Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation

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Abstract. Human activities have strong impacts on ecosystem functioning through their effect on abiotic factors and on biodiversity. There is also growing evidence that species functional traits link changes in species composition and shifts in ecosystem processes. Hence, it appears to be of utmost importance to quantify modifications in the functional structure of species communities after human disturbance in addition to changes in taxonomic structure. Despite this fact, there is still little consensus on the actual impacts of human-mediated habitat alteration on the components of biodiversity, which include species functional traits. Therefore, we studied changes in taxonomic diversity (richness and evenness), in functional diversity, and in functional specialization of estuarine fish communities facing drastic environmental and habitat alterations. The Terminos Lagoon (Gulf of Mexico) is a tropical estuary of primary concern for its biodiversity, its habitats, and its resource supply, which have been severely impacted by human activities. Fish communities were sampled in four zones of the Terminos Lagoon 18 years apart (1980 and 1998). Two functions performed by fish (food acquisition and locomotion) were studied through the measurement of 16 functional traits. Functional diversity of fish communities was quantified using three independent components: richness, evenness, and divergence. Additionally, we measured the degree of functional specialization in fish communities. We used a null model to compare the functional and the taxonomic structure of fish communities between 1980 and 1998. Among the four largest zones studied, three did not show strong functional changes. In the northern part of the lagoon, we found an increase in fish richness but a significant decrease of functional divergence and functional specialization. We explain this result by a decline of specialized species (i.e., those with particular combinations of traits), while newly occurring species are redundant with those already present. The species that decreased in abundance have functional traits linked to seagrass habitats that regressed consecutively to increasing eutrophication. The paradox found in our study highlights the need for a multifaceted approach in the assessment of biodiversity changes in communities under pressure.

Key words: environmental changes; estuarine ecosystem; eutrophication; fish ecomorphology; functional divergence; functional evenness; functional richness; human disturbance; seagrass; Terminos Lagoon, Gulf of Mexico.

Introduction

Anthropogenic impacts are deeply modifying (sometimes irreversibly) environments and geochemical fluxes (Vitousek et al. 1997). Estuarine and coastal ecosystems, which are among the most productive on Earth (Costanza et al. 1997), are under increasing pressure due to drastic changes in land use of watersheds, acceleration of coastal urbanization, sea rise, and global warming (Lotze et al. 2006). Among those ecosystems, tropical estuaries are marked by a high biodiversity and provide ecosystem services of high value (protein supply through fishing, water filtration, nursery habitats for

juveniles), while they are severely impacted by mangrove deforestation, overfishing, aquaculture, and increasing rates of sediment loading (Lotze et al. 2006). Tropical estuarine ecosystems also yield a high diversity of habitats such as mangrove swamps, seagrasses beds, muddy or sandy sediments. These different habitats and their associated communities can be expected to respond in different ways in the face of disturbances. For instance, many studies have reported seagrass loss following drastic environmental changes induced by human influence such as eutrophication (Lotze et al. 2006, Orth et al. 2006). In turn, these modifications in the composition of these vegetated habitats may alter their quality for associated fish and invertebrates with, as a consequence, a loss of some ecosystem functions and a decrease of the secondary productivity (Micheli and Halpern 2005). In these coastal ecosystems, the

nekton is dominated by fish that play an important role in nutrient fluxes, both along the trophic level and through space with migrations (Holmlund and Hammer 1999). Thus, we urgently need to determine the factors that maintain or threaten the biodiversity of fish communities. Here we focus on two overlooked facets of fish community structure (functional diversity and functional specialization), which are demonstrated to be more sensible than taxonomic diversity to habitat degradation.

Classically, biodiversity changes have been assessed using diversity indices that take into account the number of species present (species richness) and the evenness of abundance distribution among species (e.g., Pielou index [Pielou 1969]). However, such indices based only on taxonomic identity provide an incomplete view of biodiversity. Indeed, they do not take into account the biological identity and differences among species, while a recent consensus points out the importance of particular taxa rather than species richness per se to explain ecosystem processes in plant (Petchey 2004), animal (Valone and Schutzenhofer 2007), or aquatic communities (O'Connor et al. 2008). A step further in biodiversity assessment needs to consider the role of each species in ecosystems or species responses to environmental conditions. Let us consider two communities with five fish species each. The first one contains anchovy, jack, moray, flatfish, and butterfly fish while the second one contains five butterfly fish species. Species richness has a value of 5.0 for both communities, but biological diversity in terms of morphology, diet, swimming ability, and life history traits is clearly greater in the former community. This is actually what the functional view of biotic communities aims to quantify (McGill et al. 2006).

Functional ecology is based on the use of functional traits, which are defined as biological attributes that influence organismal performances (Violle et al. 2007). Basically, functional traits have to be related to ecosystem processes (effects traits) or to ecosystem stability through resistance and resilience (response traits). A step beyond species richness, we can thus quantify the functional diversity of communities, which is defined as the diversity of traits present in a community weighted by their abundances (e.g., Petchey and Gaston 2006). The index used in most of studies dealing with functional diversity is the number of functional groups defined a priori (for example, for plants: grasses, legumes, and herbs). This clustering may lead to a loss of information (Fonseca and Ganade 2001), or at worst, may lead to a weak explanatory power on ecosystem processes (Wright et al. 2006). As an alternative, continuous indices of functional diversity, directly based on functional traits, have been proposed (see Petchey and Gaston [2006] for a review) but they are either highly correlated to species richness (Petchey and Gaston 2002) or designed for single trait approaches (Mason et al. 2005). To overcome these two

limitations, Villéger et al. (2008a) recently generalized the framework of Mason et al. (2005) and proposed three indices to measure the three independent facets of functional diversity (richness, evenness, and divergence) designed for multi-traits case study. Splitting functional diversity into three independent components has already been relevant to elucidate processes of community assembly (e.g., Mason et al. 2008). From a practical point of view, Cornwell et al. (2006) show that habitat filtering may reduce the amount of functional diversity in plant communities under constraints, while Villéger et al. (2008a), in a more general framework, suggest that considering the three facets of functional diversity may reveal the impact of perturbations (e.g., climate change, fire, grazing, or overfishing) on biotic communities.

In addition to functional diversity measures, the degree of specialization is a complementary aspect of community structure (Julliard et al. 2006, Devictor et al. 2008). Indeed, when considering a regional pool of species, it is informative to determine whether the species of a local community are a random sample of the regional pool, or if they tend to exhibit more or less specialized trait combinations. Indeed, it has been hypothesized that specialist species are the most affected by environmental changes (e.g., for habitat specialists [in Jiguet et al. 2007]) since they are supposed to be strongly associated with particular niches. Thus if environmental changes lead to the degradation or even the loss of these niches, specialist species will be deeply affected. On the contrary, generalist species may tolerate a loss of particular habitats as they are supposed to occupy several, and the most common ones.

To our knowledge, there is no study that focuses on long-term modifications in the whole functional and multidimensional structure of communities when facing environmental changes. On the other hand, there is still no study about the impact of coastal habitat degradation on different aspects of fish biodiversity, including functional diversity and the level of community specialization. Here, through the use of a novel framework designed to measure various independent facets of functional community structure in addition to taxonomic diversity, we investigated the modifications in coastal fish communities after 18 years and a degradation of habitats with the Terminos Lagoon as a case study. Terminos Lagoon is one of Mexico's largest lagoons and is of primary interest for biological conservation and fishery activities. It has been severely impacted by anthropogenic pressures during the last decades (shrimp fishery, urbanization of Carmen Island, and deforestation of the watershed for intensive agriculture). Previous studies have underlined a strong shift in environmental conditions during the last two decades (Ramos-Miranda et al. 2005) as well as changes in the trophic structure of fish communities (Sosa-Lopez et al. 2005).

Our study aims to assess (1) how taxonomic diversity (species richness and evenness) are modified, (2) how
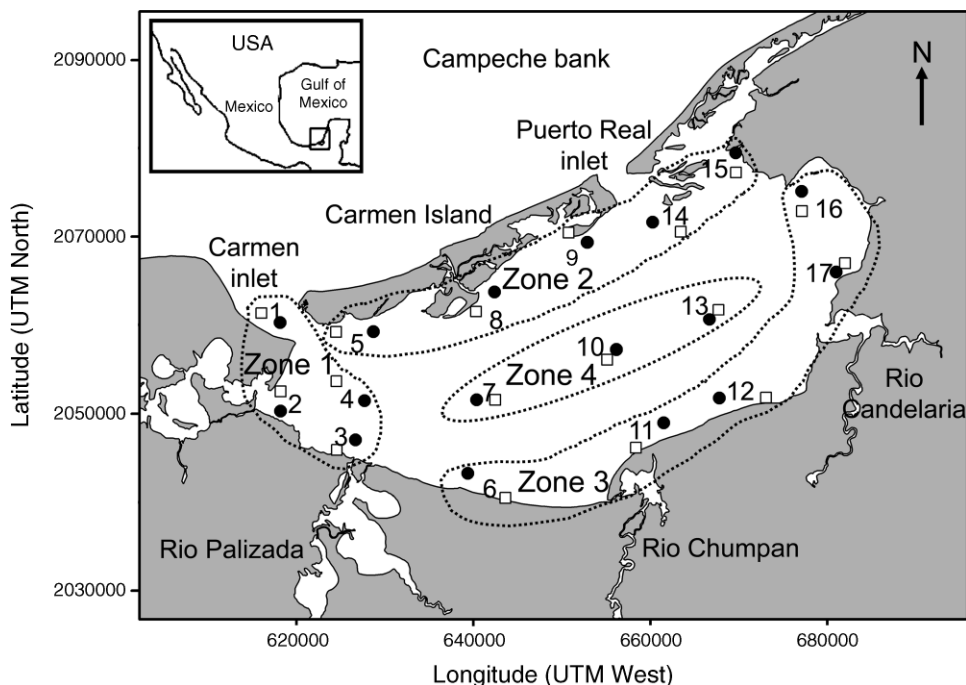
FIG. 1. Map of the study area (Universal Transverse Mercator [UTM] coordinate system). Open squares represent the 17 sampling locations in 1980–1981; solid circles are the corresponding sampling locations in 1998–1999. Environmental zones defined after environmental conditions were recorded in 1980–1981 are marked with dotted black lines.

functional diversity and functional specialization are affected, and (3) which biodiversity changes are most related to environmental modifications. We expect that indices considering functional identity of species will provide better description of habitat degradation than indices considering only species taxonomic identity and abundances, since species–environment relationships are assumed to be mediated via functional traits (e.g., Suding et al. 2008).

MATERIALS AND METHODS

The study system

Terminos Lagoon (Fig. 1) is located in the southwestern part of the Gulf of Mexico (Campeche State, Mexico). This is the largest lagoon in this area with a surface of 1660 km². The lagoon is very shallow with a mean depth of 3.5 m. Terminos Lagoon is actually an estuarine ecosystem as it is strongly influenced by freshwater discharges from three streams located on its southern part (respectively, from west to east: Palizada River, Chumpan River, and Candelaria River). The lagoon is delimited by Carmen Island (30 km long and 2.5 km wide) and thus water exchanges with the sea take place through two inlets, one on its northeastern part (Puerto Real) and the other one on the northwestern part (Carmen). Water circulation in the lagoon generally follows a clockwise direction (David and Kjerfve 1998), with seawater going inside the lagoon through the Puerto Real inlet, mixing with freshwater inputs near the

stream mouth, with the resulting brackish water going outside the lagoon through the Carmen inlet (Fig. 1).

Sampling protocol

Two similar biological surveys were conducted in 1980–1981 (Yañez-Arancibia et al. 1982) and 1998–1999 (Ramos Miranda 2000). For each campaign 17 stations were sampled monthly for a period of 12 months ($N = 204$; Fig. 1). For each station and each month, fish communities were sampled using a shrimp trawl (5 m long, with a mouth opening 2.5 m in diameter, and mesh size of 19 mm) towed for 12 minutes at a constant speed of 2.5 knots (=4.630 km/h). Each sample, therefore, consisted of a volume of 4500 m³. This active sampling method is well adapted to fishes living in this shallow coastal area, since they are relatively small (<30 cm) and slow swimmers. For each sample, all individuals were identified at the species level and weighed to the nearest decigram. Additionally, six environmental variables were recorded monthly in each station: depth (using a weighted rope), transparency (measured using a Secchi disk), and both temperature and salinity at the top and the bottom of the water column. According to the monthly environmental conditions observed in 1980–1981, the 17 stations were clustered into environmental zones (Ward agglomerative method on Euclidean distances computed on standardized environmental variables). In each zone, temporal changes between the two periods were tested for each environmental parameter using Wilcoxon pairwise rank tests.

Functional characterization of fishes

Ecomorphological traits have been used for several decades to assess fish ecological niches and then to seek (1) interregional convergence (Winemiller 1991), (2) assembly rules in fish communities (Bellwood et al. 2002, Mason et al. 2008), and (3) relationships between fish traits and environments (Wainwright et al. 2002). These traits were assimilated to functional traits as they describe how key functions are performed by fishes. For instance, the ratio of gut length to standard length is an indicator of trophic status (Kramer and Bryant 1995).

We characterized fishes for two key functions: food acquisition and locomotion. Since these functions are complex processes, they cannot be described using only one trait (Dumay et al. 2004, Mason et al. 2007). For example, swimming ability combines several performances such as speed, endurance, and maneuverability (Webb 1984), and cannot be summarized using one functional trait only. We thus selected, respectively, 7 and 10 ecomorphological traits to describe each function of interest (Appendix A). During a biological survey conducted in 2006–2007 in the same region (see Villéger et al. 2008b), a maximum of 20 individuals by species were randomly selected. On each of these individuals, morphoanatomical traits were measured and ecomorphological traits were calculated. Then, for each species, mean trait values were computed from individual measurements assuming that intraspecific variations were lower than interspecific variations (Dumay et al. 2004). Finally, for each function, trait values of all the species present in the lagoon were standardized so that the mean of each trait was 0 and its standard deviation was 1 in order to give the same weight to each trait.

Measuring taxonomic diversity, functional diversity, and functional specialization

Species evenness (i.e., among abundances) was computed using the Pielou index (Pielou 1969):

$$J = \frac{-\sum_{i=1}^{S} p_i \times \log p_i}{\log S}$$

where S is species richness and p_i are species relative abundances (here biomasses).

Measuring functional diversity has been achieved in many ways during the last two decades but progress toward continuous and multivariate measures has been made (Petchey and Gaston 2006). Villéger et al. (2008a), following the framework of Mason et al. (2005), proposed three complementary indices to evaluate the three primary and independent facets of functional diversity: functional richness (functional space occupied by the community), functional evenness (regularity in the distribution of species abundances in the functional space), and functional divergence (how species abundances diverge from the center of the functional space). See Appendix B for details on properties and compu-

tation of the indices. Here we proposed to use this multifaceted framework to evaluate the impact of environmental changes on the functional diversity of the Terminos fish communities.

Additionally, we used the index proposed by Bellwood et al. (2006b) to measure the functional specialization of a community (i.e., the average specialization of its species). When all species from the regional pool are plotted in a functional space according to the values of their traits, the degree of specialization for a species is the Euclidean distance of this species to the center of gravity (Appendix B).

Thus, functional diversity and functional specialization are two complementary views of the functional structure of communities, since functional specialization of a community depends on the positions of species relative to the center of gravity calculated from the regional pool, while functional diversity indices rely only on the functional structure of the target community.

Assessing biodiversity changes of fish communities

For each zone and for each period, species richness and species evenness were estimated. In addition, the three functional diversity indices and the specialization index were computed for each function, based on trait values and relative biomasses of species (see Appendix C for further details). Then for each zone the difference between 1998–1999 and 1980–1981 was calculated for the six indices.

These changes in index values cannot be interpreted directly since fish communities have different species numbers and different biomasses between the two periods. Thus the question is no longer whether observed diversity indices are lower in 1998–1999 than in 1980–1981, but whether diversity indices are significantly lower in 1998–1999 than in 1980–1981 after randomizing the samples between the two periods. Thus we tested the null hypothesis positing that there was no change in the structure of fish communities between the two periods. We designed an appropriate randomization procedure to test temporal changes in diversity indices for each zone (see Appendix C for details). This null model randomized the year to which each sample belongs, but without modifying the spatiotemporal structure of the sampling design, the observed species richness, and relative abundances in fish communities. Hence, this procedure takes into account any autocorrelation (temporal or spatial) among the samples. The randomization process was carried out 9999 times for each index and each zone and the P value associated with the null hypothesis (no period effect) rejection was estimated (Manly et al. 1998). In addition, a standardized effect size (SES) was calculated for each index and each zone to measure the statistical amount of deviation of the observed index of community structure from the distribution of simulated indices (Gotelli and McCabe 2002).

The clustering of stations, the computations of indices, randomizations for the null model and statistical

TABLE 1. Environmental conditions in four zones of the Terminos Lagoon (Gulf of Mexico).

Zone	Depth (m)			Secchi (m)			Bottom salinity (psu)			Substrate
	1980–1981	1998–1999	P	1980–1981	1998–1999	P	1980–1981	1998–1999	P	
1	2.8 (22%)	2.1 (45%)	***	0.6 (35%)	0.5 (50%)	*	21.3 (41%)	23.1 (47%)	NS	muddy with fine sand and clayed silt, riverine influence
2	2.6 (32%)	1.6 (45%)	***	1.1 (45%)	0.9 (49%)	**	28.5 (25%)	31.7 (18%)	***	mud near mangrove swamps and sand with seagrasses and macroalgae
3	2.5 (24%)	1.3 (35%)	***	0.9 (38%)	0.6 (39%)	***	22.4 (28%)	25.9 (22%)	***	silt–clay sediments, mangrove swamps, riverine influences
4	3.9 (11%)	3.9 (9%)	NS	1.1 (36%)	1.3 (44%)	NS	26 (25%)	31.1 (17%)	***	sand–silt sediments

Notes: For each zone, mean values are given for 1980–1981 and 1998–1999, with spatiotemporal coefficients of variation in parentheses. Results of pairwise Wilcoxon rank tests between the two periods are shown as P levels.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant.

analyses were carried out using R software (R Development Core Team 2008). Scripts used to compute functional diversity and functional specialization indices are provided in the Supplement.

RESULTS

Spatial strata

Clustering of the 17 stations according to their environmental conditions in 1980–1981 led to the discrimination of four zones (Fig. 1, Table 1). These zones are geographically continuous and reflect hydrology and sedimentology. Zone 1 grouped the stations near the Carmen Inlet and is marked by the influence of stream discharges (particularly from the Palizada River, which has the highest debit with $>4 \times 10^9 \, \text{m}^3$ per year), and thus a large amplitude for salinity (from 4 to 35 psu on the Practical Salinity Scale). Substrate in Zone 1 is muddy, with fine sand and clayed silt. Zone 2 stretched along Carmen Island up to Puerto Real inlet where stations are under marine influence (mean salinity of 28.5 psu). Substrate varies from muddy areas near mangrove swamps (*Rhizophora mangle*) to sandy zones colonized by seagrasses (*Thalassia testudinum*). Zone 3 is along the southern coast of the lagoon. These shallow waters (mean depth of 2.5 m) close to mangroves received influent from the Candelaria and Chumpan Rivers and have silt–clay sediments. Zone 4 is in the center of the lagoon, which is the deepest part (mean depth of 3.9 m) and is a transitional zone between marine and freshwater influences (salinity ranges from 15 to 36 psu for a mean of 26 psu).

Environmental changes

Comparisons between the two periods showed that the four zones experienced severe modifications in their environmental conditions (Table 1). Depth was globally decreasing, particularly in Zones 1, 2, and 3. For instance, depth in Zone 2 significantly dropped from 2.6 m on average in 1980–1981 to 1.6 m in 1998–1999 (Wilcoxon pairwise rank test: $P < 0.001$). Similarly, transparency significantly decreased in these three zones (in Zone 2 from 1.1 m to 0.9 m; $P < 0.01$). Salinity was higher in 1998–1999 than in 1980–1981, particularly in Zones 2, 3 and 4, which all showed a significant increase (a difference of >3 psu on average; $P < 0.001$).

Fish collection

A total of 10 449 and 11 946 individuals were caught in 1980–1981 and 1998–1999, respectively. These abundances converted to a biomass of 423 kg and 281 kg in each of the two sample periods. A total of 103 species were caught during the two periods of sampling. However, since the quantification of functional traits was conducted on a later sample of species, the set of trait measurements was incomplete. The 19 morpho-anatomical measures were estimated on 948 individuals belonging to 62 species. Among these 62 species, the 16 functional traits were estimated on 20 individuals for 38 species and on >10 individuals for 47 species.

Nevertheless, species for which traits have been measured represented 98.77% of total biomass and contributed to $>97\%$ of the biomass in each of the eight strata (Table 2). Additionally, species that were not functionally characterized accounted each for $<1\%$ of the total biomass within a stratum.

Changes in fish community composition and biomass

Species richness at the lagoon scale increased from 53 to 58 between the two periods, with Zone 4 being the poorest zone, while Zone 2 is the richest (Table 2). These two zones showed increasing species richness (for species functionally characterized) with, respectively, seven and six species more in 1998–1999 than in 1980–1981. When considering all species, these trends remained true with a regional increase from 77 to 89 species and with, for instance, an increase of 56 to 76 species in Zone 2.

Zone 2 had the highest biomass for the two periods (respectively $>60\%$ and 40% of total biomass) but exhibited a strong decrease from 258 kg to 120 kg after 18 years.

Species evenness was globally high ranging from 0.55 to 0.74, indicating that fish communities were composed

TABLE 2. Changes in fish community structure for each zone between the two periods of study (1980–1981 and 1998–1999).

Zone	Period	Species richness	Total biomass (kg)	Biomass described (%)	Bray-Curtis dissimilarity
1	1980–1981	42	57	98.6	0.41
	1998–1999	43	54	99.8	
2	1980–1981	42	258	99.0	0.66
	1998–1999	49	120	97.3	
3	1980–1981	45	82	99.1	0.47
	1998–1999	44	87	99.5	
4	1980–1981	25	21	99.6	0.57
	1998–1999	31	15	97.5	

Notes: Species richness and total biomass refer only to the species functionally described; the contribution of these species to total biomass is given in the fourth column. Differences in taxonomic community structure between the two periods were assessed using the Bray-Curtis index.

of both dominant and rare species but without any ultradominant species in any zone. Species evenness increased in Zones 1 and 4 and decreased in Zones 2 and 3 between 1980–1981 and 1998–1999. However, only changes in Zones 2 and 4 were statistically significant (Table 3). In Zone 4, species evenness decreased significantly from 0.74 to 0.61. Indeed, in 1980–1981 only two species were accounting for >15% of the total biomass, whereas in 1998–1999 three new dominant species accounted each for >15% of the total biomass (18%, 25%, and 27%, respectively).

Bray-Curtis dissimilarity index was calculated between the two periods for each zone. Values were relatively high, ranging from 0.41 to 0.66 (mean 0.53), revealing that fish community structures (species identity and their abundances) had been strongly modified between the two periods.

Changes in functional diversity and functional specialization

Changes in community structure were also analyzed in terms of functional diversity and functional specialization. Results of null models, testing for the period effect, provided contrasting conclusions between zones (Table 3). For instance, the central part of the lagoon (Zone 4) presented no significant modification in functional structure of fish communities, either in terms of diversity or in terms of specialization for both food acquisition and locomotion. When compared to the strong modification in community composition (Bray-Curtis dissimilarity index of 0.57), it means that even if species turnover was strong it had no influence on the functional structure of fish communities.

In contrast, the northern part of the lagoon near Carmen Island (Zone 2) was strongly affected over the study period. Indeed, for both food acquisition and locomotion, functional divergence and functional specialization were significantly lower in 1998 than in 1980 (Table 3). In this zone, drastic changes in terms of dominance occurred among the main species (i.e., those for which relative biomass is >5%). For example, the most abundant species in 1980 was the Western Atlantic seabream *Archosargus rhomboidalis* (Sparidae), while the most abundant became the striped mojarra *Eugerres plumieri* (Gerridae) in 1998. This latter species accounted for >20% of the total biomass in 1998, whereas only two individuals were caught in 1980. Another Gerridae, the caitipa mojarra, *Diapterus rhombeus*, showed the same pattern, becoming the third-ranked species in 1998 with >11% of the total biomass. On the contrary, the check-

TABLE 3. Changes in species evenness, the three functional diversity facets, and functional specialization for each zone, for food acquisition and locomotion, between the two periods of study (1980–1981 and 1998–1999).

Zone	Function	Species evenness	Functional richness	Functional evenness	Functional divergence	Functional specialization
1	Food acquisition	−0.96	−2.07†	−0.15	2.11†	1.51
	Locomotion		−1.45	0.81	−1.39	−2.43†
2	Food acquisition	−2.50†	0.47	1.61†	−2.80†	−3.17†
	Locomotion		1.34	1.29	−2.37†	−2.21†
3	Food acquisition	−1.77	0.95	−0.41	0.91	1.96†
	Locomotion		−0.27	−1.04	0.10	1.56
4	Food acquisition	2.14†	−0.12	1.78	1.85	1.70
	Locomotion		1.49	0.94	1.09	1.58

Notes: For each function, each zone, and each index, observed differences between the two periods were tested against a null model positing that there was no change between the two periods. Standardized effect sizes (SESs) are provided for each function, each zone, and each index. $SES = (I_{obs} - I_{sim})/SD_{sim}$, where I_{obs} is the observed index while I_{sim} is the mean index of the simulated communities, and SD_{sim} is the associated standard deviation.

† Significant change (bilateral risk; $P = 0.05$).

ered puffer (*Sphoeroides testudineus*, Tetraondontidae) dropped from 26% of total biomass to only 7.5% in 1998. The third "loser" species was the hardhead sea catfish *Ariopsis felis*, which almost disappeared in 1998–1999, whereas it represented >14% of fish biomass in 1980–1981. On the contrary, a species very functionally similar to *Ariopsis felis*, the dark sea catfish *Cathorops melanopus*, has slightly increased (from 6% to 9% of total biomass).

Additionally, the strong dominance shifts observed in Zone 2 provoked changes in the functional structure of fish communities in terms of functional diversity and functional specialization (illustrated for food acquisition on Fig. 2). Indeed, as the checkered puffer and the Western Atlantic seabream were specialists for food acquisition (very far from the center of gravity of the functional volume; see Fig. 2), their decrease in relative abundance coupled to the increase of the two mojarras, which were generalist species, led to a significant decrease for both functional divergence and specialization at the community scale.

Few significant changes were observed in Zones 1 and 3, assuming a low modification in the functional structure of fish communities despite a high species turnover (Tables 2 and 3). Functional richness of food acquisition decreased significantly in Zone 1, while locomotion specialization also significantly decreased. In Zone 3 we observed a significant increase in the specialization for food acquisition.

Discussion

While most previous studies dealing with environmental influences on biodiversity have focused on species richness or community composition, we proposed here to go further and to also assess changes in the functional structure of fish communities following environmental shifts and habitat degradation. We used a large data set resulting from a long-term ecological survey in an ecosystem of major interest, both ecologically and economically. Terminos Lagoon has been severely changed between 1980 and 1998. First, environmental conditions showed an increase of marine influence and an increasing turbidity as well as a global decrease of depth (Table 1). These trends are particularly severe for Zones 2 and 3, which had lost >1 m of depth after 18 years. Moreover, the mean salinity increase was associated with a decreased variation in salinity through space and time. In other words, there was a salinity homogenization across stations and months in each zone.

In the 1980s, the shallow waters along Carmen Island were mainly covered by seagrass (data from 1981 in Yañez-Arancibia and Day [1988]). During the 1990s, seagrass coverage decreased all over this zone (J. Ramos Miranda and D. Flores Hernandez, *personal observation*), especially near the city of Carmen. This disappearance of *Thallasia testudinum* in this part of the lagoon could be related to the increasing turbidity that is among the major causes of the loss of seagrass meadows

(Orth et al. 2006). These stress factors may follow the destruction of some adjacent mangrove patches (J. Ramos Miranda and D. Flores Hernandez, *unpublished manuscript*) and the rapid urbanization that occurred in the region over this period (the city of Carmen grew up from <50 000 inhabitants in 1980 to >150 000 in 2000).

Changes in fish communities examined in the current study were marked, with a global increase of 10% in species richness over the period considered. However, standing fish biomass decreased markedly over the same period, both at zone and lagoon scale. Overall, community compositions have also been deeply modified between the two periods, as illustrated by high values of Bray-Curtis dissimilarity indices in the four zones (Table 2). Ramos Miranda et al. (2005) have already observed a significant decrease in taxonomic distinctness among species in the study location, despite an increase in species richness. This finding was due to the fact that new species occurring in the lagoon in 1998 belong to a family or a genus present before in the lagoon, whereas species disappearing were not replaced by species of the same taxa. Looking at these contrasted biotic changes, it is necessary to go further by considering fish communities from a functional perspective.

In the northern part of the lagoon (Zone 2), there was not only an increase in species richness but also a twofold decrease of biomass, and drastic changes in term of species dominance and species evenness. These modifications in community composition and structure induced changes in fish functional diversity. Two particular species have partially replaced previously dominant ones and thereby deeply modified the functional structure of fish communities. The two "loser" species (the checkered puffer *Sphoeroides testudineus* and the Western Atlantic seabream *Archosargus rhomboidalis*) are functionally close with regard to food acquisition, as illustrated by their relative proximity on the PCA projection (Fig. 2). Indeed, they are characterized by similar mouth size, shape, and position, as well as a long gut adapted to a diet mainly composed of small shellfishes and epiphytic algae (McEachran and Fechhelm 2005). This highlights the importance of a functional approach to community structure, as these species are taxonomically very different while being functionally close (Appendix D). On the contrary, the two "winner" species are both mojarras and have a similar morphology, except that *Eugerres plumieri* is bigger than *Diapterus rhombeus* (standard length 155 ± 17 mm and 76 ± 22 mm [mean ± SE], respectively). They are characterized by a small median mouth ending with a long protrusion, which is a typical adaptation for invertebrates captured in the water column. Moreover, the two loser species are generally associated with seagrass beds where they find benthic molluscs and plant material (McEachran and Fechhelm 2005). By contrast, the two winner species do not have such dependence, and are often associated with bare muddy areas (McEachran and Fechhelm 2005). These results
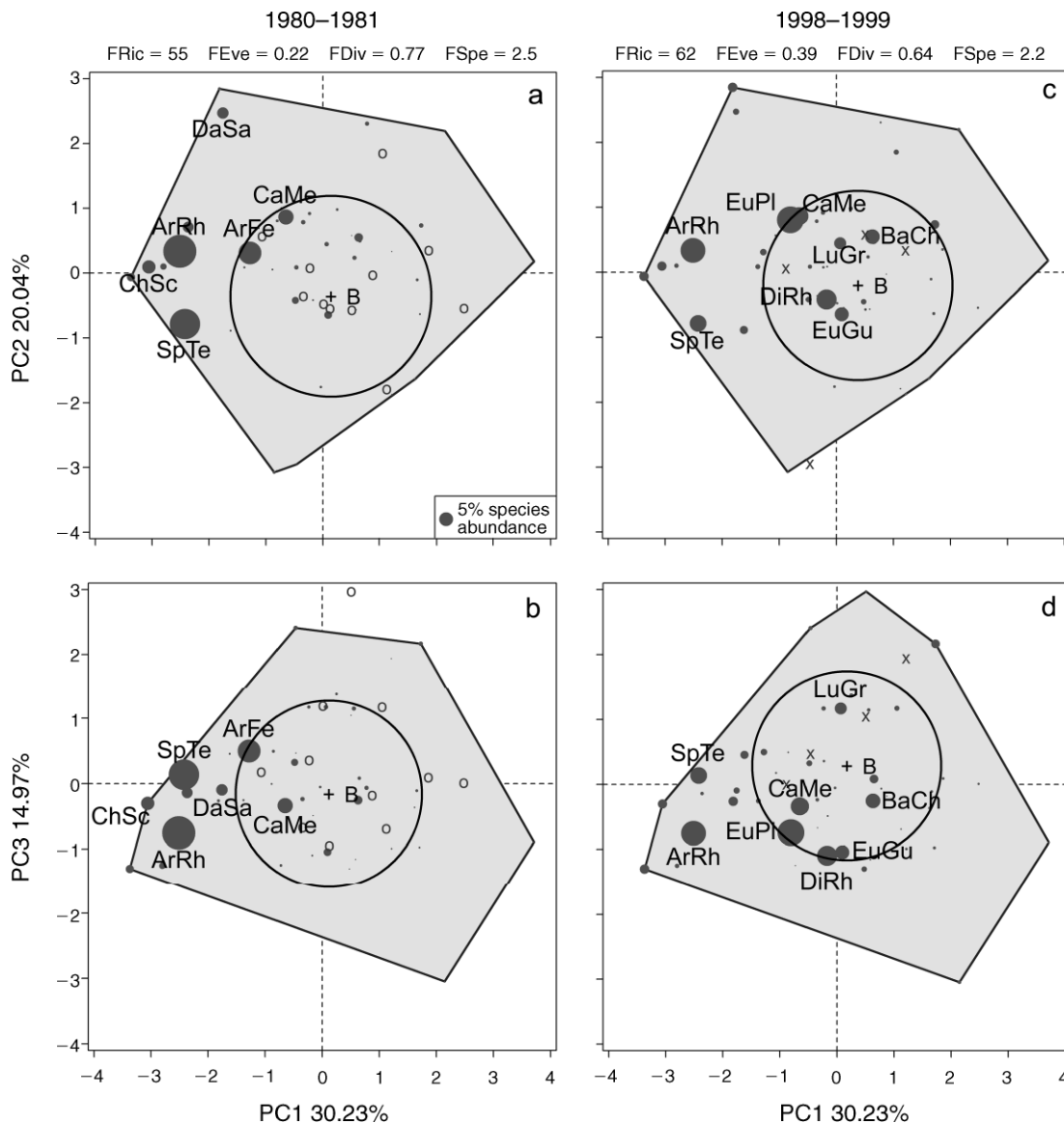
FIG. 2.   Illustration of changes in functional diversity and functional specialization for food acquisition in Zone 2 between (a, b) 1980 and (c, d) 1998. For graphical convenience we considered the PCA space where axes are either principal components 1 and 2 (panels a and c) or principal components 1 and 3 (panels b and d). They explain >65% of the total variability. Species are plotted in this functional space according to their respective trait values; areas of the dark gray disks are proportional to species abundances. Point B (+) represents the center of gravity of the vertices delimiting the convex hull (light gray enclosed area, which corresponds to functional richness). Radius of the circle equals the mean distance to B. As the proportion of the biomass close to B increases, divergence decreases. Values of functional diversity indices for the two periods are given above the graphs.

Names of dominant species: ArFe, *Ariopsis felis*; ArRh, *Archosargus rhomboidalis*; BaCh, *Bairdiella chrysoura*; CaMe, *Cathorops melanopus*; ChSc, *Chilomycterus schoepfi*; DaSa, *Dasyatis Sabina*; DiRh, *Diapterus rhombeus*; EuGu, *Eucinostomus gula*; EuPl, *Eugerres plumieri*; LuGr, *Lutjanus griseus*; SpTe, *Sphoeroides testudineus*. Small open circles in panels (a) and (b) represent species absent in 1980 and present in 1998. The small x symbols in panels (c) and (d) represent species present in 1980 and not in 1998. Key to abbreviations at top: FRic, functional richness; FEve, functional evenness; FDiv, functional divergence; FSpe, functional specialization.

suggest that species turnover was nonrandom, and instead was determined by habitat–trait relationships. Finally, the decrease of this very particular habitat and of its associated benthic fauna and epiphytic vegetation may be the main driver of the strong decrease of associated species. It suggests that the replacement of

seagrass patches by shallower muddy areas has benefited species of mojarras that share adapted traits. These results suggest that, in our system, trait-based mechanisms (as opposed to trait neutral ones) influence species turnover and explain functional diversity loss (Suding et al. 2008).

Furthermore, even if sea catfishes are classically associated with muddy substrate, *Ariopsis felis* adults are known to use shallow waters with seagrass as reproduction and nursery habitats (Yañez-Arancibia and Lara-Dominguez 1998). In our study, the abundance of *Ariopsis felis* was strongly decreasing, not only in the inner part of Carmen Island (Zone 2), but also in the other parts. For example, it dropped from 15% of total biomass to <5% in the central part of the lagoon (Zone 4). Moreover, the mean individual biomass of *Ariopsis felis* in this zone decreased strongly from 71 g to 19 g between the two periods, indicating a shift of occupation between mature adults and subadults. Thus, the degradation of a key habitat for reproduction could affect the entire population of *Ariopsis felis*. Conversely, *Cathorops melanopus* is described as a typical estuarine species that spends all its life cycle inside the lagoon (Yañez-Arancibia and Lara-Dominguez 1998). Juveniles feed mainly on organic matter and crustaceans in zones influenced by river discharges before migrating at the subadult stage to shallower waters near Carmen Island (Yañez-Arancibia and Lara-Dominguez 1998). Finally, adults breed in deep waters close to the center of the lagoon. Between the two periods, relative abundance of *Cathorops melanopus* has increased in the entire lagoon, especially in the zone near the stream mouth (Zone 1), as it represents half of the biomass in 1998–1999 (only 30% in 1980–1981). These observations suggest that the shift in environmental conditions and the increasing influence of streams (particularly marked for stations 2 and 3) may have favored this estuarine species to the detriment of *Ariopsis felis*.

The other parts of the lagoon seem to be functionally less affected by environmental changes that are nevertheless significant. However, community composition and structure have been deeply modified between the two periods in terms of species abundance turnover. Additionally, these zones are strongly affected by environmental seasonal variations, due to their exposure to freshwater discharges and/or marine influences. All these facts suggest that long-term environmental changes have not deeply changed these muddy or sandy bare habitats. Therefore, species replacements occur between functionally redundant species but do not lead to changes in the functional structure of communities.

The contrasting results obtained in the four zones suggest that the lagoon has not responded in the same manner between the two periods of study. The zone near Carmen Island has been the most affected, with strong changes in its functional structure for the two functions examined here. Moreover these changes were not adequately reflected when considering only species richness or evenness of their abundances. First, when looking at species richness changes in further detail, it appears, for example, that the 11 new species occurring in Zone 2 had very low abundances (<11 individuals each), while the four species lost were initially represented by one or two individuals. This pattern was similar in the three other zones, illustrating that changes in species richness are actually due to minor species that, in general, have very weak effects on ecosystem functioning (Grime 1998).

Furthermore, when species turnover also affected dominant species, a focus only on changes in species evenness may not be fully informative. For instance, species evenness increased in Zone 2 and decreased in Zone 4, while functional evenness increased in these two zones for both functions. These contrasted patterns illustrate that even if species evenness may be useful to see changes in abundance distribution among species, both a decrease and an increase of species evenness could lead to an increase in functional evenness. However, functional evenness, contrary to species evenness, indicates whether the dominant species are functionally similar, and this combination of species traits and abundances is the key toward a better understanding of community assembly rules and ecosystem functioning (Hillebrand et al. 2008). Overall, these findings reinforce the need to consider biological traits of species and community functional diversity in long-term surveys.

Our results are in accordance with the few studies dealing with the functional aspect of community changes when facing disturbance (e.g., Bellwood et al. 2006a). Indeed, Ernst et al. (2006) demonstrated that beyond a loss of species richness after selective logging, there was a dramatic loss of functional diversity in anuran communities. In the same vein, Flynn et al. (2009) showed that land use intensification reduces the functional diversity of animal communities (birds and mammals), potentially imperiling provisioning of ecosystem services. Devictor et al. (2008) found that more specialized species responded more negatively to landscape fragmentation and disturbance than generalist species. Here, as a further step, we show that different measures of biodiversity may lead to a paradox in the response to disturbance: a loss of functional diversity resulting from a loss of functional specialization while species richness increases. This result highlights that species richness may provide an incomplete signal of ecosystem recovery, and that a multifaceted framework (including functional traits) in the assessment of biodiversity changes is necessary after disturbance (Bellwood et al. 2006a). This result also suggests that conservation efforts should take into account the preservation of the diversity of functional traits in addition to the preservation of species richness and species dominance in order to sustain ecosystem processes. To this end, critical habitats such as seagrass beds need appropriate levels of assessment, within a multifaceted framework. More specifically, the use of several diversity facets seems essential to detect the real dimension of biodiversity loss after anthropogenic disturbance. Toward this objective, the estimation of three complementary functional diversity indices, in combination with the functional specialization index,

provides a complete framework for assessing changes in the functional structure of communities under threat, which may, in turn, alter the provisioning of ecosystem services.

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APPENDIX A

Functional characterization of fishes (*Ecological Archives* A020-056-A1).

APPENDIX B

Computation of the functional diversity indices (*Ecological Archives* A020-056-A2).

APPENDIX C

Summary of data analysis and randomization procedure (*Ecological Archives* A020-056-A3).

APPENDIX D

Dominant fish species in the northern part of the Terminos Lagoon (*Ecological Archives* A020-056-A4).

SUPPLEMENT

R script for computation of functional diversity and functional specialization indices (*Ecological Archives* A020-056-S1).