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Conservation and Sustainability of Mexican Caribbean Coral Reefs and the Threats of a Human-Induced Phase-Shift

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1. Introduction

Natural ecosystems around the world are continually changing, but in recent decades it has become increasingly evident that terrestrial and marine environments are degrading. It is considered that the main cause is the rapid human population growth and increasing demand of resources for our survival. In particular for coral reef ecosystems, they are experiencing a significant change as reflected in the decline of coral cover and diversity of species [1, 2].

Coral reefs are marine ecosystems of great ecological and economic importance to mankind. These ecosystems are characterized by high productivity and biodiversity [3] caused by the high diversity of habitats created by its complex, calcium carbonate threedimensional structure that facilitates the diversification of niches and space availability for the establishment of a variety species. Additionally, they serve as important spawning areas for breeding and feeding of the organisms that are part of the ecosystem [4]. The interactions that exist between the species that inhabit coral reefs create an ecological balance that maintains ecosystem functioning, which is reflected in its ability to maintain high productivity in these groups of reef-building coral species and fish, and play key roles in the regulation of ecological processes [2].

From the economic point of view, coral reefs supply mankind with such services as organisms for food, biochemical components, building materials, coastal protection against



storms and waves, recreational opportunities and aesthetic and cultural benefits (see [4]). It is estimated that more than 100 countries have coastlines with coral reefs, and tens of millions of people depend on them as part of their livelihood or as part of their intake of protein [5]. It is noteworthy that the quantity and quality of these services depends on the health of coral reefs.

Unfortunately, many of these ecosystems are in serious state of degradation and it is considered that the health of coral reefs is in a worldwide crisis [6]. By 2008 it was estimated that coral reefs had effectively lost 19% of their original area, an additional 15% was seriously threatened and was considered to it will be lost within the next 10 to 20 years, while 20% are under threat with the possibility of being lost within 20 to 40 years. These estimates were made under a scenario of 'business as usual' and do not consider the threats posed by global climate change [7].

Paleoecologic work suggests that this pattern of degradation in various areas of the Caribbean is unprecedented within the past millennia. Also, there is no convincing evidence that global stressors (e.g. induced bleaching by temperature changes and reduced calcification rates via increasing levels of atmospheric CO₂) are responsible for the overall pattern of recent coral degradation, making it more likely that local stressors are responsible for the recent degradation occurred in the Caribbean [1]. In this sense, it is particularly evident that degradation of coral reefs occurs near densely populated areas, hence indicating that anthropogenic factors work synergistically against the stability of these ecosystems. Among these factors, the increased levels of nutrients and the over-exploitation of reef organisms are the best studied and considered to be responsible for the larger part of the impacts [8-9]. However, we cannot omit mentioning other impacts such as increased discharge of sediment and pollutants, uncontrolled tourism and introduction of new species (e.g., lionfish) and diseases [2,4, 10-11]. Added to all these factors is the threat of global climate change and the increased intensity of natural phenomena such as severe storms and hurricanes, and the development of the El Niño / La Niña - Southern Oscillation phenomenon -- and their associated surface temperature change-- have contributed to the health degradation of coral reef ecosystems [12].

In many locations around the world the anthropogenic stress on coral reefs has exceeded the regenerative capacity of the ecosystems, causing dramatic changes in species composition and thus a severe economic loss [2]. This change in the structure and functioning of the ecosystem is known as "phase-shift" or alternative stable state; the most cited example is the shift from an original coral-dominated reef to one dominated by macroalgae[13-14], although several other transitions have been documented [2]. This phase-shift is a consequence of the loss of resilience, defined as the ability of an ecosystem to absorb perturbations, its resistance to change and its capability to regenerate after a natural or anthropogenic disturbance [15]. The degree to which the phase-shift --or alternative state-- is stable or reversible is poorly understood and represents one of the main challenges for research and management of coral reefs.

Given the nature of the problem and the huge importance of coral reefs to mankind, it is recognized that urgent action is needed to conserve and promote its sustainable use [7]. Thus, it

is urgent to assess current management practices that focus mainly on safeguarding the biodiversity of coral reefs by delimiting marine protected areas (MPAs) where human activities are controlled, or prohibited in the case of fishing. This kind of management is increasingly prevalent. But if it succeeds by adequately fulfilling its objective, it would provide a spatial refuge for the organisms that are distributed within the area, allowing critical functional groups to persist, and so continue to build local resilience of the ecosystem. However, only a few marine protected areas meet its conservation and functionality goals. At the global scale, 18% of the coral reef area is within the boundaries of a marine protected area and only 1.6% of these are properly managed [16]. To adequately address the crisis requires that management efforts are based on a better understanding of the ecological processes that maintain the resilience of coral reefs. Managing for improved resilience, incorporating the role of human activities as shapers of ecosystems provides a basis for addressing the uncertainty of a changing environment [2].

2. The case of coral reefs in the Mexican Caribbean

The degradation of coral reefs in the Wider Caribbean is alarming. Population growth in the region has led to a combined effect of increased pollution and reduced herbivore populations as a result of overfishing and/or diseases [1,17]. These reefs are continually cited as examples of a phase-shift.

In the case of coral reefs in the Mexican Caribbean (from the Northern tip of the Yucatan peninsula to the southern international border with Belize) studies are scarce and the poor distribution of the information generated from implemented management programs limits our knowledge of these systems and the successes of the conservation programs. In this sense, the current status and health of the coral reefs of the Mexican Caribbean at the regional scale are not well known, but at the local scale, clear signs of deterioration have been reported in some reefs despite being designated and managed as protected areas. To achieve conservation and sustainable use of coral reefs requires a better understanding of the dynamics of these ecosystems and the processes that support or undermine resilience; we need reliable scientific information that can be used for management plans at local and regional levels. This study presents the ecological and hydrological characterization of thirteen coral reefs distributed within three National Parks in the Yucatan: Isla Mujeres-Cancun-Nizuc National Park (PNIMCN), the National Park of Puerto Morelos reefs (PNAPM) and Cozumel reefs National Park (PNAC) (Figure 1) in order to present the current state of these reefs and identify possible causes of degradation, if present.

For the analysis of coral/benthic community structure we used the following benthic diversity indices: Margalef's D' index that measures species richness independently of the sample size, based on the ratio of the number of species (S) and the total number of individuals observed (N). Simpson's index of dominance (λ) that measures the probability from a non-repeated random draw of two organisms from a community, that they belong to the same species. The Shannon-Wiener's index of diversity (H') measures the degree of uncertainty in predicting to which species belongs an individual chosen at random from asample of Sspecies and Nindividuals. Pielou's index of evenness (J') which measures the proportion of the diversity observed in relation to the maximum expected diversity with values ranging from 0 to 1, where values close to 1 means that all speciesare equally abundant [18]. We used multivariate techniques in order to statistically support the comparisons between localities, both in the community structure of coral and fish. A similarity matrix was generated using the Bray-Curtis coefficient of similarity; this coefficient measures the similarity between two samples with values ranging from 0 to 1, where values close to 0 correspond to different samples and close to 1 correspond to equal samples. Using the similarity matrix we performed an Analysis of Similarity (ANOSIM) for assessing the differences in community structure between locations. In addition a cluster analysis classification was performed in order to detect if a group of samples have more similarity to others within a group [19]. In the case of nutrient concentrations we applied a variance analysis (ANOVA) to detect statistically significant differences between the parks studied.

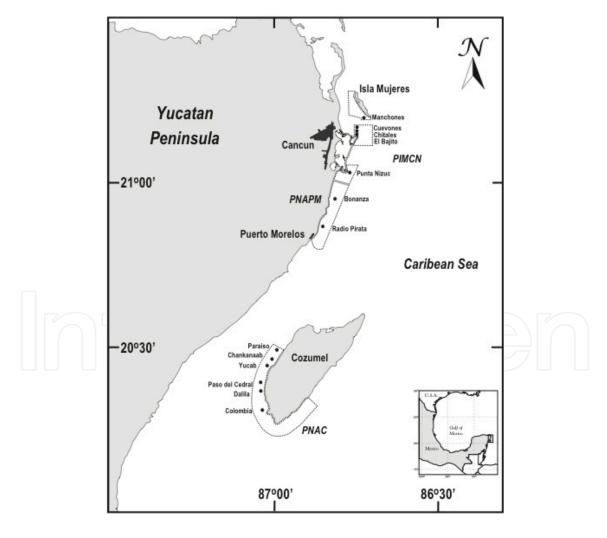


Figure 1. Sampling localities at the Marine National Parks of Isla Mujeres – Cancún – Nizuc (PNIMCN), Arrecifes de Puerto Morelos (PNAPM) and Arrecifes de Cozumel (PNAC) during 2006 - 2007.

3. Community structure of corals and benthic components

The three National Marine Parks were established to conserve the natural ecosystems found within the area, but human activities have not been restricted entirely, and instead, human settlements have increased on the coast, using these habitats for recreation and tourism as well as for fishing within in the limits of the Parks, poaching included.

In order to determine the current status of the coral reefs of the Yucatan Peninsula, an analysis of benthic components of each of these marine parks was conducted. The characterization of benthic components of the reefs provides information about the current health status of the ecosystem. The percentage of coral cover, macroalgae, seagrass, and other invertebrates, is reported from the sampled localities and subsequently analyzed their spatial and temporal variability. During the months of November 2006 (beginning of the dry season) and May 2007 (beginning of wet season) we surveyed the benthic composition of the coral reefs of the three marine parks using the Line Intercept Transect (LIT) method [20]. We surveyed five reefs at the PNIMCN, two reefs at PNAPM, and six reefs at PNAC (Table 1).

There were a total of 40 species of coral identified in the study area with the Cozumel Reefs National Park consistently containing the highest number of species: 25 coral species found at Paso del Cedral reef and 19 at Chankanaab reef (which is its maximum for this locality but the minimum for the PNAC). In general, Porites astreoides and Acropora palmata are the most abundant species in the Parks of Northern Quintana Roo, i.e., in Isla Mujeres - Cancun - Nizuc and Puerto Morelos. In the reefs of Cozumel, the most abundant species are Agaricia agaricites and Siderastrea siderea. Of all the coral reefs studied, Chitales reef, located at Punta Cancun, is the one with the lesser number of species (only seven species) (Table 1).

As for the diversity indices, we see a decrease, both in diversity and in species richness from South to North along the Quintana Roo coast; Cozumel reefs have the highest richness index, being Dalila reef the one with the highest value of D '= 6.97. Also, Chankanaab reef together with 'Colombia' reef presented the highest diversity values of H' = 2.19 nits/Ind and H' = 2.18 nits/Ind, respectively. Diversity indices decrease towards the North, with the Chitales reef having the lowest diversity value of H '= 1.60 nits/Ind. Based on the Pielou evenness index, the benthic community structure appears to be distributed evenly because the index values are relatively high; this is reinforced by the Simpson dominance index values obtained (Table 1) for Punta Nizuc reef (λ = 0.27) and for Yucab reef (λ = 0.19).

With regard to the percentage coral cover and macroalage a trend can be observed contrary to the diversity indices and the number of species as the highest percentage of coral cover was observed in the reefs of northern Quintana Roo. Particularly Yucab reef at PNAC had the highest diversity and species richness but was the one with the lowest coral cover. In the case of algae cover there is also a decrease from North to South, as the National Reef Park Isla Mujeres- Cancun -Nizuc (PNIMCN) have the highest percentages in algal cover decreasing to 17.01% in Cozumel (Figure 2). Consistently, always PNIMCN reefs have higher algal cover compared to coral. At the reefs of PNAC algal cover is consistently less than algal cover at PNPM and PNIMCN.

	Reef Loc.	Coral (%)	Algae (%)	No. of sp.	Richness (D')	Eveness (J')	H' (nits/indv)	Dominance (λ)
PNIMCN	Manchones	27.00	48.00	13	3.64	0.69	1.78	0.24
	Cuevones	26.20	41.60	10	2.76	0.73	1.68	0.24
	Chitales	16.91	49.09	7	2.12	0.82	1.60	0.25
	El Bajito	16.17	50.17	17	5.75	0.73	2.07	0.21
	Punta Nizuc	17.40	58.00	14	4.55	0.71	1.88	0.27
PNAPM	Bonanza	12.40	41.20	12	4.37	0.77	1.93	0.21
	Radio Pirata	27.60	20.60	12	3.32	0.80	2.00	0.19
PNAC	Paraiso	11.32	24.51	14	5.40	0.77	2.03	0.18
	Chankanaab	15.69	39.31	17	5.84	0.77	2.19	0.15
	Yucab	9.31	17.01	15	6.50	0.73	1.96	0.19
	Paso del Cedral	18.33	21.18	18	5.93	0.72	2.09	0.20
	Dalila	18.40	32.57	21	6.95	0.69	2.09	0.22
	Colombia	22.22	21.88	16	4.85	0.79	2.18	0.14

Table 1. Ecological Indices for the coral reefs of three marine national parks studied in northern Quintana Roo (PNIMCM: ParqueNacional Isla Mujeres, Cancún, Nizuc; PNAPM: ParqueNacionalArrecife de Puerto Morelos, PNAC: ParqueNacionalArrecifes de Cozumel)

In order to simplify comparison of benthic component data obtained from the different reef localities, we formed a single component group called abiotc components by grouping bottom components such as rocks, sand, dead coral and other non-living components.

It is important to note that while Cozumel reefs have the highest species richness and diversity, and reduced algal cover, these reefs are characterized by a higher percentage of abiotic components (above 40%). In the case of Northern reefs it is the algae that contributes to the higher percentage of benthic components (Figure 3). In the case of the reef sites of Punta Nizuc, Bonanza and Radio Pirata are characterized by the presence of seagrasses.

Applying the ANOSIM similarity analysis significant differences were detected between the various reefs studied (R = 0.497, p = 0.001), except for El Bajito reef, which in terms of the structure of benthic components it was not significantly different from Chitales reef (R = -0.006, P = 0.51), being the two reefs part of the same national park (PNIMCN). At the Cozumel Reefs National Park, the Paso del Cedral reef and Delilah reef, Paraiso reef and Chankana'ab reef are the only reefs that present no significant differences in the structure of benthic components (R = 0.047, P = 0.142; R = -0.039 p = 0.75). This can be confirmed by a cluster analysis, that based on a similarity matrix generated using the Bray-Curtis, can be seen that the diagram is clearly divided into two groups separating Cozumel reefs park (PNAC) from the parks of Puerto Morelos (PNAPM) and Isla Mujeres-Cancun-Nizuc (PNIMCN); and within this latter group, the separation between Puerto Morelos and PNIMCN can be clearly seen (Figure 4).

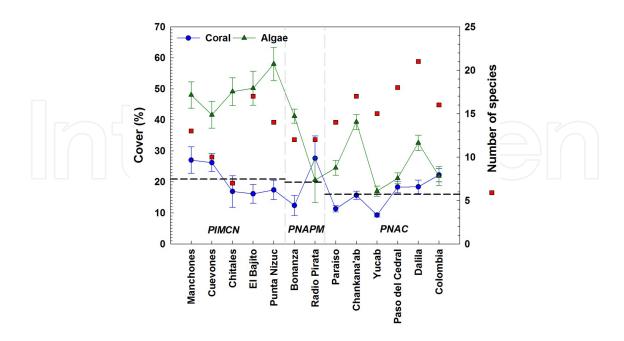


Figure 2. Coral and algal cover (percentage) at the Northern Quintana Roo National Reefs parks for the years 2006-07. The dashed line represents the average coral cover (percentage) for each park.

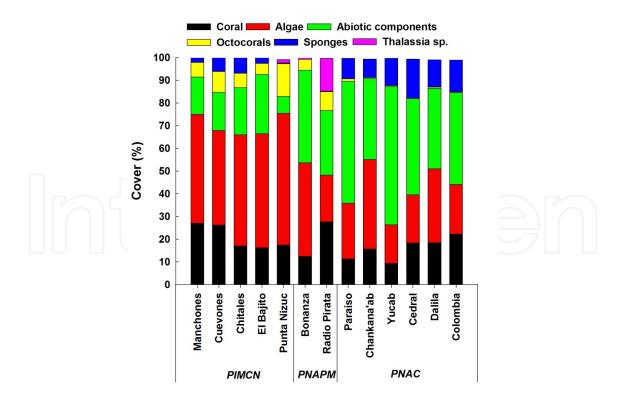


Figure 3. Benthic components of the coral reefs at three National Marine Parks in Northern Quintana Roo during 2006-2007.

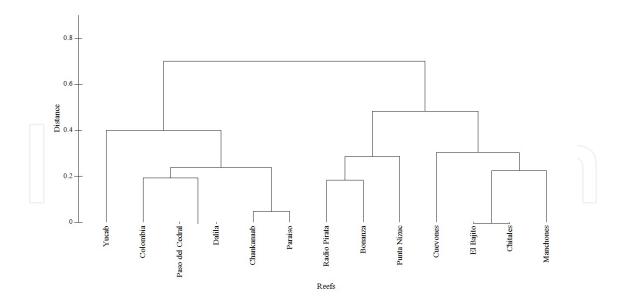


Figure 4. Cluster analysis of the coral reefs of Northern Quintana Roo (data for 2006-2007).

4. Hydrology: Nutrient concentrations

The increase of anthropogenic nutrients is attributed to be a major cause of increased algal cover in coral reef ecosystems, based on the theory that in some reefs bottom-up ecological control in food chains regulates ecosystems. In order to try to better understand the processes that regulate ecosystem resilience we additionally characterized the hydrological conditions throughout the three marine parks studied here. Samples were taken from different stations distributed on the same reefs where benthic surveying was conducted (Figure 5a,b), additionally including the hydrologic (nutrient) characterization of the Nichupte Lagoon, bounded to the north by Punta Cancun and to the south by Punta Nizuc (Figure 5a). In order to characterize the concentration of nutrients, particularly from dissolved inorganic nitrogen (DIN) species that involve inorganic nitrogen: nitrate (NO₃), nitrite (NO₂) and ammonium (NH₄), water samples were collected at two different depths: at the water surface and near the substrate. Sampling was conducted in the months representing contrasting seasonal conditions (dry and rainy seasons) in the years 2006 and 2007.

The average concentration of DIN in the sampled coral reefs is shown in Table 2. By applying a factorial ANOVA considering the different climatic seasons and parks there were no significant differences in the concentration of DIN (F = 0.422, p = 0.657) but between the dry and rainy seasons (F = 9.280, p = 0.003). Consistently, one can observe a slight increase in the concentration of dissolved inorganic phosphate (DIP) in the three parks during the rainy season; this increase is mostly evident in the PNIMCN and PNAPM, because it almost doubled the average concentration measured during the dry season (Figure 6). As was expected for Nichupté Lagoon, it was characterized by a higher concentration of DIN with respect to the levels seen at the reef sites. In addition, Ni-

chupté lagoon presents an opposite behavior to reef sites as a function of seasonality: while during the rainy season the DIN increases reefs, the concentration decreases in the lagoon, probably due to dilution effect (Table 2, Figure 6).

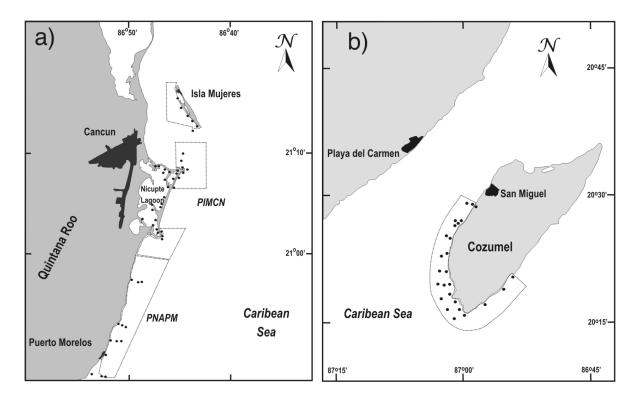


Figure 5. Sampling locations in the PNIMCN and PNAPM (a) and in the PNAC (b), used for characterizing the nutrient levels in the coral reefs of Northern Quintana Roo during 2006 – 2007.

Location	Season	DIN (μM)	Nitrate (μM)	Nitrite (μM)	Ammonium (μM)	Phosphate (μM)	Silicate (μM)
Nichupté-	Dry	14.77	2.08	1.08	11.61	0.18	5.50
Lagoon	Rainy	4.18	1.08	0.16	2.94	0.33	7.98
PNAC	Dry	1.26	0.60	0.09	0.58	0.26	6.48
	Rainy	1.96	0.54	0.09	1.33	0.29	4.58
PNAPM	Dry	0.91	0.25	0.09	0.57	0.24	3.15
	Rainy	2.15	0.53	0.04	1.58	0.16	1.85
PNIMCN	Dry	0.86	0.17	0.10	0.59	0.23	4.42
	Rainy	1.50	0.46	0.07	0.98	0.28	2.30

Table 2. Average nutrient concentration in the Nichupté-Lagoon and the coral reefs of three National reef parks of Northern Quintana Roo during 2006 – 2007.

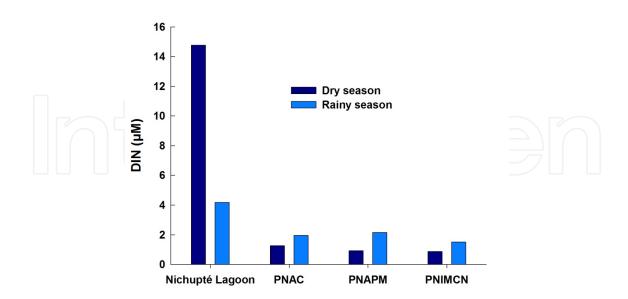


Figure 6. Average DIN concentration (μ M) in in the Nichupté-Lagoon and the coral reefs of three National reef parks of Northern Quintana Roo (PNAC, PNIMCN, PNAPM) during 2006 – 2007 in two climatically contrasting seasons (rainy and dry).

Ammonium (NH₄) is the most important DIN species in the reef waters. Its concentration is consistently higher than nitrates and nitrites, except for the PNAC during the dry season in which ammonium and nitrate have approximately the same concentration (Figure 7). It was expected that ammonia were the most important DIN species, since the success of high productivity of coral reefs results from the high nutrient recycling that takes place within the ecosystem. Most of the new nitrogen entering the reef is through N2 fixation, so it is absorbed and converted to organic nitrogen which can be later consumed and passed through the food webs or returned to the system as ammonia by passing through the process of ammonification, so it is excreted in the urine of organisms [21].

During the dry season, there is no significant difference among the three species of DIN in the three parks, however the average concentration of nitrate is higher in the PNAC. During the rainy season nitrate concentration is high in all parks but ammonium is significantly higher, being PNAPM the park with the highest ammonium concentration (Table 2, Figure 7).

The hydrographic information generated in this study indicates that there is no evidence of eutrophication in reef areas in the Mexican Caribbean. In general, nutrient concentrations are low, typical of the reef zones of the Wider Caribbean. The general average of DIN (1.3 \pm 1.6 μ M) in the Northern Quintana Roo reef parks is lower than that reported for the Florida reef tract (4.3 \pm 7.4 μ M; [22]) and within the observed range of the coral reefs of Tobago (1.6 \pm 1.1 μ M; [23]).

It has been shown that groundwater seepage into the coastal area of this region can supply significant amounts of nutrients to the water column [24-25]. However, a study in

seagrass meadows of Thalassia testudinum in Puerto Morelos reef lagoon has shown that water seeping through the springs (locally called 'ojos') can enrich the water column -and seagrasses-- with phosphorus, but not with nitrogen [25]. These authors found that in T. testudinum meadows of Puerto Morelos, the pore water contains extremely low levels of nutrients (1.2 - 3.42 µM of ammonium and 1 - 1.5 µM of phosphate) compared with the world average for seagrass meadows (~ 86 µM of ammonium and 12 µM of phosphate). This low DIN concentration in the water column of Puerto Morelos suggests that nitrogen could be limiting the growth of seagrass meadows. The nitrogen content in the tissue T. testudinum in the reef lagoon (% N> 1.8), however, is high enough to not show this limitation [25].

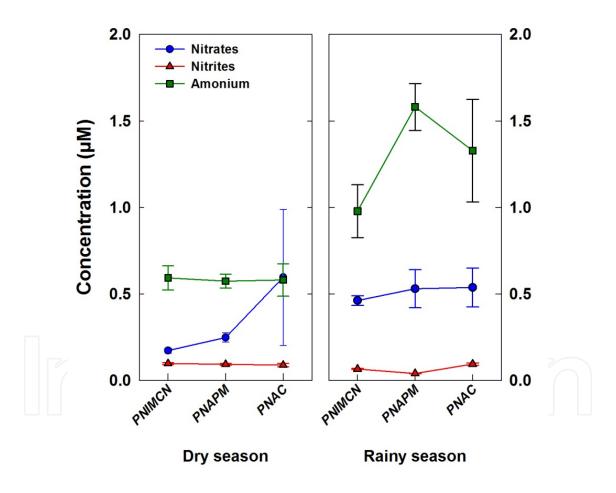


Figure 7. Average DIN concentration in the coral reefs of three National reef parks of Northern Quintana Roo (PNAC, PNIMCN, PNAPM) during 2006 - 2007 in two climatically contrasting seasons (rainy and dry). ANOVA statistical test (bars represent Std. Error).

In contrast to the typical oligotrophic conditions that characterize coral reef areas, nutrient concentration inside the Nichupté Lagoon system is much higher. The weighted average concentration of DIN inside this lagoon system (14.7 \pm 11.6 μ M for winter and 4.18 \pm 1.98 μ M

for summer) is between 2-7 times higher than the DIN average measured in Puerto Morelos, the coral reef area with the highest average DIN concentration ($2.15 \pm 0.84 \,\mu\text{M}$) of our study area. These results, however, were expected because this lagoon system receives wastewater from the surrounding developments. After a few decades of continuous supply, there are now evident signs of eutrophication [25-26]. In spite of this situation, our results indicate that reef areas developing outside this lagoonal system are not affected, so far, in their hydrographic characteristics.

Favorably, the reef systems along the Mexican Caribbean coast still thrive under low nutrient concentrations. However, the low concentrations of DIN in the coastal waters and the evident overgrowth of macroalgae on the reefs studied suggest the existence of diffuse nitrogen sources fueling their growth. Nitrogen fixation could be a major source for these reefs (see further evidences of this in the isotopic section),and if this nitrogen source dispersed through the water column, it would raise the DIN up to 0.3 μ M day-1[25]. This assumption is reasonable, especially when considering that the nitrogen isotope values (δ^{15} N) in the tissues of macroalgae growing on these reefs (see below) are very close to the isotopic composition of atmospheric nitrogen (δ^{15} N₂ = 0‰). This new nitrogen, however,may pass "undetected" in our monitoring sampling because it may be immediately assimilated by the macrophytes upon entering the coastal zone where the coral reefs develop. In this regard, the actual macrophyte biomass itself may be the best evidence of large nitrogen inputs into the otherwise oligotrophic environments that characterize coral reefs, where macrophytes' occurrence is commonly very scarce.

5. Isotope systematics of δ^{15} N in macroalgae

In order to differentiate potential sources of nitrogen to the reef zones we analyzed the nitrogen isotopic composition (δ^{15} N) of the tissue of several species of macroalgae collected from reefs studied. The δ^{15} N of macroalgae has been a widely used as tracer of nutrient dynamics [27] This approach has been applied mainly in areas where nutrient sources are diffuse or little obvious, but also in areas where sources are very different, such as nutrient inputs from sewage. However, the spatial extent of its influence is not clear [28-29].

The δ^{15} N values of macroalgae from the different reefs of the three national marine parks are shown in Figure 8. The more common genus found in the study area were *Dyctiota* spp. and *Halimeda* spp., followed by *Penicillus pyriformis*, *Ulotrix* spp. and the seagrass *Thalassia testudinum*. We grouped all species by location and compared the average- δ^{15} N (\pm 1SD) of macroalgae between locations and sampling period (Figure 8a for winter-2006, and Figure 8b for summer-2007). For reference, we have included in this figure the average nitrogen isotopic composition of nitrate (δ^{15} NO₃ = 4.37 \pm 2.5 %) for the three parks (Carriquiry unpublished data). The validity of this reference comparison rests on the assumption that nitrate is a major source of nitrogen for macroalgae.

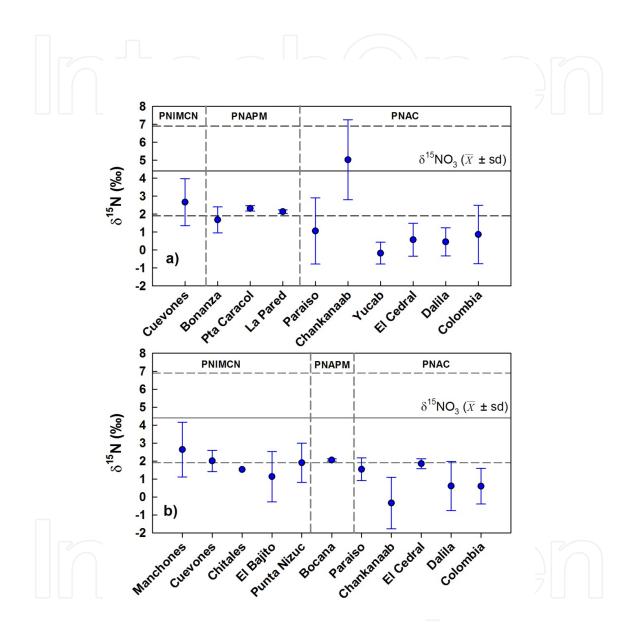


Figure 8. Average δ^{15} N composition (± 1SD) of macroalgae collected at each site during the winter of 2006 (a) and the summer of 2007 (b). The average isotopic composition of nitrate ($\delta^{15}NO_3$) in the coastal waters (Carriquiry, unpublished data) of the three coral reef national parks studied here is included as a thin horizontal line in each diagram.

A common feature for both collection periods is the low $\delta^{15}N$ values of macroalgae. During winter-2006, with the exception of Chankanaab reef at PNAC ($\delta^{15}N$ of 5.0 ± 2.2 ‰), the $\delta^{15}N$ of macroalgae is less than 3 ‰ and is markedly smaller than the isotopic value of nitrate ($\delta^{15}NO_3$) (Figure8a). As in the winter of 2006, the average $\delta^{15}N$ of macroalgae during the summer of 2007 varied from ~ 0.5 to 2.5 ‰, being always below the average $\delta^{15}NO_3$ (Figure 8b).

It is noteworthy to highlight the results obtained from Chankanaab reef (at PNAC) which shows the greatest contrast in the average $\delta^{15}N$ of macroalgae between sampling seasons: while the average $\delta^{15}N$ of macroalgae was the most positive of all sampling stations during the winter of 2006 (Figure 8a), during the summer of 2007 Chankanaab reef presented the most negative $\delta^{15}N$ values (-0.34 ± 1.43 %) of all the studied sites (Figure 8b). One factor that may explain this discrepancy is the difference in species composition between sampling sites. While in the winter of 2006 the $\delta^{15}N$ was measured in *Dyctiota* spp. and *Penicilluspyriformis*, during summer 2007 the species analyzed were *Lobophoravariegata*, *Dictyosphaera cavernous*, *Anadyomenestellata* and *Ulotrix* spp. The results for species indicates that the $\delta^{15}N$ of *Dyctiota* spp. and *P. pyriformis* were characterized by positive values in both sampling periods, while the species *L. variegata* always showed low $\delta^{15}N$ values, including *A. stellata* whose measured $\delta^{15}N$ was the most negative (-1.67 and -1.42 % for Chankanaab and Dalila, respectively) in both sampling periods.

There are several alternatives to explain the low $\delta^{15}N$ values of macroalgae in this region. N_2 fixation in coral reefs is regarded as a major component of the nitrogen cycle that provides new nitrogen for these ecosystems. It has been estimated that fixed nitrogen can supply from one quarter to one half of the nitrogen requirements for the primary producers in these oligotrophic environments [30]. It has been shown in coral reef areas where nitrogen fixation is predominant that $\delta^{15}N$ value of macroalgae is close to 0 ‰, or even negative [31,32]. In agreement, the range of $\delta^{15}N$ values measured in the different species of macroalgae (<0 to <2.5 ‰) in our study, indicates that N_2 fixation may be playing an important role in fulfilling the macrophytes' nitrogen demand. This conclusion is also supported by [25] who found that the $\delta^{15}N$ values of 1.9 ‰ in the seagrass *Thalassia testudinum*, in Puerto Morelos lagoon, were the result of nitrogen fixation.

Alternatively, another possibility is the low concentration of dissolved inorganic nitrogen (DIN) in the studied reefs. Different studies have shown a positive relationship between the $\delta^{15}NO_3$ versus nitrate concentration [NO₃], both in temperate and tropical areas. It was found in a Massachusetts estuary that the $\delta^{15}NO_3$ values approach 0 % when the nitrate concentration is reduced to levels <1 uM [33]. Similarly, other results obtained by [34]from the Mexican Caribbean reported that $\delta^{15}NO_3$ decreases linearly with the concentration of nitrate in the water column. Thus, considering the low DIN concentrations that characterizeour study area it would be expected that the $\delta^{15}N$ -DIN available for macroalgae should be characterized by lower values.

Lastly, changes in the proportion of the different nitrogen species available for photosynthesis could explain the lower values in $\delta^{15}NO_3$. In our study, ammonia accounts for 60 to 76% of the DIN levels. This implies that ammonium, but not nitrate, could be the main source of nitrogen to seaweeds in the region. Hence, the $\delta^{15}N$ of macroalgae largely

reflects the isotopic signature of ammonia. This hypothesis, although plausible, depends on the metabolic capacity of each species for using ammonium, depending on its availability in the environment.

6. The functional role of reef fish

Fishes are particularly recognized for their role as the main drivers of energy flow in coral reefs and can be separated into two major functional groups: the grazers or herbivores that regulate the abundance and community structure of algae; and corallivorous that selectively feed on coral tissue. Its importance, in addition to controlling the population of primary producers is that their feeding activity promotes biodiversity, since consumption of algae and coral leaves available space for colonization of new individuals or species [35]. Another important group are the predators as they play an important role in the ecosystem because they occupy the highest level in food webs, and from this position they regulate the organisms that are in the lower trophic levels. Additionally, they connect the dynamics of other communities and ecosystems that are apparently distinct as they often travel long distances. It has been suggested that the predator's ability to travel great distances in response to changes in prey abundance is important for maintaining stability of food webs [36]. Consequently, the loss of top predators could destabilize ecosystems through a chain reaction that eventually propagate down through the food web. With this in mind, the biomass of herbivorous and predatory fish have been calculated in order to determine whether there is spatial variability in these functional groups.

There is a close link between the fish community and benthic components, as any change in the structure of one of these communities has an effect on the structure of the other. [37] pointed out that in quantitative studies during the 80's reported high densities of predators, like sharks and groupers, associated with areas of high coral cover. Currently, the presence of large top predators is rare and is considered that the decrease in the abundance of this group has strongly affected the trophic flow patterns in reef communities [38]. In addition, the decrease in coral cover in coral reefs has been related to the decrease in the abundance and diversity of reef fishes [39].

In order to gain a better understanding of the role of fishes in our study area, we analyzed the community structure of reef fish sampled at PNAPM and PNAC; for PNIMCN we only had data for Manchones reef. By applying a similarity analysis (ANOSIM) to the abundance data, significant differences in the structure of the fish community were detected in these locations (R = 0.442, p < 0.0001). Paired tests showed significant differences between all locations, except Yucab and Paraiso Reefs (p = 0.09), and Yucab and Paso Cedral reefs (p = 0.23); also Dalila and Colombia do not show significant differences (p = 0.20). Using cluster analysis, based on a similarity matrix generated using the Bray-Curtis index, can be seen again the grouping of localities from each national park, leaving the Manchones reef alone as an isolated entity (Figure 9).

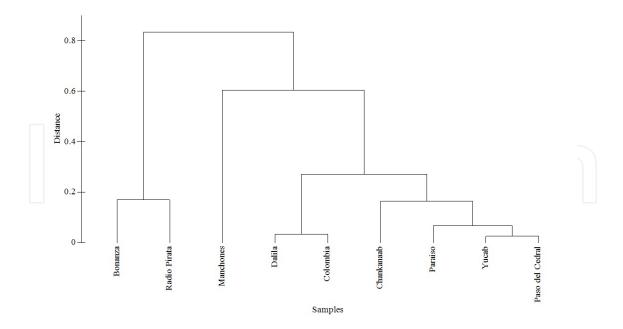


Figure 9. Cluster analysis of the reef fish community in northern Quintana Roo (2007 data).

The differences in the structure of the fish community, can be as well associated with structural differences in the benthic composition of the reefs, as the decline in coral cover reduces the structural complexity of the reef and therefore the space available for shelter and feeding [39] (Figure 10).

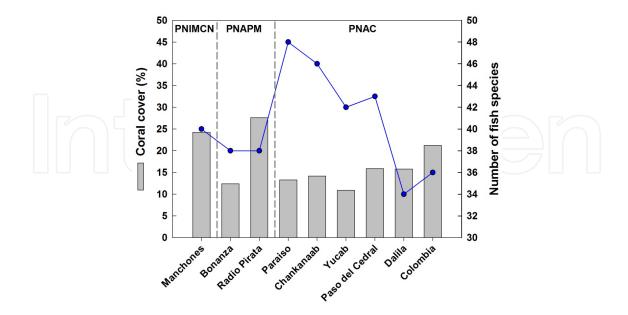


Figure 10. Trends in fish species richness and coral cover in the three national coral reef parks of Northern Quintana Roo, Mexico.

As to the relative abundance of trophic guilds, we can observe that higher predators generally have little relative abundance or simply not recorded during surveys, being Radio Pirate reef in Puerto Morelos, as well as Dalila and Colombia reefs in Cozumel were the only coral reefs where this trophic guild was recorded. The relative abundance of carnivores is up 50% Chankana'ab and Paso del Cedral reefs, however this trophic group also characterized by small fish whose dietary components include small invertebrates. Another group that has a high relative abundance of 60% and 50%, in Colombia and Dalila reefs respectively, are the herbivores (Figure 11).

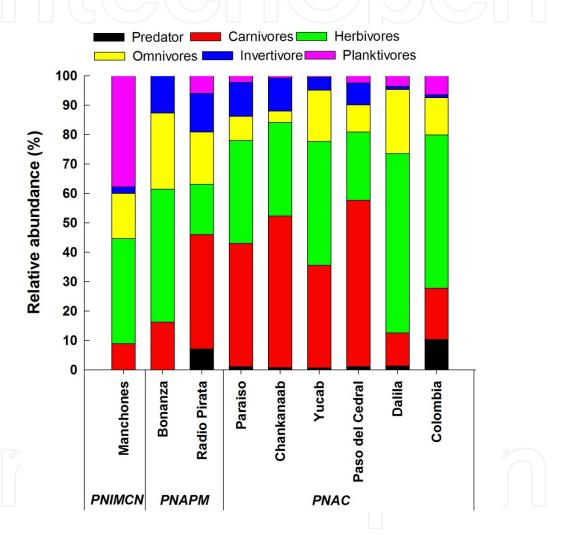
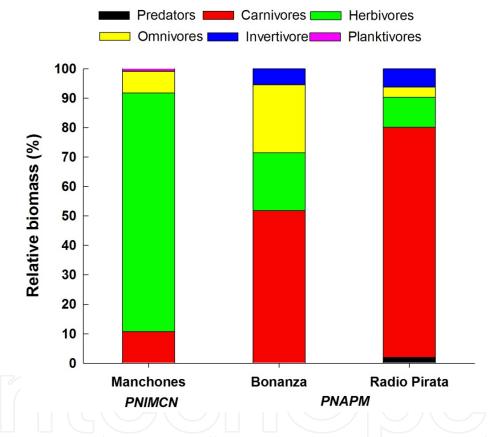


Figure 11. Relative abundance of the trophic guilds of the fish community associated with the coral reefs of northern Quintana Roo (2007 data).

Using the information of the size structure of three reefs (Manchones, Bonanza and Radio Pirata reefs) we calculated the relative biomass of the different trophic guilds using length – weight parameters for each species available at fish base [40]. This information allows assessing the degree of disturbance in the communities of each reef studied. In stable conditions or of low-disturbance, the dominant species of large size and longevity (K-strategists) are dominant in biomass and have low abundance. There are also present in the communities r-strategy spe-

cies, opportunistic species with a short lifetime that are dominate in abundance but have low biomass contribution. When a community is disturbed, K-strategy species are usually not favored and opportunistic species increase in numbers and biomass [19].

For Radio Pirate and Bonanza reefs we can see that the relative biomass of carnivores is high (>50% of the biomass), however, the relative biomass of larger predators is virtually nonexistent. In the case of Manchones reefs, the herbivores contribute in greater proportion to the biomass (Figure 12). Such inverted biomass pyramids of fish have been reported in coral reefs characterized by low coral cover. To maintain these typesof biomass pyramids, however, a high primary production is required [37].



 $\textbf{Figure 12.} \ Relative\ biomass\ of\ trophic\ guilds\ in\ reef\ fish\ communities\ of\ northern\ Quintana\ Roo\ coral\ reefs\ (2007\ data).$

Additionally, a comparison analysis chart of abundance/biomass (Abundance / Biomass Comparison - ABC plots) was performed. This method presents a statistical test (W) that represents the abundance over biomass in a range of -1 to +1; if the statistical test generates a +1, biomass dominates over abundance and represents a system with no impact. On the contrary, when the result is -1, abundance dominates over biomass indicating that the system has been highly impacted. Values near zero indicate an intermediate disturbance [19].

In the case of reefs for which we had data on both, abundance and biomass, we obtained W = 0.146, indicating that the fish communities of these reefs are under a scenario of intermedi-

ate disturbance (Figure 13) that may result either from the degradation of their habitat or the effect of fishing and poaching that take place in these reef locations [41-43]. This analysis allow us to conclude that It is essential to conduct a monitoring program of the fish community structure, and their biomass, to better assess their status and how they contribute to the functioning of these ecosystems.

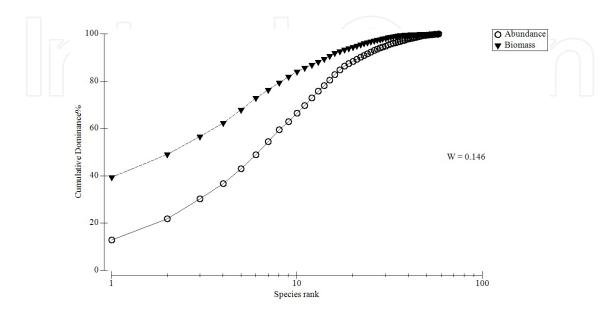


Figure 13. ABC-plot of reef fish for three coral reefs (Manchones, Bonanza and Pirate Radio) of northern Quintana Roo (2007 data).

7. Conclusion

The isotopic composition of algal tissue, along with the concentration of DIP and its various species, suggests that the low coral cover on reefs is caused by other factors rather than eutrophication of ecosystems. Plausibly, this may be an indication of reduced herbivorous-fish biomass, which is a key factor that regulates the abundance of macroalgae.

With regard to the fish community structure our results suggest an evident impact in the way biomass is distributed per trophic level, where large predators and consumers have significantly decreased. This type of inverted pyramids in fish biomass has been documented in other reef systems that show signs of anthropogenic disturbance, mainly by overfishing [37].

Fishing is the major environmental and economic problem facing most marine ecosystems, where pressure is exerted mainly on higher trophic levels in search of the largest fishes, and consecutively reducing the abundance and biomass of large predators, planktivorous and herbivorous fish, thus lowering the trophic level of the catches [2]. The ecological function of the fish is of great importance in the recovery and resilience of coral reefs and is likely to depend not only on food preferences of a trophic guild (e.g. herbivory), but also in the abundance and biomass of fish. Unfortunately, the limited information about fish populations

prevent us to establish a reliable baseline for the coral reefs in the northern Mexican Caribbean describing an undisturbed ecosystem that can be used to compare with other coral reefs in the wider Caribbean. Most of fish studies mostly focus only on single fish taxon, which does not provide relevant information required to describe the conditions of the community. Thus, assessing the ecological effects of the loss of predators is difficult, but it is well documented that the decrease of fish diversity and of important functional groups (herbivores) brings significant structural impacts through food webs and benthic community, and ultimately in the functioning of coral reefs [8, 38].

The ecological symptoms of a coral reef with probabilities of collapsing (a phase-shift) are likely to include the loss of macro-fauna, reduced fish stocks, a change in the ecological role of herbivorous fish that are replaced by only one species of echinoid, destructive over-grazing and bioerosion due to food limitation suffered by sea urchins, and reduced coral recruitment. To be able to efficiently address the current global crisis of coral reefs, it is urgently needed to be able to generate information that allows us to assess the current status of these ecosystems. It is also required the active management of human activities that modify the essential ecological processes and functions of coral reef ecosystems.

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