

Environmental state and tendencies of the Puerto Morelos CARICOMP site, Mexico

Rosa E. Rodríguez-Martínez, Francisco Ruíz-Rentería, Brigitta van Tussenbroek, Guadalupe Barba-Santos, Edgar Escalante-Mancera, Guillermo Jordán-Garza & Eric Jordán-Dahlgren

Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. Ap. Postal 1152, 77500 Cancún, Q. Roo, México; rosaer@cmarl.unam.mx, renteria@cmarl.unam.mx, vantuss@cmarl.unam.mx, isis@cmarl.unam.mx, escalant@cmarl.ail.com, nadroj_ome@hotmail.com, jordan@cmarl.unam.mx

Received 10-VII-2009. Corrected 22-II-2010. Accepted 12-VII-2010.

Abstract: The CARICOMP site at Puerto Morelos, Mexico was monitored from 1993 to 2005. No significant changes in air temperature, wind patterns, periodicity and quantity of rainfall, sea-surface temperature and water transparency were observed between sampling years. During the study four hurricane impacts were registered. At the coral reef site overall mean cover of fleshy algae (47%) and turf algae (36%) were high, whereas cover of corals (2%) and sponges (3%), and abundance of sea-urchins (0.04 org m^{-2}) were consistently low. Gorgonians were dominant and showed changes in their community structure; the number of species increased from 1993 to 1995, their abundance decreased after Hurricane Roxanne (1995) and recovered by 2001. At four seagrass sites total community biomass remained constant ($707.1\text{-}929.6 \text{ g dry m}^{-2}$) but the above-ground biomass of the seagrass *Syringodium filiforme* and fleshy algae increased gradually. Total biomass ($531\text{-}699 \text{ g dry m}^{-2}$) and leaf productivity ($0.89\text{-}1.56 \text{ g dry m}^{-2} \text{ d}^{-1}$) of the seagrass *Thalassia testudinum* remained constant, but the species invested proportionally more biomass in above-ground leaf tissues at the end of the study. The minor hurricanes from 1993 until 2005 had no detectable impacts on the seagrass beds, however, the major Hurricane Wilma (October 2005) changed the community composition at three stations and caused complete burial of the vegetation at a coastal station. The gradual changes in the seagrass and reef communities recorded in the 12 years of continuous monitoring of the CARICOMP site may reflect the increased pollution caused by the rapid augment in urban and tourist developments along the coasts and inland from Puerto Morelos, coupled with poor water management practices. *Rev. Biol. Trop.* 58 (Suppl. 3): 23-43. Epub 2010 October 01.

Key words: environmental monitoring, CARICOMP, Mexico, coral reef, seagrass.

Typical Caribbean coastal systems consist of the highly complex and productive coral reefs, seagrass beds and mangrove forests (Moberg & Folke 1999), interconnected and linked to the open ocean and the nearby inland areas. Subject to many types of stressors, which often have community-specific impacts and may act in a synergistic rather than additive manner (Hughes & Connell 1999), the community dynamics of these systems have yet to be fully understood (Hughes *et al.* 1992, Done *et al.* 1996). In addition, the serious decline of coral reefs (Hughes 1994), seagrass beds (Short

& Echeverría 1996) and mangroves (Farnsworth & Ellison 1997) worldwide in the last decades led to a radical reassessment of the way these systems were monitored. Studies at small spatio-temporal scales provide information on the behavior of the system at a particular place and time but, can not be extrapolated to understand regional or long-term processes, because community dynamics are highly variable, even at local scales (Bythell *et al.* 2000, Fourqurean *et al.* 2001). Also, the effect of major impacts, such as hurricanes, and subsequent possible primary or secondary succession, can only be

evaluated with longer-term assessments of the communities.

In 1992, the Caribbean Coral Reef Productivity (CARICOMP) Program was established with the objective of conducting a long-term region-wide monitoring program to analyze changes in the structure of the principal Caribbean coastal ecosystems: coral reefs, mangroves and seagrasses (CARICOMP 1994). To achieve this goal, a relatively simple sampling protocol was developed, such that could be implemented easily at any site in the region, regardless of the local infrastructure for scientific studies.

In this study we report on the variations recorded in environmental variables and changes at the level of reef and seagrass communities between 1993 and 2005 at the Puerto Morelos CARICOMP site. Possible correlations between environmental parameters and changes at the reef and seagrass communities were assessed. The results obtained in this study provide a baseline that will allow for the evaluation of present and future potential impacts of the continuous increasing human developments along the Caribbean coasts of Mexico and global natural and anthropogenic disturbances.

MATERIALS AND METHODS

Study site: The CARICOMP site in Mexico is located near Puerto Morelos on the NE coast of the Yucatan Peninsula (Fig. 1). An extended fringing reef forms a 3-4m deep reef-lagoon, characterized by calcareous sand that is stabilized by seagrass meadows. The reef has well-developed back-reef and crest zones and a relatively flat fore-reef that descends gradually to 20-25m into an extensive sand platform. Inland wetlands are separated from the sea by a 2-3m high, and 100-200m broad, sand bar. A detailed description of the study area is found in Ruíz-Rentería *et al.* (1998). Puerto Morelos was a small fishing village until the early 1980's, when it developed rapidly as tourism became the main economic activity. During the course of our study (1993-2005) the population and number of hotel rooms experienced a three-fold increase (Table 1). By mid-2009, the local population was estimated at 15 000 and there were 6 000 hotel rooms. Coastal development poses several threats to the well-being of coastal systems including the increase of nutrients and pollutant levels in coastal waters due to the general lack of sewage treatment plants in the area (with the exception of some hotels),

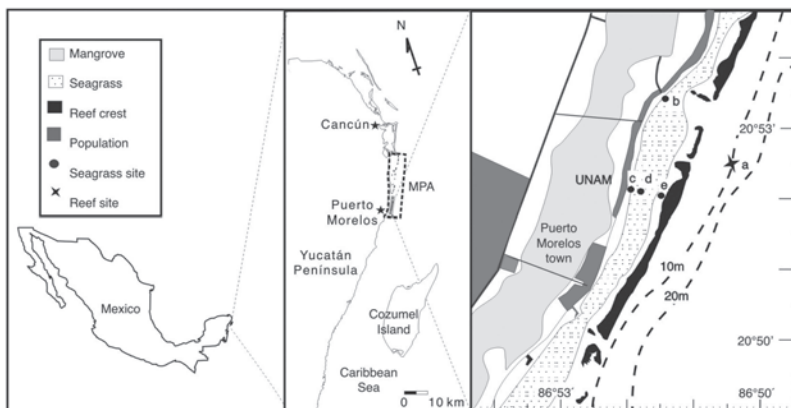


Fig. 1. Location of the Puerto Morelos Mexico CARICOMP site. The distribution of the CARICOMP stations are indicated: (a) coral reef; (b) seagrass high productivity; (c) seagrass coastal; (d) seagrass typical and (e) seagrass reef.

TABLE 1

Socio-demographic parameters and major disturbance events in the Puerto Morelos CARICOMP site from 1993 to 2005

Year	Population ¹	Hotel rooms ²	Hurricanes ³	Bleaching ⁴	Diseases
1993	-	-	-	0	nd
1994	-	-	-	0	nd
1995	2224	401	Roxane (3) ⁵	severe	nd
1996	-	-	-	0	nd
1997	-	-	-	low	nd
1998	-	-	-	moderate	WB, WPx
1999	-	-	-	0	nd
2000	3438	401	-	0	DS, WB, WP, WPx, YB
2001	-	-	-	0	BB, DS, WB, WP, WPx, YB
2002	-	-	-	low	nd
2003	-	-	-	moderate	BB, DS, WB, WP, WPx, YB
2004	-	-	Ivan (5) ^{5,6}	moderate	BB, DS, WB, WP, WPx, YB
2005	7726	1455	Emily (2) ⁶ Wilma (5)	severe	BB, DS, WB, WP, WPx, YB

nd: no data, BB: Black-band disease, DS: dark-spots disease, WB: white-band diseases, WP: white-plague disease, WPx: white-pox disease, YB: yellow-band disease.

¹ Source: Censos de Población y Vivienda, INEGI (1995, 2000, 2005)

² Source: Secretaría de Turismo del Estado de Quintana Roo (<http://sedetur.qroo.gob.mx/index.php>)

³ Hurricane categories marked in parenthesis according to the Saffir-Simpson scale

⁴ Bleaching events intensity as: low =<20% of colonies, moderate=21-50%, severe=<51%

⁵ Hurricane Ivan passed over 200km away from Puerto Morelos reef but caused high waves than produced detachment of benthic organisms

⁶ Survey on the reef site were conducted before the hurricanes stroke in 1995 and 2004.

an underground water circulation system that outfalls in mangrove wetlands and submarine springs and the seepage through the sand bar in response to rain inputs (Rodríguez-Martínez 2008). Sedimentation is not a major problem due to the lack of superficial rivers in the Yucatan peninsula, although beach restoration projects and construction of piers are potential sources of sediment inputs to the site. In 1998, Puerto Morelos reef was declared a marine protected area and in average it receives *ca.* 200 000 visitors per year (<http://www.conanp.gob.mx>).

Monitoring of environmental parameters. From 1993 to 2005, sea-surface temperature, maximum-minimum air temperature and accumulated precipitation were sampled

on near-daily basis following the CARICOMP level I protocol (CARICOMP 1994). Sea surface temperature was measured at the pier of the Universidad Nacional Autónoma de México (UNAM) research facilities at Puerto Morelos, Mexico where the depth is about 2.5m. Sea-surface temperature and refractometer readings of salinity were measured weekly at the Reef, Typical and High-productivity seagrass stations (Fig. 1). Weekly Secchi disk (30cm diameter) measurements were carried at the Typical and High-productivity seagrass stations (horizontal measurements) and 2-3km east from the reef crest (vertical measurement). On some occasions measurements were taken at different times than the ones established by the protocol and usually no measurements were conducted on weekends and vacation periods.

Monitoring of the coral reef site: The reef site was established in 1993, approximately 3km offshore (20°53.11' N-86°50.28' W) on a typical low-relief fore-reef as indicated by the CARICOMP protocol (Fig. 1). Five permanent 10m transects were deployed randomly perpendicular to the slope at a depth of 10m. The end-points of each permanent transect were fixed with stainless steel stakes. Line intercept measurements were taken using a brass chain (link length=1.4cm) deployed between the fixed stakes. The number of chain-links covering a given benthic category/species provided an estimate of its proportion of relative cover along the chain, the main benthic categories where coral, gorgonian, algae (fleshy, calcareous, turf, coralline), sponges, rock and sediment. Identification of corals and gorgonians was carried out to species level. Gorgonians were counted when their branches or fronds crossed the transect line under the normal surge conditions, and in order to follow the standardization of the CARICOMP database were assigned to the following growth form categories: rod, feather and, fan. Sea urchin density was estimated by a visual inspection of 2m wide belt transect, whose center was the brass chain. Surveys were conducted between May and September, except those in 1994 and 1996 which were realized in October, and those of 2000 and 2002 that were omitted. The last survey was conducted in 2004. Some of the information reported here on coral bleaching and diseases was obtained using different protocols and surveys on other reef habitats (back-reef and scarce high relief sites on the fore-reef) of Puerto Morelos.

Monitoring of the seagrass community: From 1993 to 2005, four stations were sampled within the Puerto Morelos reef lagoon representing the local seagrass range of environments (Fig. 1): High Productivity (20°53.76' N, 86°51.072' W), (2) Typical (20°52.063' N, 86°52.913' W), (3) Reef (20°51.851' N, 86°51.487' W) and (4) Coast (20°52.038' N, 86°52.025' W). The first two stations were located in the middle of the reef lagoon; the

High Productivity station (High Prod) was in the vicinity of marine springs venting water from the mangrove wetlands, whereas the Typical station was away from obvious point sources of groundwater. The Reef station was ~200m shoreward from the reef tract, in an area with a relative high hydrodynamic regime, and the Coast station was ~30m from the coastline and represented the dense fringe vegetation. Depths at these stations varied between 2.5-3.5 m. Further descriptions of the study sites can be found in Van Tussenbroek (1995, 1998). Biomass and community composition of the seagrass communities were determined following the CARICOMP Level I protocol with the following modifications: a metal corer of 22cm diameter and depth of 30-35cm was employed instead of a PVC pipe (diameter 15cm) and three (rarely two), instead of four, haphazardly chosen replicates were collected at each sampling time per station. In addition to standard procedures, the number of foliar shoots of *Thalassia testudinum* and the number of leaves of *Syringodium filiforme* were determined for each sample. Foliar dynamics of *T. testudinum* were determined according the standard CARICOMP methods employing 6 randomly placed quadrats of 10x20cm per site per sampling time. Weight per shoot was calculated by dividing the leaf biomass by the number of shoots per quadrat and the time interval between the beginning of two successive leaves or leaf plastochron (PI_{leaf}) following Van Tussenbroek (1998). On occasions, one or two quadrats were lost reducing the number of samples. Sampling times were winter (December of the previous year until February of the sampling year) and summer (June until August). In addition to the above-mentioned CARICOMP study period of 1993-2005, sampling was conducted in 2006 and 2009 to evaluate the impact of Hurricane Wilma which passed over the area in October 2005.

Statistical analyses: Parametric statistical tests (e.g. repeated measures ANOVA, t-test, Tukey's Honestly Significant Difference) were employed whenever assumptions of normality

and homoscedasticity were satisfied; otherwise non-parametric procedures (e.g. Friedman ANOVA, Wilcoxon) were employed. The coral reef database had missing data, as two stakes were lost on occasions and two years were not sampled, and missing values were estimated using multiple linear regression and adding a random component from a t distribution to the regression estimates. To discern seasonal differences in the parameters of community biomass and foliar dynamics of *T. testudinum*, summer data of all sampling years were pooled and compared with a Student t-test with the pooled data collected during the winter. To obtain an annual value of all sampled parameters the winter and summer values were pooled per sampling year. A two-way ANOVA was applied to latter parameters as independent factors, and station and year as fixed factors because they were specifically chosen as specified by the CARICOMP protocol. If necessary, the data were log transformed to comply with the

prerequisites of the analysis of variance. Inter-annual fluctuations were of special interest; the interaction factor of the two-factor ANOVA indicated whether temporal tendencies were similar or distinct at the four sampling sites. If a station were to be responsible for significant interaction it will be eliminated from the two-way ANOVA analyses because general temporal patterns were of interest for the study. For all analyses alpha was set at 0.05. Statistical analyses were completed using Statistica version 6 software.

RESULTS

Environment: Air and sea-water temperature showed seasonal variability throughout the study (Figs. 2, 3). Monthly averaged annual air temperature ranged from 20.7-30.4°C and sea surface temperature from 25.1-29.9°C, (Table 2). The general trend was higher air

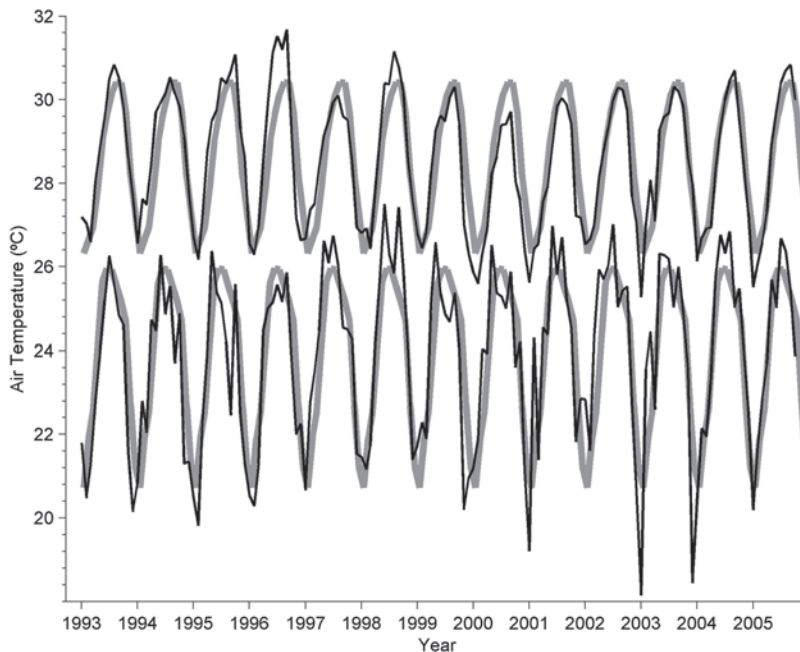


Fig. 2. Monthly average of daily values of maximum air temperature (upper black line) and minimum air temperature (lower black line) from 1993 to 2005 in Puerto Morelos, Mexico. The grey lines superimposed on the figure correspond to the average year values shown in Table 2 in order to detect irregular events.

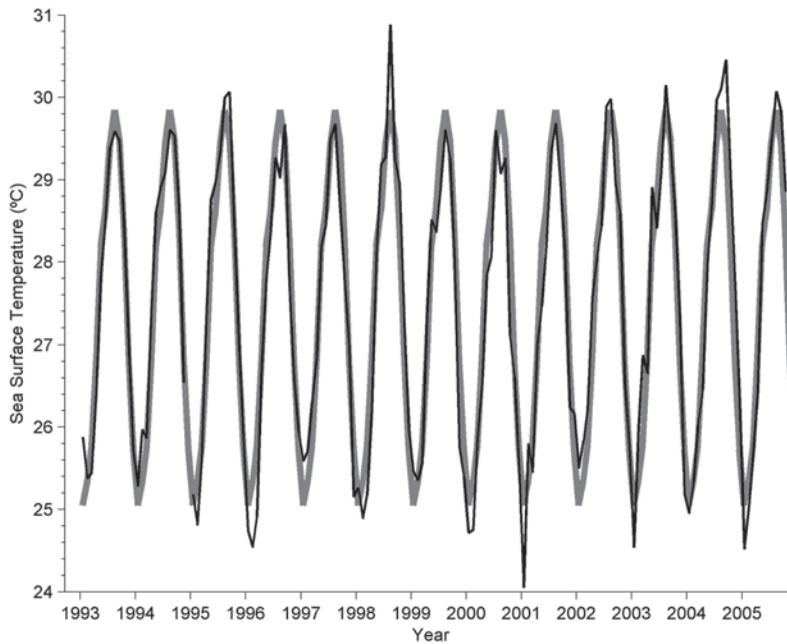


Fig. 3. Sea surface temperature monthly average of daily values (black line) at UNAM's pier in Puerto Morelos, Mexico from 1993 to 2005. The grey line superimposed on the figure corresponds to the average year values shown in table 2 in order to detect irregular events.

TABLE 2

Average year values of rainfall, minimum and maximum air temperature and sea surface temperature at Puerto Morelos, Mexico. The values were calculated using the average of all daily data per month for the period 1993-2005

Month	Rainfall (mm)		Minimum air temperature (°C)		Maximum air temperature (°C)		Sea surface temperature (°C)	
	mean	SE	mean	SE	mean	SE	mean	SE
January	66.6	12.8	20.7	0.3	26.3	0.2	25.1	0.1
February	45.4	14.9	21.9	0.4	26.7	0.2	25.3	0.1
March	45.4	12.3	22.5	0.3	27.0	0.1	25.8	0.1
April	21.1	5.1	24.1	0.3	27.9	0.2	26.8	0.1
May	53.5	20.1	25.6	0.3	29.0	0.2	28.2	0.1
June	149.0	25.4	26.0	0.2	29.6	0.2	28.6	0.1
July	59.2	14.9	25.9	0.2	30.1	0.2	29.4	0.1
August	66.6	7.7	25.5	0.2	30.4	0.1	29.9	0.1
September	127.9	18.4	25.3	0.3	30.4	0.2	29.5	0.1
October	161.4	22.1	24.7	0.2	29.7	0.2	28.4	0.1
November	111.9	31.1	22.7	0.4	28.2	0.2	26.8	0.2
December	72.4	18.9	21.2	0.3	27.3	0.2	25.7	0.1

(29.0-29.7°C) and sea surface (28.2-29.5°C) temperatures from May to October and a reduction of approximately ~1-4°C during the rest of the year (Table 2). From November to April cold fronts (“Nortes”) produced a drop in the temperature and cool the surface of the ocean. From 1993 to 2004 the average rainfall was 1 060.6mm/year (± 171.4). Average year rainfall values were minimum in April (21.1mm) and maximum in October (161.4mm). The dry season and the rainy season were not clearly defined, but there were two rain peaks, one in June and another from September to November (Table 2). The hurricane season extends from June to November, peaking between August and September. Between 1993 and 2005, four hurricanes passed close to the study area (Table 1) and lowered the sea surface temperature. Between 2000 and 2005 there appeared to be a gradual increase in maximum sea surface temperature and, with the exception of 2002, a slight decrease in minimum temperature (Fig. 3). The maximum sea surface temperature exceeded the average year values in the summers of 1995, 1998, 2002, 2003, 2004 and 2005 (Fig. 3). In all of these years bleaching events of different magnitude were recorded in Puerto Morelos reef (Table 1). A mild bleaching event also occurred in 1997 (Table 1) but sea surface temperature was not above the average year values (Fig. 3). Secchi disk visibility distance was on average 5 m less in the lagoon zone (mean=15.4 m) than in the open ocean (21.2m) and had no noticeable pattern with the wet and dry seasons and no important variation throughout the study period. All refractometer salinity readings had a monthly average of 36ppt, except in a very few occasions consistent with periods of heavy rains and mangrove swamp runoff.

Coral reef site: The main characteristic of the Puerto Morelos CARICOMP reef site were a low coral and sponge cover and a high cover of fleshy and turf algae (Fig. 4). This type of benthic coral community “coral grounds” is typical for the low-relief and low-slope fore-reef environments found in the northeastern

Mexican Caribbean coast (Jordán-Dahlgren & Rodríguez-Martínez 2003) and are also found colonizing similar hard ground environment all over the Caribbean (Goreau 1959). Coral cover was low (mean <3%) because, although colony density is relatively high, colonies were small (over 75% of the colonies had diameters <10cm), suggesting high coral recruitment rates but low probabilities of survival to larger sizes. Coverage by scleractinians remained without significant changes throughout the study (Friedman ANOVA (χ^2 [n=5, df=11]=10.6, p=0.46). Of the 26 species of scleractinian corals known for the fore-reef of Puerto Morelos (Jordán-Dahlgren 1979), 12 were recorded in the CARICOMP site throughout the study. *Montastraea cavernosa*, *Dichocoenia stokesii* and *Meandrina meandrites* were the most abundant coral species. Sponge cover fluctuated from 1.5 to 6.5%, it decreased significantly from 1993 to 1998 (rep ANOVA, F=2.2, df=11, p=0.03), and recovered by 2004 (Fig. 4). Encrusting species (*Cliona* spp.) were

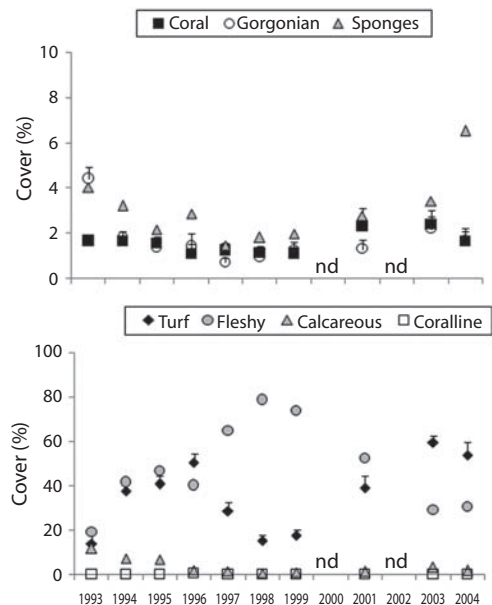


Fig. 4. Mean cover of biotic benthic groups at the Puerto Morelos CARICOMP reef station between 1993 and 2004. The bar represents upper Standard Errors. nd: no data.

most commonly recorded. Fleishy algae cover oscillated between 19% and 79% and changed significantly through the sampled years (χ^2 [n=5, df=11]=39.8, $p<0.001$), the highest values were recorded from 1997 to 1999 and the lowest in 1993, 2003 and 2004 (Fig. 4); differences were significant in all cases (Wilcoxon matched pairs tests, $p<0.05$). The composition of fleshy algae remained relatively constant throughout the study, with *Sargassum* spp. and *Dictyota* spp. being the dominant species. Turf algae cover also fluctuated throughout the study (14-60%) increasing significantly from 1993 to 1996 (Tukey post-hoc tests, $p<0.03$ all cases), decreasing by 1998, when it had a similar value as in 1993 (Tukey, $p=1.0$), and increasing again by 2003 and 2004 (Fig. 4). The cover by fleshy algae and turf algae had a significant inverse correlation ($R^2=-0.97$, $p<0.001$, $N=9$). Calcareous algae cover declined from 12% to 0.5% between 1993 and 1998 and remained low afterwards (Fig. 4); changes in time were significant (Friedman ANOVA, (χ^2 [n=5, df=11]=37.3, $p=0.001$). The more abundant calcareous algae species in all surveys were *Halimeda tuna*, *Rhipocephalus phoenix* and *Penicillus capitatus*. Sediment cover declined significantly ($p<0.05$) from 1993 ($37.4\pm 10.5\%$) to 1995 ($0.5\pm 0.8\%$) and remained without subsequent changes afterward. Crustose coralline algae and bare rock were rarely recorded.

Gorgonians were the most conspicuous benthic fauna in the fore-reef environment. The density and composition of the gorgonian community was highly dynamic throughout the study. The number of gorgonian species

increased from 9 in 1993 to 16 in 2004 (Table 3), more likely due to a recovery process following the impact of Hurricane Gilbert (1988): as colonies grew they were more prone to be intercepted by the line intercept transect. Gorgonian density increased significantly between 1993 and 1995 (Tukey, $p=0.02$) and stabilized afterwards (Fig. 5). Gorgonian species with feather and rod growth forms were more abundant than those with fan forms (Table 3). The proportion between gorgonian colony growth forms changed significantly in time (Contingency table. $G=53.27$, $df=14$, $p<0.01$). Between 1993 and 1997, feather growth forms were more abundant while in later surveys rod forms became more abundant (Table 3). The dominant species throughout the study were *Pseudopterogorgia americana*, *Eunicea mammosa* and *Plexaura flexuosa*. From 1993 to 1997, these three species contributed with

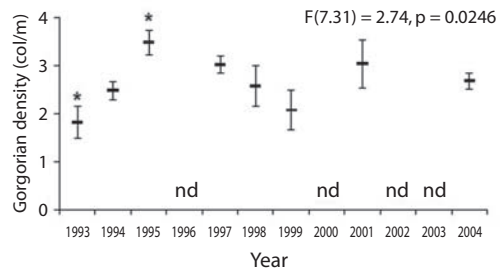


Fig. 5. Change in the density of gorgonian colonies (colonies m^{-1}) between 1993 and 2004 in the Puerto Morelos CARICOPM reef site. The bar represents upper Standard Errors. The asterisk on top of bars denotes significant difference between sampling periods (Tukey NHS). nd: no data.

TABLE 3

Number of gorgonian species (S), number of colonies (N) and percentage of colonies regarding their colony growth form in the Puerto Morelos CARICOMP site in different sampling periods

	1993	1994	1995	1997	1998	1999	2001	2004
S	9	8	11	5	13	15	17	16
N	91	124	174	151	129	83	150	104
Rod (%)	30.8	35.5	41.4	35.8	60.5	56.6	50.7	52.9
Feather (%)	53.8	43.5	55.7	61.6	36.4	38.6	44.0	41.3
Fan (%)	11.0	4.0	2.9	2.6	3.1	4.8	5.3	5.8

over 70% of all of the colonies recorded in the transects. In later surveys, their combined relative importance diminished gradually to 43% in 2004, as other species (*P. acerosa*, *E. tourneforti* and *Muricea muricata*) became more abundant. Other gorgonian species had low abundances throughout the study.

Sea urchins were rare in all sampling years. Overall density fluctuated between 0 and 0.06 urchins m⁻² between 1993 and 2003, and increased slightly in 2004 (0.14 ind m⁻²),

due to a relatively higher number of *Diadema antillarum* and *Echinometra viridis*. Other species recorded in the course of the study were *Eucidaris tribuloides* and *Meoma ventricosa*.

Seagrass site: From 1993 to 2005, the total biomass of the seagrass community was consistently higher in the High Prod and Coast sites than at the other two sites (Table 4). Total biomass (of above- and below-ground tissues) of *T. testudinum* was always higher than that

TABLE 4
General mean values (SD) of the seagrass community parameters in four sampling stations in Puerto Morelos, Mexico 1993-2005

	High Prod	Typical	Reef	Coast
Community biomass (cores): g dry m ⁻²				
N _{total} core samples	78	78	78	77
Above-ground	126.7 (30.8)	104.5 (46.8)	62.8 (18.3)	325.9 (116.5)
Total	929.6 (161.2)	707.1 (154.1)	768.1 (162.4)	1280.5 (190.3)
Above-ground biomass (cores): g dry m ⁻²				
<i>Thalassia testudinum</i>	70.1 (17.0)	38.4 (13.5)	37.7 (15.0)	55.3 (15.1)
<i>Syringodium filiforme</i>	19.8 (11.8)	11.5 (7.6)	4.3 (4.2)	41.1 (17.2)
Fleshy algae	12.1 (18.1)	28.0 (39.5)	0.2 (0.8)	192.5 (119.2)
Calcareous algae	24.9 (14.5)	26.6 (16.5)	20.5 (10.2)	36.7 (22.2)*
Total biomass (cores): g dry m ⁻²				
<i>Thalassia testudinum</i>	699.0 (144.7)	531.4 (143.0)	689.7 (167.6)	720.7 (152.8)
<i>Syringodium filiforme</i>	184.6 (92.8)	109.6 (61.2)	48.1 (34.6)	312.2 (107.8)
Calcareous algae	33.9 (19.2)	35.4 (23.4)	29.4 (15.1)	43.6 (26.2)
% of total biomass above substratum				
<i>Thalassia testudinum</i>	10.1 (1.9)	7.3 (2.1)	5.5 (1.8)	7.8 (2.0)
<i>Syringodium filiforme</i>	10.7 (4.2)	10.3 (3.2)	7.8 (4.7)	13.3 (3.4)
Calcareous algae	73.2 (9.3)	76.6 (12.2)	72.7 (13.9)	81.3 (7.2)
Shoot density (cores + quadrats): no m ⁻²				
<i>Thalassia testudinum</i>	545 (165)	499 (168)	731 (210)	555 (162)
Leaf density (cores): no m ⁻²				
<i>Syringodium filiforme</i>	1827 (951)	1357 (876)	625 (526)	3139 (929)
<i>Thalassia testudinum</i> foliar dynamics (quadrats)				
N _{total} quadrats	156	152	140	140
Productivity (g dry m ⁻² d ⁻¹)	1.6 (0.6)	0.9 (0.4)	0.9 (0.4)	1.5 (0.6)
P:B ratio	2.4 (0.5)	2.7 (0.5)	3.1 (0.5)	2.6 (0.5)
Growth (mg dry shoot ⁻¹ d ⁻¹)	3.0 (0.8)	1.9 (0.6)	1.3 (0.5)	2.9 (1.0)
Weight per shoot (mg dry)	125.9 (27.6)	71.3 (23.6)	42.9 (14.7)	111.4 (38.8)

Community biomass: sum of biomass of all vegetation groups. Total biomass: sum of above- and below ground plant sections. Biomass of calcareous algae was based on somatic weight determined after decalcification.

of the other vegetation groups, the highest values were found in the High Prod and Coast sites, followed by the Typical site, whereas the lowest values were recorded in the more hydrodynamic Reef station. Foliar productivity of *T. testudinum* was highest at the High Prod and Coast stations, where the shoots attained comparable density size and growth rates. The Typical site showed intermediate values of all parameters, while in the Reef site *T. testudinum* shoots were shorter, had a lower growth-rate, and were more abundant than at the other sites (Table 4). Calcareous algae, mainly comprising species of the genera *Halimeda*, *Penicillus*, *Rhizocephalus* and *Udotea*, attained a similar biomass in all four sampling sites, although the relative contribution of these genera varied between sites (Table 4). In the Coast site, a large portion of the above-ground biomass belonged to the group “fleshy algae” (mainly *Avrainvillea* spp. and *Cladocephalus* spp.).

Seasonal variations were appreciated in the foliar dynamics of *T. testudinum*, presenting, in general, higher leaf growth (Fig. 6) and productivity, and lower PI_{leaf} during the summer than in the winter (Table 5). Shoot density, in contrast, remained constant throughout the year (Table 5), and leaf biomass did not vary significantly between summer and winter in the High Prod site. The pooled summer values of the above-ground- and total biomass of all other vegetation groups did not vary from the pooled winter data, and the p of the Student t -test exceeded 0.1 in all cases.

Interannual fluctuations of the studied parameters of the seagrass community did not show the same trends at all sampling stations, as indicated by their significant interaction between station and year of the two-way ANOVA (Table 6). However, excluding the Coast station resulted in, interactions becoming insignificant for most parameters (except for total community biomass and for the biomass of the fleshy algae), and thus this station was omitted from further analysis. Differences between years were then significant for all parameters (Table 6), but interannual variations of the parameters of foliar dynamics of

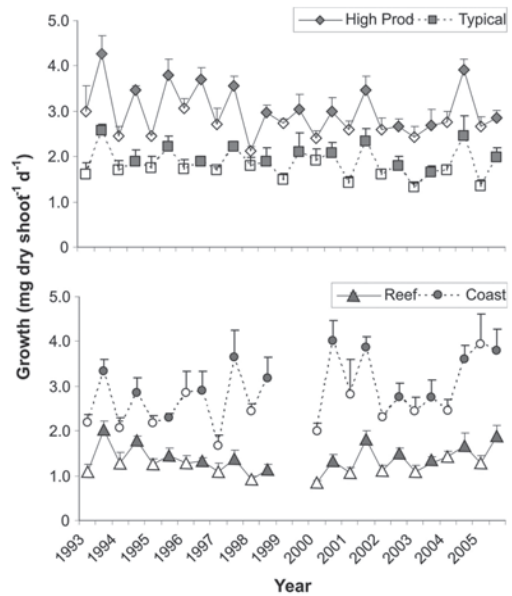


Fig. 6. *Thalassia testudinum* growth per shoot at four sampling stations in Puerto Morelos reef lagoon from 1993 to 2005. The open symbols represent mean values for the winter and filled symbols for the summer months. Bars represent upper Standard Errors (SE), N=6, except for rare occasions when 1-2 quadrats were lost.

T. Testudinum (Fig. 7) and the biomass of the other seagrasses (*S. filiforme*), calcareous and fleshy algae were erratic, without an obvious pattern. The clearest signals of changes in time, from 1993 until 2005, were ascending tendencies in the total biomass of the seagrass *Syringodium filiforme* (corresponding to the group “other seagrasses”) and in the fleshy algal group (Table 7). *S. filiforme* also showed increased leaf density and both seagrass species (*T. testudinum* and *S. filiforme*) showed an increment in the proportion of the biomass allocated to the above-ground leaves (% above-ground biomass) in the course of the study (Table 7, Fig. 7).

The impact of the major Hurricane Wilma (October 2005) on the sampling stations in the seagrass beds of Puerto Morelos reef lagoon was not severe, with exception of the vegetation at the Coast site, which was buried by a

TABLE 5

Thalassia testudinum leaf dynamics. General mean values (SD) per station of pooled summer and pooled winter data from 1993-2005, at four stations in Puerto Morelos reef lagoon

	High Prod	Typical	Reef	Coast
Summer				
Productivity (g dry m ⁻² d ⁻¹)	1.7 (0.6)	1.0 (0.4)	1.1 (0.4)	1.8 (0.6)
Biomass (g dry m ⁻²)	66.0 (22.7)	36.7 (15.9)	33.8 (13.1)	67.8 (27.4)
P:B ratio	2.6 (0.5)	2.7 (0.6)	3.2 (0.5)	2.7 (0.5)
Growth (mg dry sht ⁻¹ d ⁻¹)	3.3 (0.8)	2.1 (0.7)	1.5 (0.5)	3.3 (1.0)
Weight per shoot (mg dry)	128.5 (25.7)	76.9 (25.5)	46.6 (15.9)	121.0 (39.2)
Density (shoots m ⁻²)	519 (164)	495 (185)	740 (224)	569 (174)
PI _{leaf} (d)	26.1 (6.7)	23.2 (6.5)	26.4 (10.5)	29.3 (10.4)
N	78	77	72	70
Winter				
Productivity (g dry m ⁻² d ⁻¹)	1.5 (0.6)	0.8 (0.3)	0.8 (0.3)	1.2 (0.5)
Biomass (g dry m ⁻²)	66.0 (23.5)	31.9 (13.3)	27.6 (9.1)	50.5 (19.5)
P:B ratio	2.2 (0.3)	2.5 (0.3)	3.0 (0.5)	2.4 (0.4)
Growth (mg dry shoot ⁻¹ d ⁻¹)	2.7 (0.7)	1.6 (0.4)	1.1 (0.4)	2.5 (0.9)
Weight per shoot (mg dry)	123.4 (29.4)	65.7 (20.1)	39.0 (12.2)	101.8 (36.2)
Density (shoots m ⁻²)	546 (180)	493 (163)	728 (191)	513 (165)
PI _{leaf} (d)	30.6 (8.3)	25.8 (5.6)	28.2 (6.6)	34.1 (10.8)
N	78	75	68	70
Student t				
Productivity	2.45 *	3.47 ***	4.38 ***	5.97 ***
Biomass	0.01 n.s.	1.98 *	3.20 **	4.30 ***
P:B ratio	5.67 ***	3.56 ***	2.73 **	4.21 ***
Growth per shoot	4.74 ***	5.26 ***	4.39 ***	4.87 ***
Weight per shoot	1.15 n.s.	2.98 ***	3.13 ***	3.00 ***
Density	0.95 n.s.	0.017 n.s.	0.35 n.s.	1.97 n.s.
PI _{leaf}	1.53 n.s.	0.46 n.s.	0.50 n.s.	1.12 n.s.

Results of the Student t-test which compared the values of the summers and winters. n.s. not significant, * p≤0.05, ** p≤0.01, *** p≤0.005. N as indicated in the Table 1P. For PI_{leaf}: N=26 for High Prod and Typical, and N=24 for Reef and Coast.

~1-1.5m thick sand layer. In the persistent beds, above-ground biomass, shoot density, % of total biomass allocated to above-ground tissue and productivity of *T. testudinum* were often slightly lower, but within the range of “normal” fluctuations at these sites (Fig. 8). In comparison with 2005, the abundance of *S. filiforme*, and fleshy and calcareous algae, decreased slightly after passage of the hurricane at the High Prod and Typical sites (Fig. 8), but at the Reef site declines in these vegetation groups were less notable or

absent. In early 2009, three years after Hurricane Wilma, the composition of the vegetation in the High Prod, Typical and Reef sites were similar to those recorded during the CARICOMP observation period, although not always comparable with the pre-hurricane values recorded in 2005 (Fig. 8). In 2009, the previously bare sandy area at the Coast station was sparsely colonized by calcareous and fleshy algae (*Caulerpa* spp.) and the seagrasses *Halodule wrightii* and *Syringodium filiforme* (Fig. 8).

TABLE 6

Two-way ANOVA applied to the parameters of the seagrass community and foliar dynamics of *Thalassia testudinum* in Puerto Morelos reef lagoon with station and sampling year as fixed factors

	All stations		Excluding Coast	
	F _{interaction}	F _{interaction}	F _{station}	F _{year}
Community biomass (core)				
Above-ground	2.74***	1.28 n.s.	90.08***	3.61***
Total	1.84**	1.90 *	45.98***	1.74 ^{n.s.}
Above –ground biomass (core)				
<i>T. testudinum</i>	1.55 *	1.51 n.s.	146.97***	5.21***
<i>S. filiforme</i>	1.70 *	1.00 n.s.	578.68***	4.35***
Fleshy algae	3.67***	2.44 ***	29.42***	2.37**
Calc. algae	3.31***	1.27 n.s.	4.32*	2.59***
Total Biomass				
<i>T. testudinum</i>	1.47 *	1.53 n.s.	35.46***	3.52***
<i>S. filiforme</i>	1.78 *	1.28 n.s.	101.82***	4.47***
Calc. Algae	3.62***	1.51 n.s.	2.33 ^{n.s.}	2.83***
Shoot density (core and quadrat)				
<i>T. testudinum</i>	1.54 *	1.33 n.s.	97.39***	2.52**
<i>S. filiforme</i> (core)	2.54 ***	0.97 n.s.	11.11 ***	3.97***
<i>T. testudinum</i> leaf dynamics (quadrats)				
Productivity	1.80 **	1.45 n.s.	102.87***	4.51***
Growth per shoot	2.18 ***	1.41 n.s.	287.99***	5.29***
Weight per shoot	2.00 ***	1.36 n.s.	530.75***	2.19*

Significant interactions between station and year indicate that the trends with time were distinct at the stations. n.s. not significant, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.005$ for N see Table 4.

DISCUSSION

The longer-term monitoring at the Puerto Morelos CARICOMP site revealed gradual almost imperceptible changes in various parameters. The sea surface temperature showed a trend towards a slight increase in the maximum and a decrease in the minimum values, the coral reef community showed no recovery of hard corals 15 years after Hurricane Gilbert (1988), and the seagrass community slowly shifted towards a relative higher dominance of faster growing seagrasses and fleshy algae, and higher investment in above-ground plant parts. The relationships between the changes in the benthic community of the seagrasses and reefs were neither general nor straightforward, but rather system-, place- and time-specific.

At the reef site, the benthic community remained relatively stable throughout the study. Hard coral cover was consistently low (<2.5%) and represented the lowest extreme of the coral cover values recorded in all of the CARICOMP sites. Species richness, cover and density values recorded were considerably lower than those reported for the same reef area in 1978 (Jordán-Dahlgren 1979), before the reef was impacted by major Hurricane Gilbert (1988, class V). That single event resulted in a reduction in species richness from 16 to 12, in coral cover from 8.4% ($\pm 3.1\%$) to 3.1% ($\pm 1.2\%$) and in coral colony density from 0.9 col m^{-1} (± 0.2) to 0.3 col m^{-1} (± 0.2), at a depth of 10m (Rodríguez-Martínez 1993). Fifteen years later, the reef community showed little recovery,

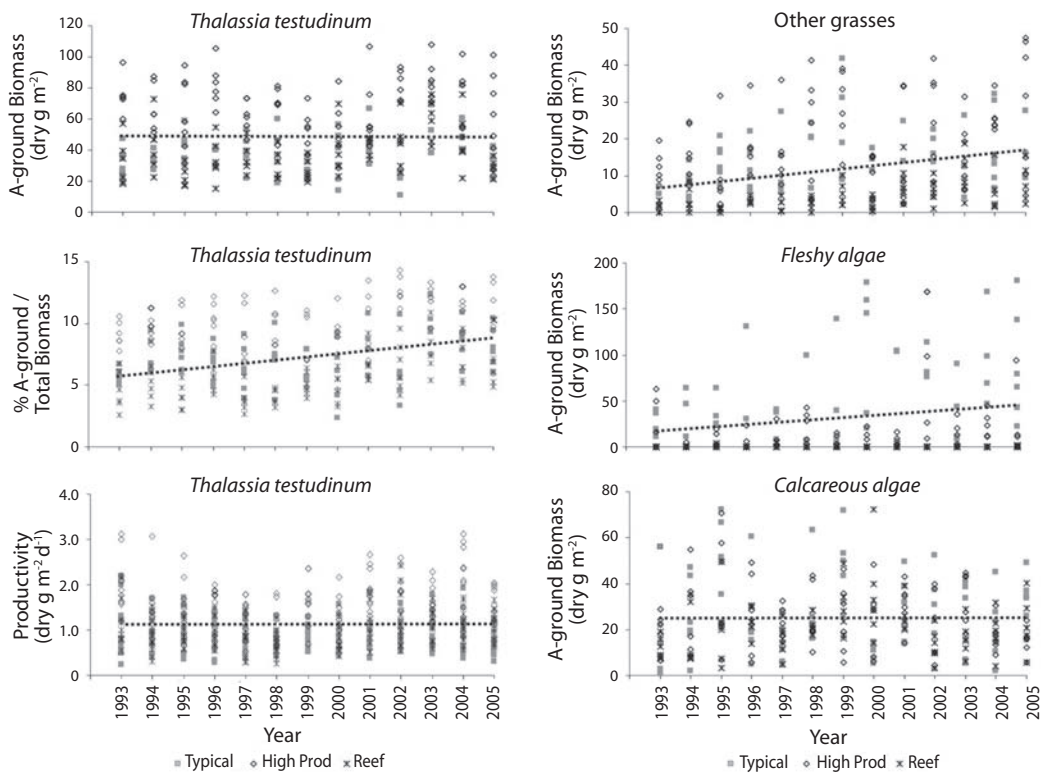


Fig. 7. *Thalassia testudinum* above-ground biomass, percentage of the total biomass allocated to above-ground tissue and productivity, together with the above-ground biomass of other grasses (*Syringodium filiforme* at all sites), fleshy algae and calcareous algae at Typical, High Prod and Reef stations in Puerto Morelos reef lagoon from 1993 until 2005. Each point represents a sample. A regression line is drawn through grouped sample of all the three stations. A-ground biomass = Above-ground biomass.

which could be attributed to the locally low rugosity fore-reef. Although relatively frequent recruitment events could account for the relatively abundant small coral colonies, only a few of these recruits reached larger sizes (over 75% of the colonies had diameters <10cm). Suggested forcing functions responsible for this type of community include high re-suspension of sediments, due to the gentle slope (<5°), that drive the selection of resistant species such as *Montastraea cavernosa*, *Diploria strigosa*, *Dichocoenia stokesiis* and *Siderastrea siderea* (Loya 1976, Jordán-Dahlgren 1979). Further sediment abrasion and colony detachment during storms and hurricanes also accounted for

dominance of juvenile stages in the population (Jordán-Garza 2004).

During the study period the major forcing factors that affected the coral community were hurricanes, coral diseases and bleaching events. The effects of the minor hurricanes were small, considering that the community suffered a major impact by Hurricane Gilbert in 1988. In 1993, when the CARICOMP project started, gorgonians hadn't fully recovered from the impact of Hurricane Gilbert, as their density ($1.8 \pm 0.7 \text{ org m}^{-1}$) was lower than that recorded in the same area in 1978 ($2.8 \text{ org m}^{-1} \pm 0.5$; Jordán-Dahlgren 1979) but by 1995 gorgonian density ($3.5 \pm 0.6 \text{ org m}^{-1}$)

TABLE 7

Slopes of the linear regression of the parameters of the seagrass community and foliar dynamics of *Thalassia testudinum* with sampling year to discern possible increasing or decreasing trends in the course of the study (1993-2005)

Parameter	Slope	Sign. slope
Community biomass (Cores)		
Above-ground	2.873	0.000
Total	-	0.409
Above-ground biomass (Cores)		
<i>Thalassia testudinum</i>	-	0.058
<i>Syringodium filiforme</i>	0.705	0.000
Fleshy algae	1.391	0.004
Calcareous algae	-	0.812
Total Biomass (Cores)		
<i>Thalassia testudinum</i>	-	0.084
<i>Syringodium filiforme</i>	5.824	0.000
Calcareous algae	-	0.521
% Above-ground biomass (Cores)		
<i>Thalassia testudinum</i>	0.184	0.000
<i>Syringodium filiforme</i>	0.256	0.001
Shoot density (Quadrats + cores)		
<i>Thalassia testudinum</i>	-	0.715
Leaf density (Core)		
<i>Syringodium filiforme</i>	23.181	0.005
<i>T. testudinum</i> leaf dynamics (quadrats)		
Productivity	-	0.143
P:B ratio	-	0.071
Growth per shoot	-	0.781
Weight per shoot	-	0.326

Regressions were applied to the pooled data of the stations High Prod, Typical and Reef. N as in Table 4. – slope not indicated because it was not significant at $\alpha = 0.05$.

surpassed pre-hurricane values. In 1995, Hurricane Roxanne (class III) made land 100km south of Puerto Morelos and did not cause major damage to the reef, but in the next three years gorgonian density showed a down-trend pattern coupled with a change in the dominant gorgonian growth forms, from feather to rod, which could be the result of differential recruitment, different growth rates or competitive outcomes (Connell *et al.* 2004). By 2004, gorgonian composition and density ($2.7 \pm 0.4 \text{ org m}^{-1}$) was very similar to that of 1978. Fluctuations through time in the cover of fleshy algae and turf algae were more likely the result of the time of the year when the surveys were conducted and the life history characteristics of

the component species; when the surveys were done in the summer the abundance of fleshy algae, mainly *Sargassum* spp., increased and overgrew the turf algae. Coverage by fleshy and turf algae (84%) was higher than that found in other CARICOMP sites like Panamá (21%; Guzmán *et al.* 2005), Puerto Rico (maximum 38%, Linton & Fisher 2004), Costa Rica (63%; Fonseca *et al.* 2006) and Jamaica (73%; Linton & Fisher 2004). Density of sea urchins throughout the study ($< 0.2 \text{ org m}^{-2}$) was low and comparable to that reported for other CARICOMP sites (Linton & Fisher 2004). The population of *Diadema antillarum* increased slightly in our last survey but we can't determine if this was the beginning of the recovery

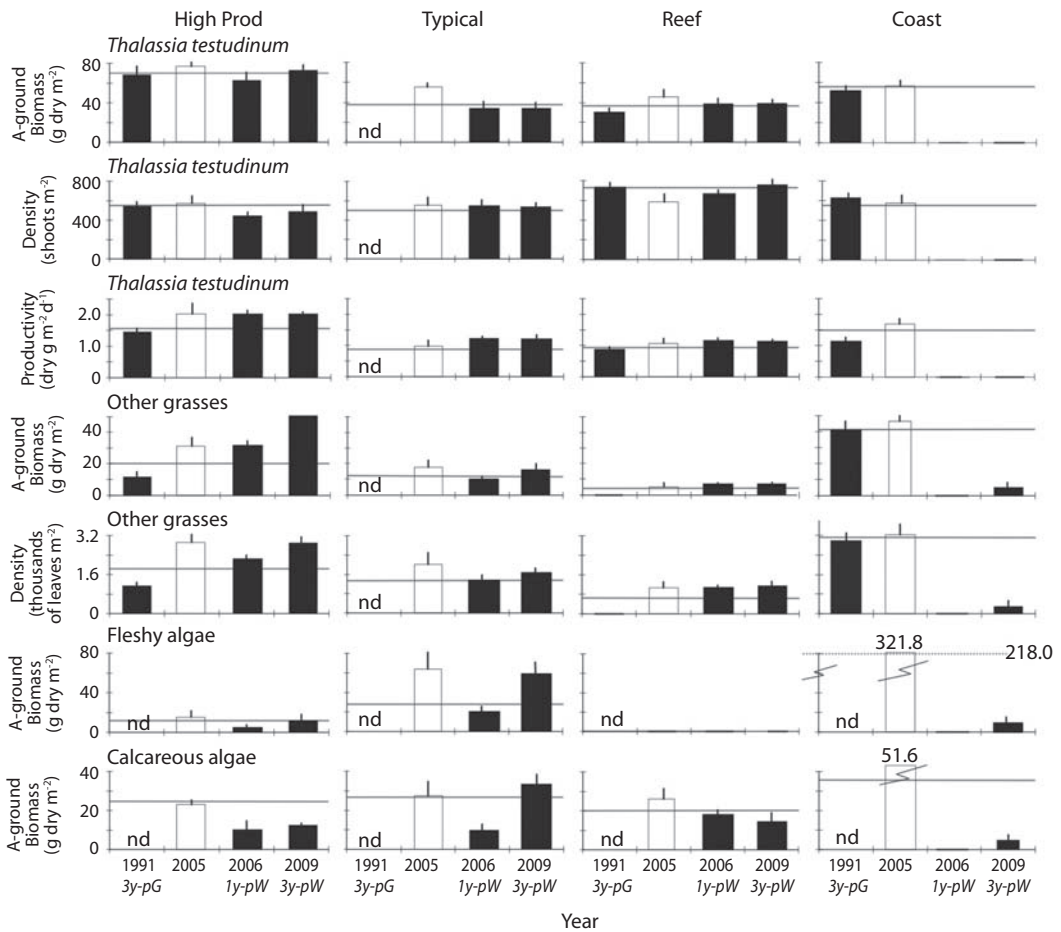


Fig. 8. Values of selected parameters of the seagrass community during post-hurricane years at four stations in Puerto Morelos reef lagoon (black bars), together with the values previous to Hurricane Wilma in 2005 (white bar). N=12 for 1991 and 2005, N=10 for 2006, N=6 for 2009, except at the Coast station (N=12). The small vertical top-bar represents upper SE. The grey horizontal line represents the average value from 1993 until 2005. Biomass of calcareous algae was based on somatic weight. The group "Other grasses" consisted of *Syringodium filiforme*, except at the Coast station in 2009, when both *Halodule wrightii* and *S. filiforme* were registered. Values of 1991 are from Van Tussenbroek (1994a, 1995, 1998). pG: post-Hurricane Gilbert (September 1988), pW: post-Hurricane Wilma (October 2005), A-ground biomass: Above-ground biomass, nd: not determined.

process. Density of *D. antillarum*, however, has increased in other Mexican reefs, such as Mahahual (7.3 ± 4.2 org m^{-2} ; Jordán-Garza *et al.* 2007) and Akumal (Rodríguez-Martínez pers. obs.) but mostly in shallow back-reef areas.

Disease outbreaks were recorded and their effects measured throughout the study period in many areas of Puerto Morelos reef. The data set from the CARICOMP reef site showed no

significant increase in the prevalence of coral diseases. However, the increment in the number and prevalence of coral diseases elsewhere in Puerto Morelos (Rodríguez-Martínez *et al.* 2001, Jordán-Dahlgren *et al.* 2005) suggest that higher sea surface temperature trends observed in present study may be a causative factor, either by thermal stress on the host reducing coral resistance to infections or

TABLE 8

Total Carbon (C), Nitrogen (N) and Phosphorus (P) content on leaves of *Thalassia testudinum* from Puerto Morelos reef lagoon determined during distinct studies (Van Tussenbroek, Unpublished data, courtesy T.J.B. Carruthers, J.W. Fourqurean)

Station	Date	%C	%N	%P	C:N	C:P
High Prod	Dec 2001	32.5	2.1	0.1	18.2	532.0
	Jul 2003	38.3	2.4	0.2	18.6	540.6
	Jun 2005	32.4	1.9	0.2	20.4	566.2
Typical	Jun 1998	33.4	1.9	0.1	20.9	799.9
	Apr 2001	33.1	1.9	0.1	20.8	607.7
	Jun 2005	36.9	1.9	0.1	22.7	697.8
Reef	Jul 1991	34.2	1.6	0.1	25.3	1004.0
	Jul 2003	35.2	1.9	0.2	21.9	607.4
	Jun 2005	37.9	2.0	0.2	22.5	581.1
Lagoon	Aug 1991*	34.7	1.8	0.2	22.7	608.9
	Apr 2001	34.0	2.1	0.2	19.0	522.4
	Jul 2003	33.3	1.1	0.2	19.8	404.8
	Jun 2005	34.8	1.9	0.2	21.7	510.0

* From Gallegos *et al.* 1993.

thermally induced increase in pathogens' virulence (Bruno *et al.* 2007, Harvell *et al.* 2007). In 1998, only two diseases, white-band and white-pox, were recorded affecting colonies of *Acropora palmata*, in the back-reef of Puerto Morelos. In 2000, the number of recorded diseases had increased to five and by 2004 to six, reflecting the same situation that has been observed throughout the Caribbean. The first thermal bleaching event of corals and other reef organisms recorded at Puerto Morelos was in 1995 (CARICOMP 1997) and, since then, bleaching occurred in all of the years when the maximum sea surface temperature exceeded 30°C in the summer, except in the year of 1997. During the study period, however, no mass mortality of scleractinian corals associated with thermal coral bleaching was recorded on Puerto Morelos reef. The most severe bleaching events were recorded in 1995 and 2005 (Table 1), when it was estimated that over 50% of the coral colonies were bleached at different intensities. The bleaching event of 1998, which

caused catastrophic mortalities of corals around the world (Aronson *et al.* 2000), was recorded as moderate in Puerto Morelos reef (Table 1). At the CARICOMP reef site, no significant bleaching was recorded possibly because surveys were carried out at months that coincided with the onset of the bleaching events.

Variations in the seagrass community were in many aspects distinct from those in the reef community and subject to different forcing factors. For example, the possible rise in seawater temperature most likely did cause detectable changes in the seagrass community structure during the study period. The temporal dynamics of the seagrass community occurred at three levels: (1) season, (2) gradual changes from 1993 until 2005, probably forced by increased nutrient inputs, and (3) perturbations due to the major Hurricanes Gilbert (1988) and Wilma (2005). In general, biomass, growth rates, and productivity, were lower in the winter than in the summer. Such seasonal fluctuations in the foliar dynamics of *Thalassia testudinum* have

already been reported by Van Tussenbroek (1995) and were most likely related to variations in the solar cycle. In the present study, in some of the years the contrast between the summer highs and the winter lows in the growth rates and productivity were less obvious, more likely because the 7-10 days lasting observation periods were not always representative of the prevailing conditions during that season. Seasonal trends were not observed in the biomass of the other vegetation groups, but at this point it can't be discerned whether this is a real trend or a sampling effect. The general-purpose and simple sampling design for the study of the composition seagrass communities of the CARICOMP project allowed for comparison between sites within a wide geographical area but possibly did not have the necessary resolution to discern small changes in the seagrass community. Sampled areas were limited to the small area covered by the cores and there was a very wide spread of the individual sampling points, as is demonstrated in figures 7 and 8. Therefore, a signal of change must be exceptionally strong to be discerned and it is possible that the seasonal changes in biomass of the different vegetation groups remained undetected.

Most parameters varied significantly between sampling years, but the interannual fluctuations did not coincide with extreme environmental conditions such as storms, periods of heavy rain, or extreme temperatures. On the other hand, the continuous sampling scheme detected low, but significant, changes in the course of the CARICOMP study from 1993 to 2005, as indicated by the positive and significant slopes of the regressions of these parameters against sampling year. These gradual, almost imperceptible changes in community structure most likely could be explained by an increasing nutrient load into this reef lagoon. Nutrient availability to seagrasses may be derived from C:N:P ratios in the leaf tissues (Duarte 1992, Fourqurean *et al.* 1992). Carbonate systems, such as Puerto Morelos reef lagoon are phosphorus limited (Powell *et al.* 1989, Short *et al.* 1990, Fourqurean *et*

al. 1992, Carruthers *et al.* 2005) and the P contents in *T. testudinum* leaves, sampled on several occasions in the reef lagoon, gradually increased at all sites, except for the High Prod station, located near a mangrove discharge, which presented high P throughout the whole period (Table 8). The gradual shifts of relatively higher biomass invested in above-ground tissues of *T. testudinum* and *S. filiforme* were consistent with an increasing nutrient load, as seagrasses tend to show higher proportional above-ground biomass under more eutrophic conditions (Zieman & Wetzel 1980, Erftemeijer & Middelburg 1993, Van Tussenbroek *et al.* 1996). At the level of the seagrass community, the competitive superiority tends to shift to species with faster relative growth rates at increasing nutrient availability (Fourqurean *et al.* 1995, Rose & Dawes 1999, Fourqurean & Rutten 2003), which in the case of the study sites in Puerto Morelos reef lagoon, corresponded with the faster-growing seagrass *S. filiforme* and rooted and drifting fleshy algae. Latter vegetation groups gradually became more abundant, but they did not replace the dominant *T. testudinum*, causing an increment in total above-ground community biomass. Very noteworthy was the increasing presence of *S. filiforme* at the Reef station. Before the CARICOMP sampling program, during 1990-1991, this seagrass was almost absent (Van Tussenbroek 1994a). In 1993, the majority of the samples had *S. filiforme* but at low densities (average density 329 leaves m⁻², SD=377), but by 2005, all samples contained this seagrass reporting on average 1070 leaves per m⁻² (SD=525). Above-mentioned gradual changes in the seagrass community, the increased P content of the *T. testudinum* leaves, and the finding of high phosphorus inputs through groundwater discharges into the system after heavy rain (Carruthers *et al.* 2005), together are strong indications that the Puerto Morelos reef system is slowly changing from a pristine to a more eutrophic system.

The impact of Hurricane Wilma (class 4, duration >60 h, October 2005), evaluated through comparison of pre- (2005) and

post- (2006) hurricane values of selected parameters of the seagrass community, showed only small changes in the community of the persistent beds. Not all vegetation groups were affected equally and at the High Prod and Typical Stations, *Syringodium filiforme* and the algae were more affected than *T. testudinum*. These findings are consistent with the selective removal hypothesis of Cruz-Palacios and Van Tussenbroek (2005) and Van Tussenbroek *et al.* (2008), which postulate that different vegetation groups show differential susceptibility to removal by hurricane-induced burial, sediment-removal or abrasion. In addition, the magnitude of the effects on the distinct groups was site-dependent, and the reef station, situated in a high hydrodynamic area, was least affected by Hurricane Wilma. The impact of Hurricane Gilbert (1988) on the seagrass community was not assessed directly, but retrospective analysis of shoots of *T. testudinum* indicated a decreased shoot density at the High Prod, Typical and Coast stations, whereas the number of shoots at the Reef station was not affected by this hurricane (van Tussenbroek 1994b). The seagrass community at the Coast station was wiped out completely by Hurricane Wilma, but this site presented a very lush and well-developed *T. testudinum*-dominated seagrass bed after Hurricane Gilbert (van Tussenbroek 1994a,b, 1995). Thus, the perturbations caused by Hurricanes Gilbert (1988) and Wilma (2005) on the same seagrass beds differed, which emphasizes again that the impacts of hurricanes are, in addition to the nature of the hurricane itself, site- and community-dependent (Fourqurean & Rutten 2004, Cruz-Palacios & Van Tussenbroek 2005, Cabaço *et al.* 2008). The sampling years 1991 (data from Van Tussenbroek, 1994,1995,1998) and 2009, were three years post Hurricanes Gilbert and Wilma respectively, and recovery of the persistent beds was relatively fast. Van Tussenbroek (1994b) registered rapid population growth of *T. testudinum* 1-3 years after Hurricane Gilbert and in 2009 the biomass values of the vegetation groups at the High Prod, Typical and Reef

stations, were comparable to those observed during the CARICOMP observation period. Three years after complete eradication, the vegetation of the Coast station presented few calcareous algae and the early seagrass colonizers *Halodule wrightii* and *Syringodium filiforme* following the characteristic primary succession sequences described by Patriquin (1975), Williams (1990), Fourqurean & Rutten (2004) and Van Tussenbroek *et al.* (2006) for seagrass communities in tropical Atlantic reef lagoons.

CONCLUSION

The CARICOMP research in Puerto Morelos, Mexico provided a baseline data set to detect environmental changes which will allow for the evaluation of present and future potential impacts of the continuous coastal development and global rise in temperature. Between 1993 and 2005, the benthic coral and seagrass communities at Puerto Morelos CARICOMP appeared stable, although some trends of potential permanent changes were discerned. Gorgonian and seagrass communities recovered relatively fast from the impact of major hurricanes suggesting high ecological resilience (Nyström *et al.* 2008). Coral cover at the reef site was expected to recover from Hurricane Gilbert (1988) but remained low. The coral community seems to be on a semi-permanent initial phase of development where recruitment is high but mortality is also high, seeming in a sense resilient to present conditions. However, algal outbreaks may change this situation as there is an ongoing increase in coastal development and there is no control of residual waters. Gradual changes in the seagrass community structure suggest an increasing nutrient load into the reef lagoon. We recommend the implementation of regulation measurements for the adjacent coastal zone, mainly for sewage and garbage treatment, in order to prevent deterioration of the coral reef and seagrass communities.

ACKNOWLEDGMENTS

This project was financed by the National University of Mexico and CARICOMP. We thank Miguel Angel Maldonado, Leonardo Vázquez, Daniel Gasca and all of the students that collaborated with the field work. Paul Blanchon and three anonymous reviewers made valuable comments to improve the manuscript.

RESUMEN

El sitio CARICOMP en Puerto Morelos, México, se monitoreo de 1993 a 2005. No se registraron cambios significativos en la temperatura del aire, los patrones de viento, la periodicidad y cantidad de lluvia, la temperatura superficial del mar y la transparencia del agua entre los años de muestreo. Durante el estudio se registraron cuatro huracanes menores. En el sitio del arrecife coralino la cobertura global promedio de algas carnosas (47%) y de algas tipo tapete (36%) fue elevada, mientras que la cobertura de corales (2%), esponjas (3%) y la abundancia de erizos (0.04 m^{-2}) fue consistentemente baja. Los gorgonáceos fueron dominantes y mostraron cambios en su estructura comunitaria; el número de especies aumentó de 1993 a 1995, su abundancia disminuyó después del Huracán Roxanne (1995) y se recuperó en el 2001. En cuatro estaciones de pastos marinos la biomasa total de la comunidad permaneció constante ($707.1-929.6 \text{ gps m}^{-2}$) pero la biomasa sobre el sustrato del pasto *Syringodium filiforme* y de algas carnosas aumentó gradualmente. La biomasa total ($531-699 \text{ gps m}^{-2}$) y productividad de hojas ($0.89-1.56 \text{ gps m}^{-2} \text{ d}^{-1}$) del pasto *Thalassia testudinum* permaneció constante, pero la especie invirtió proporcionalmente más biomasa en el tejido de hojas sobre el sustrato al final del estudio. Los huracanes menores entre 1993 y 2005 no produjeron impactos detectables en las camas de pastos, sin embargo, el huracán mayor Wilma (Octubre 2005) cambió la composición de la comunidad en tres estaciones y causó el enterramiento completo de la vegetación en la estación costera. El cambio gradual en las comunidades de pastos marinos y arrecife registrado en 12 años de monitoreo continuo en el sitio CARICOMP puede reflejar un aumento en la contaminación causada por el rápido incremento en desarrollo urbano y turístico a lo largo de la costa y tierra adentro de Puerto Morelos, acompañado por malas prácticas de manejo del agua.

Palabras clave: monitoreo ambiental, CARICOMP, México, arrecife coralino, pastos marino.

REFERENCES

- Aronson, R.B., W.F. Precht, I.G. Macintyre & T.J.T. Murdoch. 2000. Coral bleach-out in Belize. *Nature* 405: 36.
- Bythell, J.C., Z.M. Hillis-Starr & C.S. Rogers. 2000. Local variability but landscape stability in coral reef communities following repeated hurricane impacts. *Mar. Ecol. Prog. Ser.* 204: 93-100.
- Bruno, J.F. & E.R. Selig. 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE*: 2: e711.
- Cabaço, S., R. Santos & C.M. Duarte. 2008. The impact of sediment burial and erosion on seagrasses: A review. *Est. Coast. Shelf Sci.* 79: 354-366.
- CARICOMP. 1994. CARICOMP Methods Manual-Level I: Manuals of methods for Mapping and monitoring of physical and biological parameters in the coastal zone of the Caribbean. Kingston, Jamaica: CARICOMP Data Management Centre, University of the West Indies.
- CARICOMP. 1997. Studies on Caribbean coral bleaching 1995-96. *Proc. 8th Int. Coral Reef Symp, Panamá* 1: 673-678.
- Carruthers, T.J.B., B.I. van Tussenbroek & W.C. Dennison. 2005. Influence of submarine springs and wastewater on nutrient dynamics of Caribbean seagrass meadows. *Est. Coast. Shelf Sci.* 64: 191-199.
- Connell, J.H., T.E. Hughes, C.C. Wallace, J.E. Tanner, K.E. Harms & A.M. Kerr. 2004. A long-term study of competition and diversity of corals. *Ecol. Monogr.* 74: 179-210.
- Cruz-Palacios, V. & B.I. van Tussenbroek. 2005. Simulation of hurricane-like disturbances on a Caribbean seagrass bed. *J. Exp. Mar. Biol. Ecol.* 324: 44-60.
- Done, T.J., J.C. Ogden, W.J. Wiebe & B.R. Rosen. 1996. Biodiversity and ecosystem function of coral reefs, 393-429. *In* H.A. Mooney, J.H. Cushman, E. Medina, O.E. Sala & E.D. Schulze (eds.). *Functional Roles of Biodiversity: A Global Perspective*. SCOPE 1996, John Wiley and Sons, New York. USA.
- Duarte, C.M. 1992. Nutrient concentrations of aquatic plants: patterns across species. *Limnol. Oceanogr.* 37: 882-889.

- Erftemeijer, P.L.A. & J.J. Middelburg. 1993. Sediment-nutrient interactions in tropical seagrass beds: a comparison between a terrigenous and carbonate sedimentary environment in South Sulawesi (Indonesia). *Mar. Ecol. Prog. Ser.* 102: 187-198.
- Farnsworth, E.J. & A.M. Ellison. 1997. The global conservation status of mangroves. *Ambio* 26: 328-334.
- Fonseca A.C., E. Salas & J. Cortés. 2006. Monitoreo del arrecife coralino Meager Shoal, Parque Nacional Cahuita, Costa Rica (sitio CARICOMP). *Rev. Biol. Trop.* 54: 755-763.
- Fourqurean, J.W., A. Willsie, C.D. Rose & L.M. Rutten. 2001. Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Mar. Biol.* 138: 341-354.
- Fourqurean, J.W., G.V.N. Powell, W.J. Kenworthy & J.C. Zieman. 1995. The effects of long-term manipulation of nutrient supply on competition between seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos* 72: 349-358.
- Fourqurean, J.W. & L.M. Rutten. 2003. Competing goals of spatial and temporal resolution: monitoring seagrass ecosystem on a regional scale, p. 257-288. *In* D.E. Busch & J.C. Trexler (eds.). *Monitoring ecosystems*. Island Press, Washington D.C., USA.
- Fourqurean, J.W. & L.M. Rutten. 2004. The impact of hurricane Georges on soft-bottom, back reef communities: site- and species-specific effects in South Florida seagrass beds. *Bull. Mar. Sci.* 75: 239-257.
- Fourqurean, J.W., J.C. Zieman & G.V.N. Powell. 1992. Phosphorus limitation of primary production in Florida Bay: Evidence from C:P:N ratios of the dominant seagrass *Thalassia testudinum*. *Limnol. Oceanogr.* 37: 162-171.
- Goreau, T.F. 1959. The Ecology of Jamaican Coral Reefs. I. Species composition and zonation. *Ecology* 40: 67-90.
- Guzmán, H.M., P.A.G. Barnes, C.E. Lovelock & I.C. Feller. 2005. A site description of the CARICOMP mangrove, seagrass and coral reef sites in Bocas del Toro, Panama. *Carib. J. Sci.* 4: 430-440.
- Harvell, D., E. Jordán-Dahlgren, S. Merkel, E. Rosenberg, L. Raymundo, G. Smith, E. Weil & B. Willis. 2007. Coral disease, environmental drivers, and the balance between coral and microbial associates. *Oceanography* 20: 58-81.
- Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551.
- Hughes, T.P., D. Ayer & J.H. Connell. 1992. The evolutionary ecology of corals. *Trends Ecol. Evol.* 7: 292-295.
- Hughes, T.P. & J.H. Connell. 1999. Multiple Stressors on Coral Reefs: A Long-Term Perspective. *Limnol. Oceanogr.* 44: 932-940.
- Jordán-Dahlgren, E. 1979. Estructura y composición de arrecifes coralinos en la región noreste de la Península de Yucatán, México. *An. Centro Cienc. del Mar y Limnol. Universidad Nacional Autónoma México* 6: 69-86.
- Jordán-Dahlgren, E. & R.E. Rodríguez-Martínez. 2003. The Atlantic coral reefs of México, p. 131-158. *In* J. Cortés (ed.). *Latin American Coral Reefs*. Elsevier, Amsterdam, Holland.
- Jordán-Dahlgren, E., M.A. Maldonado & R.E. Rodríguez-Martínez. 2005. Incidence of coral diseases and colony mortality in the *Montastraea annularis* complex in reefs on the Southeastern Gulf of Mexico and Northwestern Mexican Caribbean. *Dis. Aqua. Org.* 63: 3-12.
- Jordán-Garza, A.G. 2004. Efecto de la rugosidad del substrato sobre *Siderastrea siderea*, *Diploria strigosa* y *Montastraea cavernosa* en la costa Noreste de la Península de Yucatán, México. Bachelor Thesis, Facultad de Ciencias, Universidad Nacional Autónoma México, México D.F.
- Jordán-Garza, A.G., Maldonado M.A., Baker D.M. & Rodríguez-Martínez R.E. 2008. High abundance of *Diadema antillarum* on a Mexican reef. *Coral Reefs* 27: 295.
- Linton, D. & T. Fisher. 2004. Caribbean Coastal Marine Productivity Program, 1993-2004. CARICOMP, Kingston, Jamaica.
- Loya, Y. 1976. Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. *Bull. Mar. Sci.* 26: 450-466.
- Moberg, F. & C. Folke 1999. Ecological goods and services of coral reef ecosystems. *Ecol. Econ.* 29: 215-233.
- Nyström, M., N.A.J. Graham, J. Lokranz & A.V. Nyström. 2008. Capturing the cornerstones of coral reef resilience: linking theory to practice. *Coral Reefs* 27: 795-809.

- Patriquin, D.G. 1975. "Migration" of blowouts in seagrass beds at Barbados and Carriacou, West Indies, and its ecological and geological implications. *Aquat. Bot.* 1: 163-189.
- Powell, G.V.N., W.J. Kenworthy & J.W. Fourqurean. 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bull. Mar. Sci.* 44: 324-340.
- Rodríguez-Martínez, R.E. 1993. Efectos de un ciclón en la estructura comunitaria de corales escleractinios. Bachelor Thesis. E.N.E.P. Iztacala. Universidad Nacional Autónoma México, México.
- Rodríguez-Martínez, R.E. 2008. Community involvement in marine protected areas: the case of Puerto Morelos reef, México. *J. Environ. Manag.* 88: 1151-1160.
- Rodríguez-Martínez, R.E., A.T. Banaszak & E. Jordan-Dahlgren. 2001. Necrotic patches affect *Acropora palmata* (Scleractinia: Acroporidae) in the Mexican Caribbean. *Dis. Aquat. Org.* 47: 229-234.
- Rose, C.D. & C.J. Dawes. 1999. Effects of community structure on the seagrass *Thalassia testudinum*. *Mar. Ecol. Prog. Ser.* 184: 83-95.
- Ruíz-Rentería, F., Van Tussenbroek B.I. & E. Jordán-Dahlgren. 1998. Puerto Morelos, Quintana Roo, Mexico, p 57-66. In B.J. Kjerfve (ed.). CARICOMP-Caribbean Coral Reef, Seagrass and Mangrove Sites. UNESCO, Paris.
- Short, F.T. & S.W. Echeverria. 1996. Natural and human-induced disturbance of seagrasses. *Environm. Conserv.* 23: 17-27.
- Short, F.T., W.C. Dennison & D.G. Capone. 1990. Phosphorus limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. *Mar. Ecol. Prog. Ser.* 62: 169-174.
- Van Tussenbroek, B.I. 1994a. Spatial and seasonal variability in biomass and leaf morphology of the manatee grass *Syringodium filiforme* in a tropical coral reef lagoon, Mexico. *An. Inst. Cienc. del Mar y Limnol. UNAM* 21: 15-22.
- Van Tussenbroek, B.I. 1994b. The impact of Hurricane Gilbert on the vegetative development of *Thalassia testudinum* in Puerto Morelos reef lagoon, Mexico: a retrospective study. *Bot. Mar.* 37: 421-428.
- Van Tussenbroek, B.I. 1995. *Thalassia testudinum* leaf dynamics in a Mexican Caribbean reef lagoon. *Mar. Biol.* 122: 33-40.
- Van Tussenbroek, B.I. 1998. Above- and below-ground biomass and production of *Thalassia testudinum* in a tropical reef lagoon. *Aquat. Bot.* 61: 69-82.
- Van Tussenbroek, B.I., K. Hermus & T. Tahey. 1996. *Thalassia testudinum* (Banks ex König) biomass and growth in a shallow tropical lagoon system, in relation to tourist development. *Carib. J. Sci.* 32: 357-364.
- Van Tussenbroek, B.I., J.A. Vonk, J. Stapel, P.L.A. Erfemeijer, J.J. Middelburg & J.C. Zieman. 2006. The biology of *Thalassia*, p. 409-439. In A.W.D. Larkum, R.J. Orth & C.M. Duarte (eds.). *Paradigms and Recent Advances in Research Seagrass Biology*. Springer, The Netherlands.
- Van Tussenbroek, B.I., M.G. Barba Santos, J.K. van Dijk, S.N.M. Sanabria Alcaraz & M.L. Téllez Calderón. 2008. Selective elimination of rooted plants from a tropical seagrass bed in a back-reef lagoon: a hypothesis tested by Hurricane Wilma (2005). *J. Coast. Res.* 24: 278-281.
- Williams, S.L. 1990. Experimental studies of Caribbean seagrass bed development. *Ecol. Monogr.* 60: 449-469.
- Zieman, J.C. & R.G. Wetzel. 1980. Productivity in seagrasses: methods and rates, p. 87-116. In R.C. Phillips & C.P. McRoy (eds.). *Handbook of Seagrass Biology: An Ecosystem Perspective*. Garland STPM, New York, USA.