

Seawater turbidity and fish communities on coral reefs of Puerto Rico

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ABSTRACT: We investigated the variations of reef fish assemblages on coral reefs that experience different turbidity regimes, by assessing the association between the vertical extinction coefficient for photosynthetically active radiation ($K_{d\text{PAR}}$) and communities of fishes and corals at 21 reef sites in La Parguera, southwest Puerto Rico. Statistical correlations and non-metric multidimensional scaling (NMS) identified turbidity as an important environmental parameter affecting ecological processes on coral reefs, as reflected by changes in the composition and abundance of reef fishes and benthic communities. Lower fish density and species richness was found at turbid sites. Turbidity was also negatively correlated to percent coral cover, which together with rugosity, were additional habitat parameters shaping reef fish assemblages. Bluehead wrasse *Thalassoma bifasciatum* and yellowtail damselfish *Microspathodon chrysurus* were species rarely present at turbid sites and abundant at clear ones. The yellowtail hamlet *Hypoplectrus chlorurus* and sharknose goby *Elacatinus evelynae* had the opposite distribution along the turbidity gradient. We identified seawater turbidity as an additional predictor of the reef fish community structure in La Parguera, in addition to live coral cover and reef rugosity. Because coral reefs and reef fishes were less complex (lower rugosity, less species richness, less diversity) in more turbid sites, managing for clear water conditions within the coastal area of La Parguera should lead to improved ecosystem resilience and stability, and should become a primary goal of management.

KEY WORDS: Coral reef · Fish community · Turbidity · Vertical attenuation · Coefficient of light (K_d)

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INTRODUCTION

Tropical coastal regions are increasingly affected by anthropogenic disturbances such as urban and industrial development, population pressure, poor land-use practices, and the extensive exploitation of marine resources (Gardner et al. 2003, Hughes et al. 2010). These stressors alter the dispersal of water, sediments, nutrients and contaminants, often reducing coastal water quality and affecting marine ecosystems. Although reef organisms are adapted to tolerate variations in water quality, e.g. corals, zooxanthellae (Rogers 1983), fish (Amesbury 1981), barnacles (Wolanski et al. 2003), and algae (Fabricius et

al. 2005), when critical thresholds are exceeded they may be adversely affected. Because coral reefs support multiple products and services (Moberg & Folke 1999), their deterioration results in real ecological and economic loss. Human stresses in coastal areas are predicted to increase (Cohen 2003); hence the need to enhance knowledge of the interacting physical and biological factors affecting the structure of reef assemblages. Over recent decades, suspended sediments and eutrophication in Puerto Rico have increased and caused higher seawater turbidity than in the past (Morelock et al. 2001, Warne et al. 2005, Ryan et al. 2008). Turbidity refers to the loss of water clarity and is caused by suspended organic and inor-

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ganic particulates in the water column, such as sediments, tannins, bacteria or plankton, as well as by dissolved organic compounds. Turbidity is an important ecological variable determining fish distribution (Amesbury 1981, Fabricius et al. 2005, Mallela et al. 2007). In excess, turbidity can disrupt basic physiological functions such as respiration, growth, or feeding (Meager et al. 2005). Most fishes depend on visual cues as a main source of sensory information and, therefore, reduced light intensity due to turbidity has the potential to change fish social and mating behavior (Järvenpää & Lindström 2004), affecting predator avoidance and foraging success (Leahy et al. 2011). As a consequence, increased turbidity that significantly lowers light intensity can reduce fish abundance and diversity (Amesbury 1981, Mallela et al. 2007) and modify trophic structures (Harmelin-Vivien 1992).

The reduction in light penetration and photosynthetically active radiation (PAR) available for benthic primary producers (e.g. algae) due to increased turbidity can also affect the distribution and abundance of reef organisms, with deleterious consequences in the ecosystem balance (Souter & Linden 2000). Fishes that specialize on coral reefs for food or habitat are highly susceptible to disturbances that affect these systems (Wilson et al. 2006). Thus, fish community parameters, such as abundance and diversity, are usually correlated with specific habitat features, such as live coral cover (Lewis 1997, Syms & Jones 2000), complexity (Risk 1972, Friedlander & Parrish 1998, Kuffner et al. 2007) and density of macroalgae (Levin 1993). However, there are also feedback mechanisms whereby the fish community may have a significant role in maintaining reef function, for example through herbivory (Mumby 2006, Burkepile & Hay 2008), bioerosion (Ceccarelli et al. 2001) or nutrient and energy cycling. Thus, coral reef ecosystems can be evaluated in terms of fish abundance and the composition of fish assemblages.

We sought to understand how coral reef fish assemblages vary in relation to turbidity levels. Although several processes, such as sediment and nutrient runoff, phytoplankton blooms, and sediment resuspension can affect reef turbidity, within this study it was not

possible to control for all of these factors. Turbidity was measured as the extinction coefficient of photosynthetic active radiation ($K_{d\text{ PAR}}$). This coefficient quantifies the rate at which light is attenuated with increasing depth. This information can be used to improve conservation strategies that control environmental effects on coral reefs.

MATERIALS AND METHODS

Study area

This study was conducted between February and October 2005 at 21 reef sites along La Parguera, southwest Puerto Rico (Fig. 1). The distribution of coral reef habitats in the area was determined using the Puerto Rico benthic habitat characterizations of Kendall et al. (2001). Using existing bathymetry data, 10 m depth contours were created using Spatial Analyst and these were combined with reef habitats within ArcMap 9.1 to select potential sampling reef sites at 10 m depth. The final sampling sites were selected to obtain coverage of areas of known differing seawater turbidity.

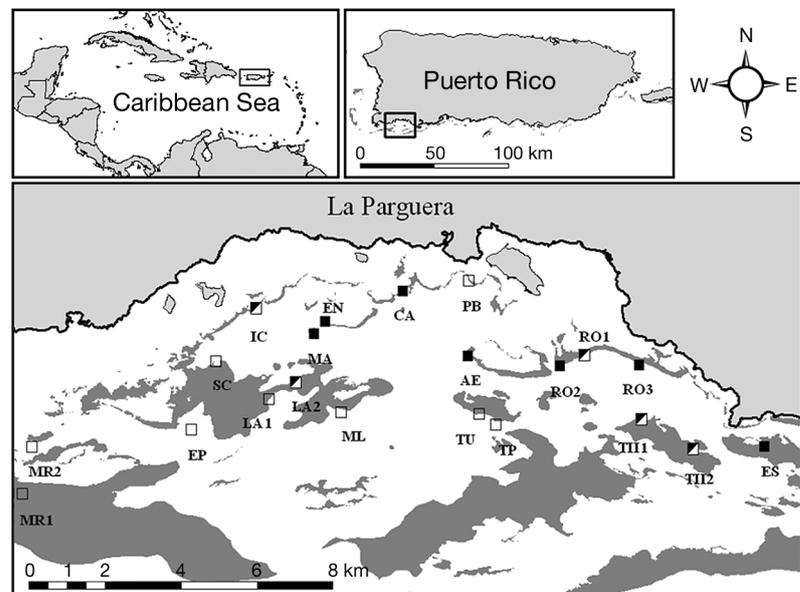


Fig. 1. La Parguera, southwest Puerto Rico, showing coral reef areas (dark gray), sampling sites on the reefs, and turbidity of the seawater at the sampling sites, measured as the extinction coefficient of photosynthetic active radiation ($K_{d\text{ PAR}}$): □ clear ($K_{d\text{ PAR}} \leq 0.17 \text{ m}^{-1}$); ■ turbid ($K_{d\text{ PAR}} \geq 0.20 \text{ m}^{-1}$); ▣ intermediate ($K_{d\text{ PAR}} = 0.18 \text{ to } 0.19 \text{ m}^{-1}$). Sampling sites codes: San Cristobal (SC), El Palo (EP), the Pinnacles (TP), Margarita (MR1, MR2), Media Luna (ML), Laurel (LA1, LA2), Turrumote (TU), Phosphorescent Bay (PB), Romero (RO1, RO2, RO3), East Station (ES), Enmedio (AE), Caracoles (CA), Enrique (EN), Mario (MA), Isla Cueva (IC), and Turrumote II (TII1, TII2)

Reef habitats south of La Parguera have developed on a broad carbonate shelf, with emergent fringing reefs, bank-barrier reefs and submerged patch reefs (Kendall et al. 2001, Morelock et al. 2001). Because there are no rivers discharging directly along this coast (Ewel & Whitmore 1973), waters are generally clear; however, reefs located east of La Parguera are affected by river plumes coming from Guanica and Guayanilla, ~15 and 30 km up-current respectively, resulting in a variety of seawater turbidity levels within the area. Similarly, salinities at eastern reefs, such as Romero, can sporadically decline in response to significant increases in freshwater runoff after strong storm events (Otero 2009).

Field methods

Vertical profiles of PAR were obtained from underwater light measurements taken at 1 m intervals from the surface to 10 m depth using a submersible irradiance meter (Li-Cor). In order to standardize the characterization of site specific turbidity, irradiance measures were made only between 08:00 and 10:00 h on days with clear skies and light winds. Sampling was omitted 2 to 3 d after heavy rains or strong winds to avoid bias from sporadic events. The $K_{d\text{ PAR}}$ values (m^{-1}) were estimated following Beer's Law as:

$$K_{d\text{ PAR}} = \ln E_d(z) = -K_d(z) + \ln E_d(0) \quad (1)$$

where $E_d(z)$ is the ascendant irradiance at depth z (m), and $E_d(0)$ is the ascendant irradiance at 0 m depth, measured underwater as close as possible to water surface. Per site through time, 6 to 9 measurements were obtained, including wet and dry season, to consider possible temporal variability in K_d values. Although the number of K_d measures was limited, turbidity categorization was similar to that reported by Cardona-Maldonado (2008) for La Parguera reefs.

The fish community was characterized using an adaptation of the underwater visual census method (UVC) of Brock (1954) standardized to 15 min per transect. Fish were identified and enumerated at 10 m depth within 6 replicate belt-transects at each site. Fish species saturation curves showed that few species were added after the sixth transect at all stations. Because water turbidity varied between sites, and the minimum visibility was ~10 m, transect dimensions were standardized to $10 \times 3 \text{ m}^2$ (180 m^2 per site), to ensure sufficient visibility for fish observation and identification at all sites. Large mobile fish were counted first to minimize possible diver avoidance bias. Fish species were classified into 1 of 6

trophic groups (zooplanktivore, herbivore, sessile invertebrate feeder, mobile invertebrate feeder, omnivore and piscivore) following Randall (1967).

The benthic composition and percent live coral cover at 10 m depth was determined along 6 replicate 10 m line transects at each site (Loya 1972). A plastic tape measure was laid along reef surface and all live coral species beneath the tape were identified to the lowest possible taxon. The lengths (cm) of each species under the tape measure were summed, and converted to percentages of the total transect length. Reef rugosity was calculated using the ratio of the horizontal distance (x m) of a chain laid over the reef structure divided by the total chain length (6 m) \times 6. Fish, coral, rugosity and turbidity data at each site was collected on the same day, every 3 mo. Additional turbidity measurements were taken on different days to add more observations of this parameter throughout the study period. Because sites were located using a field GPS, data was taken in the same reef but not exactly in the same place. A pooled overall average for each variable was obtained by site.

Data analysis

Species diversity was calculated using the Shannon-Wiener diversity index (Ludwig & Reynolds 1988) as $H' = -\sum P_i \ln P_i$, where P_i is the proportion of the total number of individuals occurring in species i . Logarithmic transformations [$\log(x + 1)$] were applied to fish density data given their large variability. Because fish densities per 30 m^2 were low, they are reported as per 100 m^2 . Normality was corroborated using a Kolmogorov-Smirnov 1-sample test and homogeneity of variance by a Levene's test. To examine the association between reefs and water quality, correlations among seawater turbidity, $K_{d\text{ PAR}}$, and fish and coral community structure (density, species richness, diversity, and density of trophic groups) were tested using linear regressions, compensated by Bonferroni corrections ($p < 0.005$). In addition, a correlation matrix of all the variables was constructed (Table 2), and partial correlations were developed among $K_{d\text{ PAR}}$ and the fish variables, controlling for coral cover and rugosity (see Tables 2 & 3 in 'Results').

Due to the non-parametric nature of the data, multivariate analysis was employed to evaluate the variation in fish species composition and abundance among varying seawater turbidity types, using non-metric multidimensional scaling (NMS) ordination

analysis in PC-ORD version 5.0 (McCune & Mefford 2006). The relationships of ordination scores to multiple potentially influential variables (physical or bio-physical: $K_{d\ PAR}$, rugosity; biological: live coral coverage, coral species richness) were examined with linear relationships depicted as joint plots. Multiresponse permutation procedure (MRPP), a non-parametric multivariate test for group differences, i.e. was used to evaluate compositional differences of fish assemblages in seawaters of varying turbidity (McCune & Mefford 2006). Both MRPP analyses and ordination used the Sorensen distance measure on untransformed mean fish densities (number of fish per transect) of all observed species. Species most frequent and abundant in clear and turbid waters were identified using indicator species analysis in PC-ORD (McCune & Mefford 2006). Compositional analyses were conducted at the species level.

RESULTS

Seawater turbidity

Varying seawater turbidity levels characterized the 21 sampling sites at La Parguera with $K_{d\ PAR}$ values ranging from 0.16 to 0.26 m^{-1} (Table 1, Fig. 1). Therefore, turbidity was classified into 3 groups using natural breaks in GIS: clear ($K_{d\ PAR} \leq 0.17\ m^{-1}$), intermediate ($K_{d\ PAR} = 0.18\ to\ 0.19\ m^{-1}$) and turbid waters ($K_{d\ PAR} \geq 0.20\ m^{-1}$). Clear water was found offshore westward, at San Cristobal (SC), El Palo (EP), The Pinnacles (TP), Margarita (MR1, MR2), Media Luna (ML), Laurel (LA1) and Turrumote (TU). An exception to this pattern was Phosphorescent Bay (PB), which had clear waters, despite being located close to land. Turbid water was observed at nearshore eastward areas such as Romero (RO2, RO3), East Station (ES), Enmedio (AE), Caracoles (CA), Enrique (EN), and Mario (MA). Sites with intermediate turbidity, Isla Cueva (IC), Laurel (LA2), Turrumote II (TII1, TII2), and Romero (RO1) were located between turbid and clear sites.

Table 1. Biotic and abiotic parameters (means \pm SD) measured at coral reef sites in La Parguera, southwest Puerto Rico. Sample size $n = 6$, except for ^a; measurements of $K_{d\ PAR}$ with $n = 9$. See Fig. 1 legend for sampling site codes. Trophic guild codes: H = herbivore, Z = zooplanktivore, P = piscivore, MI = mobile invertebrate feeder, O = omnivore, SI = sessile invertebrate feeder. Densities are number of fish per 100 m^2 (ind. 100 m^{-2})

Sampling site	$K_{d\ PAR}$	Fish		Coral cover (%)	Rugosity	Density of trophic guild					SI	
		Density	Species richness			Diversity (H')	H	Z	P	MI		O
EP ^a	0.16 \pm 0.05	143 \pm 11	12.3 \pm 2.3	2.1 \pm 0.1	37 \pm 6	1.21 \pm 0.04	67 \pm 8.3	19 \pm 1.5	9 \pm 0.4	30 \pm 2.7	7 \pm 0.5	19 \pm 1.5
SC ^a	0.16 \pm 0.03	133 \pm 34	15.7 \pm 2.2	2.2 \pm 0.2	45 \pm 15	1.39 \pm 0.06	50 \pm 9.3	35 \pm 7.0	11 \pm 0.8	50 \pm 9.2	15 \pm 0.8	11 \pm 1.8
TP ^a	0.16 \pm 0.02	87 \pm 6	12.7 \pm 6.2	2.3 \pm 0.1	46 \pm 5	1.36 \pm 0.03	50 \pm 17.0	22 \pm 15.1	4 \pm 0.5	24 \pm 6.0	19 \pm 1.8	11 \pm 2.4
MR1	0.17 \pm 0.02	163 \pm 26	12.2 \pm 4.4	1.9 \pm 0.1	28 \pm 6	1.21 \pm 0.03	67 \pm 6.6	20 \pm 1.2	7 \pm 24.4	28 \pm 11.8	4 \pm 1.8	11 \pm 1.2
PB	0.17 \pm 0.02	143 \pm 15	14.0 \pm 3.1	2.0 \pm 0.2	42 \pm 19	1.28 \pm 0.02	31 \pm 3.2	22 \pm 12.1	9 \pm 0.0	44 \pm 3.9	24 \pm 5.0	15 \pm 4.2
MR2	0.17 \pm 0.02	120 \pm 8	11.8 \pm 4.0	2.1 \pm 0.1	26 \pm 6	1.25 \pm 0.04	41 \pm 4.6	28 \pm 8.8	11 \pm 4.4	22 \pm 3.7	20 \pm 1.3	9 \pm 1.2
ML	0.17 \pm 0.01	113 \pm 18	10.0 \pm 4.6	1.8 \pm 0.1	43 \pm 6	1.36 \pm 0.07	37 \pm 4.3	37 \pm 12.8	7 \pm 0.8	7 \pm 5.5	20 \pm 0.8	4 \pm 4.0
TU	0.17 \pm 0.02	107 \pm 23	11.2 \pm 2.8	1.9 \pm 0.2	42 \pm 13	1.48 \pm 0.03	44 \pm 5.7	22 \pm 24.6	4 \pm 2.9	28 \pm 0.8	19 \pm 0.8	6 \pm 0.8
LA1 ^a	0.17 \pm 0.03	90 \pm 33	9.0 \pm 4.3	1.8 \pm 0.1	30 \pm 10	1.10 \pm 0.02	50 \pm 3.1	19 \pm 18.6	6 \pm 0.4	11 \pm 13.6	9 \pm 0.8	6 \pm 0.5
RO1	0.18 \pm 0.05	107 \pm 14	10.2 \pm 2.1	1.8 \pm 0.2	24 \pm 4	1.30 \pm 0.03	17 \pm 2.3	24 \pm 7.1	11 \pm 0.4	26 \pm 10.6	24 \pm 1.4	11 \pm 1.1
TII2	0.18 \pm 0.01	73 \pm 12	9.2 \pm 3.4	1.8 \pm 0.1	25 \pm 12	1.06 \pm 0.03	47 \pm 6.9	9 \pm 1.6	2 \pm 0.8	24 \pm 1.8	27 \pm 2.1	9 \pm 2.6
IC	0.19 \pm 0.01	150 \pm 30	12.3 \pm 2.3	1.8 \pm 0.1	20 \pm 13	1.36 \pm 0.11	63 \pm 12.2	13 \pm 15.6	11 \pm 5.6	35 \pm 5.0	15 \pm 3.2	19 \pm 3.1
TII1	0.19 \pm 0.01	67 \pm 6	9.2 \pm 5.7	1.9 \pm 0.1	16 \pm 3	1.12 \pm 0.04	26 \pm 5.0	7 \pm 0.0	4 \pm 0.0	35 \pm 3.4	22 \pm 1.9	9 \pm 2.2
LA2	0.19 \pm 0.04	63 \pm 8	10.8 \pm 4.0	2.1 \pm 0.2	31 \pm 5	1.17 \pm 0.02	30 \pm 6.0	13 \pm 0.8	9 \pm 0.5	35 \pm 3.5	26 \pm 1.2	7 \pm 1.0
EN ^a	0.20 \pm 0.06	90 \pm 9	10.5 \pm 1.9	2.1 \pm 0.1	35 \pm 11	1.31 \pm 0.02	37 \pm 6.3	17 \pm 5.1	4 \pm 0.0	20 \pm 1.6	24 \pm 1.2	7 \pm 1.2
RO2	0.21 \pm 0.01	90 \pm 15	6.5 \pm 3.2	1.5 \pm 0.2	11 \pm 10	1.14 \pm 0.03	20 \pm 4.5	15 \pm 0.8	6 \pm 0.0	22 \pm 12.1	22 \pm 2.4	6 \pm 1.8
AE	0.22 \pm 0.05	63 \pm 9	9.4 \pm 2.7	2.0 \pm 0.2	18 \pm 10	1.20 \pm 0.07	22 \pm 5.1	19 \pm 6.4	7 \pm 0.4	37 \pm 1.1	13 \pm 0.4	11 \pm 2.3
CA ^a	0.22 \pm 0.02	67 \pm 8	9.3 \pm 3.0	1.8 \pm 0.1	24 \pm 13	1.20 \pm 0.05	35 \pm 5.4	13 \pm 7.9	4 \pm 0.4	26 \pm 1.5	20 \pm 0.4	2 \pm 0.4
RO3 ^a	0.22 \pm 0.05	60 \pm 10	8.3 \pm 2.9	1.8 \pm 0.1	25 \pm 8	1.14 \pm 0.03	15 \pm 4.5	2 \pm 8.0	2 \pm 0.4	26 \pm 1.7	22 \pm 1.5	6 \pm 2.7
MA	0.23 \pm 0.11	60 \pm 7	9.7 \pm 2.6	2.0 \pm 0.1	17 \pm 11	1.30 \pm 0.07	25 \pm 3.9	8 \pm 1.8	3 \pm 1.2	30 \pm 2.4	24 \pm 1.2	16 \pm 2.4
ES	0.26 \pm 0.03	57 \pm 8	7.0 \pm 1.7	1.7 \pm 0.1	17 \pm 4	1.14 \pm 0.04	20 \pm 3.3	2 \pm 0.0	2 \pm 0.0	24 \pm 1.6	20 \pm 0.9	9 \pm 1.5

Fish and coral communities and turbidity

A total of 85 fish species from 32 families were identified. Fish density and species richness had on average low values in turbid waters and higher values under clearer conditions (Table 1). Fish densities

Table 3. Partial correlation coefficients among $K_{d\ PAR}$ and fish variables surveyed in 21 coral reef sites (10 m depth) in La Parguera, southwest Puerto Rico. Bold values correspond to the significant correlations ($p < 0.05$). Trophic guild codes: H = herbivore, Z = zooplanktivore, P = piscivore

	$K_{d\ PAR}$			Fish			Density of trophic guild		
	Density	Species richness	Diversity (H')	H	Z	P	H	Z	P
$K_{d\ PAR}$	-0.69	-0.47	0.01	-0.51	-0.64	-0.58			
Density		0.55	-0.27	0.58	0.52	0.66			
Species richness			0.52	0.46	0.25	0.63			
Diversity (H')				0.12	-0.06	0.1			
H					0.23	0.23			
Z									0.69
P									

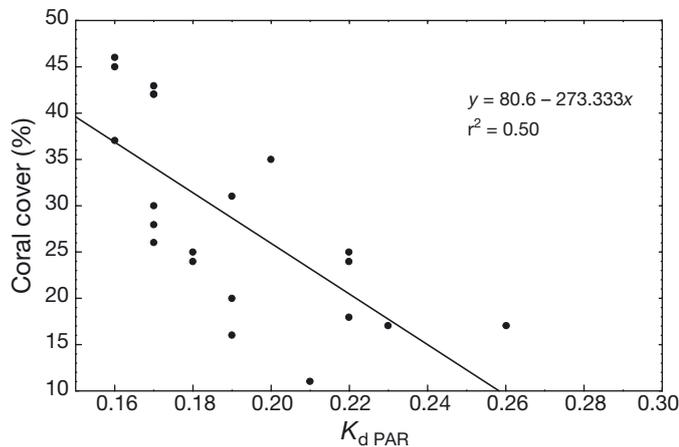


Fig. 3. Relationship between the extinction coefficient of photosynthetic active radiation ($K_{d\ PAR}$) and percent live coral cover at 21 reefs at La Parguera, southwest Puerto Rico

coverage ($y = 0.06 + 0.05x$, $r^2 = 0.44$, $p = 0.001$) (Table 2). Fish species richness ($y = -4.8 + 12.4x$, $r^2 = 0.38$, $p = 0.0031$) and zooplanktivore density ($y = -4.2 + 1.9x$, $r^2 = 0.37$, $p = 0.0033$) were positively related with reef rugosity (Table 2).

Multivariate analysis

The NMS ordination on species composition and abundance converged on a stable, 3-dimensional solution (final stress = 9.46, final instability = 0.000001) and demonstrated greater structure than expected by chance (Monte Carlo procedure, $p = 0.004$) (Fig. 4). The 2 most explanatory ordination axes (3 and 2) were independent (orthogonality = 94%) and explained 81% of the fish assemblage variance, calculated as a proportion of the variation in the reduced matrix relative to that in the original data matrix. Axis

3 represented most of the variance (64%), and the overlay of potentially influential habitat variables showed this axis to be strongly associated with seawater turbidity ($r = 0.62$). Coral cover ($r = 0.59$) and rugosity ($r = 0.21$) were also correlated to this axis. Axis 2, which represented an additional 17% of the ordination variance, was correlated with seawater turbidity ($r = 0.61$), coral cover ($r = 0.51$), and rugosity ($r = 0.46$). Thus, compared with the other variables tested, $K_{d\ PAR}$ had a greater influence on fish composition and abundance. These results

confirmed a negative response of the fish assemblage to high seawater turbidity. The number of fishes and species was lower at turbid sites, located at the lower and right portion of Fig. 4, compared to clear water sites, located at the upper and left end of the figure. Sites with intermediate water turbidity were located between these extremes. Fish species composition

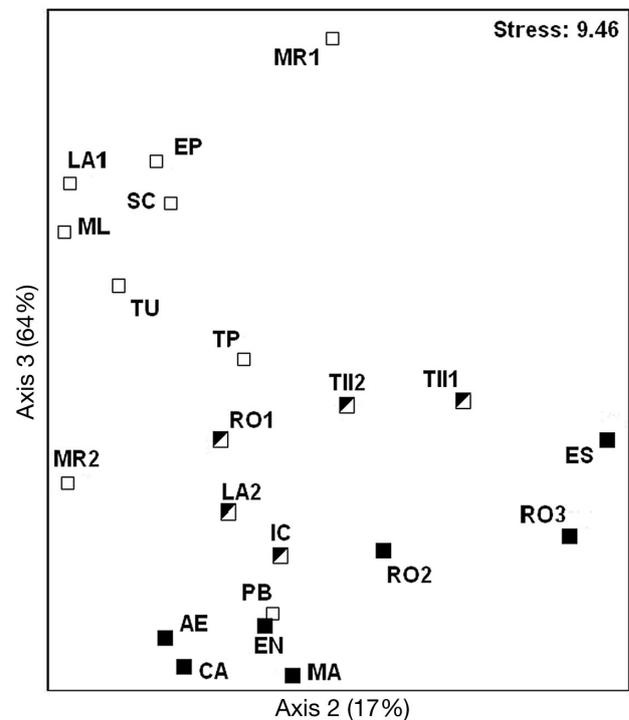


Fig. 4. Non-metric multidimensional scaling plot based on Bray-Curtis similarities of fish assemblages of La Parguera, southwest Puerto Rico, at reef sampling sites with (□) clear ($K_{d\ PAR} \leq 0.17\ m^{-1}$), (◐) intermediate ($K_{d\ PAR} = 0.18$ to $0.19\ m^{-1}$), and (■) turbid seawaters ($K_{d\ PAR} \geq 0.20\ m^{-1}$). See Fig. 1 legend for reef sampling site codes

variation among the different water turbidity types was confirmed (MRPP, $p = 0.002$, $A = 0.20$), with the more dissimilar assemblages being those of clear and turbid waters (MRPP, $p = 0.0007$, $A = 0.27$). Indicator species analysis showed that frequency and abundance of yellowtail damselfish *Microspathodon chrysurus* and bluehead wrasse *Thalassoma bifasciatum* decreased with turbidity, while those of sharknose goby *Elacatinus evelynae* and yellowtail hamlet *Hypoplectrus chlorurus* increased. Based on these results we infer that seawater turbidity was an important environmental parameter in determining the spatial distribution of some reef fishes (Table 4).

DISCUSSION

Our results suggest that seawater turbidity is an important factor affecting ecological processes on coral reefs of La Parguera, as reflected by changes in the composition and abundance of reef fishes and benthic communities. This point is based on the strong negative relations found between $K_{d\text{ PAR}}$ and fish and coral community characteristics, and within the NMS 3-dimensional ordination.

Low values of both the number of fish species and their densities in sites with more turbid water may reflect fish avoiding sites of high turbidity. Coral reefs subject to continuous increases in seawater turbidity can suffer habitat degradation and community shifts (Loya 1976, Reopanichkul et al. 2009). Reef fishes, in particular, may change their community structure and trophic composition in response to water quality degradation (Fabricius et al. 2005, Mallela et al. 2007, Reopanichkul et al. 2009). Thus, high turbidity could affect both ecosystem stability and key properties of the fish assemblage associated to it.

The general pattern of fish abundance decreasing with higher turbidity might result from a different availability of resources that co-vary with turbidity, such as light, sediments, nutrients, and benthic cover. The particular processes that affect turbidity (e.g. sedimentary runoff, eutrophication, colored dissolved organic matter,

Table 4. Species-specific densities (mean number of ind. 100 m^{-2}) of the 10 main fish species found at 21 coral reef sites (10 m depth) in La Parguera, southwest Puerto Rico, ranked in order of increasing turbidity ($K_{d\text{ PAR}}$). See Fig. 1 legend for sampling site codes

Sampling site	$K_{d\text{ PAR}}$	<i>Acanthurus coeruleus</i>	<i>Chromis cyanea</i>	<i>Chromis multilineata</i>	<i>Elacatinus evelynae</i>	<i>Hypoplectrus chlorurus</i>	<i>Halichoeres garnoti</i>	<i>Microspathodon chrysurus</i>	<i>Stegastes fuscus</i>	<i>Stegastes leucostictus</i>	<i>Stegastes partitus</i>	<i>Thalassoma bifasciatum</i>
EP	0.16	4.3	0.0	22.3	1.7	0.7	1.7	6.7	12.3	1.0	9.3	11.0
TP	0.16	1.7	0.7	0.0	5.0	1.7	1.7	0.7	0.0	2.7	5.0	6.0
SC	0.16	14.0	2.7	6.0	6.0	0.7	0.7	5.0	0.7	4.3	13.3	25.7
PB	0.17	0.0	0.0	0.0	5.7	4.0	0.0	0.0	1.7	10.0	2.3	2.3
LA1	0.17	1.0	2.7	22.3	3.3	0.7	1.0	2.7	6.7	0.0	4.0	17.3
ML	0.17	1.0	3.3	34.0	4.0	0.7	0.0	4.3	3.3	2.7	9.0	16.0
MIR1	0.17	9.3	0.0	0.0	0.0	0.0	4.3	5.7	6.7	2.3	7.7	32.3
MIR2	0.17	0.0	0.0	0.0	0.7	0.0	2.3	0.0	0.0	7.7	10.0	6.0
TU	0.17	3.3	2.7	29.3	4.0	1.7	0.7	1.7	1.7	3.3	1.7	2.3
RO1	0.18	0.7	0.0	0.0	3.3	1.0	0.7	0.7	0.0	9.3	0.7	21.0
TH2	0.18	0.0	2.7	0.0	8.7	1.3	0.0	1.3	2.0	4.7	3.3	0.0
IC	0.19	0.7	0.0	0.0	5.7	3.3	0.7	0.0	0.0	5.7	1.7	0.0
LA2	0.19	1.0	0.7	0.0	4.0	0.7	0.7	0.0	1.0	6.0	3.3	4.3
TH1	0.19	0.0	0.0	0.0	8.3	1.0	2.3	0.0	0.0	2.7	4.3	0.0
EN	0.20	1.0	0.0	0.0	9.0	6.0	0.0	0.0	1.0	10.7	1.0	0.0
RO2	0.21	0.0	0.0	0.0	7.7	0.7	0.0	0.0	0.0	8.3	0.7	0.0
AE	0.22	0.0	0.0	0.0	4.3	4.0	0.0	0.0	1.0	3.3	4.0	0.0
CA	0.22	0.0	0.0	0.0	5.7	2.7	0.0	1.0	1.7	5.0	3.3	0.0
RO3	0.22	1.0	0.0	0.0	6.0	1.0	0.0	0.0	0.0	7.7	0.0	0.0
MA	0.23	0.0	0.0	0.0	3.7	5.3	0.0	0.0	0.0	4.3	1.3	0.0
ES	0.26	0.0	0.0	0.0	10.0	0.7	1.7	0.0	0.0	8.3	0.7	0.0

etc.) cannot be identified from this study. However, there is a significant relationship between turbidity and sedimentation in La Parguera (Otero 2009). In addition, if turbidity were mainly caused by nutrients or phytoplankton, greater abundances of herbivore and planktivore fishes would be expected in more turbid sites (Fabricius et al. 2005), opposite to the results of this study. The lower density of herbivores at turbid reefs is in agreement with Wolanski et al. (2003), but in our study it coincides with a lower algal cover in turbid sites compared with that at clear ones (Cardona-Maldonado 2008). Presumably, when turbidity gets too high, productivity and algal cover are reduced and can only support small populations of herbivores. Considering the extensive fishing pressure occurring throughout Puerto Rico (Appeldoorn et al. 1992, Appeldoorn 2008), overfishing is a probable explanation for the lack of correlation between turbidity and fish density observed in piscivores, mobile invertebrate feeders, omnivores, and sessile invertebrate feeders. These groups were scarce, and represent the snappers, groupers, grunts and jacks, which are the largest and most targeted species in the area (Matos-Caraballo 2004). Nevertheless, the limited area covered by each transect (30 m²) also contributed to this result because these species are patchily distributed and not likely to be encountered along the transect.

As with several other reef studies, turbidity was found to be negatively related with percent coral cover (Loya 1976, Reopanichkul et al. 2009) and, although with more variability, rugosity also tended to decrease with higher turbidity. The loss of reef structure because of turbidity is a long process that depends on the strength and duration of exposition. Even when coral cover decreases, reef framework can persist long after the death of corals. All this has potential ramifications over the short and long term, since both fish species richness and zooplanktivore density were significantly correlated with percent coral cover and rugosity, both of which are dependent upon coral growth or loss (Table 3). Losses in live coral and structural complexity are well documented to cause losses in fish diversity and abundance (Luckhurst & Luckhurst 1978, McCormick 1994, Wilson et al. 2006); however separating their effects is complicated because most live corals usually possess high structural complexity. When live coral cover is lost many fish species decline in abundance due to loss of settlement habitat and habitat structural complexity (Munday et al. 2008). Therefore, in conclusion, the variations in coral cover and rugosity observed in this study, which may or may not be

independent or co-vary with seawater turbidity, affected reef fish assemblages.

The NMS ordination highlighted turbidity as a major factor shaping reef fish communities in La Parguera, followed by coral cover and reef rugosity. This ordination showed a general tendency towards reduced fish density and species richness as turbidity increased and coral cover and reef rugosity decreased. A more specific analysis of this trend found 4 species as the main ones responsible for the observed differences: the bluehead wrasse, yellowtail damselfish, sharknose goby, and yellowtail hamlet. The first 2 were more abundant in clear water reefs and seemed to avoid sites with high turbidity, while the latter 2 were more abundant in turbid water reefs. In agreement with these results, the bluehead wrasse and yellowtail damselfish were previously reported to be common in reefs farthest from land in La Parguera, which have clearer waters, and the yellowtail hamlet to be more abundant in the nearshore reefs (McGehee 1994), which are more turbid. In addition, bluehead wrasse and damselfishes were reported to decrease in abundance when water quality or live coral cover diminish (González-Sanson & Aguilar 2010).

We identified seawater turbidity as an additional predictor of the reef fish community structure in La Parguera, in addition to live coral cover and reef rugosity. Because coral reefs and reef fish communities were less complex (lower rugosity, less species richness, less diversity) in more turbid sites, managing for clear water conditions within the coastal area of La Parguera should lead to improved ecosystem health through increases in diversity, resilience and stability (Walker & Salt 2006), and should become a primary goal of management. As the attenuation coefficients of light can be measured from boats and even satellites (e.g. MODIS Kd 490 product) (Wang et al. 2009), the relationships between water optical properties and coral reef and fish community parameters reported in this study may be used to monitor changes in water quality as a precursor of change in coral and reef fish communities, as well as to identify problem areas and efficiently monitor progress toward management goals (clear water).

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LITERATURE CITED

- Amesbury SS (1981) Effects of turbidity on shallow-water reef fish assemblages in Truk, Eastern Caroline Islands. Proc 4th Int Coral Reef Symp, Manila 1:155–159
- Appeldoorn RS (2008) Transforming reef fisheries management: application of an ecosystem-based approach in the USA. *Caribb Environ Conserv* 35:232–241
- Appeldoorn RS, Beets J, Bohnsack J, Bolden S, Matos D, Mayers S, Rosario A, Sadovy Y, Tobias W (1992) Shallow water reef fish stock assessment for the US Caribbean. NOAA Tech Mem NMFS-SEFSC-304
- Brock RE (1954) A preliminary report on a method of estimating reef fish populations. *J Wildl Manag* 18: 297–308
- Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proc Natl Acad Sci USA* 105: 16201–16206
- Cardona-Maldonado MA (2008) Assessment of coral reef community structure using water optical properties. MS dissertation, University of Puerto Rico, Mayaguez, PR
- Ceccarelli DM, Jones GP, McCook LJ (2001) Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. *Oceanogr Mar Biol Annu Rev* 39:355–389
- Cohen JE (2003) Human population: the next half century. *Science* 302:1172–1175
- Ewel JJ, Whitmore JL (1973) The ecological life zones in Puerto Rico and the US Virgin Islands. USDA Forest Service, Institute of Tropical Forestry, Rio Piedras, PR
- Fabricsius K, De'ath G, McCook L, Turak E, Williams DM (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Mar Pollut Bull* 51:384–398
- Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *J Exp Mar Biol Ecol* 224:1–30
- Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960
- González-Sansón G, Aguilar C (2010) Reef fish diversity components as indicators of cumulative effects in a highly impacted fringe reef. *Ecol Indic* 10:766–772
- Harmelin-Vivien H (1992) Impact of human activities on coral reef fish communities in French Polynesia. *Cybiurn* 16:279–289
- Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. *Trends Ecol Evol* 25:633–642
- Järvenpää M, Lindström K (2004) Water turbidity by algal blooms causes mating system breakdown in a shallow water fish, the sand goby *Pomatoschistus minutus*. *Proc Biol Sci* 271: 2361–2365
- Kendall MS, Monaco ME, Buja KR, Christensen JD, Kruer CR, Finkbeiner M, Warner RA (2001) Methods used to map the benthic habitats of Puerto Rico and the US Virgin Islands. www.ccma.nos.noaa.gov/products/biogeography/usvi_pr_mapping/manual.pdf
- Kuffner I, Brock J, Grober-Dunsmore R, Bonito V, Hickey T, Wright C (2007) Relationships between reef fish communities and remotely sensed rugosity measurements in Biscayne National Park, Florida, USA. *Environ Biol Fishes* 78:71–82
- Leahy SM, McCormick MI, Mitchell MD, Ferrari MCO (2011) To fear or to feed: the effects of turbidity on perception of risk by a marine fish. *Biol Lett* 7:811–813
- Levin PS (1993) Habitat structure, conspecific presence, and spatial variation in the recruitment of a temperate reef fish. *Oecologia* 94:176–185
- Lewis AR (1997) Effects of experimental coral disturbance on the structure of fish communities on large patch reefs. *Mar Ecol Prog Ser* 161:37–50
- Loya Y (1972) Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Mar Biol* 13:100–123
- Loya Y (1976) Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. *Bull Mar Sci* 26:450–466
- Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Mar Biol* 49:317–323
- Ludwig JA, Reynolds JF (1988) *Statistical ecology: a primer on methods and computing*. Wiley, New York, NY
- Mallela J, Roberts C, Harrod C, Goldspink CR (2007) Distributional patterns and community structure of Caribbean coral reef fishes within a river-impacted bay. *J Fish Biol* 70:523–537
- Matos-Caraballo D (2004) Puerto Rico/NMFS Cooperative Fisheries Statistics Program. April 2001–March 2004. Final report to the National Marine Fisheries Service, NOAA. Fisheries Research Laboratory, Department of Natural and Environmental Resources, San Juan, PR
- McCormick MI (1994) Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Mar Ecol Prog Ser* 112:87–96
- McCune B, Mefford M (2006) PC-ORD. Multivariate analysis of ecological data. Version 5.0. MjM Software, Gleneden Beach, OR
- McGehee MA (1994) Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. *Mar Ecol Prog Ser* 105:243–255
- Meager JJ, Solbakken T, Utne-Palm AC, Oen T (2005) Effects of turbidity on the reactive distance, search time, and foraging success of juvenile Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 62:1978–1984
- Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. *Ecol Econ* 29:215–233
- Morelock J, Ramirez WR, Bruckner AW, Carlo M (2001) Status of coral reefs, southwest Puerto Rico. *Carib J Sci Special Pub* 4
- Mumby PJ (2006) The impact of exploiting grazers (Scariidae) on the dynamics of Caribbean coral reefs. *Ecol Appl* 16:747–769
- Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for coral reef fishes. *Fish Fish* 9:261–285
- Otero E (2009) Spatial and temporal patterns of water quality indicators in reef systems of southwestern Puerto Rico. *Caribb J Sci* 45:168–180
- Randall JE (1967) Food habits of reef fishes of the West Indies. *Stud Trop Oceanogr* 5:665–847
- Reopanichkul P, Schlacher TA, Carter RW, Worachananant S (2009) Sewage impacts coral reefs at multiple levels of ecological organization. *Mar Pollut Bull* 58:1356–1362
- Risk W (1972) Fish diversity on a coral reef in the Virgin Islands. *Atoll Res Bull* 153:1–6
- Rogers CS (1983) Sublethal and lethal effects of sediments applied to common Caribbean Reef corals in the field.

- Mar Pollut Bull 14:378–382
- Ryan KE, Walsh JP, Corbett DR, Winter A (2008) A record of recent change in terrestrial sedimentation in a coral-reef environment, La Parguera, Puerto Rico: A response to coastal development? Mar Pollut Bull 56:1177–1183
- Souter D, Linden O (2000) The health and future of coral reef systems. Ocean Coast Manag 43:657–688
- Syms C, Jones GP (2000) Disturbance, habitat structure, and the dynamics of a coral reef fish community. Ecology 81: 2714–2729
- Walker B, Salt D (2006) Resilience thinking: sustaining ecosystems and people in a changing world. Island Press, Washington, DC
- Wang M, Son S, Harding LW Jr (2009) Retrieval of diffuse attenuation coefficient in the Chesapeake Bay and turbid ocean regions for satellite ocean color applications. J Geophys Res 114:C10011, doi:10.1029/2009JC005286
- Warne AG, Webb RMT, Larsen MC (2005) Water, sediment, and nutrient discharge characteristics of rivers in Puerto Rico, and their potential influence on coral reefs. US Geological Survey Scientific Investigations Report 2005-5206, Reston, VA
- Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Glob Change Biol 12:2220–2234
- Wolanski E, Richmond R, McCook L, Sweatman H (2003) Mud, marine snow and coral reefs. Am Sci 91:44–51

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