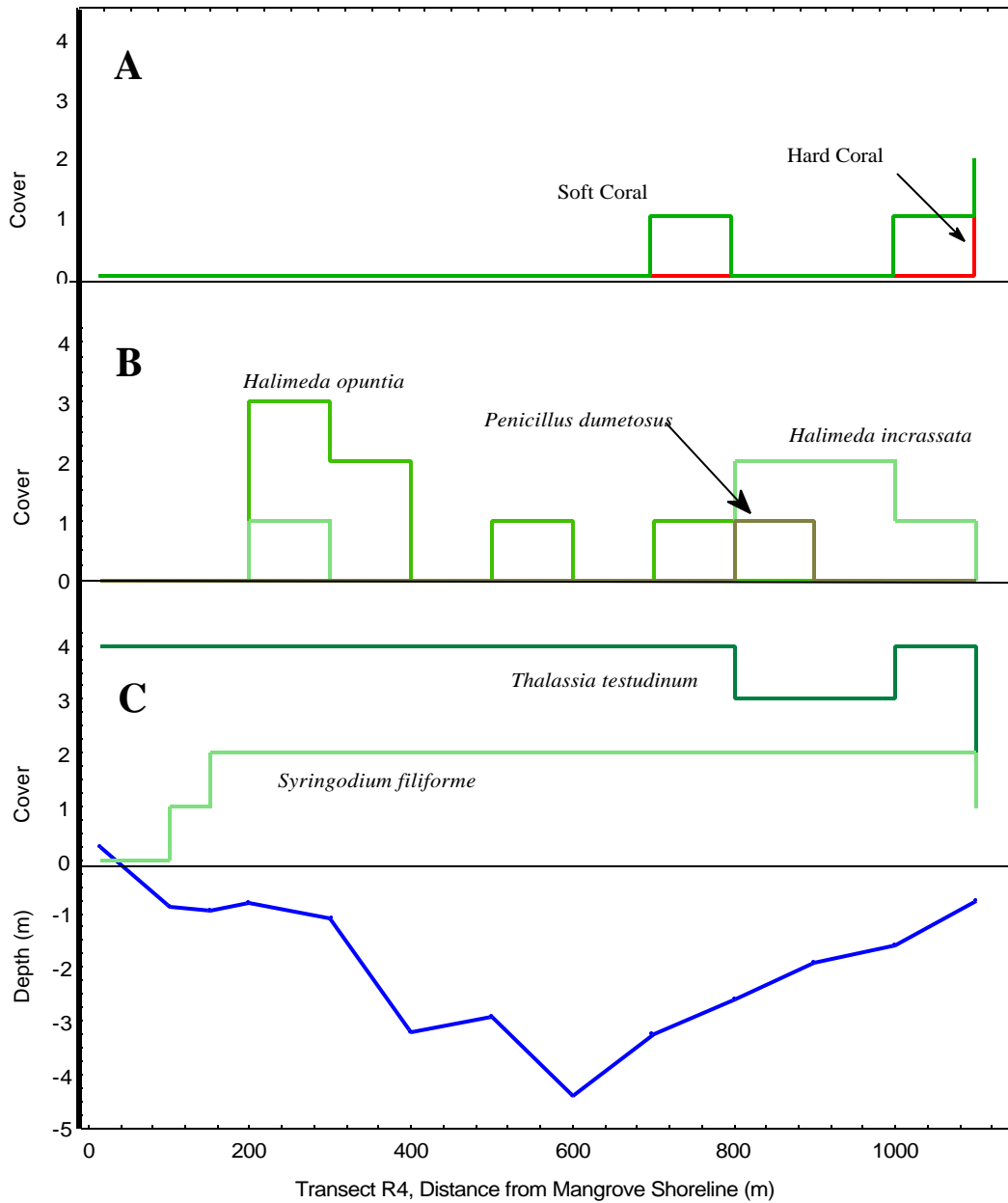


Figure 11. Transect R4, Roatan-north, Honduras. Windward side of the island with intermediate disturbance from winds expected. Depth and bottom communities: Depth (bottom graph) and Cover estimates are indicated at distances from the mangrove shoreline (beginning of transect) offshore. Cover values are visual estimates of bottom coverage by bottom community components: 0- no cover noted, 1- 1% to 15% cover, 2- 16% to 45% cover, 3- 46% to 75% cover, 4- 76% to 100% cover. **A:** hard coral and soft coral; **B:** calcareous algae; **C:** seagrasses.

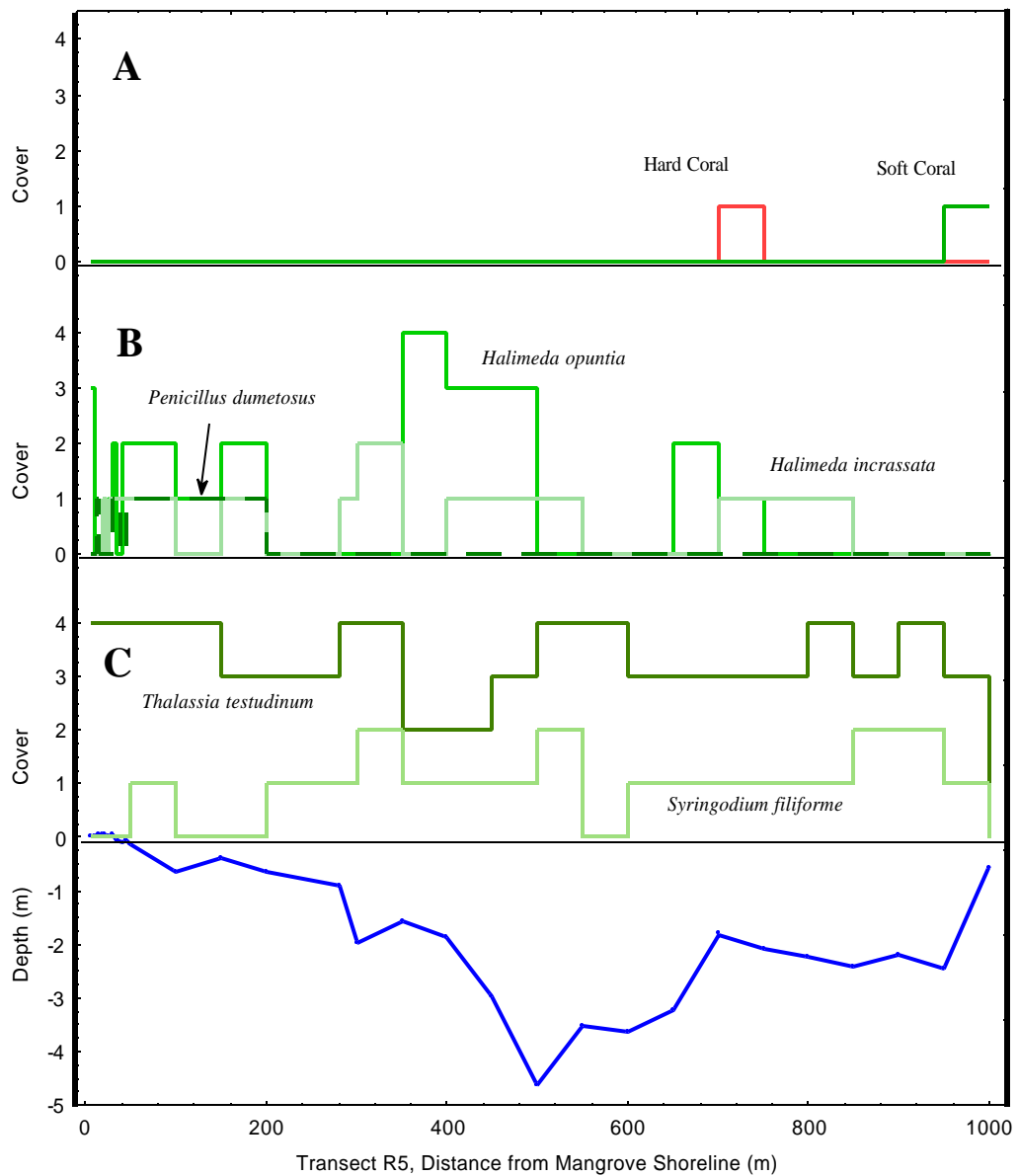


Figure 12. Transect R5, Roatan-north, Honduras. Windward side of the island with intermediate disturbance from winds expected. Depth and bottom communities: Depth (bottom graph) and Cover estimates are indicated at distances from the mangrove shoreline (beginning of transect) offshore. Cover values are visual estimates of bottom coverage by bottom community components: 0- no cover noted, 1- 1% to 15% cover, 2- 16% to 45% cover, 3- 46% to 75% cover, 4- 76% to 100% cover. **A:** hard coral and soft coral; **B:** calcareous algae; **C:** seagrasses.

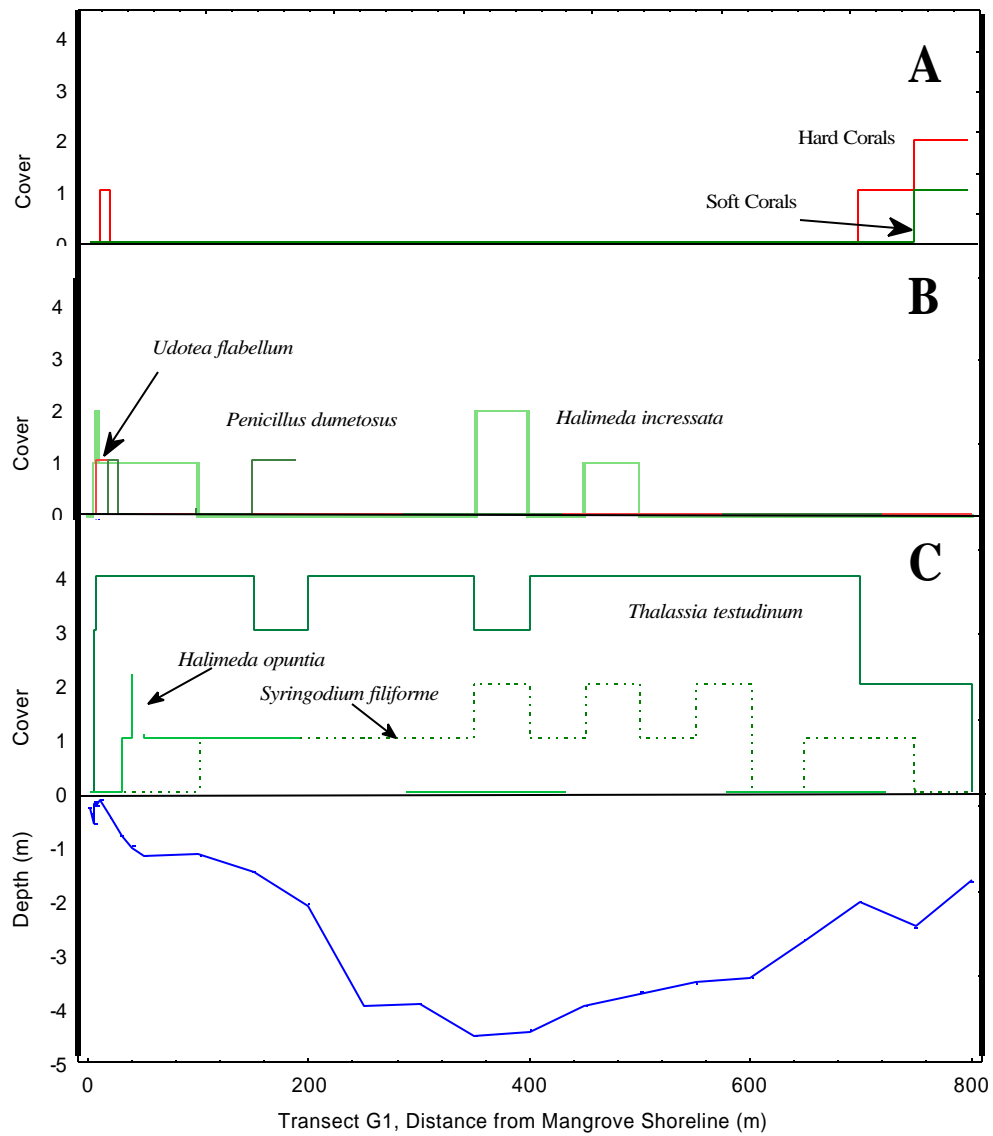


Figure 13. Transect G1, Guanaja, Honduras. Windward side of the island with high disturbance from winds expected. Depth and bottom communities: Depth (bottom graph) and Cover estimates are indicated at distances from the mangrove shoreline (beginning of transect) offshore. Cover values are visual estimates of bottom coverage by bottom community components: 0- no cover noted, 1- 1% to 15% cover, 2- 16% to 45% cover, 3- 46% to 75% cover, 4- 76% to 100% cover. **A:** hard coral and soft coral; **B:** calcareous algae; **C:** seagrasses and calcareous alga *Halimeda opuntia*.

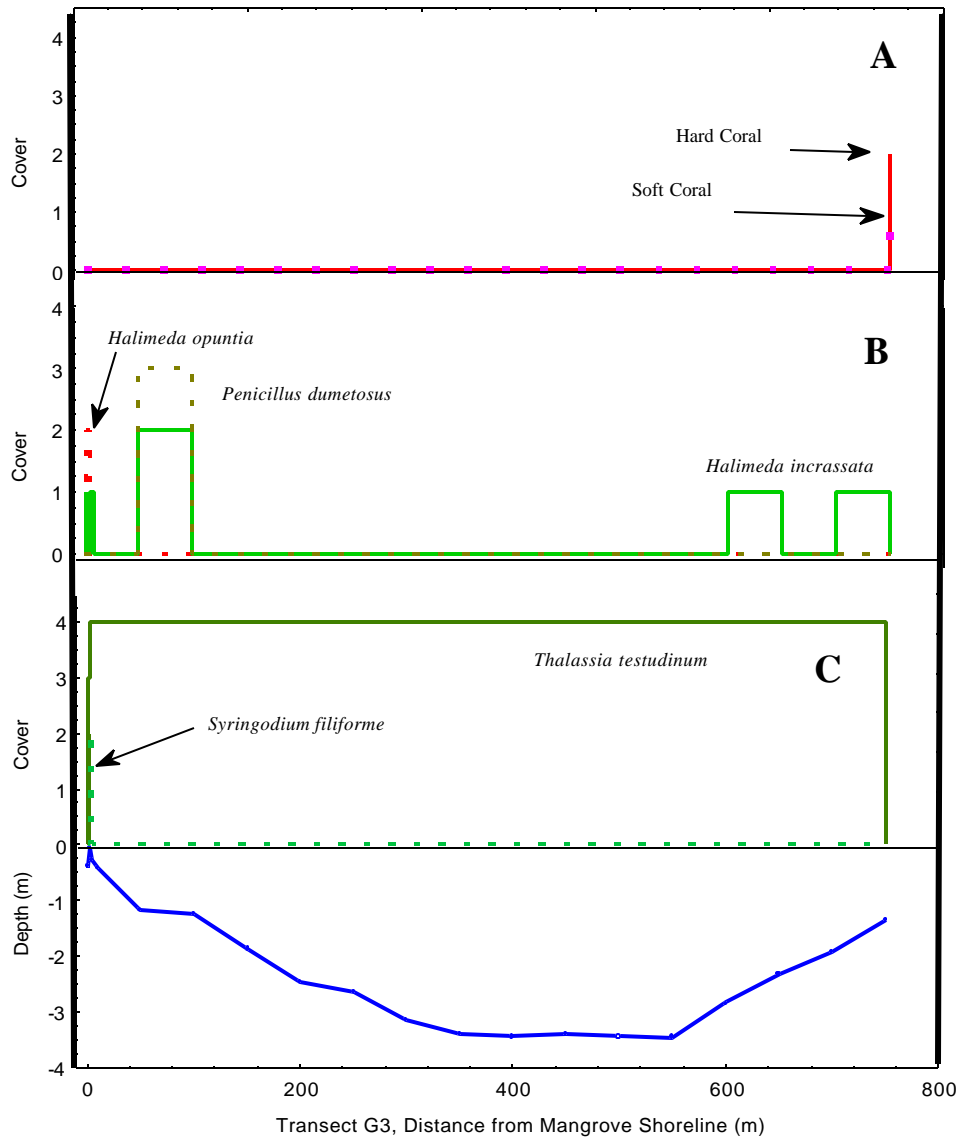


Figure 14. Transect G3, Guanaja, Honduras. Windward side of the island with high disturbance from winds expected. Depth and bottom communities: Depth (bottom graph) and Cover estimates are indicated at distances from the mangrove shoreline (beginning of transect) offshore. Cover values are visual estimates of bottom coverage by bottom community components: 0- no cover noted, 1- 1% to 15% cover, 2- 16% to 45% cover, 3- 46% to 75% cover, 4- 76% to 100% cover. **A**: hard coral and soft coral; **B**: calcareous algae; **C**: seagrasses.

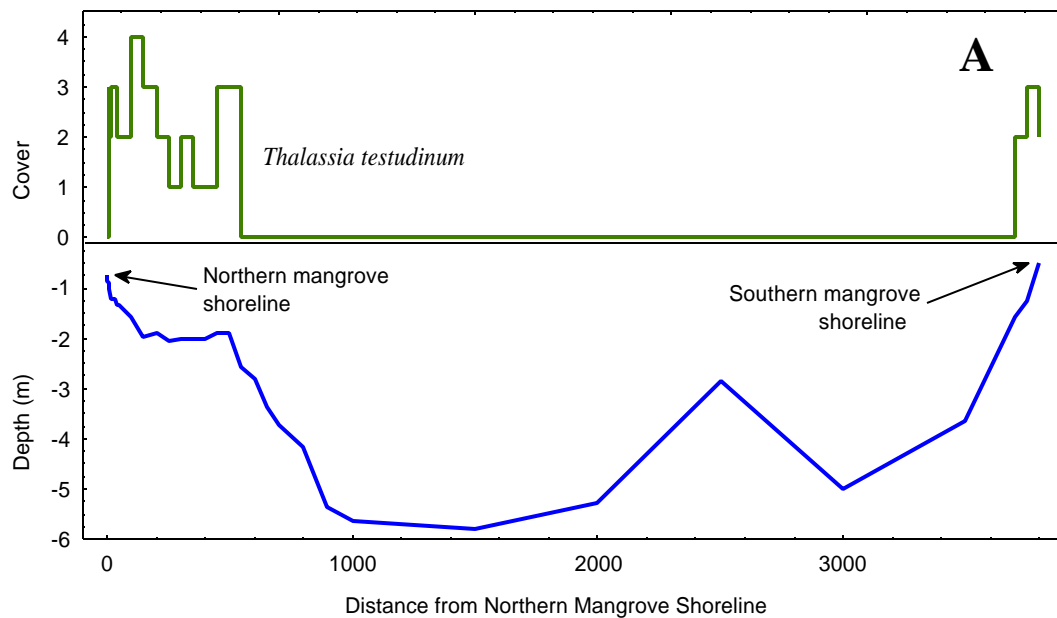
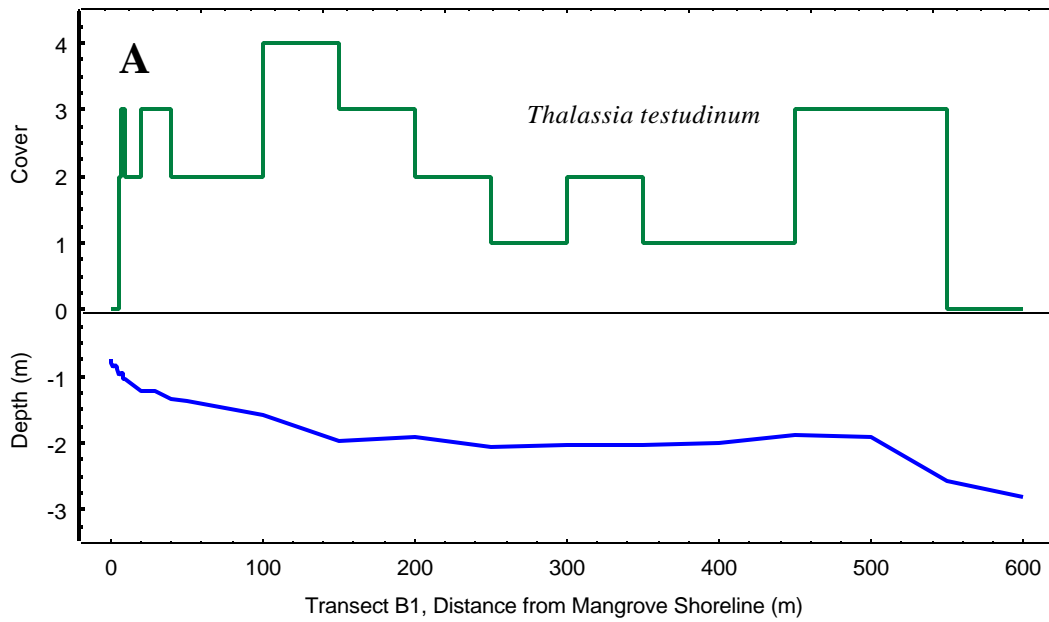


Figure 15. Transect B1 across Bahia la Graciosa, Guatemala. Top graph shows a close up of the nearshore zone from the northern mangrove shoreline to 600 m. Bottom graph shows the profile of the bay bottom from the northern mangrove shoreline to the southern mangrove shoreline. Graph A (both figures) shows *Thalassia testudinum* communities in shallow waters near shorelines. Bay waters were turbid during observations, so that the bottom was not visible below about 2 m. Depth (bottom graph) and Cover estimates are indicated at distances from the mangrove shoreline (beginning of transect) offshore. Cover values are visual estimates of bottom coverage by bottom community components: 0- no cover noted, 1- 1% to 15% cover, 2- 16% to 45% cover, 3- 46% to 75% cover, 4- 76% to 100% cover. A: seagrass cover.

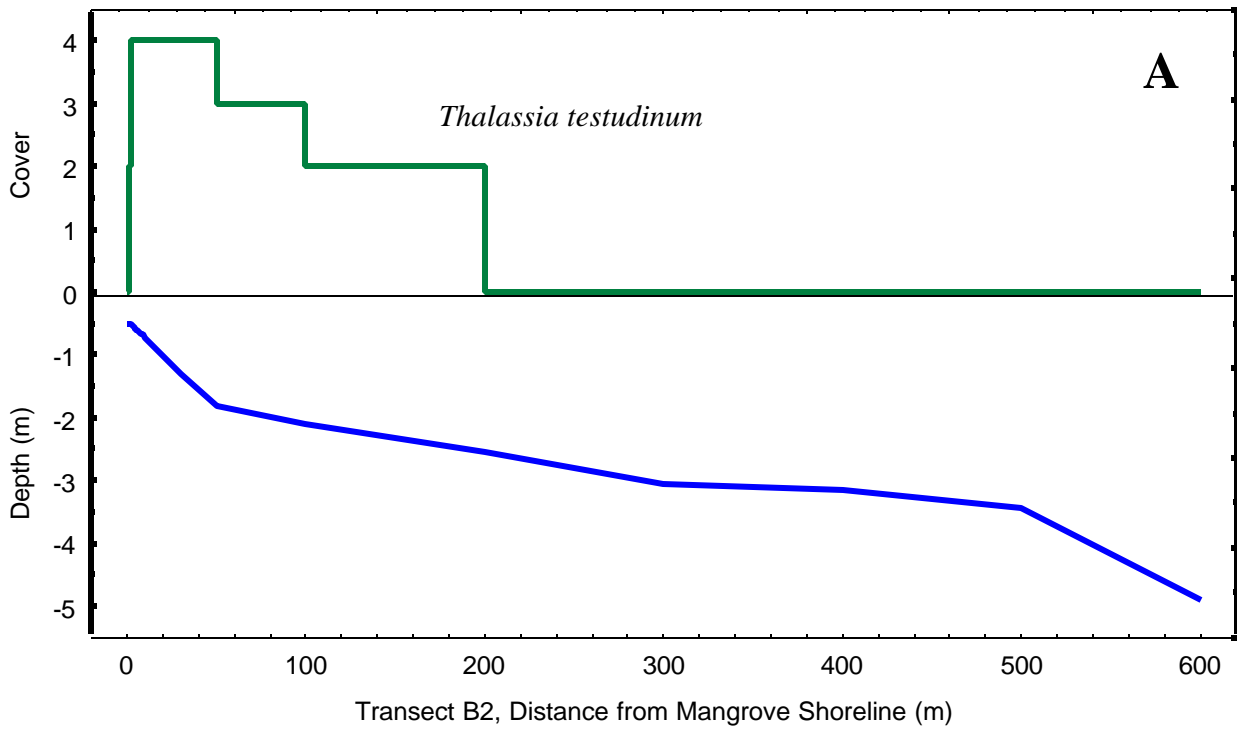


Figure 16. Transect B2, Bahia la Graciosa, Guatemala. Northern shore of the Bahia la Graciosa with low disturbance from sedimentation expected. Depth and bottom communities: Depth (bottom graph) and Cover estimate are indicated at distances from the mangrove shoreline (beginning of transect) offshore. Cover values are visual estimates of bottom coverage by bottom community components: 0- no cover noted, 1- 1% to 15% cover, 2- 16% to 45% cover, 3- 46% to 75% cover, 4- 76% to 100% cover. A: seagrass cover.

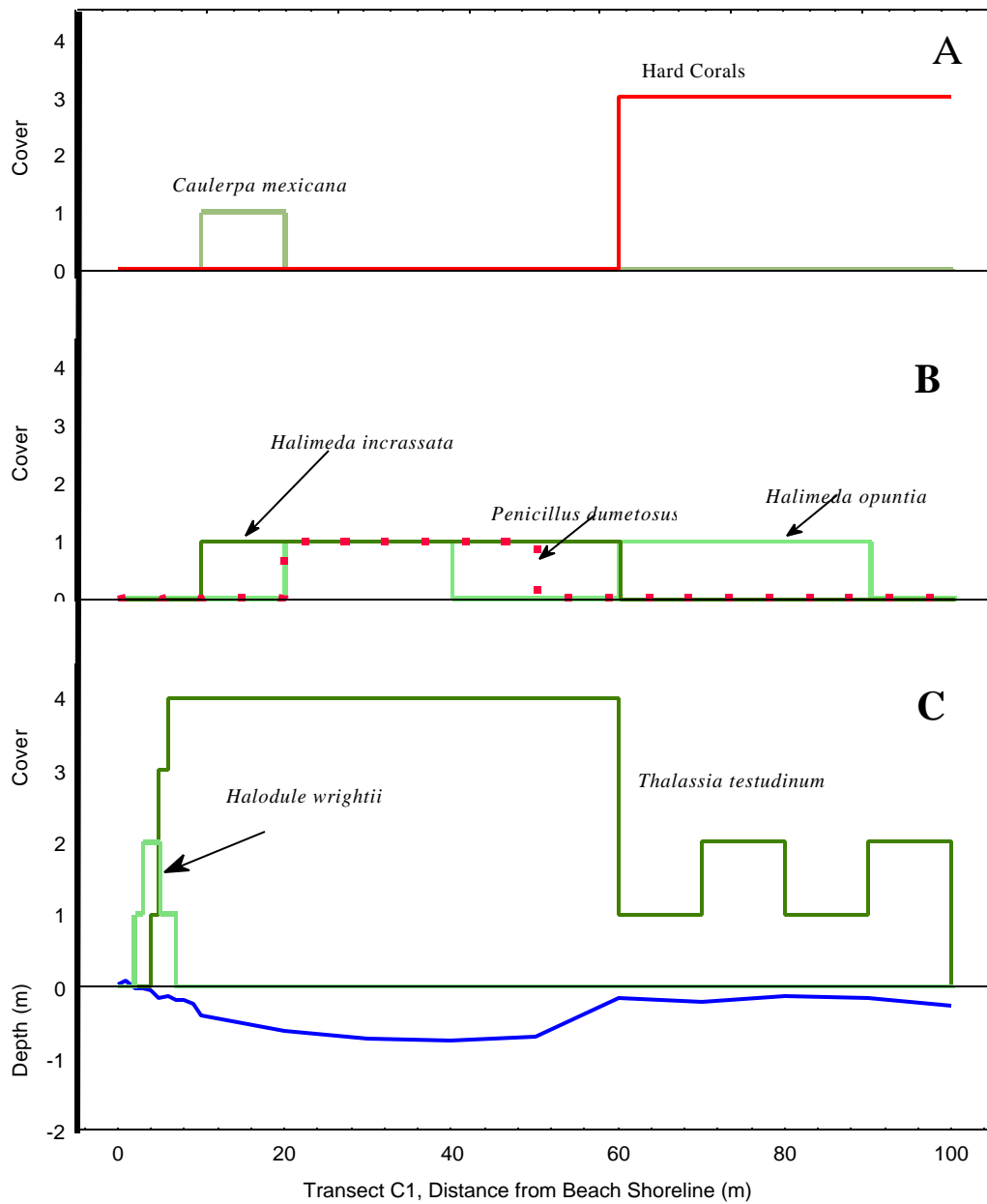


Figure 17. Transect C1, Cayos Cochinos, Honduras. Offshore islands with intermediate disturbance from sedimentation expected. Depth and bottom communities: Depth (bottom graph) and Cover estimate are indicated at distances from the beach shoreline (beginning of transect) offshore. Cover values are visual estimates of bottom coverage by bottom community components: 0- no cover noted, 1- 1% to 15% cover, 2- 16% to 45% cover, 3- 46% to 75% cover, 4- 76% to 100% cover. **A**: hard corals and alga *Caulerpa mexicana*; **B**: calcareous algae; **C**: seagrass cover.

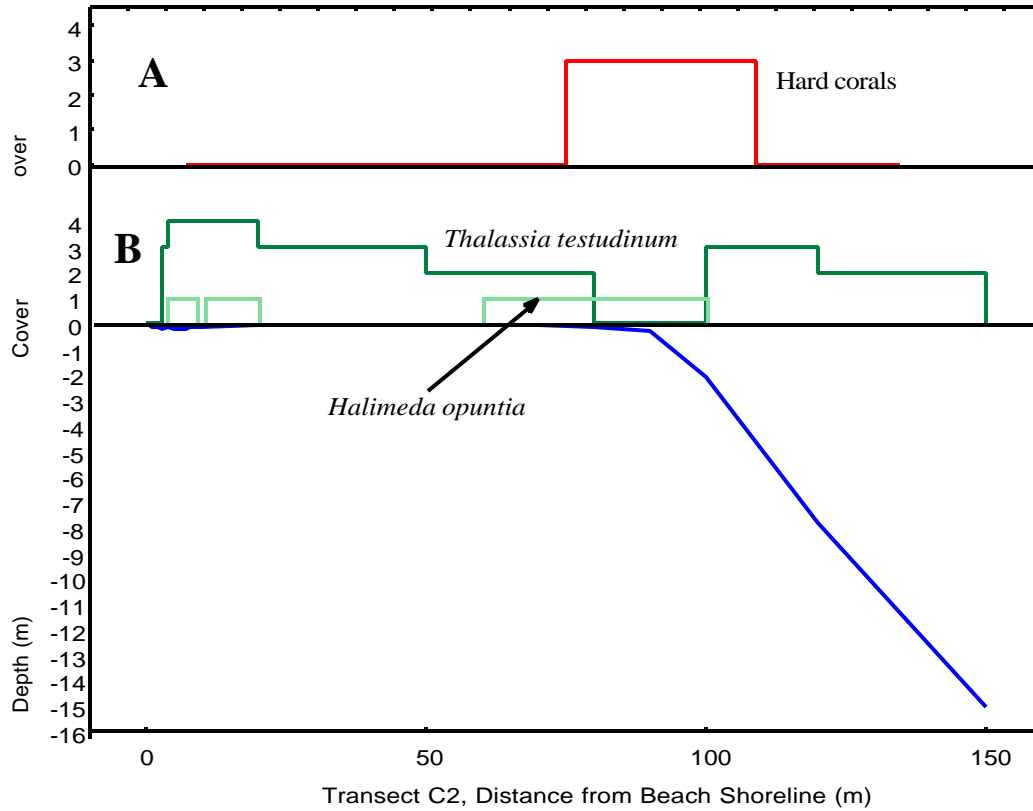


Figure 18. Transect C2, Cayos Cochinos, Honduras. Offshore islands with intermediate disturbance from sedimentation expected. Depth and bottom communities: Depth (bottom graph) and Cover estimate are indicated at distances from the beach shoreline (beginning of transect) offshore. Cover values are visual estimates of bottom coverage by bottom community components: 0- no cover noted, 1- 1% to 15% cover, 2- 16% to 45% cover, 3- 46% to 75% cover, 4- 76% to 100% cover. **A**: hard corals; **B**: seagrass (*Thalassia testudinum*) and calcareous alga (*Halimeda opuntia*) cover.

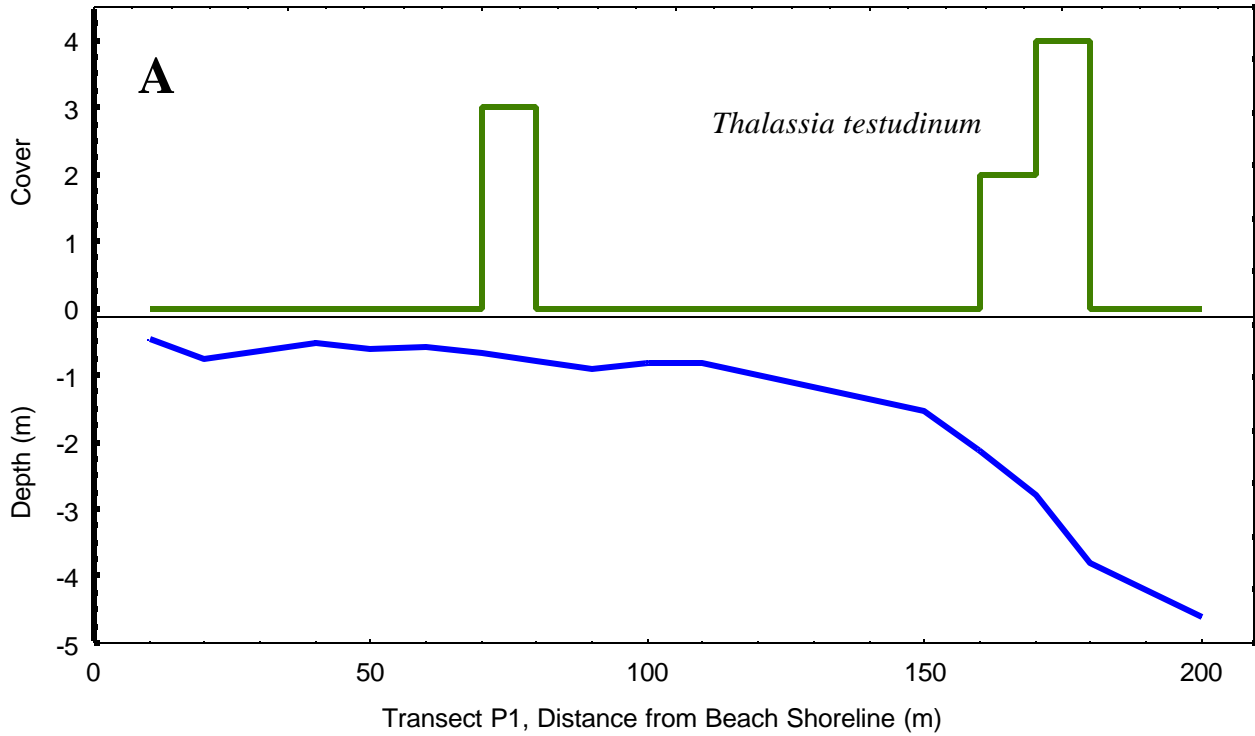


Figure 19. Transect P1, Punta Manabique, Guatemala. Western shoreline with high disturbance from sedimentation expected. Depth and bottom communities: Depth (bottom graph) and Cover estimate are indicated at distances from the beach shoreline (beginning of transect) offshore. Cover values are visual estimates of bottom coverage by bottom community components: 0- no cover noted, 1- 1% to 15% cover, 2- 16% to 45% cover, 3- 46% to 75% cover, 4- 76% to 100% cover. **A**: seagrass cover.

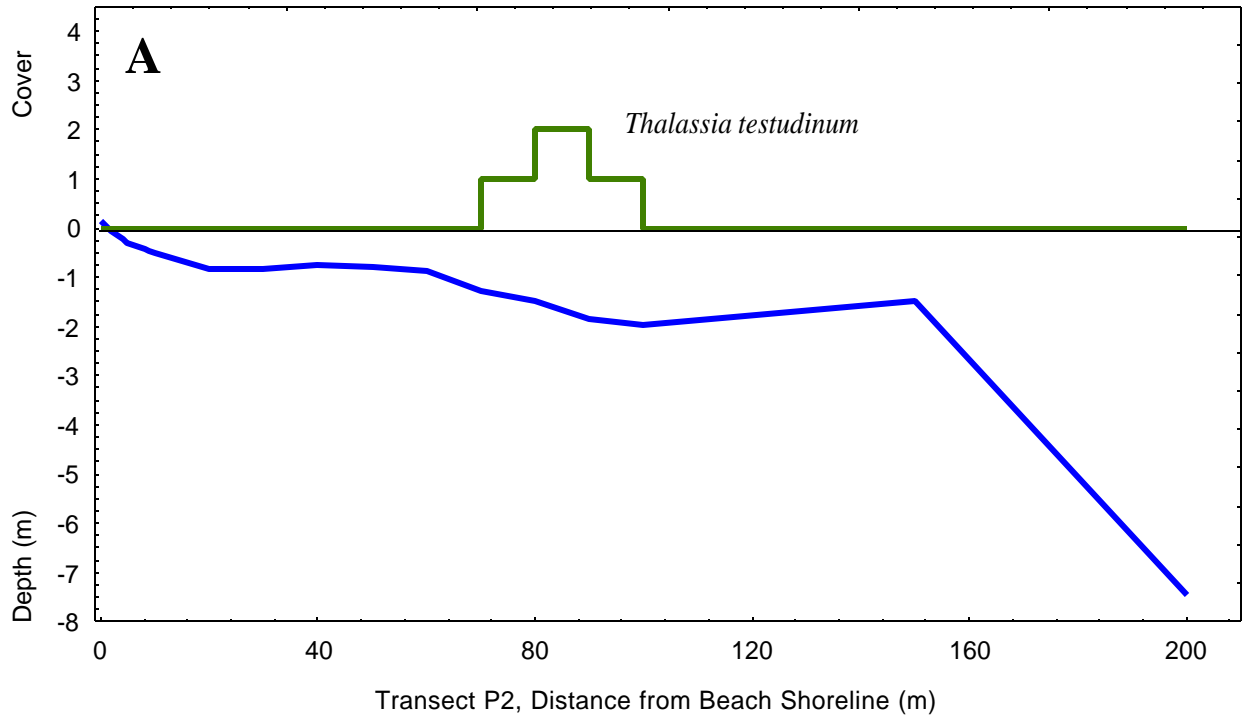


Figure 20. Transect P2, Punta Manabique, Guatemala. Western shoreline with high disturbance from sedimentation expected. Depth and bottom communities: Depth (bottom graph) and Cover estimate are indicated at distances from the beach shoreline (beginning of transect) offshore. **A**: sparse bottom cover of *Thalassia testudinum* was recorded.

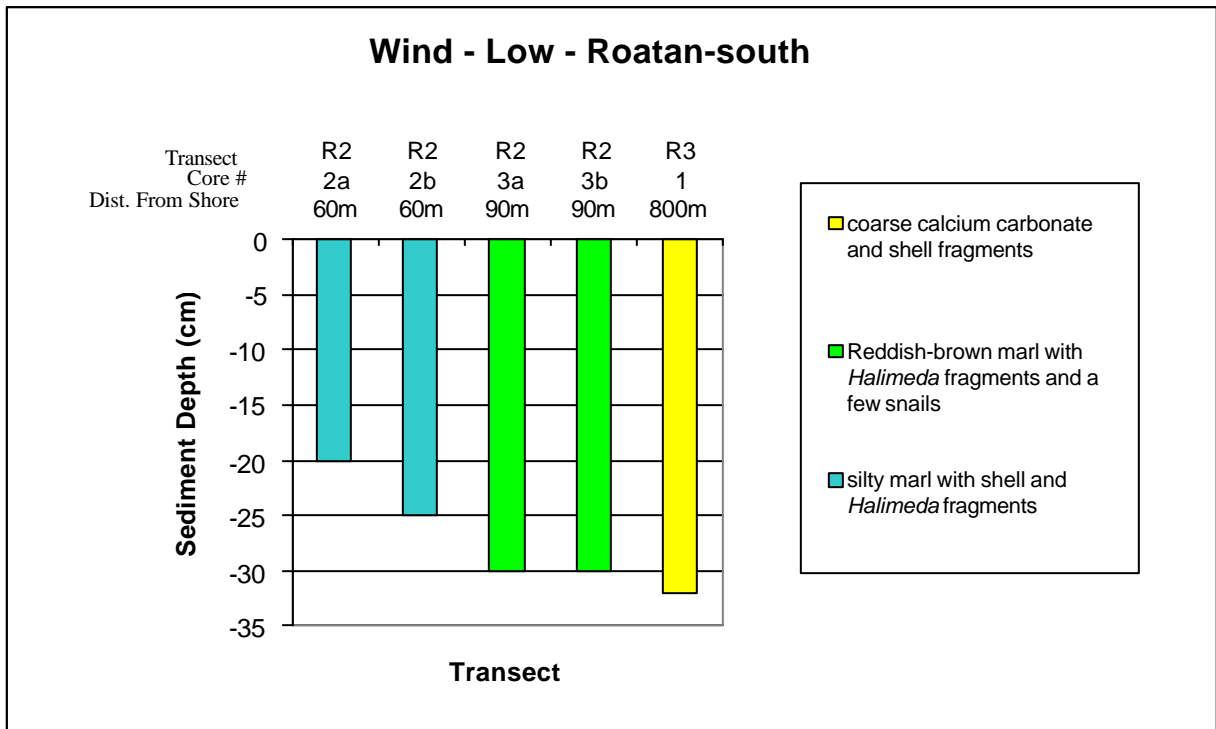


Figure 21. Sediment core profile for wind disturbance, low impact transects - Roatan-south, Honduras.

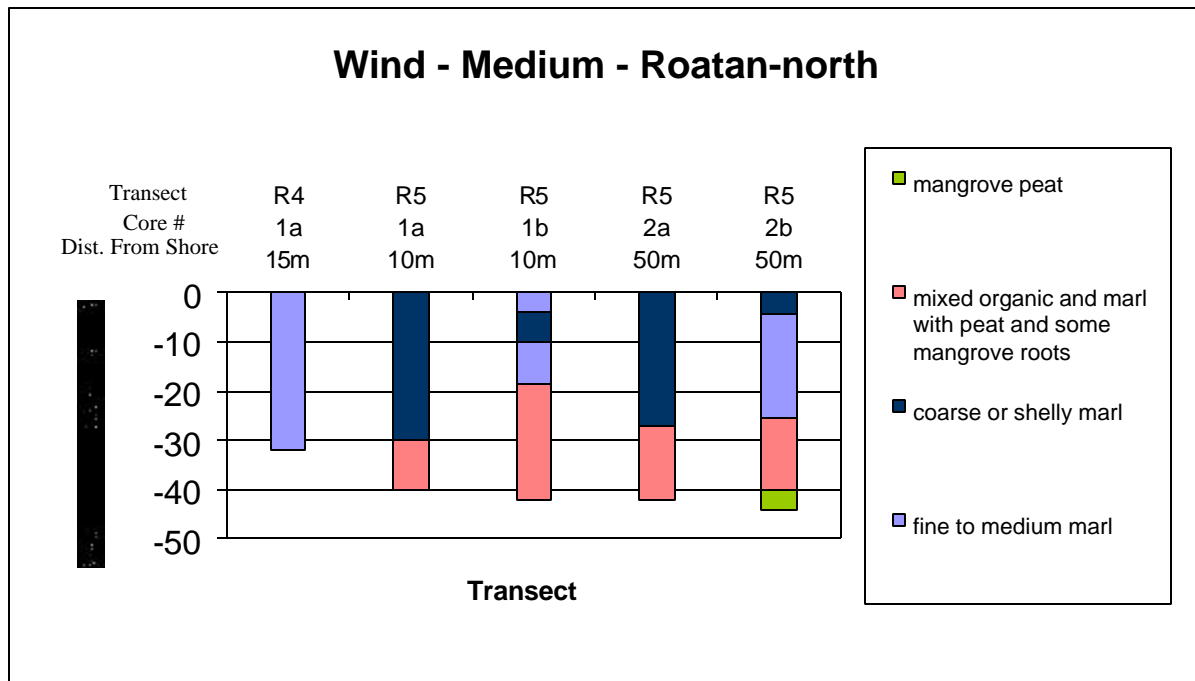


Figure 22. Sediment core profile for wind disturbance, medium impact transects - Roatan-north, Honduras.

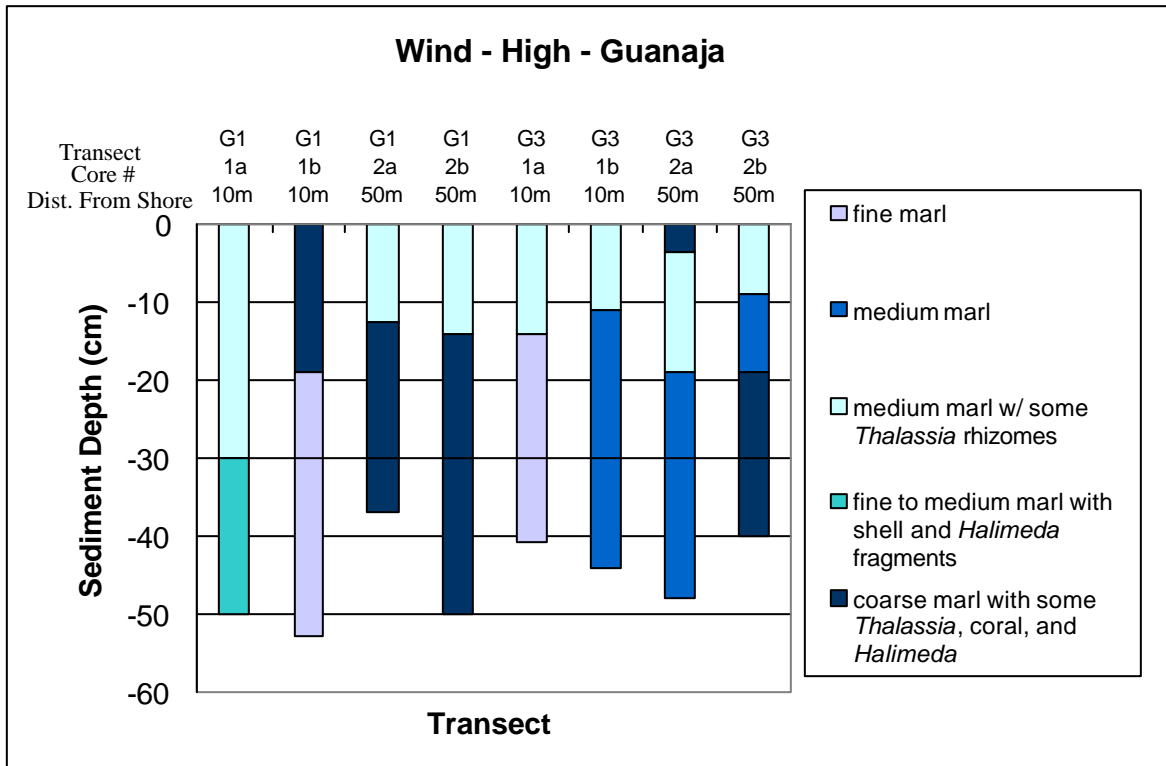


Figure 23. Sediment core profile for wind disturbance, high impact transects - Guanaja, Honduras.

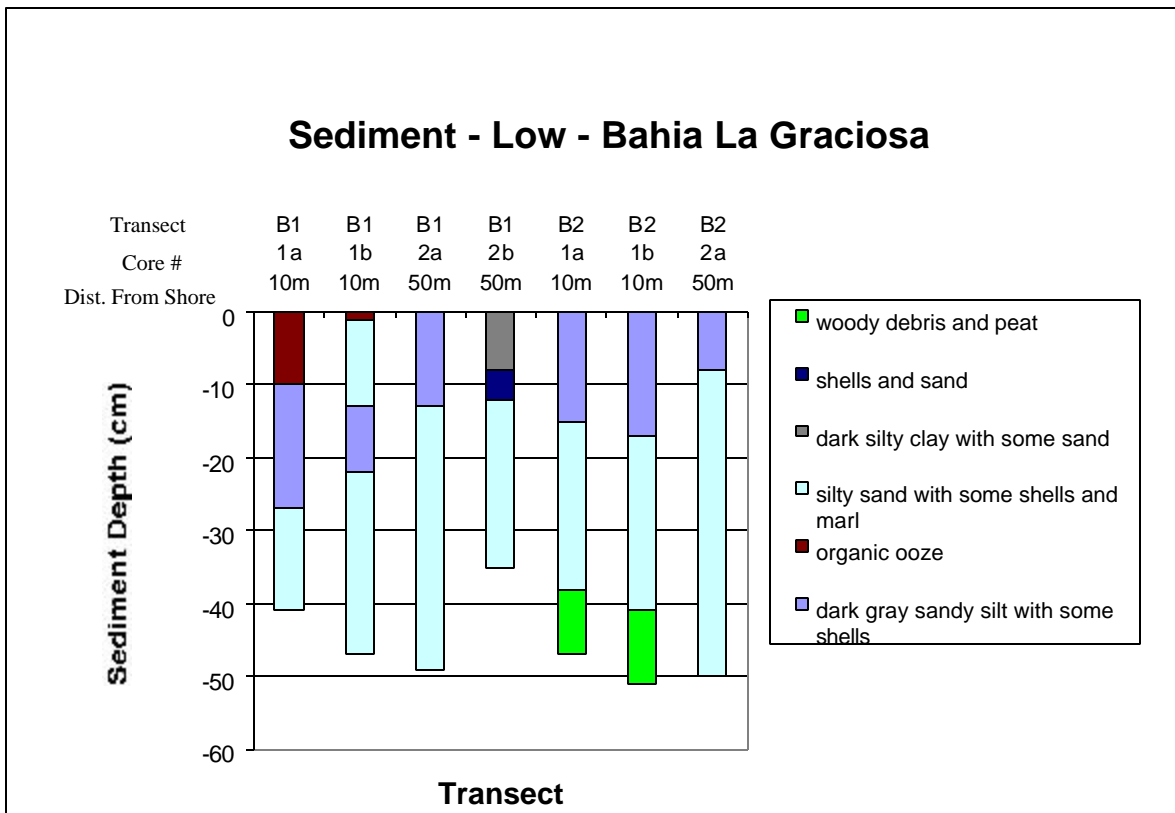


Figure 24. Sediment core profile for sediment disturbance, low impact transects - Bahia la Graciosa, Guatemala.

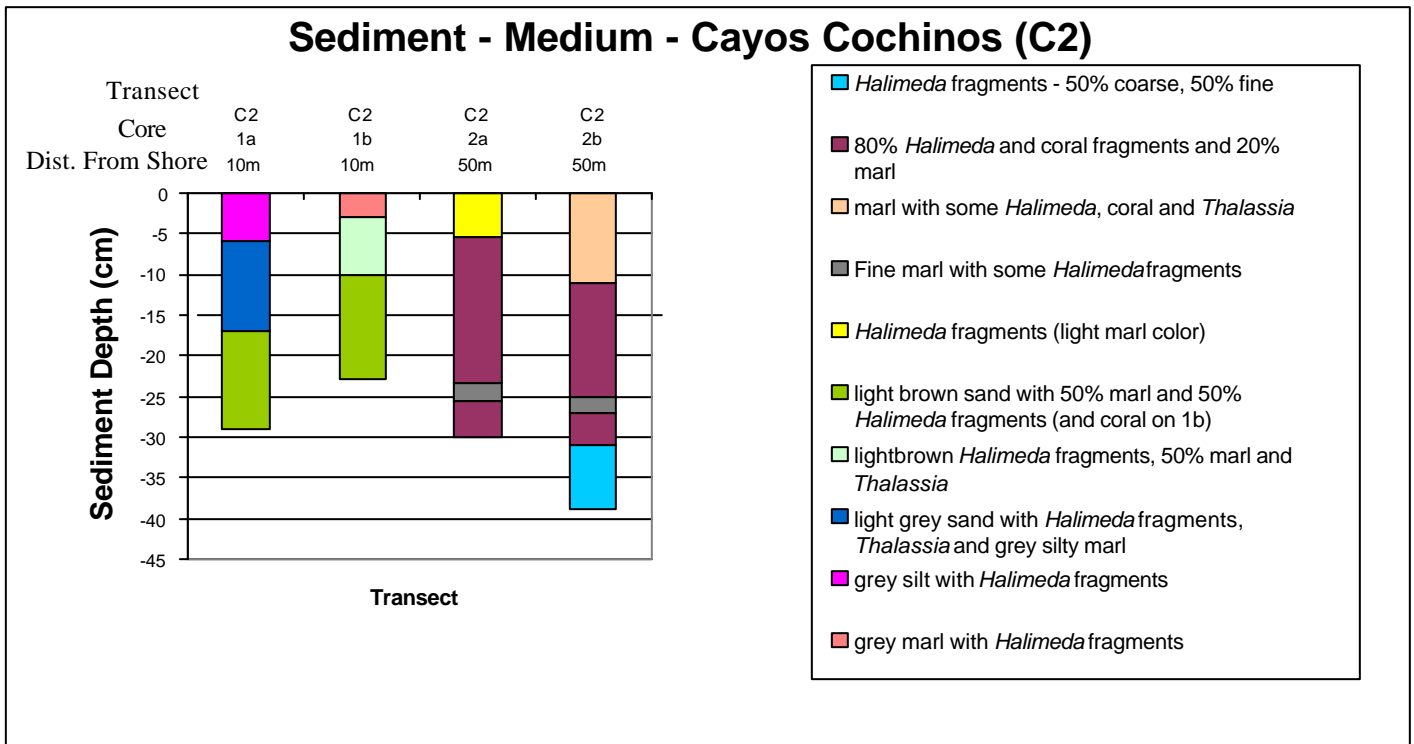
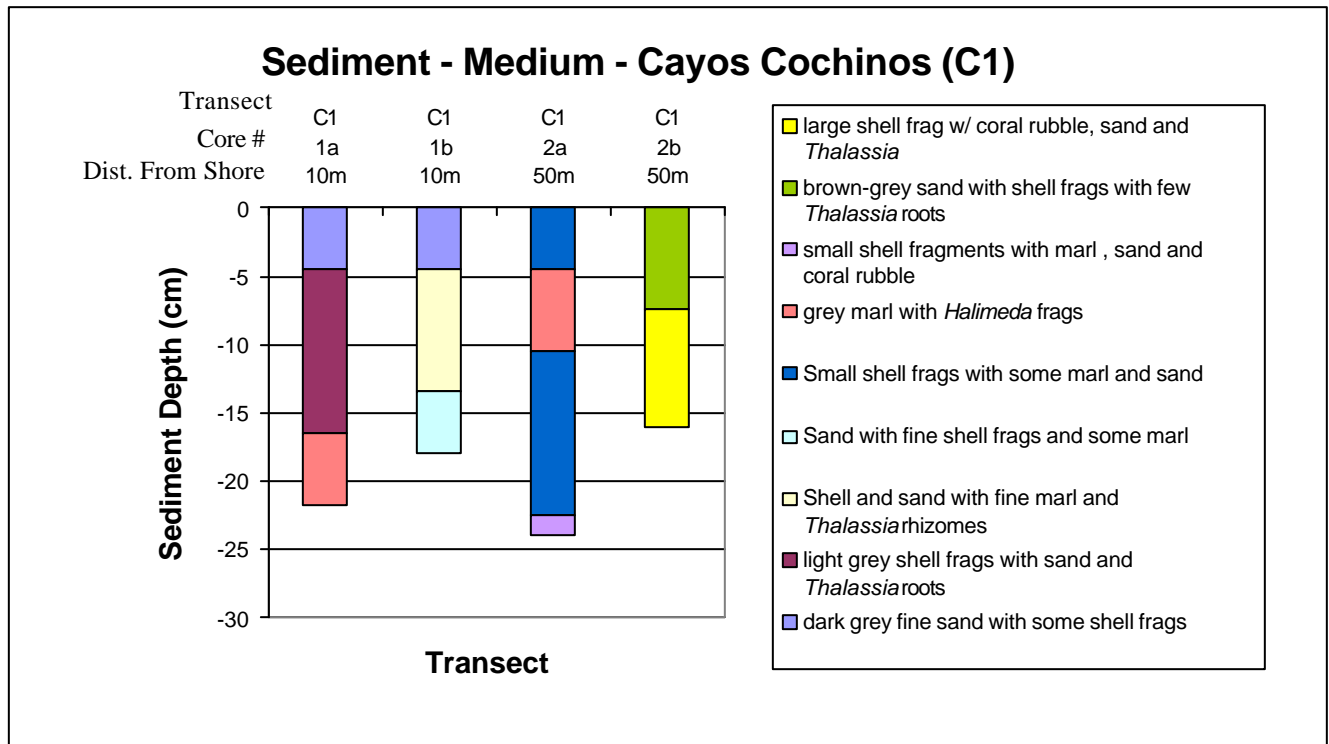


Figure 25. Sediment core profile for sediment disturbance, medium impact transects - Cayos Cochinos, Honduras (Transects C1 and C2).

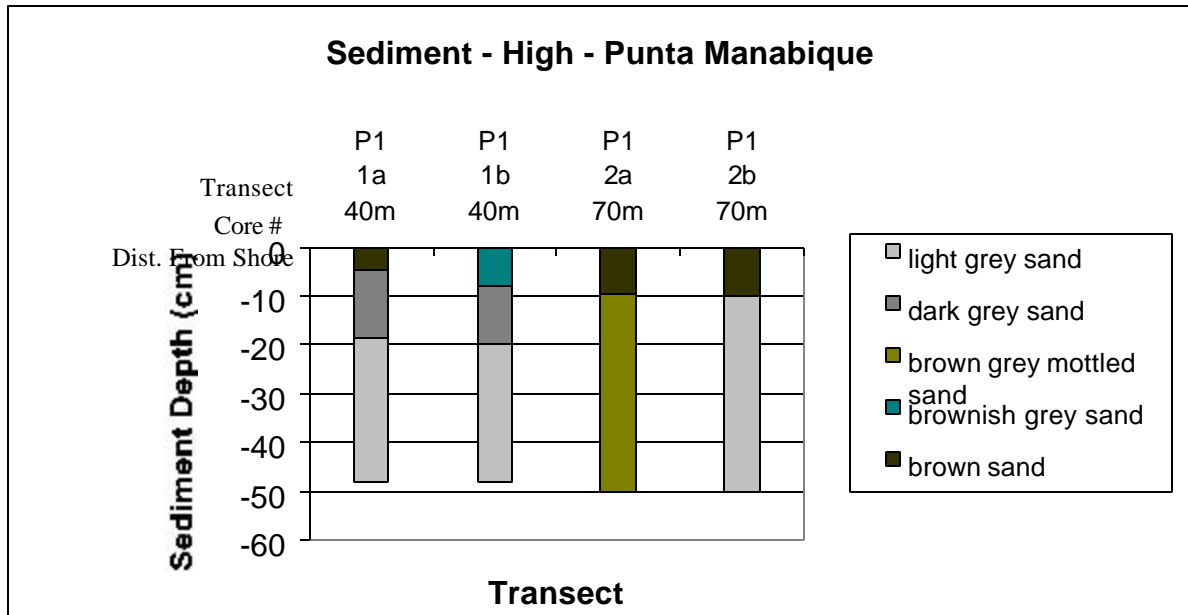


Figure 26. Sediment core profile for sediment disturbance, high impact transects - Punta Manabique, Guatemala.