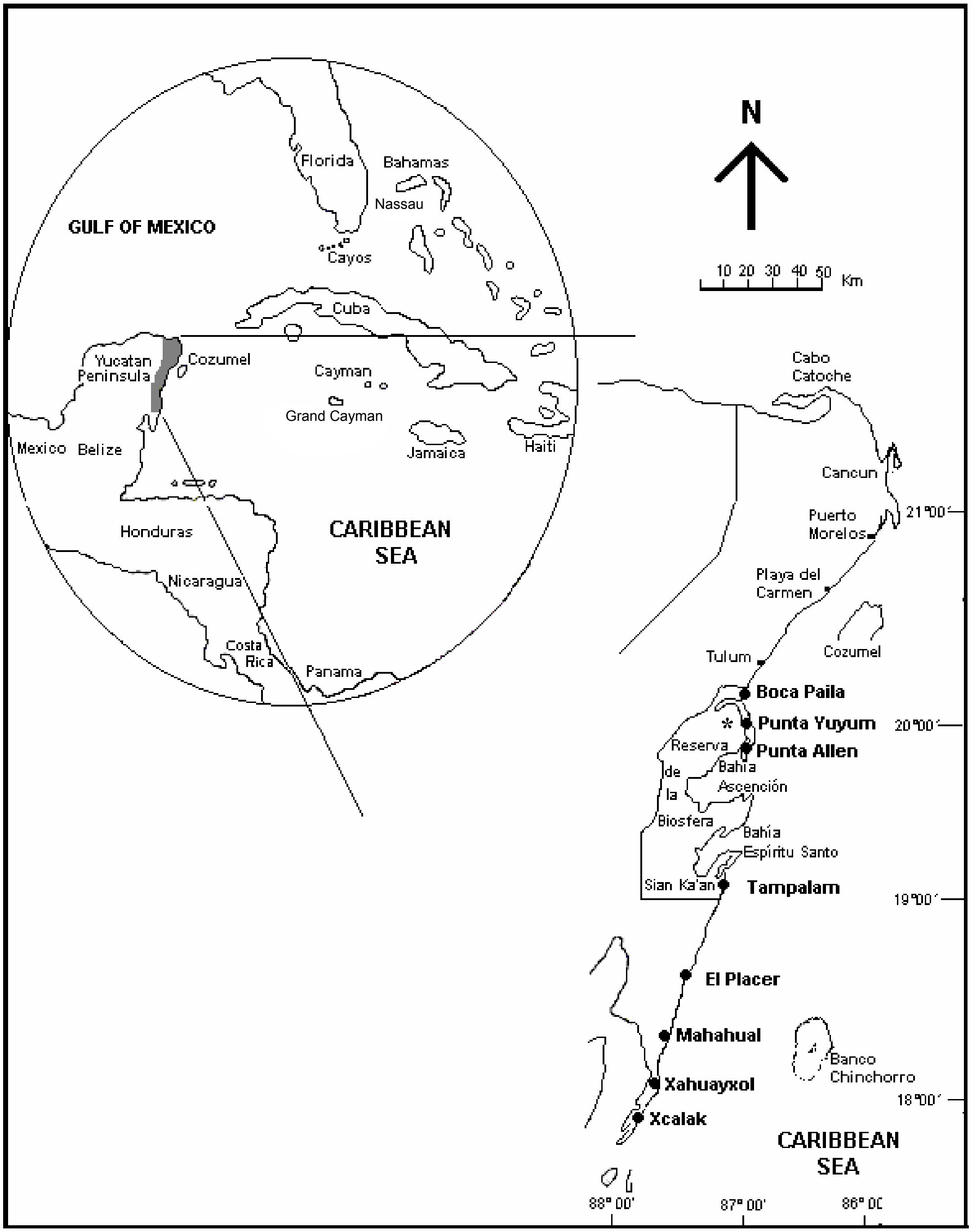

Figure 1. AGRRA survey reefs in central-southern Quintana Roo, Mexico. Modified from Núñez-Lara and Arias-González (1998).

CONDITION OF CORAL REEF ECOSYSTEMS IN CENTRAL-SOUTHERN QUINTANA ROO (PART 2: REEF FISH COMMUNITIES)

BY

ENRIQUE NÚÑEZ-LARA,[1] CARLOS GONZÁLEZ-SALAS,[1, 2]
MIGUEL A. RUIZ-ZÁRATE,[1] ROBERTO HERNÁNDEZ-LANDA,[1]
and J. ERNESTO ARIAS-GONZÁLEZ[1]

ABSTRACT

Increases of fishing and tourism threaten the natural relationships between reef fish communities and their environments. All species of reef fishes were visually assessed in the central and southern Mexican Caribbean in eight fringing reefs, four of which are in a protected biosphere reserve. The sampling design included three spatial scales from tens of meters to tens of kilometers. A total of 9,908 individuals belonging to 128 species and 43 families were identified in 144 belt transects. Zooplankton feeders were the most important trophic group by number of individuals; plant and detritus feeders dominated by number of species. Herbivores were larger in unprotected reefs than in the reserve. Regression analyses showed significant inverse relationships between total fish species density and macroalgal index (a proxy for macroalgal biomass) and, for "large" (≥25 cm diameter) stony corals, partial-colony mortality and live/dead ratio. Significant inverse relationships were also found between mean abundance of the plant and detritus feeders guild and macroalgal index and macroalgae abundance. Geomorphological factors and anthropogenic impacts, both positive (protection) in the reserve and negative (fishing and tourism) in unprotected areas, may explain these spatial patterns in reef-fish community structure.

INTRODUCTION

The reefs of the Mexican Caribbean run along the eastern margin of the Yucatán Peninsula. They are distributed parallel to the coastline of Quintana Roo state as a fringing reef system which originated during Miocene-Pleistocene rifting of the carbonate platform (Weidie, 1985). Eight reefs with similar structural configurations were chosen for the present study (Fig. 1). The reef profile can generally be divided into three main

[1] Laboratorio de Ecología de Ecosistemas Arrecifes Coralinos, Centro de Investigación y de Estudios Avanzados IPN, Carretera Antigua a Progreso Km 6, AP 73, Mérida, Yucatán, México. Emails: enunez@mda.cinvestav.mx, earias@mda.cinvestav.mx

[2] Ecole Pratique des Hautes Etudes, Laboratoire d'Ichtyoécologie Tropicale et Méditerranéenne, ESA 8046 CNRS, Université de Perpignan, 66860 Perpignan cedex FRANCE. E-mail: cgonzale@univ-perp.fr

Pp. 338-358 in J.C. Lang (ed.), Status of Coral Reefs in the western Atlantic: Results of initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Research Bulletin 496.

zones: reef lagoon, reef crest, and fore reef (mostly spur-and-groove). Four of the reefs are located within the Sian Ka'an Biosphere Reserve, which extends from 19° 05'N to 20° 06'N. The reserve, which was created in 1986 by presidential decree, has approximately 120,000 ha of coastal environments including 37,000 ha of coral reefs that were added in 1998. Natural ecological conditions within the reserve have been conserved due to the long distance from large population centers, limited access, and the restrictions on fishing and tourism. Punta Allen (Rojo Gómez) and Punta Herrero are the reserve's two largest human communities, both having less than 300 inhabitants. The villagers are principally dedicated to lobster fishing and less effort is given to catching bony fishes of which the main species are mojarras *(Gerres* spp.), snappers (lutjanids), barracudas *(Sphyraena barracuda*), grunts (haemulids), and groupers (serranids).

The remaining reefs are located between the southern boundary of the Sian Ka'an Biosphere Reserve and the frontier with Belize. The predominant activity in this area is fishing, mainly for local consumption. Most fish are caught in Banco Chinchorro, a shelf-edge bank reef system located about 45 km seaward of Mahahual town. The principal fishing methods employed are trotlines, traps, gill nets and harpoons [Oficina Regional de Pesca (SEMARNAP), unpublished report]. The Regional Fishing Office for 1997 reported a total fish catch of 335,443 kg from the zone between Punta Herrero, in the southern of Sian Ka'an reserve, and Xcalak, near the Belize border. However, locality-specific information was not provided.

Tourism has recently begun to grow rapidly along the unprotected southern coast of the Mexican Caribbean. The reefs under greatest threat, Mahahual and Xcalak, are in the path of large developers. Tourism potentially constitutes a relatively benign and lucrative use of coral reef resources. However, this benefit can be counteracted by damage and overexploitation (Hawkins and Roberts, 1993). The relationship between tourism and reef fishes is mainly indirect, being felt through the effects on fish habitat (Russ, 1991) including coral breakage and death due to vessel anchors, sedimentation, dredging, and other coastal zone activities (Dollar, 1982; Grigg, 1994; Muthiga and McClanahan, 1997). A direct effect of tourism is the extraction of fishes for consumption by visitors. Changes in community structure are caused by overexploitation of fishes of the high trophic levels (Russ, 1991). Thus, effects of fishing are partially attributable to the high demand of fishes for tourists and partially to the continuous increase in the numbers of fishermen and local inhabitants.

There are relatively few studies of reef fish communities in the Mexican Caribbean (e.g., Fenner, 1991; Díaz-Ruiz and Aguirre-León, 1993; Schmitter-Soto, 1995; Arias-González, 1998; Díaz-Ruíz et al., 1998; Núñez-Lara and Arias-González, 1998). In the present study we tried to detect the main structural forces affecting reef fish communities, and to measure the influence of fisheries and tourism on fishes and their habitat. The data generated represents a basis for comparative analyses of reef fish community structure at different spatial scales.

METHODS

Reef fishes were visually censused at eight fringing reef localities along Mexico's central and southern Caribbean coast. The reefs were selected on the basis of a mixture of strategic and representative criteria, including their spatial separation distance (usually 20-30 km), natural geographic barriers (such as the two large bays that divide the Sian Ka'an Biosphere Reserve), and their type of use by humans. For the purpose of this study, every reef was assigned to one of three geographical areas (Fig. 1): Northern Sian Ka'an (NSK) at 19º-20° N (3 reefs about 25 km apart); Southern Sian Ka'an (SSK) at 18º-19° N (2 reefs about 30 km apart–one being outside the reserve); and Southern (S) at 17º-18° N (3 reefs about 30 km apart). The distance parallel to the reef crest that constituted each reef was approximately three kilometers. This distance was subdivided into three 0.9-1 km subreefs (north, center, and south). Subreefs were geographically localized with GPS and described in terms of distance from the coast and degree of exposure to oceanic currents. Six replicate belt transects, each measuring 50 m long by 2 m wide, were swum parallel to the coast at every subreef. Transects were spaced approximately 100 m apart and all surveys were made between 0900 and 1700 hours by one diver (Nuñez-Lara). All transects were made at an average depth of 12 meters in the fore reef. The dominant habitat was spur and groove, except in northern Tampalam, where the calcareous substratum was largely covered with benthic algae, gorgonians, and sponges.

All reef fishes ≥3cm in body length within the transects were counted and their sizes estimated in six categories: 3-10 cm, 11-20 cm, 21-30 cm, 31-40 cm, 41-50 cm and > 50 cm. The Atlantic and Gulf Rapid Reef Assessment (AGRRA) fishes constitute a subset of the "all species" data: in this paper, "serranids" are species of *Epinephelus* (including *E. fulvus* but excluding *E. cruentatus,* which is here classified as *Cephalopholis cruentata)* and *Mycteroperca*; "haemulids" and "scarids" (parrotfishes) refer to fishes that are ≥3 cm in total length.

In order to describe the reef fish community structure, the following ecological descriptors were calculated: species richness, abundance, density, trophic structure and size structure. Three different spatial scales were used for the analysis: subreef (hundreds of meters), reef (kilometers) and area (tens of kilometers). Trophic structure was analyzed by calculating the percentage of individuals and fish species belonging to each of Randall's (1967) feeding categories: plant and detritus feeders; zooplankton feeders; sessile invertebrate feeders; "shelled" invertebrate feeders; generalized carnivores; ectoparasite feeders; and fish feeders.

A multiple regression technique was used to relate the total fish density with the following benthic habitat variables assessed by Ruiz et al. (this volume): total live stony coral cover; total (recent + old) partial-colony mortality, old partial-colony mortality, recent partial-colony mortality, live:dead ratio and maximum diameter for "large" (≥25 cm in diameter) stony corals; and relative abundance and macroalgal index (relative abundance x height, a proxy for biomass) for macroalgae. Simple regression was used to examine the relationship between total fish herbivore density and the two macroalgal descriptors (index and relative abundance). Densities were log+1 transformed to meet the assumptions for parametric regression tests. Classification analysis was performed to determine the degree of similarity among subreefs, based on the abundance values of their recorded fish species. The Bray-Curtis (1957) distance index was used as a similarity measure and the Unweighted Pair Grouping Method Average (UPGMA) as a clustering method.

Pp. 338-358 in J.C. Lang (ed.), Status of Coral Reefs in the western Atlantic: Results of initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Research Bulletin 496.

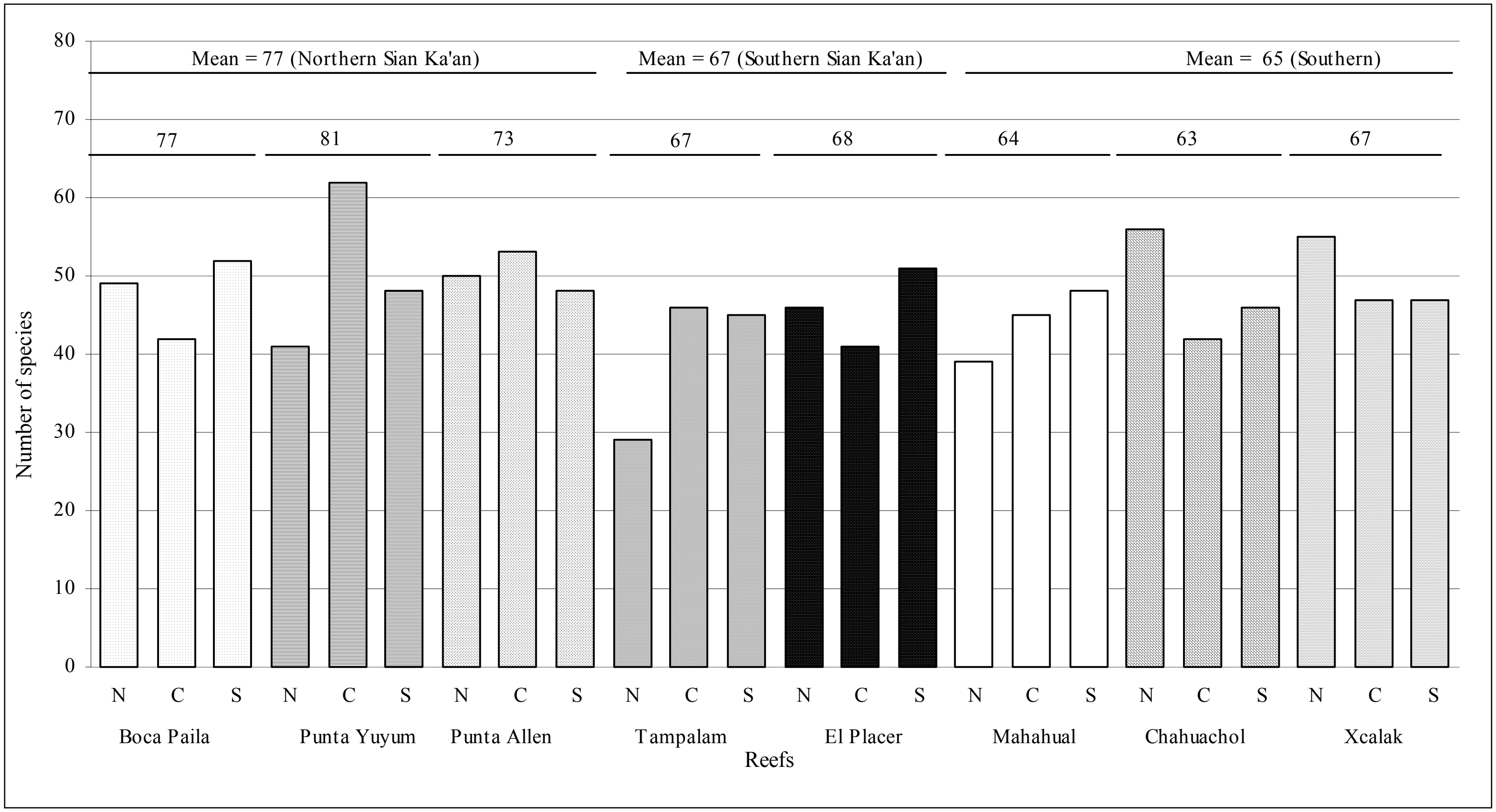

Figure 2. Species richness (all fishes ≥3 cm long) by subreef at 12 m depth in central-southern Quintana Roo, Mexico.

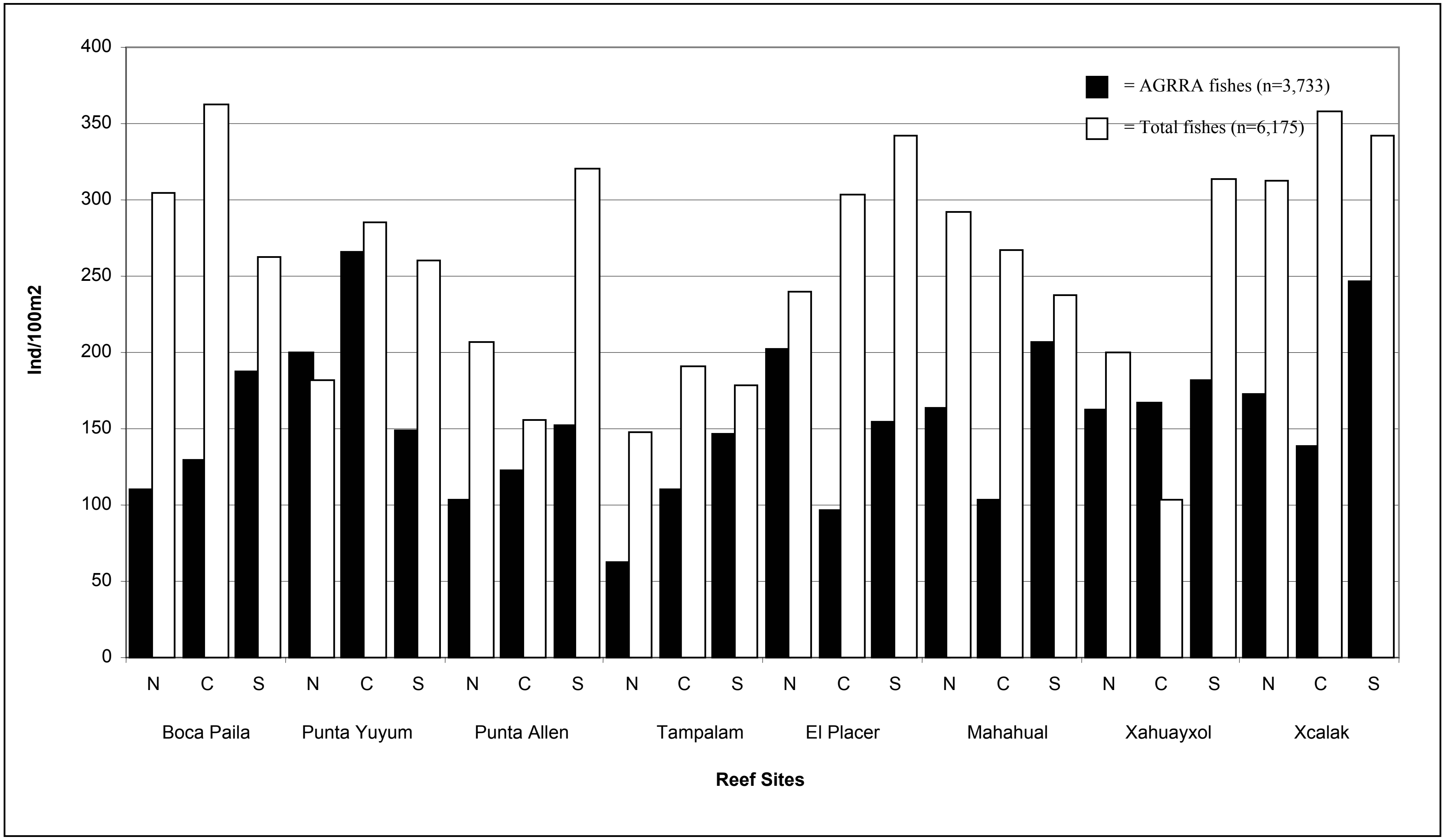

Figure 3. Mean density (no. individuals/100 m^2) of all fishes (≥3 cm long), and of AGRRA fishes, by subreef at 12 m depth in central-southern Quintana Roo, Mexico.

Pp. 338-358 in J.C. Lang (ed.), Status of Coral Reefs in the western Atlantic: Results of initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Research Bulletin 496.

RESULTS

Species Composition and Richness

A total of 128 reef fish species belonging to 43 families were identified in 144 belt transects. The greatest number was found in the NSK area and the lowest in the S area (Table 1, Fig. 2). Particularly notable was the large number of species belonging to the families Holocentridae (squirrelfish), Serranidae (grouper) and Haemulidae (grunts) in the NSK area and the relatively low number of species from such "typical" reef fish families as Pomacentridae (damselfish), Labridae (wrasse), and Scaridae (parrotfishes) in the SSK area. A somewhat different pattern was evident for AGRRA fishes (Table 1) as species numbers overall were rather similar in the NSK and S areas (23-32, n = 18 subreefs). In the SSK area, the number of AGRRA species was slightly lower at El Placer (21-27, n = 3 subreefs), but much smaller at Tampalam (n = 5-15, n = 3 subreefs).

The 25 dominant fish species in terms of sighting frequency and density belonged to the following families: Labridae, Acanthuridae (surgeonfish), Scaridae, Pomacentridae, Haemulidae, Serranidae, Lutjanidae (snappers), Pomacanthidae (angelfish), Holocentridae and Grammatidae (basslet). *Thalassoma bifasciatum* was the most frequently sighted and abundant species in all the studied reefs, followed by *Acanthurus coeruleus*, *Sparisoma aurofrenatum* and *Halichoeres garnoti* (Table 2). Forty percent of these dominant fish species are included in the AGRRA fish list.

Abundance and Density

A total of 9,908 fishes were counted in the 144 transects, 3,733 of which belonged to the species on the AGRRA list. Total densities were highest in Xcalak S and Punta Yuyum C and lowest in Tampalam N and Xahuayxol C (Fig. 3). In an examination of the key AGRRA families, regardless of scoring mode (all individuals or restricted counts for haemulids, scarids, and serranids), the Scaridae was found to have the greatest density,

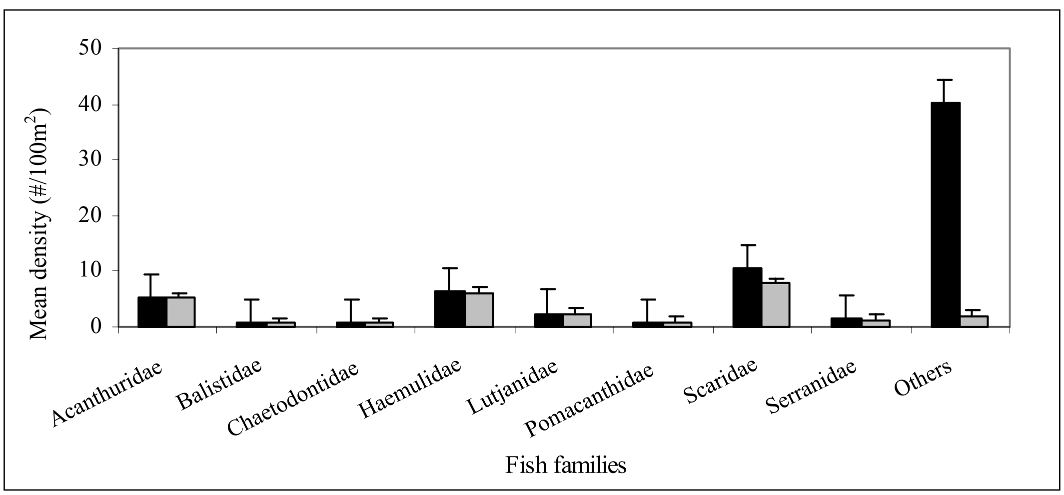

Figure 4. Mean density (no. individuals/100m^2 ± se) of all fishes (≥3 cm long), and of AGRRA fishes, by family in central-southern Quintana Roo, Mexico. Other AGRRA fishes = *Bodianus rufus, Caranx ruber, Lachnolaimus maximus, Microspathodon chrysurus, Sphyraena barracuda.*

followed by the Haemulidae and Acanthuridae (Fig. 4). Although less abundant, the Lutjanidae and Serranidae were more plentiful than the Balistidae (leatherjackets), Chaetodontidae (butterflyfish), and Pomacanthidae.

Parrotfishes ≥3cm and surgeonfishes were most abundant overall in the S area, although the density of parrotfishes was also high at Punta Allen (in the NSK area). Surgeonfishes were relatively scarce at Mahahual (in the S area) where scarid density was highest (Table 3). The density of snappers was highest in Boca Paila and Punta Yuyum reefs in the NSK area and in Xcalak in the S area. Grunts ≥3cm were also abundant in Punta Yuyum (especially) and Boca Paila as well as in El Placer (SSK area). The density of groupers (*Epinephelus, Mycteroperca*) was low in all the reefs.

Trophic Structure

Considering total abundances, the trophic structure of the fish community was dominated by zooplankton feeders (39%), followed by plant and detritus feeders (28%) and shelled invertebrate feeders (16%). In term of total species richness, the three most important of Randall's (1967) trophic groups were the plant and detritus feeders (24%), "shelled" invertebrate feeders (21%), generalized carnivores (15%) and sessile invertebrate feeders (14%). Ectoparasite feeders and fish feeders showed the lowest percent contribution for both individuals and species (Fig. 5). Similar patterns were detected for every area and each of the sampled reefs, with zooplankton feeders dominating by number of individuals and the plant and detritus feeders being the most important group by numbers of species, closely seconded by "shelled" invertebrate feeders (Table 4). Among the most abundant of the herbivorous fish species were *Scarus iserti (=S. croicensis)*, *Acanthurus coeruleus*, *A. bahianus*, *Sparisoma aurofrenatum* and *S. viride*.

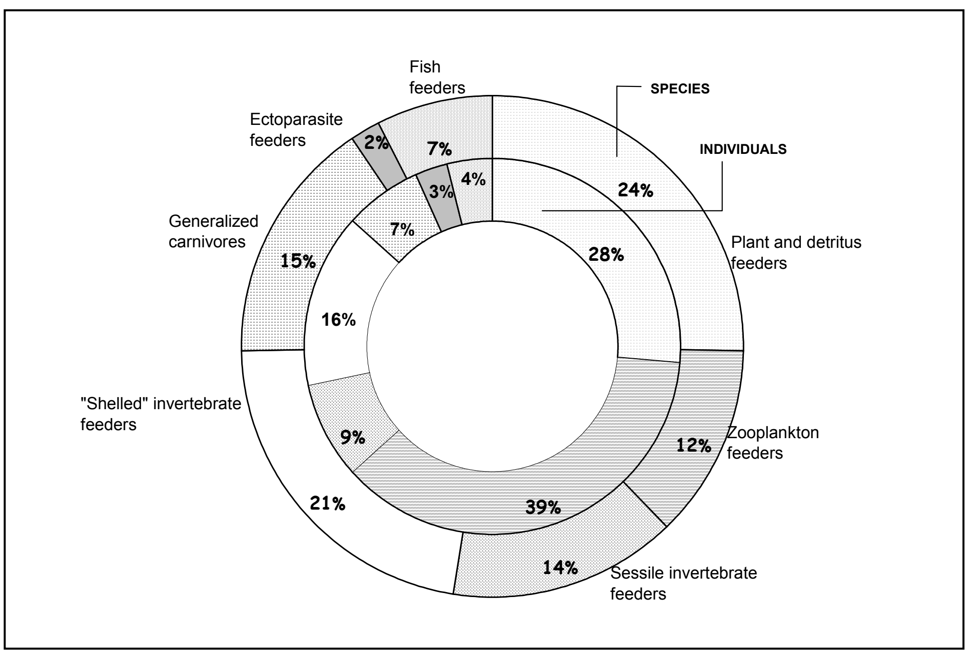

Figure 5. Trophic structure (as percent of species and individuals) for all fishes ≥3 cm long at 12 m in central-southern Quintana Roo, Mexico.

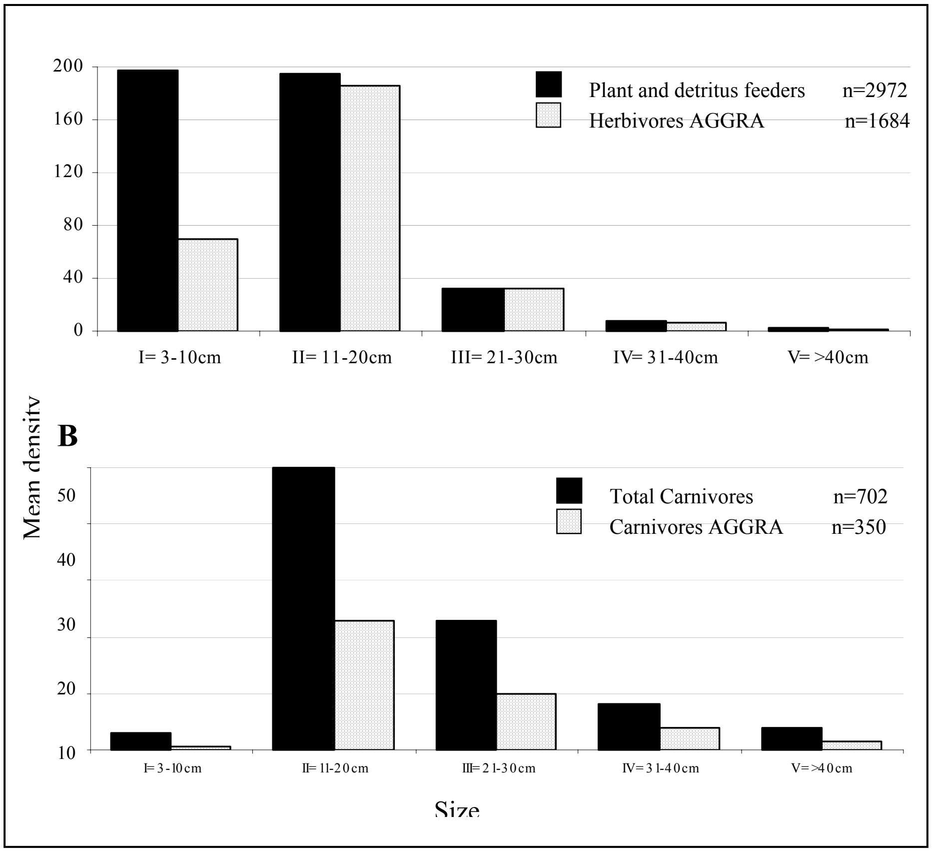

Figure 6. Size frequency distribution of **(A)** all plant and detritus feeders ≥3 cm (acanthurids, kiphosids, pomacentrids except *Chromis*, and scarids) and AGRRA herbivores ≥3 cm (acanthurids, scarids, *Microspathodon chrysurus*) and **(B)** all carnivores ≥3 cm [carangids, lutjanids, scombrids, select serranids (*Epinephelus* and *Mycteroperca*), sphyraenids] and AGRRA carnivores ≥3 cm [lutjanids, *Epinephelus* (except for *E. cruentatus*) and *Mycteoperca*] at 12 m in central-southern Quintana Roo, Mexico.

Lengths

Very few of the surveyed fishes exceeded 30 cm in length. The most common size classes for "all herbivores" (acanthurids, kyphosids, pomacentrids except *Chromis,* and scarids) were equally divided between the 3-10 cm and 11-20 cm length intervals (Fig. 6A). In a more detailed analysis, we observed proportionately more fishes in the 11-20cm size class in the S area (particularly in Mahahual and Xcalak) than in the NSK and SSK areas where smaller herbivores (3-10cm) were relatively more abundant (Table 5). Key herbivores (acanthurids, scarids ≥3cm, *Microspathodon chrysurus*) were slightly larger (10-20 cm) overall (Fig. 6A) and also attained their largest sizes in the S area.

Both for "all carnivores" (carangids, lutjanids, scombrids, sphyraenids, plus *Epinephelus* and *Mycteroperca*) and for the AGRRA carnivores (lutjanids, select serranids), the most common size class was 11-20 cm (Fig. 6B). Among the more abundant carnivores (total and AGRRA species) were the relatively small-sized *Epinephelus fulvus*, *Lutjanus apodus* and *L. synagris*. However, carnivores were slightly larger in the reefs in which they were most abundant (Xcalak, Boca Paila and Yuyum) (Table 5).

Classification Analysis

Classification analysis divided the sites into two large clusters according to the affinity criteria based on total fish abundances. The first cluster of 10 subreefs includes only sites located in the NSK and SSK areas. The second cluster includes all nine of the subreefs of the S area, three of the NSK area and El Placer S subreef (SSK area). Tampalam N subreef was markedly different from all the other survey sites (Fig. 7).

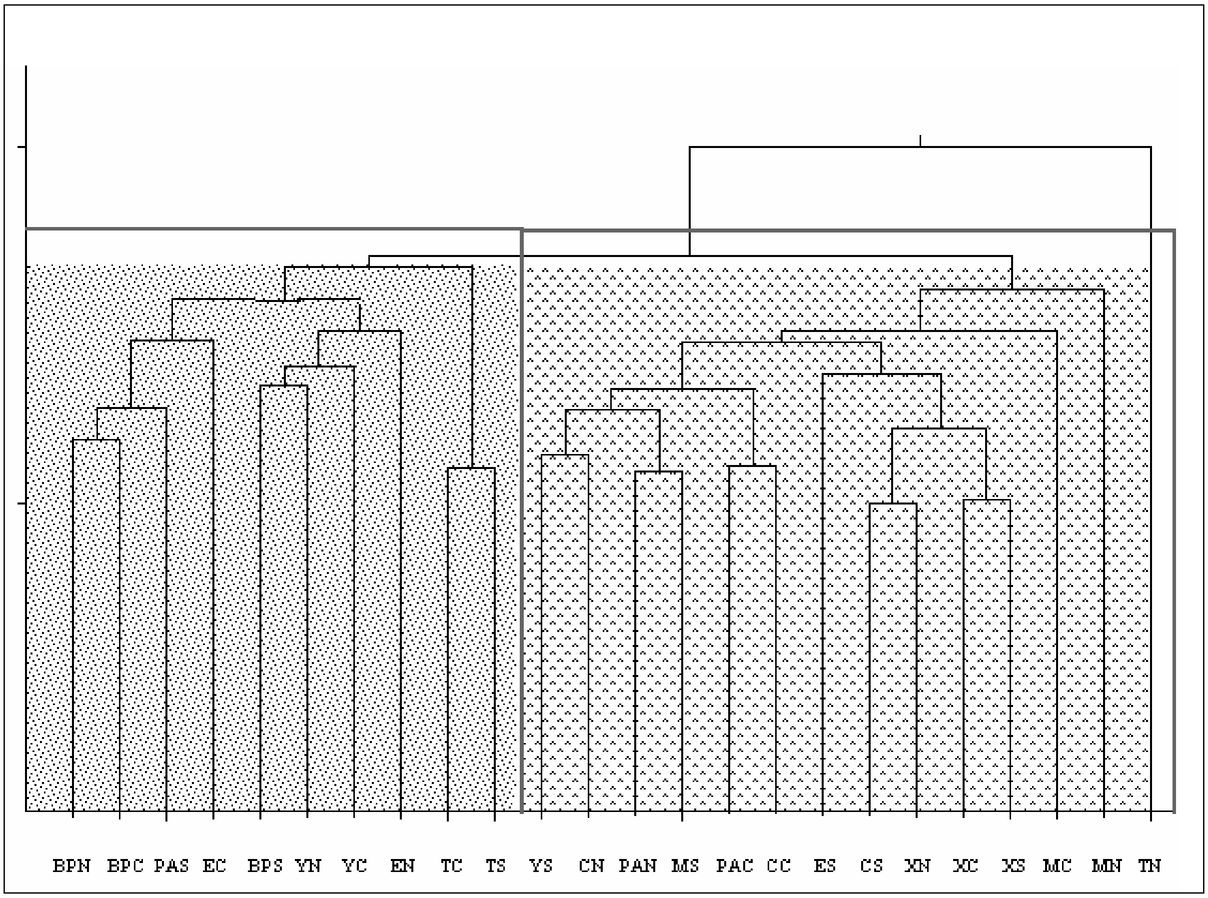

Figure 7. Hierarchical classification analysis based on total fish abundance, by subreef at 12 m in central-southern Quintana Roo, Mexico.

Relationships

Multiple regression analyses between the total density of all the fish species and the benthic habitat variables (Ruiz et al., this volume) showed statistically significant inverse relationships ($P < 0.05$) with the macroalgal index, live/dead stony coral ratio, and total (recent + old) partial-colony mortality (Fig. 8). The r^2 statistic indicates that the model of multiple regression, when all six benthic variables are included, explains 86.96% of the variability in the fish density data. Statistically significant, inverse relationships were also found between the means for the total plant and detritus guild and those for the macroalgal index and relative abundance of macroalgae (Fig. 9).

Pp. 338-358 in J.C. Lang (ed.), Status of Coral Reefs in the western Atlantic: Results of initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Research Bulletin 496.

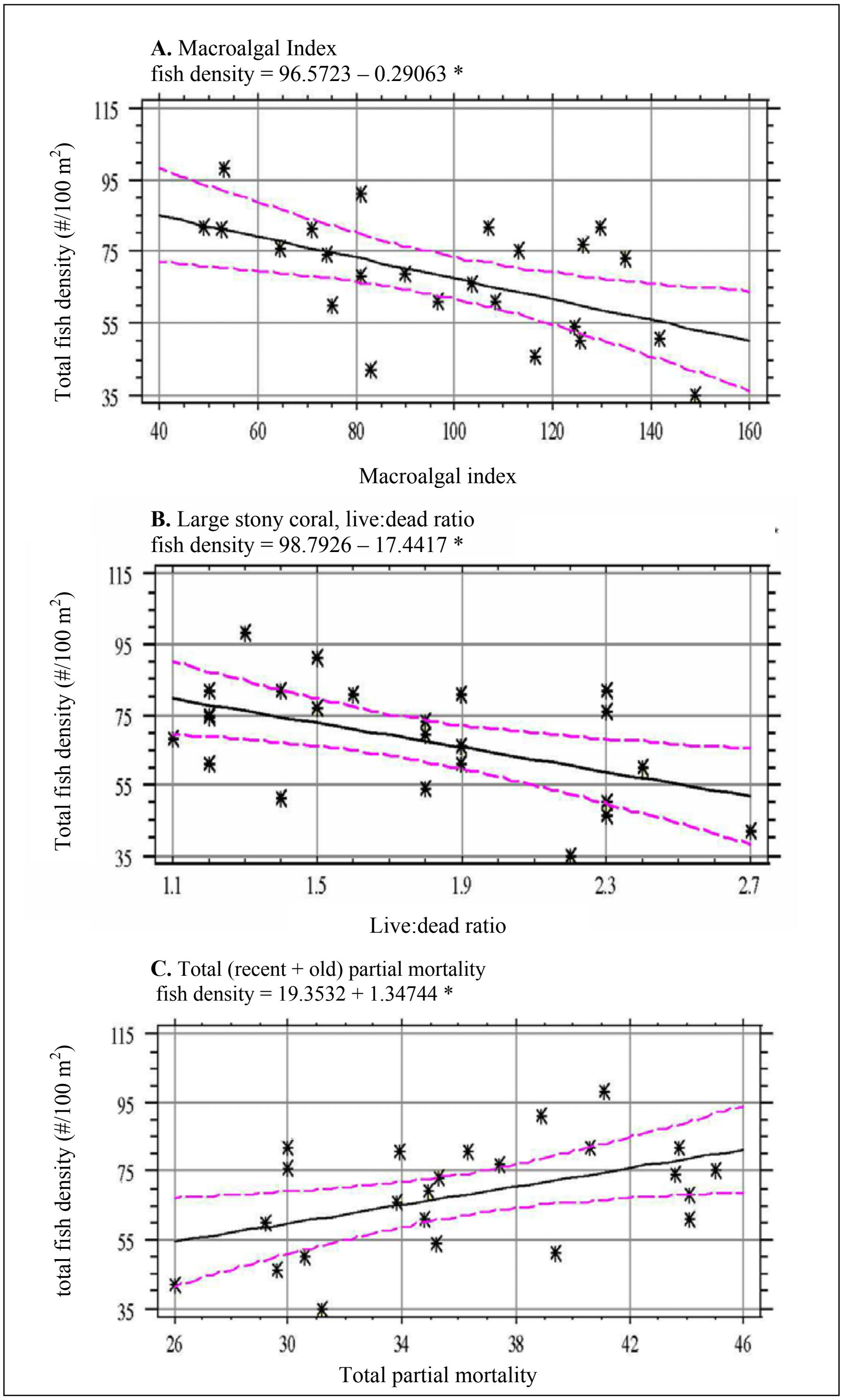

Figure 8. Regression plot and 95% confidence intervals between mean total fish density (no. individuals/100m^2) and (**A**) mean macroalgal index (P<0.01, 29.2% of the variability in fish density explained), and for large (≥25 cm in diameter)stony corals (**B**) mean live:dead ratio (P<0.05, 26.3% explained), (**C**) mean total (recent + old) partial colony mortality (P<0.05, 22.5% explained) by subreef at 12 m in central-southern Quintana Roo, Mexico.

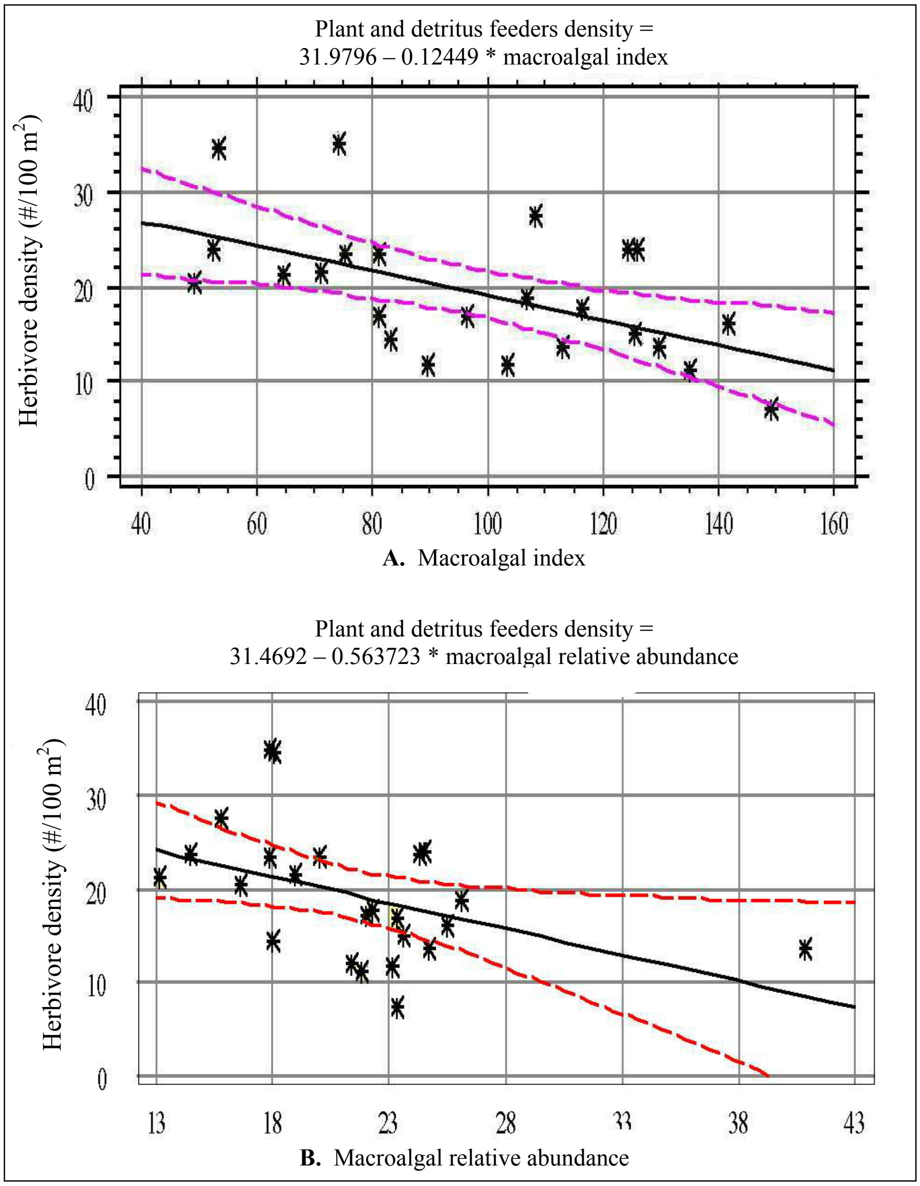

Figure 9. Regression plot and 95% confidence interval between mean herbivore (plant and detritus feeders) density (no. individuals/100m^2) and (**A**) mean macroalgal index ($P=0.005 < 0.01$, 30.3% of the variability in fish density explained) and (**B**) mean macroalgal relative abundance ($P=0.03<0.05$ 19.5% explained), by subreef at 12 m in central-southern Quintana Roo, Mexico.

DISCUSSION

The principal factors involved in the evolution and maintenance of coral reef fish community structure are historical, biogeographical, geomorphological and bio-ecological (Harmelin-Vivien, 1989). The present study suggests the participation of some of these factors in the regulation of fish communities in the Mexican Caribbean as well as human intervention in the form of both environmental protection and deterioration.

Pp. 338-358 in J.C. Lang (ed.), Status of Coral Reefs in the western Atlantic: Results of initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Research Bulletin 496.

The ecological descriptors used to describe reef fish community structure (species richness, abundance, density) showed a gradient from greater to lesser running from north to south along the Mexican Caribbean coast. The grouping of subreefs in the cluster analysis also approximately followed this pattern. This gradient not only coincides with latitudinal variation but with variation in protection against human exploitation. Indeed, Arias-González's (1998) trophic structural analysis had previously demonstrated that top-level fish production could be two to three times higher in relatively unfished Mexican Caribbean reefs than in those which are unprotected. At first we thought the degree of conservation was the most obvious explanation for the observed geographic gradient found during these surveys. However, it is also possible that other factors aided in determining this pattern.

It is well known that coral reefs have a fragmented environmental distribution and are characterized by diverse substrate types and complexity. The biology of reef fishes is set to the multi-scalar coral reef systems by ecological processes that act upon them and by the architectural patchiness of the reef environment (Sale, 1998). Geomorphological and habitat structural features may be an alternative explanation for the differences found in fish communities, at least for one of the spatial scales investigated in this study. The greatest numbers of species and families were recorded in the NSK reefs, especially in Punta Yuyum and Boca Paila, where coral reef structures visually appear to have a high degree of topographical complexity because the spurs are of high relief, and are covered with a large variety of benthic fauna. Conditions here naturally appear to be particularly favorable for the establishment and persistence of resident reef fishes. At the same time, the Boca Paila and Punta Yuyum reefs receive the least amount of anthropogenic disturbance. Therefore, the fact that these two reefs had higher fish species and family richness, along with higher abundances and larger sized carnivores than those in the SSK and S areas, could be a response to a combination of favorable geomorphological and human factors. Similarly, the relatively low species richness and abundances observed at Punta Allen, which is also located within the NSK, may be explained as a response either to the effects of fishing activity in the community of Rojo Gómez (Punta Allen) and/or to the natural influence of the large freshwater masses associated with La Ascención and Espíritu Santo Bays.

The Tampalam and El Placer reefs in the SSK area experience reduced human activity in the form of few fishing boats (<five per locality) and low numbers of fishermen (5-10 per locality). This fishing activity sometimes occurs immediately over the coral reefs, which can affect fish community structure directly by decreasing the abundance of top predators and indirectly by causing damage to the habitat with fishing gear (Russ and Alcala 1996). Nevertheless, the most probable explanation for the reduced numbers of fish species and individuals at Tampalam was the low structural complexity clearly seen in this system. The spur-and-groove formations on the fore reef were not continuous along the coast, being interrupted by a flat calcareous substratum at Tampalam N, with consequent reduction of suitable habitat spaces for fishes. We conclude that fishing activity was not sufficiently intense and frequent at Tampalam to modify the reef fish community structure. However, habitat structure appeared to be a determining factor, not only of differences among the geographical areas but between the reefs within the SSK area and among the subreefs at Tampalan (Fig. 7).

Fishing and seasonal tourism activities are highest in the S area as reflected in the lower number of fish species and families relative to the NSK and SSK areas. Evident effects of fishing were the loss of intermediate- to large-sized fishes (mainly carnivores) and the clear dominance of the trophic structure by species of plant and detritus feeders. The depletion of large top predators can modify the community structure of reef fishes via an increase in the abundance, size, and biomass of fish prey (Russ, 1991; Jennings and Polunin, 1996; McClanahan, 1997). The three reefs located in the S area are subject to comparable levels of fishing exploitation and have similar geomorphological and habitat structures which probably explains the similar values for their reef fish community descriptors.

A general trend in the size structure of fish species at all three spatial scales was the high abundance of plant and detritus feeders that were <20 cm in length and of carnivores that were between 10 and 30 cm long. As the size of the plant and detritus feeders was greatest in the S area, where large predatory fishes were particularly scarce, their greater lengths here could also be a result of local fishing practices.

The significant inverse relationship that we found between plant and detritus feeders and macroalgae indicates that herbivorous fishes have a measurable effect on the abundance of this important algal group in the Mexican Caribbean. Hence, overfishing of top predators may have ecological effects that cascade through reef ecosystems.

Overall, the results of this work suggest that the general condition and spatial patterns found in the ecological descriptors of reef fish communities at the different spatial scales studied were partially due to effects of human activities (mainly fishing) and partially attributable to geomorphological and habitat structure characteristics. Studies evaluating the condition of reefs and their fish communities appear to be an efficient management tool, given the need for rapid, integrated information useful in short-term planning of coastal resource administration projects. The systematic continuation of this kind of assessment will be beneficial for social, economic, and, of course, environmental purposes.

ACKNOWLEDGMENTS

This project was financed by the Caribbean Environment Programme of the United Nations Environment Programme, Consejo Nacional de Ciencia y Tecnología (CONACYT) and CINVESTAV. The AGRRA Organizing Committee also facilitated financial support as described in the Forward to this volume. We express our sincere thanks to the Secretaría de Medio Ambiente, Recursos Naturales y Pesca (SEMARNAP) in Quintana Roo for allowing us to use their facilities at Mahahual. Thanks are also due to Biol. Alfredo Arrellano Guillermo, Director, Sian Ka'an Biosphere Reserve (RBSK) for his invaluable logistical assistance during the work within the Reserve, to Amigos de Sian Ka'an for permission to use Pez Maya as a work base within the Reserve, and to Chente, Chepe, Felipe, Fredy and Vidal for their valuable help during the fieldwork.

REFERENCES

Arias-González, J E.
1998. Trophic models of semi-protected and unprotected coral reef ecosystems in the South of the Mexican Caribbean. *Journal of Fish Biology* 53 (Supplement A):236-255.

Bray, R.J., and J.T. Curtis
1957. An ordination of the uplands communities of the southern Wisconsin. *Ecological Monographs* 27:325-349.

Díaz-Ruíz, S., and A. Aguirre-León
1993. Diversidad e ictiofauna de los arrecifes del sur de Cozumel, Quintana Roo Pp. 818-832. In: S.I. Salazar-Vallejo, and N.E. González (eds.), *Biodiversidad Marina y Costera de México*. Comision Nacional de Biodiversidad y CIQRO. México.

Díaz-Ruíz, S., A. Aguirre-León , and E.A. Arias González
1998. Habitat interdependence in coral reef systems: a case of study in Mexican Caribbean reef. *Journal of Aquatic Health Management* 1:387-397.

Dollar, S.J.
1982. Wave stress and coral community structure in Hawaii. *Coral Reefs* 1:71-81.

Eschmeyer,W.N. (editor)
1998. *Catalog of Fishe*s. Special Publication No. 1 of the Center for Biodiversity Research and Information, California Academy of Science, San Francisco, CA. Volumes 1-3, 2905 pp.

Fenner, D.
1991. Effects of Hurricane Gilbert on coral reef fish and sponges of Cozumel, Mexico. *Bulletin of Marine Sciences* 48:719-730.

Grigg, R.W.
1994. Effects of sewage discharges, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Marine Ecology Progress Series* 103:25-34.

Harmelin-Vivien, M.L.
1989. Reef fish community structure: An Indopacific comparison. *Ecologique Etudes*. 69:21-60.

Hawkins, J.P., and C.M. Roberts
1993. Effects of recreational scuba diving on coral reefs: trampling on reef flat communities. *Journal of Applied Ecology* 30:25-30.

Houston, M.A.
1991. A general hypothesis of species diversity on coral reefs. *American Naturalist*. 113:81-110.

Jennings, S., and N. V. C. Polunin
1996. Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef fish communities. *Journal of Applied Ecology* 33: 400-412.

McClanahan, T. R.
1997. Primary succession of coral-reef algae: differing patterns on fished versus unfished reefs. *Journal Experimental Marine Biology and Ecology* 218:77-102.

Muthiga, N.A., and T.R. McClanahan
1997. The effects of visitors use on the hard coral communities of the Kisite Marine Park, Kenya. *Proceedings of the Eighth International Coral Reef Symposium* II:1879-1882.

Núñez-Lara, E.
1998. *Factores que determinan la estructura de la comunidad de peces arrecifales en el sur del Caribe Mexicano: un análisis multivariado*. MC Thesis, Marine, CINVESTAV-Merida, Yucatán, México. 113 pp.

Núñez-Lara, E., and J.E. Arias-González
1998. The relationship between reef fish community structure and environmental variables in the southern Mexican Caribbean. *Journal of Fish Biology* 53(A):209-221.

Randall, J.E.
1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* 5:665-847.

Russ, G.R.
1991. Coral reef fisheries: effects and yields. Pp. 601-635. In: P. F Sale (ed*.), The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego.

Russ, G. R., and Alcala, A. C.
1996. Marine reserves: Rates and patterns of recovery and decline of large predatory fish. *Ecological Applications*. 6:947-961.

Sale, P.F.
1998. Appropriate scale for studies of coral reef fish ecology. *Australian Journal of Ecology* 23:202-208.

Weidie, A.E.
1985. Geology of the Yucatán Platform. Pp. 1-19. In: W.C. Ward, A.E. Weidie, and W. Back (eds.), *Geology and Hydrology of the Yucatan and Quaternary Geology of Northeastern Yucatan Peninsula*. New Orleans.

Pp. 338-358 in J.C. Lang (ed.), Status of Coral Reefs in the western Atlantic: Results of initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Research Bulletin 496.

Table 1. Site information for AGRRA fish surveys in central-southern Quintana Roo, México.

Site name	Site code	Reef type	Latitude (° ' " N)	Longitude (° ' " W)	Survey date	Depth (m)	≥25 cm stony corals (#/10 m)[1]	% live stony coral cover (mean ± sd)[1]	50 m fish transects (#)	Species in transects (#) AGRRA[2]	Total
Northern Sian Ka'an											
Boca Paila North	BPN	Fringing	20 06 51	87 27 23	Aug.30 99	12	6	15.5 ± 4.5	6	30	49
Boca Paila Center	BPC	Fringing	20 06 21	87 27 34	Aug.31 99	12	6	19.0 ± 9.5	6	24	42
Boca Paila South	BPS	Fringing	20 05 51	87 27 47	Aug.31 99	12	2	8.5 ± 2.5	6	30	52
Punta Yuyum North	PYN	Fringing	19 58 30	87 27 10	Aug.27 99	12	4.5	10.5 ± 5.5	6	21	41
Punta Yuyum Center	PYC	Fringing	19 58 00	87 27 06	Aug.26 99	12	4	12.5 ± 6.0	6	33	62
Punta Yuyum South	PYS	Fringing	19 57 30	87 26 52	Aug.25 99	12	4.5	10.5 ± 6.0	6	23	48
Punta Allen North	PAN	Fringing	19 50 30	87 26 15	Aug.20 99	12	4.5	11.5 ± 3.5	6	27	50
Punta Allen Center	PAC	Fringing	19 50 00	87 26 36	Aug.21 99	12	4.5	14.5 ± 7.5	6	25	52
Punta Allen South	PAS	Fringing	19 49 30	87 26 52	Aug.22 99	12	3.5	10.5 ± 4.5	6	25	48
Southern Sian Ka'an											
Tampalam North	TN	Fringing	19 09 15	87 32 00	Sep.30 99	12	1.5	8.5 ± 5.5	6	5	29
Tampalam Center	TC	Fringing	19 08 45	87 32 10	Sep.30 99	12	5	15.0 ± 9.0	6	11	45
Tampalam South	TS	Fringing	19 08 15	87 32 13	Sep.29 99	12	6	18.0 ± 6.5	6	15	44
El Placer North	EPN	Fringing	18 54 48	87 37 03	Sep.25 99	12	2	6.0 ± 2.5	6	27	45
El Placer Center	EPC	Fringing	18 54 08	87 37 24	Sep.24 99	12	2.5	9.0 ± 3.5	6	21	41
El Placer South	EPS	Fringing	18 53 38	87 37 36	Sep.23 99	12	4	12.0 ± 4.0	6	25	51
Southern											
Mahahual North	MN	Fringing	18 43 05	87 41 56	Jun.27 99	12	5	17.0 ± 7.0	6	24	39
Mahahual Center	MC	Fringing	18 42 35	87 42 09	Jun.26 99	12	4.5	17.0 ± 6.0	6	23	45
Mahahual South	MS	Fringing	18 42 05	87 42 20	Jun.25 99	12	6	16.5 ± 5.5	6	27	48
Xahuayxol North	XN	Fringing	18 30 55	87 45 02	Jul.20 99	12	3.5	11.5 ± 3.0	6	31	55
Xahuayxol Center	XC	Fringing	18 30 25	87 45 13	Jul.21 99	12	2.5	12.0 ± 5.5	6	25	41
Xahuayxol South	XS	Fringing	18 29 55	87 45 22	Jul.22 99	12	3.5	11.5 ± 5.5	6	26	45
Xcalak North	XCN	Fringing	18 13 43	87 49 51	Jul.13 99	12	3.5	9.0 ± 4.5	6	32	54
Xcalak Center	XCC	Fringing	18 13 09	87 49 54	Jul.14 99	12	3.5	9.5 ± 3.0	6	28	45
Xcalak South	XCS	Fringing	18 12 39	87 49 47	Jul.15 99	12	3	7.5 ± 4.5	6	31	45

[1]Data from Ruiz et al. (this volume); [2]Excluding any *Epinephelus cruentatus.*

Table 2. Sighting frequency and mean density of the 25 most frequently sighted fish species in "all species" belt transect surveys in central-southern Quintana Roo, México. * = AGRRA species.

Species	Sighting frequency (%)[2]	Density (#/100m^2)
Thalassoma bifasciatum	97	9.76
**Acanthurus coeruleus*	97	2.68
**Sparisoma aurofranatum*	94	2.35
Halichoeres garnoti	93	2.00
Chromis cyanea	92	9.39
Stegastes partitus	92	4.00
**Acanthurus bahianus*	85	1.82
**Sparisoma viride*	84	1.88
**Haemulon flavolineatum*	78	1.64
Stegastes fuscus	76	1.31
**Scarus iserti (=S. croicensis)*[1]	74	2.96
**Haemulon sciurus*	69	2.15
**Epinephelus fulvus*	68	0.94
**Ocyurus chrysurus*	67	1,06
**Sparisoma chrysopterum*	66	1.04
**Microspathodon chrysurus*	65	0.90
Stegastes leucostictus	64	0.85
**Haemulon plumieri*	60	0.85
**Holacanthus tricolor*	52	0.55
**Scarus taeniopterus*	51	1.01
Holocentrus adscensionis	45	0.63
**Anisotremus virginicus*	41	1.03
**Bodianus rufus*	39	0.50
Stegastes variabilis	37	0.52
Gramma loreto	28	0.69

[1]Species names according to Eschmeyer's (1998) revision.
[2]Sighting frequency (%) = percentage of transects in which the species was recorded.

Pp. 338-358 in J.C. Lang (ed.), Status of Coral Reefs in the western Atlantic: Results of initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Research Bulletin 496.

Table 3. Density (mean ± standard deviation) of AGRRA fishes, by subreef in central-southern Quintana Roo, México.

Site name	Herbivores (#/100m^2)		Carnivores (#/100m^2)		
	Acanthuridae	Scaridae (≥3 cm)	Haemulidae (≥3 cm)	Lutjanidae	Serranidae[1]
Northern Sian Ka'an					
Boca Paila N	4.7 ± 2.4	5.8 ± 3.5	3.5 ± 1.5	2.7 ± 3.1	2.0 ± 0.8
Boca Paila C	8.0 ± 7.3	2.0 ± 1.5	11.7 ± 8.1	3.0 ± 3.3	0.7 ± 1.0
Boca Paila S	7.7 ± 6.8	3.8 ± 1.8	13.3 ± 10.4	6.8 ± 1.2	1.2 ± 2.5
Yuyum N	7.5 ± 2.0	8.0 ± 5.5	12.0 ± 7.6	2.5 ± 2.6	1.5 ± 2.0
Yuyum C	4.7 ± 3.7	8.2 ± 2.5	24.3 ± 14.9	9.5 ± 7.6	2.0 ± 2.5
Yuyum S	4.8 ± 5.5	11.0 ± 4.0	7.3 ± 4.1	1.2 ± 0.8	1.2 ± 0.5
Punta Allen N	3.2 ± 5.1	9.8 ± 5.7	2.0 ± 1.2	1.3 ± 2.2	1.8 ± 0.8
Punta Allen C	4.2 ± 1.5	9.8 ± 5.7	3.0 ± 1.9	1.0 ± 0.6	2.3 ± 2.0
Punta Allen S	3.5 ± 2.5	15.7 ± 12.1	6.3 ± 8.7	1.3 ± 1.5	1.3 ± 0.8
Southern Sian Ka'an					
Tampalam N	5.0 ± 4.0	2.0 ± 2.0	5.0 ± 0.5	0	1.7 ± 4.0
Tampalam C	4.7 ± 9.7	6. 5 ± 5.0	7.0 ± 4.4	2.5 ± 1.3	0.3 ± 0.8
Tampalam S	4.0 ± 8.0	10.8 ± 5.9	9.0 ± 6.7	2.7 ± 2.2	0.2 ± 0
El Placer N	3.8 ± 4.2	5.2 ± 2.9	15.5 ± 18.7	0.7 ± 0.5	2.3 ± 4.2
El Placer C	1.8 ± 0.8	9.0 ± 5.1	4.0 ± 2.5	0.2 ± 0.6	1.0 ± 2.0
El Placer S	3.8 ± 3.7	12.2 ± 7.4	6.3 ± 5.7	1.8 ± 1.5	1.8 ± 3.5
Southern					
Mahahual N	2.5 ± 0.5	15.0 ± 12.0	1.0 ± 1.3	1.2 ± 0	1.5 ± 1.3
Mahahual C	2.5 ± 3.5	21.8 ± 17.8	2.3 ± 1.5	0.3 ± 0	0.8 ± 0.8
Mahahual S	3.3 ± 3.5	25.0 ± 13.4	2.3 ± 1.0	1.0 ± 0.6	1.5 ± 0.9
Xahuayxol N	6.7 ± 7.7	13.0 ± 4.7	2.8 ± 1.3	1.0 ± 10.3	1.8 ± 0.6
Xahuayxol C	4.5 ± 4.6	8.3 ± 4.8	2.5 ± 0.8	1.0 ± 0.6	2.8 ± 6.5
Xahuayxol S	6.2 ± 4.8	11.3 ± 6.7	7.5 ± 6.0	2.0 ± 3.0	2.3 ± 3.5
Xcalak N	4.0 ± 4.0	13.2 ± 5.1	2.7 ± 0.6	6.7 ± 12.4	1.7 ± 1.0
Xcalak C	5.0 ± 3.3	10.0 ± 4.3	4.3 ± 3.0	2.7 ± 3.5)	1.2 ± 2.5
Xcalak S	16.7 ± 22.4	14.2 ± 6.4	3.0 ± 1.1	4.7 ±6.0	2.3 ± 2.7

[1]*Epinephelus* spp. (excluding any *E. cruentatus)* and *Mycteroperca* spp.

Table 4. Mean percentage of species and individuals in Randall's (1967) reef fish feeding categories by reef in central-southern Quintana Roo, México.

Reef name	Plant and detritus feeders (%)		Zooplankton feeders (%)		Invertebrate feeders sessile (%)		Invertebrate feeders "shelled" (%)		Generalized carnivores (%)		Ectoparasite feeders (%)		Fish feeders (%)	
	Spp[1]	Ind[2]	Spp	Ind	Spp	Ind	Spp	Ind	Spp	Ind	Spp	Ind	Spp	Ind
Northern Sian Ka'an														
Boca Paila	24	17	10	37	12	16	23	16	19	14	1	1	10	3
Punta Yuyum	20	23	11	30	13	15	22	26	15	11	4	1	10	2
Punta Allen	23	32	14	38	16	7	18	11	16	7	4	1	8	4
All Northern Sian Ka'an	**23**	**24**	**12**	**36**	**12**	**12**	**21**	**18**	**16**	**11**	**3**	**1**	**7**	**4**
Southern Sian Ka'an														
Tampalam	27	33	13	32	9	5	24	20	13	7	9	2	3	3
El Placer	25	18	13	50	13	5	19	19	13	3	6	1	10	4
All Southern Sian Ka'an	**24**	**26**	**13**	**41**	**11**	**5**	**22**	**20**	**13**	**5**	**1**	**7**	**7**	**3**
Southern														
Mahahual	22	39	11	37	17	9	19	9	18	3	1	1	10	3
Xahuayxol	25	32	13	38	17	7	21	15	17	4	1	1	6	4
Xcalak	22	30	10	48	19	4	24	9	15	4	1	1	9	6
All Southern	**24**	**34**	**11**	**41**	**18**	**6**	**22**	**10**	**17**	**4**	**1**	**1**	**8**	**4**

[1]Spp = Species
[2]Ind = Individuals

Pp. 338-358 in J.C. Lang (ed.), Status of Coral Reefs in the western Atlantic: Results of initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Research Bulletin 496.

Table 5. Mean abundance by size category for herbivorous and carnivorous reef fishes (all species and AGRRA list) by reef in central-southern Quintana Roo, México.

Reef name	Fish trophic category	Abundance (#/reef)				
		3-10 cm	11-20 cm	21-30 cm	31-40 cm	41-50 cm
Northern Sian Ka'an						
Boca Paila	All herbivores	**219**	132	28	8	7
	AGRRA herbivores[1]	35	**128**	28	4	4
	All carnivores	2	**70**	29	12	6
	AGRRA carnivores[1]	1	**52**	12	8	3
Yuyum	All herbivores	**195**	163	33	7	0
	AGRRA herbivores	76	**163**	33	7	0
	All carnivores	9	**86**	27	6	1
	AGRRA carnivores	3	**65**	10	1	0
Punta Allen	All herbivores	**176**	188	21	7	2
	AGRRA herbivores	92	**184**	20	7	1
	All carnivores	0	**25**	19	5	5
	AGRRA carnivores	0	5	**10**	5	5
Southern Sian Ka'an						
Tampalam	All herbivores	**204**	111	14	9	3
	AGRRA herbivores	78	**107**	14	9	1
	All carnivores	0	**32**	16	3	3
	AGRRA carnivores	0	**21**	8	2	0
El Placer	All herbivores	**285**	99	35	7	0
	AGRRA herbivores	**97**	90	35	7	0
	All carnivores	0	**51**	12	6	8
	AGRRA carnivores	0	**14**	0	2	0
Southern						
Mahahual	All herbivores	173	**334**	65	4	0
	AGRRA herbivores	60	**306**	65	4	0
	All carnivores	4	**33**	11	2	3
	AGRRA carnivores	0	**9**	5	0	1
Xahuayxol	All herbivores	146	**218**	29	9	0
	AGRRA herbivores	76	**199**	29	9	0
	All carnivores	6	**51**	19	1	1
	AGRRA carnivores	0	**13**	10	0	0
Xcalak	All herbivores	181	**317**	35	11	0
	AGRRA herbivores	49	**316**	35	11	0
	All carnivores	6	**53**	50	25	4
	AGRRA carnivores	0	26	**34**	22	3
All Reefs	**All herbivores**	**197.4**	**195.3**	**32.5**	**7.8**	**1.5**
	AGRRA herbivores	**70.4**	**186.6**	**32.4**	**7.3**	**0.8**
	All carnivores	**3.4**	**50.1**	**22.9**	**7.5**	**3.9**
	AGRRA carnivores	**0.4**	**22.8**	**9.9**	**4.4**	**1.3**

[1]See Methods for AGRRA species as defined in this paper.