Coral Reefs (2010) 29:277–288
DOI 10.1007/s00338-009-0582-9

REPORT

Reef habitats and associated sessile-benthic and fish assemblages across a euphotic–mesophotic depth gradient in Isla Desecheo, Puerto Rico

Jorge R. Garcia-Sais

Received: 15 April 2009 / Accepted: 27 December 2009 / Published online: 7 February 2010

Abstract Quantitative surveys of sessile benthos and fish populations associated with reef habitats across a 15–50 m depth gradient were performed by direct diver observations using rebreathers at Isla Desecheo, Puerto Rico. Statistically significant differences between depths were found for total live coral, total coral species, total benthic algae, total sponges and abiotic cover. Live coral cover was higher at the mid-shelf (20 m) and shelf-edge (25 m) stations, whereas benthic algae and sponges were the dominant sessile-benthic assemblage at mesophotic stations below 25 m. Marked shifts in the community structure of corals and benthic algae were observed across the depth gradient. A total of 119 diurnal, non-cryptic fish species were observed across the depth gradient, including 80 species distributed among 7,841 individuals counted within belt-transects. Fish species richness was positively correlated with live coral cover. However, the relationship between total fish abundance and live coral was weak. Abundance of several numerically dominant fish species varied independently from live coral cover and appeared to be more influenced by depth and/or habitat type. Statistically significant differences in the rank order of abundance of fish species at euphotic vs mesophotic stations were detected. A small assemblage of reef fishes that included the cherubfish, *Centropyge argi*, sunshine chromis, *Chromis insolata*, greenblotch parrotfish, *Sparisoma atomarium*, yellowcheek wrasse, *Halichoeres cyanocephalus*, sargassum triggerfish, *Xanthichthys ringens*, and the longsnout butterflyfish, *Chaetodon aculeatus* was most abundant or only present from stations deeper than 30 m, and thus appear to be indicator species of mesophotic habitats.

Keywords Mesophotic · Fishes · Corals · Puerto Rico · Isla Desecheo · Caribbean

Introduction

Characterizations of reef habitats and associated sessile-benthic and fish communities at depths between 30 and 100 m (mesophotic) are rare in the Caribbean, and mostly available from submersible surveys. Colin (1974, 1976) described the taxonomic composition of reef fishes at depths between 90 and 305 m off the coasts of Jamaica, Belize and the Bahamas as a mixed assemblage of shallow reef (<30 m) and true "deep-reef" species seldom present shallower than 50 m. Colin (1974) argued that the vertical distribution of some reef fish species was more related to habitat features than depth, and noted ontogenetic trends in the vertical distribution of "deep-reef" species, where juvenile stages were typically observed at shallower depths than adults. In Puerto Rico, the Seward Johnson– Sea Link submersible survey (Nelson and Appeldoorn 1985) provided a qualitative characterization of benthic habitats and associated fishes of the insular slope, encompassing depths between 100 and 1,250 m. Despite observations of a "rich and highly complex" reef fish community associated with the upper insular slope (30–100 m), these habitats were left virtually undescribed by the Seward Johnson—Sea Link survey.

Communicated by Guest Editor Dr. John Marr

J. R. Garcia-Sais (✉)
Department of Marine Sciences, University of Puerto Rico,
Mayaguez, Puerto Rico
e-mail: goingdeep49@gmail.com

J. R. Garcia-Sais
P. O. Box 3424, Lajas 00667, Puerto Rico

Mesophotic coral ecosystems (MCEs) are characterized by the presence of light-dependent corals and associated communities that are typically found at depths between 30 and 150 m in tropical and subtropical regions (Hinderstein et al. 2010). Quantitative assessments of reef substrate cover by sessile-benthic communities from mesophotic reef habitats in the Caribbean include the autonomous underwater vehicle (AUV) surveys of the La Parguera shelf-edge (Singh et al. 2004) and the Marine Conservation District (MCD) coral reef system located south of St. Thomas, USVI (Armstrong et al. 2006). Menza et al. (2007) reported on coral taxonomic composition, percent substrate cover, and recent degradation of a mesophotic coral reef system (MSR-1) on the outer shelf south of St. Croix, USVI using video and still-camera images dropped from the NOAA R/V Nancy Foster. The aforementioned studies identified major differences of sessile-benthic community structure associated with the various mesophotic habitat types and depth gradients, but lacked inferences about their reef fish communities. Beets and Friedlander (1997) and Nemeth (2005) conducted quantitative surveys of the red hind (*Epinephelus guttatus*) population within the MCD, a known spawning aggregation site for this species. These studies provided a baseline and an assessment of the effectiveness of the closed fishing regulation for the recovery of the red hind population within the MCD, but do not include information on fish–habitat associations for other species. A more general description of the fish community at the MCD from AGRRA surveys is available from Nemeth et al. (2008).

García-Sais et al. (2004) performed a survey of non-cryptic reef fish abundance and sessile-benthic substrate cover measurements from Black Jack Reef, a mesophotic coral reef in the south coast of Vieques Island. Most of the 54 fish species observed within a depth range of 30–40 m were common shallow (<30 m) reef species previously reported from reefs systems surveyed by García-Sais et al. (2004) within the neritic shelf of Vieques Island. Notable exceptions to the shallow reef assemblage were the presence of adult tiger groupers (*Mycteroperca tigris*) and mutton snappers (*Lutjanus analis*). Recent surveys of fish communities associated with mesophotic reefs in Puerto Rico have highlighted the relevance of these systems as habitats for large groupers and snappers and proposed management alternatives for their protection (García-Sais et al. 2005a, 2007). From diver visual surveys and ichthyocide collections, Dennis et al. (2005) reported 111 fish species from reef sites in Mona Passage, including 32 from depths below 30 m at Mona Island. They proposed that the relatively impoverished ichthyofauna, compared to the mainland Puertorrican shelf reflects the limited habitat diversity of the island, and the “imperfect filtering” effect of the oceanic (Mona) passage on ichthyofaunal connectivity between islands.

In this paper, I describe variations of the sessile-benthic coral community and associated non-cryptic fish assemblages surveyed by direct diver observations using rebreathers along a euphotic-mesophotic gradient encompassing depths from 15 to 50 m off the shelf and upper insular slope of Desecheo Island, in Mona Passage, Puerto Rico. Although sampling stations in the 15–25 m range here examined are out of the MCE as defined range (Hinderstein et al. 2010), the comparative analysis with mesophotic stations provides direct inferences of upper insular slope habitats at the upper limit of MCEs as a transitional ecological zone of coral reef communities.

Materials and methods

During 2004–2005, Desecheo was selected as the site for two independent studies directed to provide a quantitative assessment of the reef benthic and non-cryptic fish community structure from mesophotic habitats of the upper insular slope down to 50 m (García-Sais et al. 2005a), and to monitor coral reef communities within the insular shelf from previously established permanent transects (García-Sais et al. 2005b). Both studies were performed by the same field survey team using Inspiration rebreathers.

Study site

Desecheo (Figs. 1, 2) is an oceanic island in Mona Passage, located approximately nine nautical miles off Rincón, northwest coast of Puerto Rico. The island that used to be a US Navy shooting range during World War II was designated as a Natural Reserve in 1999. Marine communities of Desecheo are influenced by clear waters, strong currents, and seasonally high wave action from North Atlantic winter swells. Coral reefs are established off the west and southwest coasts at depths between 15 and (at least) 70 m. Shallow coral reef community surveys were performed at depths of 15, 20 and 25 m within the Puerto Botes/Puerto Canoas reef system of the main insular shelf platform in the southwest coast. The survey of Agelas mesophotic reef system (García-Sais et al. 2005a) included stations at 30 and 40 m down a steep slope (wall) and at 50 m on a gently sloping terrace of the insular slope (Fig. 2).

Sessile-benthic reef communities

At depths of 15, 20 and 25 m reef sessile-benthic communities were characterized from existing sets of 5–10 m long permanent transects at each station as part of the sampling protocol of the Puerto Rico Coral Monitoring

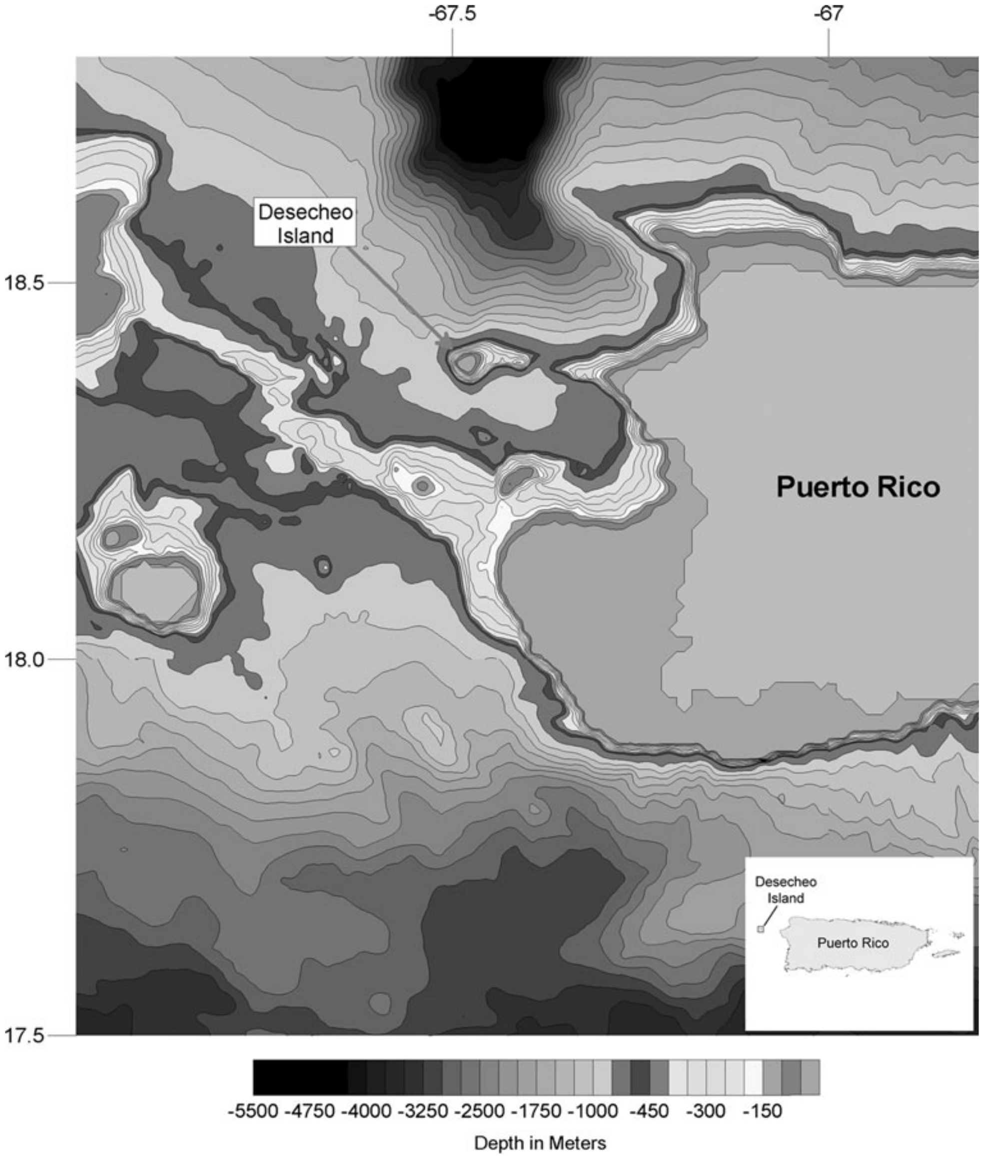


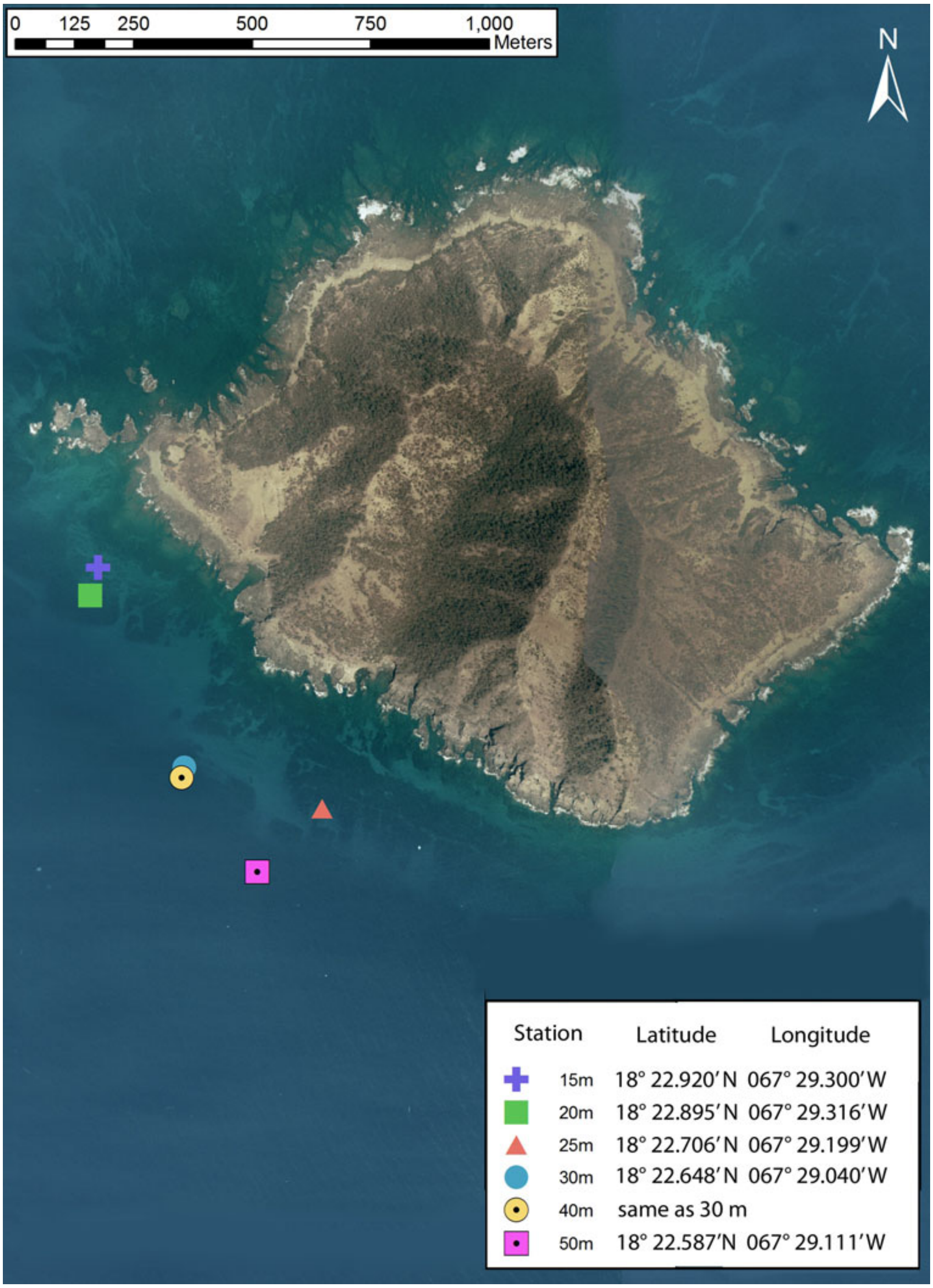
Fig. 1 General bathymetry map of Mona Passage showing location of study site at Isla Desecheo, west coast of Puerto Rico

Program sponsored by NOAA and administered by the PR Department of Natural and Environmental Resources (PRDNER) since 1999 (García-Sais et al. 2005b). Data on percent substrate cover by sessile-benthic categories was produced by the continuous intercept chain-link method (CARICOMP 1994), as modified from Porter (1972).

At depths of 30, 40 and 50 m the percent substrate cover by reef sessile-benthic categories was measured from sets of 5–10 m long permanent transects established during this study as baseline for future monitoring activities. Digital videos of each transect were taken maintaining constant lens to reef substrate distances. A total of 10 non-overlapping digital video images were analyzed from each transect using the Coral Point Count software v.3.2 (García-Sais et al. 2005a). Common and scientific names of sessile-benthic organisms here reported follow the identification guides of Humann and Deloach (2003), except for *Montastraea annularis*, which is here reported as a species complex.

Reef fish surveys

Diurnal, non-cryptic fish species present within three meters from the reef substrate were surveyed by a set of five replicate belt-transects at each station (depth). Transects were centered over the reference line of transects used for benthic community characterizations, producing five survey areas of 30 m^2 (10 m long x 3 m wide) at each station. Fish species saturation curves were prepared and showed that more than 90% of all species were reached by the fifth transect at all stations (García-Sais et al. 2005a). Each transect was surveyed during 12–15 min. A survey



	Station	Latitude	Longitude
✚	15m	18° 22.920′N	067° 29.300′W
🟩	20m	18° 22.895′N	067° 29.316′W
▲	25m	18° 22.706′N	067° 29.199′W
●	30m	18° 22.648′N	067° 29.040′W
⊙	40m	same as 30 m	
⊡	50m	18° 22.587′N	067° 29.111′W

Fig. 2 Aerial photograph of Desecheo Island showing location of sampling stations, geographic coordinates and depth. Station coordinates here reported correspond to the start of transect 3, at the midpoint of the transect sequence for all stations

protocol in which groups of fish species were counted in sequence was followed to minimize diver avoidance/attraction bias (García-Sais et al. 2005a). Common and scientific names of fishes here reported followed the identification guides of Humann and Deloach (2006).

Data analysis

Variations with depth of the percent reef substrate cover by sessile-benthic categories (e.g., total live coral, total benthic algae, total sponges, total abiotic) and total fish abundance and species richness were analyzed with one-way ANOVAs and Tukey's multiple mean comparison procedures after checking for normality using the Shapiro-Wilks normality test. Variations of fish abundance with depth for numerically dominant species were tested using ANOVAs and Tukey's multiple mean comparison procedures after (ln +1) transformation. Patterns of benthic habitat and ichthyofaunal similarities between depths were examined using a non-metric multidimensional scaling (MDS) procedure on the data of percent substrate cover by benthic categories and fish abundance from replicate transects (5) at each depth. Double standardization of the fish abundance data was performed to smooth the effects of numerically dominant species with highly aggregated spatial distributions. Data ordination was based on Bray-Curtis Euclidean distances. ANOSIM and SIMPER routines in the PRIMER statistical package were used to analyze similarities of benthic and fish community structure between depths, and to identify relevant species contributions to similarity/dissimilarity percentages within and between depths. Lloyd's Patchiness Index (1967) was used to describe dispersion patterns of numerically dominant fish species from stations surveyed. Patchiness (P) was calculated as $\mathrm{P} = [\mathrm{S}^2 - \mathrm{X})/\mathrm{X}^2$, where S^2 = variance of abundance at each depth, and X = meanabundance at each depth.

Results

Reef sessile-benthic community structure

Variations of mean substrate cover by the principal benthic categories at different depths surveyed off Desecheo are presented in Fig. 3. Statistically significant differences between depths were found for total live coral ($F_{5,24} = 70.4$, $P < 0.001$), total coral species ($F_{5,24} = 6.4$, $P < 0.001$), total benthic algae ($F_{5,24} = 14.8$, $P < 0.001$), total sponges ($F_{5,24} = 50.5$, $P < 0.001$) and abiotic cover ($F_{5,24} = 42.4$, $P < 0.001$). Live coral cover peaked at shelf stations 25 and 20 m with means of 48.1 and 47.2%, respectively. Mesophotic reef stations at the slope wall 30 m and deeper presented means of live coral cover ranging between 6.0 and 9.2, significantly lower than euphotic stations within the shelf (Fig. 3). Massive corals of *Montastraea* spp., particularly *M. annularis* (complex) were the dominant coral assemblage down to 40 m, representing from 32.9 to 69.5% of the total cover by corals at those stations (Fig. 4). At 50 m, *Montastraea* spp. declined to approx 6.1% of the total cover by corals, whereas the *Agaricia lamarcki/grahamae* complex exhibited their peak cover (mean: 6.0%), representing 68.3% of the total cover by corals at 50 m. Although not measured, it was visually evident that *Agaricia* spp. were the predominant coral assemblage down to a depth of at least 60 m.

In contrast to the observed decline of reef substrate cover by corals, sponges exhibited an opposite pattern of increasing cover with depth (Fig. 3). A sharp increment of substrate cover by sponges was measured at 30 m relative to insular shelf stations. Peak substrate cover by sponges was reached at the two deepest stations surveyed (e.g., 40 and 50 m). Large branching sponges, mostly *Agelas conifera*, *A. clathrodes* and *Aplysina* spp. typically grew attached to relatively small corals, creating sponge-coral bioherms that were observed to function as habitat for juvenile fishes (*Chromis cyanea*, *C. insolata*, *Clepticus parrae*) and invertebrates. Basket sponges, *Xestospongia muta* were common throughout the depth range, including both euphotic and mesophotic stations.

Benthic algae presented higher reef substrate cover at both ends of the depth gradient, peaking at 15 m and at 50 m (Fig. 3). Minimum cover by benthic algae was associated with the 20 and 25 m stations, which had the

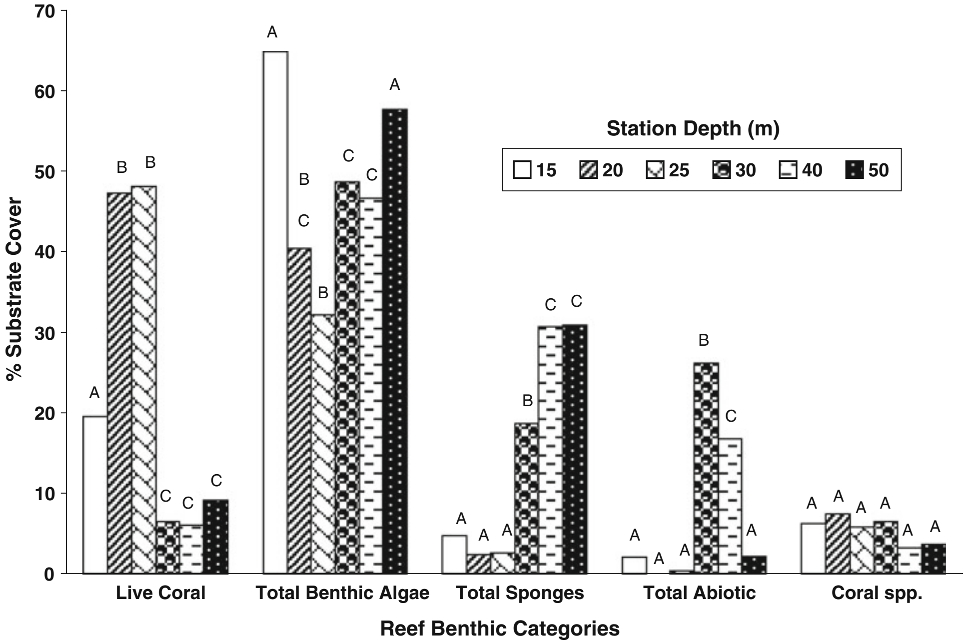


Fig. 3 Mean percent substrate cover by the main reef sessile-benthic categories surveyed across a 15–50 m depth gradient from Isla Desecheo during 2004–2005. *Letter* changes over *bars* identify statistically significant differences (One-way ANOVA; $P < 0.001$) between depths for the various benthic categories

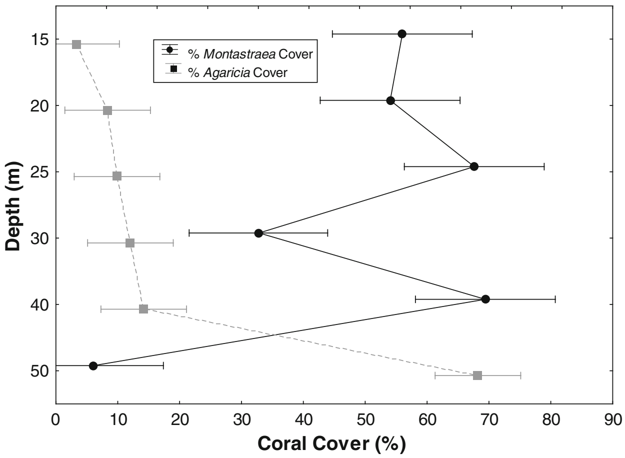


Fig. 4 Variations of the mean percent composition of *Montastraea* spp. and *Agaricia* spp. corals into the total substrate cover by live corals at reef stations surveyed across a 15–50 m depth gradient in Isla Desecheo

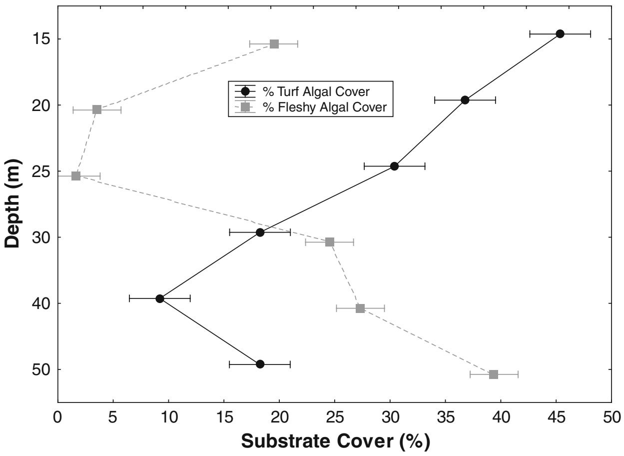


Fig. 5 Variations of the percent cover by turf and fleshy macroalgae at reef stations surveyed across a 15–50 m depth gradient in Isla Desecheo

highest live coral cover. The taxonomic structure of benthic algae across the depth gradient was characterized by a contrasting pattern of turf and fleshy algae. Turf algae, comprised by a mixed assemblage of short red and brown macroalgae growing as a carpet over reef hard substrates exhibited a pattern of declining cover with depth (Fig. 5). Conversely, fleshy macroalgae, largely comprised of encrusting *Lobophora variegata* increased sharply with depth. At 50 m, *L. variegata* represented 69.6% of the total cover by benthic algae and was observed growing as a dense carpet over a vast deposit of algal nodules, or rhodoliths (Ballantine et al. 2008).

Abiotic cover by reef substrate categories included sand, gravel, and coral rubble. Reef stations at 30 m and 40 m in the slope wall presented significantly higher abiotic cover than other reef stations along the depth gradient (Fig. 3). Active transport of sand from the shelf down the slope wall was evidenced by a sandy plain fringing the base of the wall that produced a “rise” of slope inclination. Abiotic cover was less than 3% at 50 m. Minimum abiotic cover (<1%) was measured from the 20 and 25 m stations.

Mesophotic stations 30, 40, and 50 m, and euphotic stations 15, 20, and 25 m exhibited the maximum dissimilarity within the depth gradient examined (Fig. 6). Differences of benthic community structure between euphotic and mesophotic stations were statistically significant for all pairwise comparisons (ANOSIM; $r > 0.867$; $P < 0.001$). Mesophotic stations 30 and 40 m and euphotic stations 15, 20, and 25 m were not significantly different from each other (ANOSIM; $r < 0.867$, $P > 0.001$). Station 50 m was significantly different from all other stations in the gradient (ANOSIM; $r > 0.95$, $P < 0.001$). From the analysis of similarity percentages (SIMPER), substrate cover by fleshy algae, sponges and abiotic categories combined for more than 69% of the cumulative similarity at mesophotic stations, whereas cover by live corals and turf algae combined for more than 70% of the cumulative similarity at euphotic stations. Substitution of abiotic cover for turf algae at 50 m separated this station from other mesophotic stations in terms of community structure similarities.

Reef fish community structure

A total of 80 diurnal, non-cryptic fish species distributed among 7,841 individuals were identified within belt-transects across the depth gradient. In addition, another 39 fish species were observed outside transect areas (García-Sais et al. 2005a, b). Thus, the quantitative fish data base from belt-transects here analyzed represents approximately 67% of the total non-cryptic fish species identified within the study area. Reef species observed outside transect areas include mid-water pelagics (jacks, mackerels, sharks, barracudas), large demersals that avoid divers (large groupers and snappers), and demersals that occur in very low abundance and/or are semi-cryptic (moray eels, blennies, small basses, hamlets, etc.). An assemblage of 42 species accounted for more than 99.5% of the total fish abundance within belt-transects (Table 1). At any given station, 12 species or fewer accounted for more than 90% of the total fish abundance. Sixteen species were present within belt-transects across the entire depth range (all six stations), and another 12 were present in at least 5 of the 6 stations surveyed. A total of 66 fish species were observed from mesophotic depths 30–50 m, including 51 within belt-transects.

A non-metric, resemblance plot of Bray-Curtis similarities based on the rank order of fish abundance from belt-transects is presented in Fig. 7. Fish assemblages from

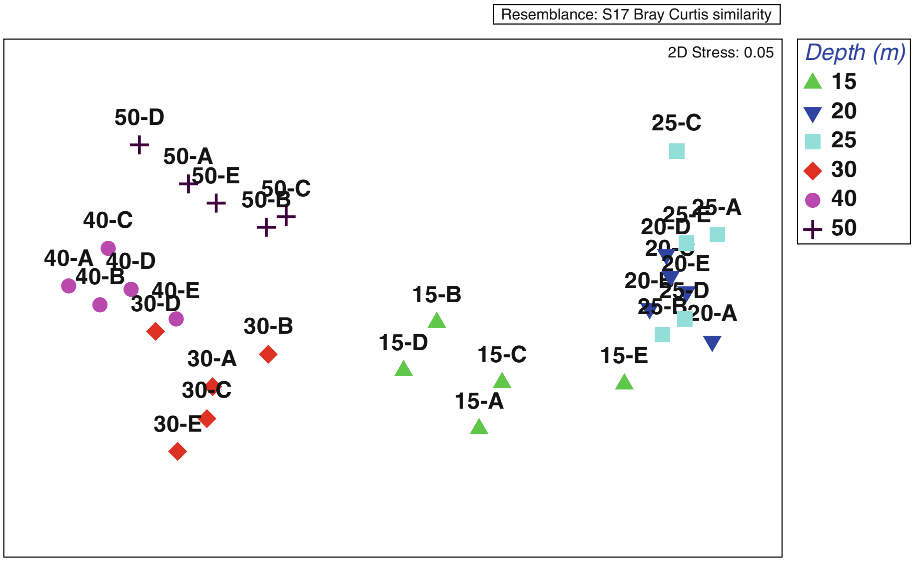


Fig. 6 Non-metric, multidimensional scaling (MDS) plot of Bray Curtis similarities based on the percent substrate cover by sessile-benthic categories (live coral, turf algae, fleshy algae, sponges, abiotic) from sets of five replicate line transects surveyed at six stations encompassing a 15–50 m depth gradient in Isla Desecheo. Primer statistical package

mesophotic stations 30, 40, 50 m were dissimilar from those of euphotic stations 15, 20, and 25 m (ANOSIM, $r > 0.87$; $P < 0.01$). Differences were not significant between stations 15 and 20 m, and between 30 and 40 m (ANOSIM, $r > 0.87$; $P < 0.001$). Stations 15 and 20 m presented the highest similarity, sharing the three most abundant species (*Chromis cyanea*, *Thalassoma bifasciatum*, *Stegastes partitus*), and 10 of the top 15 from each station (Table 1). Dissimilarity between shelf stations 15–20 m and mesophotic stations was mostly contributed by differences in rank abundance of Clown and Bluehead wrasses, *Halichoeres maculipinna* and *Thalassoma bifasciatum*, Yellowtail Damselfish, *Microspathodon chrysurus*, and Blue Tang, *Acanthurus coeruleus*. Schoolmaster and mahogany snappers (*Lutjanus apodus*, *L. mahogany*), respectively were observed to be the most common demersal predators from shelf stations.

Slope wall stations 30 and 40 m presented the second highest similarity between stations sharing the three most abundant species (*C. cyanea*, *Clepticus parrae*, *Coryphopterus personatus*) and 15 of the top 20 from each station (Table 1). *Paranthias furcifer*, *Serranus tigrinus*, *Coryphopterus personatus*, *C. glaucofraenum*, *C. insolata*, *Epinephelus guttatus* and *Xanthichthys ringens* were the main taxa contributing to ichthyofaunal dissimilarity between slope wall and shelf stations. *Mycteroperca venenosa*, *E. guttatus* and *Balistes vetula* were among the most common top demersal predators at slope wall stations.

Reef fish assemblages at stations 25 m and 50 m were significantly different from all other stations in the gradient (ANOSIM, $r > 0.87$; $P < 0.001$). Station 25 m was numerically dominated by *C. personatus*, *Gramma loreto* and *C. lipernes*, all of which exhibited peak abundances at 25 m. In addition to the aforementioned species, *Balistes vetula*, *Lactophrys triqueter*, *Melichthys niger*, *Mulloides martinicus*, *Neoniphon marianus*, and *Liopropoma rubre* contributed markedly to dissimilarity from other stations (Table 1). Large demersal predators, such as *E. striatus and M. venenosa* were observed in higher numbers at 25 m than at other stations. These species were generally observed within the large and irregular *Montastraea* coral buildups and appeared to be using these structures as residential habitat.

Station 50 m presented the highest ichthyofaunal dissimilarity to other stations within the depth gradient. The assemblage of *Centropyge argi*, *Chaetodon aculeatus* and *Sparisoma atomarium* contributed the highest dissimilarity (SIMPER). *Centropyge argi* and *S. atomarium* were only observed within transects at mesophotic stations (30, 40, and 50 m). *Chaetodon aculeatus*, although also present at stations 20 and 25 m, ranked highest (8th) at station 50 m. Other species observed only from mesophotic stations include *C. insolata*, and *Halichoeres cyanocephalus*. Large demersal predators, such as *M. venenosa* and *Ginglymostoma cirratum* were observed foraging or transient at 50 m. There were no reef structures large enough to serve as residential habitats for large demersal fishes at 50 m. The queen triggerfish, *Balistes vetula* was the only mid-size demersal predator consistently observed at 50 m.

Total fish abundance and species richness peaked at the outer shelf station 25 m with means of 443.2 Ind/transect and 32.2 spp/transect (Fig. 8). Statistically significant differences were found between depths for total fish abundance (ANOVA; $F_{5,24} = 10.8$; $P = 0.0002$) and species richness (ANOVA; $F_{5,24} = 21.2$, $P < 0.001$). Both abundance and species richness were significantly lower at the deepest mesophotic station 50 m relative to all other stations surveyed. All of the numerically dominant fish

Table 1 Rank order of the 20 most abundant fish species surveyed within belt-transects across a 15–50 m depth gradient off Desecheo Island during 2004–2005

Fish species	Sampling stations (Depths, m)					
	15	20	25	30	40	50
Acanthurus coeruleus	16	12				
Amblycirrhitus pinos	10	10	15			11
Canthigaster rostrata						17
Centropyge argi						5
Cephalopholis cruentatus		14	15		19	20
Cephalopholis fulva	8	12		13	13	9
Chaetodon aculeatus					19	8
Chromis cyanea	1	1	4	1	1	2
Chromis insolata				14	4	4
Chromis multilineata	4	7	5	9		15
Clepticus parrae			6	2	3	
Coryphopterus glaucofraenum				6	5	
Coryphopterus lipernes	7	4	3	11	11	3
Coryphopterus personatus		8	1	4	2	6
Epinephelus guttatus					19	13
Elacatinus sp.	6	5	9	10	16	
Gramma loreto	13	6	2	5	6	15
Halichoeres garnoti	5	9	8	7	8	10
Halichoeres maculipinna	9	14	14			
Holacanthus tricolor					16	20
Holocentrus rufus	18			18	9	
Kyphosus bermudensis			12			
Lutjanus apodus	16		17			
Melichthys niger	12					
Microspathodon chrysurus	13	11				
Mulloides martinicus			11			
Myripristis jacobus		17				
Neoniphon marianus			17			
Opistognathus aurifrons				20		
Paranthias furcifer				12	11	
Pseudupeneus maculatus				15		
Scarus iserti	16	17			19	11
Serranus tigrinus					17	15
Sparisoma aurofrenatum	11	14	17	18	19	17
Sparisoma atomarium						14
Sparisoma radians	18	17	13			
Sparisoma viride	18					
Stegastes partitus	2	3	10	3	7	1
Stegastes planifrons		17				
Thalassoma bifasciatum	3	2	7	8	10	7
Xanthichthys ringens					14	

Species listed represent more than 99.5% of the total abundance from each station. Rank based on the mean abundance of five replicate transects per station

species across the depth gradient (*Chromis cyanea*, *Coryphopterus personatus*, *Stegastes partitus*, *T. bifasciatum*, *C. lipernes*, and *G. loreto*) presented significantly lower abundance at 50 m (ln transformed data) than at one or more stations shallower in the gradient (Fig. 9). The higher fish abundance at 25 m was driven by peak abundances of *C. personatus*, *C. lipernes* and *G. loreto*, but also by the significantly higher number of species per transect (mean: 32.2). Positive correlations between live coral cover and both fish species richness ($r = 0.72$, $P = 0.036$) and abundance ($r = 0.31$, $P = 0.10$) were found, but the relationship of live coral cover and total fish abundance appeared to be weakened by the presence of numerically dominant species with aggregated (patchy) distributions, such as *C. cyanea* and *C. parrae* (Table 2) at stations with relatively low coral cover (e.g., 30 and 40 m). Bluehead wrasse (*T. bifasciatum*) another numerically dominant species with patchy distributions throughout most of the depth gradient displayed a pattern of gradual decline of abundance with increasing depth that was unrelated to coral cover.

Discussion

The coral reef system of Desecheo reached its peak development at stations 20 and 25 m, as evidenced by the significantly higher percent substrate cover by live corals relative to other stations. This is the deepest section of the insular shelf and appears to provide optimal conditions for sustained coral growth, resulting in massive structural buildup by corals, particularly centenary colonies of *M. annularis* (complex) that exceed 10 m in diameter and rise more than 5 m from the seafloor (García-Sais et al. 2005a, b). Shallower colonized pavement habitats of the insular shelf, represented here by station 15 m were colonized by corals, but mostly small encrusting colonies prevailed and massive structural buildups were generally absent. This may be associated with the disruptive mechanical effects of extreme wave action induced by hurricanes and other physical disturbances that operate on timescales of decades at the inner shelf. Peak reef substrate cover at 15 m by turf algae, which is highly resilient to wave action and its associated surge and abrasion effects may be indicative of the physical controlling forces prevailing at the inner shelf.

Coral growth below the shelf-edge declined sharply in Desecheo. The upper insular slope from 30 to 40 m appears to receive substantial sediment from the shelf, as evidenced by the significantly higher cover by abiotic (mostly sand and rubble) substrates relative to other stations. Fleshy macroalgae, largely *L. variegata* significantly increased its

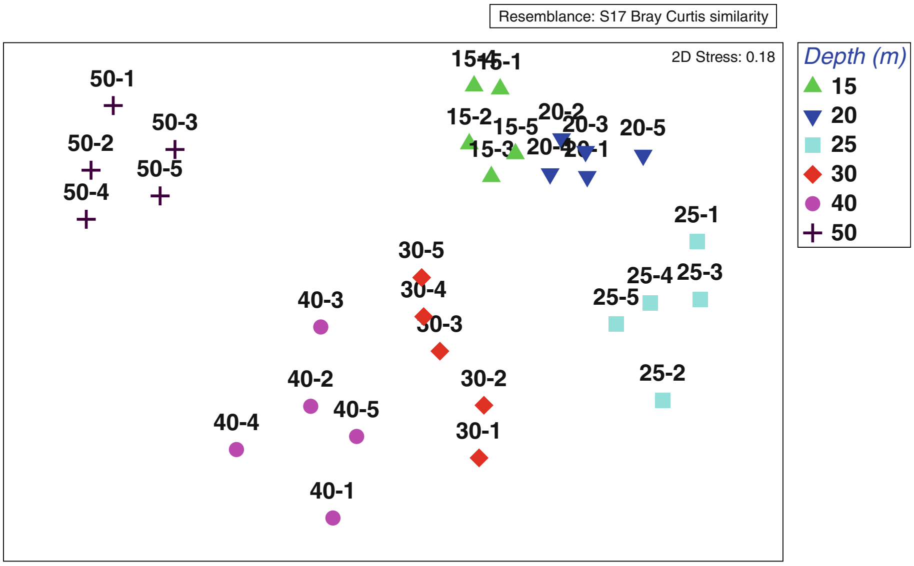


Fig. 7 Non-metric, multidimensional scaling (MDS) plot of Bray Curtis similarities based on the rank order abundance of reef fishes from sets of five replicate belt-transects surveyed at six stations encompassing a 15–50 m depth gradient in Isla Desecheo. Primer statistical package

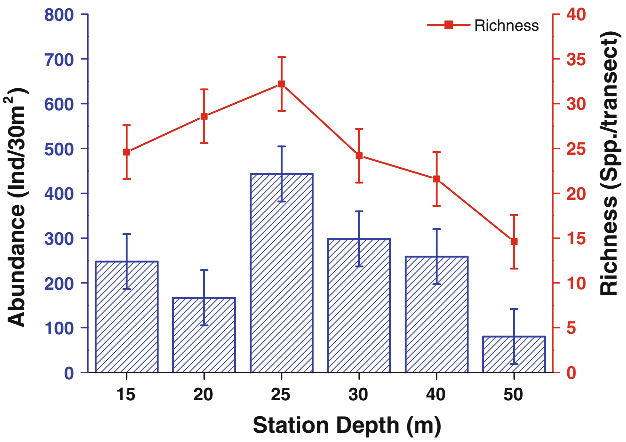


Fig. 8 Mean fish abundance and species richness from sets of five replicate belt-transect surveys encompassing a 15–50 m depth gradient at Isla Desecheo

cover at slope wall stations relative to shelf stations and prevailed as the dominant sessile-benthic category in terms of reef substrate cover down to 50 m. Substrate cover by abiotic and fleshy macroalgae precludes settlement of coral planulae and may limit the growth and development of existing colonies due to sedimentation stress (Rogers 1983; Acevedo and Morelock 1988). The vast deposit of crustose algal nodules or rhodoliths that accumulated in a gently sloping terrace at depths between 45 and 70 m in Desecheo structurally resemble the “algal-sponge zone” described by Bright et al. (1984) for the Flower Garden Bank in the northwest Gulf of Mexico. Rhodoliths are mostly covered by the encrusting alga, *L. variegata* and by branching sponges, but were observed to serve also as attachment substrates for *Agaricia* spp.

Sponges, particularly branching *Agelas* spp. and *Aplysina* spp. increased markedly in substrate cover at slope wall stations relative to shelf stations. Because of their relatively low body mass, branching sponges can attach to small corals and other anchoring substrates in the wall and grow out to the water column, where the swift current created by the steep wall morphometry creates an ideal filter feeding environment. Sponges were also the dominant sessile-benthic invertebrate at the 50 m station where they represented the largest structure contributing topographic relief that could serve as protective habitat for fishes and invertebrates. The role of sponges as protective habitats for fishes in mesophotic habitats was previously noted by Collete and Rutzler (1977) off the mouth of the Amazon River in northern Brazil. Light penetration within the 30–40 m range at Desecheo is not considered a limiting factor for coral growth and development. *Montastraea* spp. was the dominant coral assemblage down to the base of the wall at 40 m and was also present within transects at 50 m. The *M. annularis* complex is known to construct large coral colonies and extensive reefs at depths of 30–40 m in clear waters of the Caribbean Sea (Nemeth et al. 2004; García-Sais et al. 2004, 2008; Armstrong et al. 2006; Menza et al. 2007) and the Flower Garden Banks (Bright et al. 1984; Hickerson et al. 2008) in the northwestern Gulf of Mexico. In contrast, *Agaricia* spp. dominated reef substrate cover by live corals at the 50 m station in Desecheo, which is more consistent with the findings at Pulley Ridge (Halley et al. 2007).

The community structure of reef fishes at Desecheo exhibited statistically significant variations across the depth gradient. Species richness and abundance were positively correlated to live coral cover, which peaked at stations of intermediate depth (25 and 20 m). This is related to the higher substrate rugosity and habitat heterogeneity available in sections of optimal reef development, as well as to

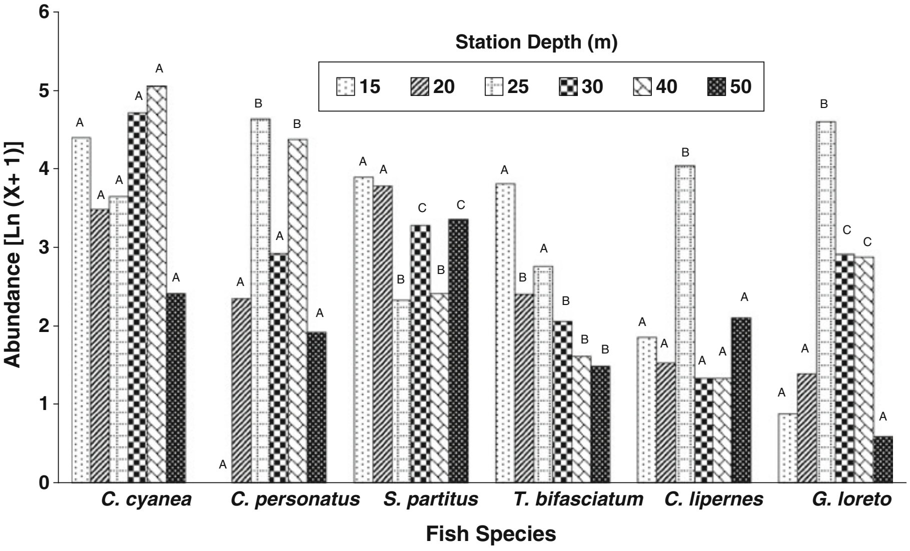


Fig. 9 Mean abundance variations with depth of the numerically dominant fish species surveyed across a 15–50 m depth gradient in Isla Desecheo. Letter changes over bars represent statistically significant differences (ANOVA; $P < 0.05$)

Table 2 Abundance variance to mean ratios and Lloyd's Patchiness Index (in parenthesis) for the numerically dominant fishes surveyed from replicate belt-transects at Isla Desecheo

Fish species	Sampling stations (m)					
	15	20	25	30	40	50
Chromis cyanea	33.8 (1.4)	8.5 (1.2)	17.7 (1.4)	12.8 (1.1)	139.7 (1.9)	5.5 (1.4)
Stegastes partitus	1.7 (1.0)	1.0 (1.0)	0.9 (1.0)	0.3 (1.0)	1.9 (1.1)	0.6 (1.0)
Thalassoma bifasciatum	6.6 (1.1)	1.5 (1.0)	3.0 (1.1)	3.6 (1.4)	9.5 (3.1)	1.0 (1.0)
Gramma loreto	2.0 (1.7)	2.2 (1.4)	25.4 (1.2)	11.5 (1.6)	2.2 (1.1)	4.0 (4.8)
Coryphopterus personatus	n/a	n/a	26.2 (1.2)	21.3 (2.2)	61.7 (1.8)	14.9 (3.4
Coryphopterus lipernes	1.3 (1.0)	1.5 (1.1)	9.8 (1.2)	2.2 (1.4)	9.5 (4.0)	1.7 (1.1)
Clepticus parrae	n/a	25.0 (5.8)	10.7 (1.4)	44.0 (1.9)	135.7 (2.9)	n/a

the direct function of live corals as microhabitats for numerically dominant species such as gobies (e.g., *C. personatus*, *C. lipernes*, and *Elacatinus* spp.). Distributions of some numerically dominant fish species, however, were observed to vary independently from live coral cover and appeared to be more influenced by depth. For example, abundance of *T. bifasciatum* declined almost monotonically with increasing depth. Such trend implies an inverse relationship with live coral cover along the first three depths of the gradient, due to the increasing pattern of live coral from station 15 m through 25 m. An assemblage of species comprised by opportunistic carnivores, *T. bifasciatum*, *Halichoeres maculipinna* and herbivores, *Microspathodon chrysurus*, *S. planifrons*, *A. coeruleus*, *S. viride*, *S. radians* distinguished euphotic (particularly 15 and 20 m) from mesophotic stations.

At the upper limit of mesophotic depth in Desecheo, the slope wall habitat exhibited a peculiar fish assemblage very strongly dominated by zooplanktivorous taxa such as *C. cyanea*, *C. insolata*, *C. parrae* and *P. furcifer*, which may be associated with the higher availability of zooplankton food coming from the shelf-edge. The most abundant fish in the study, *C. cyanea*, exhibited highly aggregated or patchy distributions at slope wall stations that introduced high abundance variability within replicate transects, rendering a homogeneous spatial distribution across the gradient. The largest aggregations were comprised by swarms of new recruits (<2 cm) associated with branching sponges (not corals) as protective habitats. Swarms of small juvenile *C. parrae* and *C. insolata* were also present at slope wall stations associated with branching sponges. The high substrate cover by branching sponges (*Agelas* spp., *Aplysina* spp.) influences the function of mesophotic reefs as important recruitment habitats for reef fishes. In this study, the relatively high abundance of *C. cyanea* and *C. parrae* in sponge dominated mesophotic reef habitats introduced high variability to the correlation between live coral cover and total fish abundance.

The lowest ichthyofaunal abundance and species richness was associated with the rhodolith reef habitat at the deepest section of this study (50 m). It is a virtually flat horizontal terrace, with only small microhabitats available for fishes contributed mostly by sponges and discontinuities within the rhodolith bank. The lack of rugosity and structural complexity of the rhodolith habitat is a limiting factor for the abundance and species richness of reef fishes. It has been noted that the abundance of basslets (*G. loreto*, *G. linki*), squirrelfishes (*H. rufus*) and groupers (*E. striatus*, *M. venenosa*, *M. bonaci*) increases in this depth with increasing substrate rugosity (J. Garcia-persersonal observation).

A small assemblage of reef fishes that includes *C. argi*, *C. insolata*, *S. atomarium*, *C. aculeatus*, *H. cyanocephalus*, *P. furcifer*, and *X. ringens* was most abundant or only present from stations deeper than 30 m and thus appear to be indicator fish species of mesophotic habitats. As for the sessile-benthic community, the fish assemblage of the "Agelas" reef system at Desecheo resembles in several relevant taxonomic components the fish assemblage described by Dennis and Bright (1988) for the "algal-sponge zone" of the Flower Garden Bank at depths between 50 and 80 m. In the *Agelas* reef system, *C. cyanea*, and *C. insolata* appear to be replacing the yellowtail reef fish (*C. enchrysurus*) as the most abundant *Chromis* spp. in mesophotic habitats. This later species has been reported for Puerto Rico at deeper habitats of the insular slope (Nelson and Appledoorn 1985), and may be part of the Agelas reef system deeper than our 50 m survey limit. Likewise, the spanish hogfish, *Bodianus rufus* appears to be a Caribbean counterpart of the spotfin hogfish, *B. pulchellus*, and the yellowfin grouper, *Mycteroperca venenosa* may be replacing in Puertorrican (perhaps Caribbean) mesophotic reefs the continental grouper species *M. interstitialis* and *M. phenax* as top demersal predators.

Acknowledgments This study was accomplished thanks to the collaboration of a field team of rebreather divers with expertise on reef benthic invertebrate (Roberto Castro, J. Sabater-Clavell) and fish identification (J. García-Sais, M. Carlo). Milton Carlo directed the planning and logistics of the saturated diving activities using rebreathers and assisted with underwater sampling protocols. Underwater photography was the responsibility of J. Sabater-Clavell. Stacey Williams assisted with the statistical analyses. Thanks to Dr. Vance Vicente for his valuable assistance and training with the taxonomy of sponges. Special thanks to Mayra García from the Department of Natural and Environmental Resources (DNER) and Graciela García-Moliner from the Caribbean Fishery Management Council (CFMC) who served as points of contact from the sponsoring agencies. This research was supported by NOAA coral monitoring grant NA04NOS4260297 administered in Puerto Rico by the DNER, and NOAA coral grant NA03NMF4410352 administered in Puerto Rico by the CFMC.

References

Acevedo R, Morelock J (1988) Effects of terrigenous sediment influx on coral reef zonation in southwestern Puerto Rico. Proc 6th Int Coral Reef Symp 2:189–194

Armstrong R, Singh H, Torres J, Nemeth R, Can A, Roman C, Justice R, Riggs L, García-Moliner G (2006) Characterizing the deep insular shelf coral reef habitat of the Hind Bank Marine Conservation District (US Virgin Islands) using the SeaBED Autonomous Underwater Vehicle. Cont Shelf Res 26:194–205

Ballantine DL, Appeldoorn RS, Yoshioka P, Weil E, Armstrong R, Garcia JR, Otero E, Pagan F, Sherman C, Hernandez-Delgado EA, Bruckner A, Lilyestrom C (2008) Chapter 9. Biology and ecology of Puerto Rican coral reefs. In: Reigl BM, Dodge RE (eds) Coral reefs of the USA. Springer, Heidelberg, pp 375–406

Beets J, Friedlander A (1997) Evaluation of the spawning aggregation closure for red hind (*Epinephelus guttatus*), St. Thomas, US Virgin Islands. Report to the Caribbean Fishery Management Council, San Juan, P. R., p 17

Bright TJ, Kramer GP, Minnery GA, Viada ST (1984) Hermatypes of the Flower Garden Banks, northwestern Gulf of Mexico: a comparison to other western Atlantic reefs. Bull Mar Sci 34:461–476

CARICOMP (1994) Manual of methods for mapping and monitoring of physical and biological parameters in the coastal zone of the Caribbean. Caribbean Coastal Marine Productivity: Data Management Center. Centre for Marine Sciences. U. West Indies. Mona, Kingston, Jamaica and Florida Institute of Oceanography. U. South Florida, p 68

Colin PL (1974) Observation and collection of deep reef fishes off the coasts of Jamaica and Honduras. Mar Biol 24 (1):29–38

Colin PL (1976) Observation of deep reef fishes in the Tongue-of-the-Ocean, Bahamas. Bull Mar Sci 26:603–605

Collete BB, Rutzler K (1977) Reef fishes over sponge bottoms off the mouth of the Amazon River. Proc 3rd Int Coral Reef Symp 1:305–310

Dennis GD, Bright TJ (1988) Reef fish assemblages on hard banks in the northwest Gulf of Mexico. Bull Mar Sci 43:280–307

Dennis GD, Smith-Vaniz WF, Colin PL, Hensley DA, McGehee A (2005) Shore fishes from islands of the Mona Passage, Greater Antilles with comments on their zoogeography. Caribb J Sci 41 (4): 716–743

García-Sais JR, Castro R, Sabater J, Carlo M (2004) Monitoring of coral reef communities from Isla de Vieques, Puerto Rico, 2004. Final Report submitted to the Department of Natural and Environmental Resources (DNER), US Coral Reef National Monitoring Program, NOAA, p 118, http://www.drna.gobierno.pr/oficinas/arn/recursosvivientes/costasreservasrefugios/coral/publicaciones

García-Sais JR, Castro R, Sabater J, Carlo M (2005a) Inventory and atlas of corals and coral reefs from the US Caribbean EEZ (Puerto Rico and the United States Virgin Islands). Final Report submitted to the Caribbean Fishery Management Council (CFMC/NOAA). p 215, www.caribbeanfmc.com/index/reni.pdf

García-Sais JR, Castro R, Esteves R, Sabater J, Carlo M (2005b) Monitoring of coral reef communities at Isla Desecheo, Rincón, Mayaguez Bay, Guanica, Ponce and Isla Caja de Muerto, Puerto Rico, 2005. Final Report submitted to the Department of Natural and Environmental Resources (DNER), US Coral Reef National Monitoring Program, NOAA, p 126, http://www.drna.gobierno.pr/oficinas/arn/recursosvivientes/costasreservasrefugios/coral/publicaciones

García-Sais JR, Castro R, Sabater J, Carlo M (2007) Characterization of benthic habitats and associated reef communities at Bajo de Sico Seamount, Mona Passage, Puerto Rico. Final Report submitted to Caribbean Fishery Management Council (CFMC/NOAA) p 91

García-Sais JR, Appeldoorn R, Batista T, Bauer L, Bruckner A, Caldow C, Carrubba, Corredor J, Díaz E Lilyestrom C, García-Moliner G, Hernández-Delgado E, Menza E, Morell J, Pait A, Sabater-Clavell J, Weil E, Williams E (2008). The state of coral reef ecosystems of the Commonwealth of Puerto Rico. In: Waddell J, Clarke AM (eds) The state of coral reef ecosystems of the United States and Pacific Freely Associated States. NOAA Technical Memorandum NOS NCCOS 73. NOAA/NOS/NCCOS. Center for Coastal Monitoring and Assessment's Biogeography Team. Silver Spring, MD, pp 75–116

Halley RB, Garrison VE, Ciembronowicz KT, Edwards R, Jaap WC, Mead G, Earle S, Hine AC, Jarret B, Locker SD, Naar DF, Donahue B, Dennis GD, Twichell DC (2007). Pulley Ridge—The United States' deepest coral reef? http://sofia.er.usgs.gov/publications/ofr/03-54/abstracts/pulleyridge_03geerab.html

Hickerson EL, Schmahl GP, Robbart M, Pretch WF, Caldow C (2008) The state of coral reef ecosystems of Flower Garden Banks, Stetson Bank, and Other Banks in the Northwestern Gulf of Mexico. In: Waddell J, Clarke AM (eds) The state of coral reef ecosystems of the United States and Pacific Freely Associated States. NOAA Technical Memorandum NOS NCCOS 73. NOAA/NOS/NCCOS. Center for Coastal Monitoring and Assessment's Biogeography Team. Silver Spring, MD, pp 189–217

Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, Pyle RL, Zawada DG, Appeldoorn R (2010) Introduction to mesophotic coral ecosystems: characterization, ecology, and management. Coral Reefs this issue

Humann P, Deloach N (2003) Reef coral identification, 2nd edn. New World Publications, Jacksonville, FL, p 278

Humann P, Deloach N (2006) Reef fish identification, 3rd edn. New World Publications, Jacksonville, FL, p 481

Lloyd M (1967) Mean crowding. J Anim Ecol 36:1–30

Menza C, Kendall M, Rogers C, Miller J (2007) A deep reef in deep trouble. Cont Shelf Res. 27: 2224–2230

Nelson WR, Appeldoorn RS (1985) Cruise Report R/V Seward Johnson. A submersible survey of the continental slope of Puerto Rico and the US Virgin Islands. Report submitted to NOAA, NMFS, SEFC, Mississippi Laboratories. University of Puerto Rico, Department of Marine Sciences, p 76

Nemeth RS (2005) Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection. Mar Ecol Prog Ser 286:81–97

Nemeth RS, Herzlieb S, Kadison ES, Taylor M, Rothenberger P, Harold S, Toller W (2004) Coral reef monitoring in St. Croix and St. Thomas, United States Virgin Islands. Final report submitted to the Department of Planning and Natural Resources, US Virgin Islands, p 79

Nemeth RS, Smith TB, Blondeau J, Kadison ES, Calnan JM, Gass J (2008) Characterization of deep water reef communities within the Marine Conservation District, St. Thomas, US Virgin Islands. Final Report submitted to the Caribbean Fishery Management Council (CFMC/NOAA), p 90

Porter JW (1972) Patterns of species diversity in Caribbean reef corals. Ecology 53:745–748

Rogers CS (1983) Sub-lethal and lethal effects of sediments applied to common Caribbean reef corals in the field. Mar Pollut Bull 14:378–382

Singh H, Armstrong R, Gilbes F, Eustice R, Roman C, Pizarro O, Torres J (2004) Imaging coral I: Imaging coral habitats with the Seabed AUV. Subsurface Sensing Technologies and Applications. 5:25–42