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Effects of depth and bottom communities on the distribution of highly territorial reef fish in the northwestern region of Cuba

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Summary

The main goal of the study was to investigate changes in reef fish species abundance and its correlation with selected environmental variables. Three main questions guided the analyses: (i) Do the analytical methods have a significant influence on the results; (ii) What are the main assemblage variation axes; and (iii) What are the factors correlating best with assemblage composition. Highly territorial fish assemblages of several coral reefs along the northwestern region of Cuba were assessed using a stationary point visual census technique. A total of 39 701 individuals of 26 species from the families Chaetodontidae, Labridae and Pomacentridae were counted in 841 censuses; almost 80% of the fish belonged to just four species: bluehead (*Thalassoma bifasciatum*), bicolor damselfish (*Stegastes partitus*), slippery dick (*Halichoeres bivittatus*) and blue chromis (*Chromis cyanea*). Several multivariate techniques (cluster analysis, non-metric multidimensional scaling and canonical correspondence analysis) were used to explore main patterns in assemblage composition variation. It was found that the results did not differ significantly when analyzing the same data set. Furthermore, it was shown that the combined use of different multivariate techniques enhanced the interpretation of fish assemblage composition changes. Depth was the main variable explaining variation in the composition of fish assemblages in the studied reefs. The densities of corals and gorgonians were also strongly associated with depth. Sponge density made an additional significant contribution to the explanatory model. Results of this research could be used as a baseline reference for future analyses of the impact of human actions in the study area. (e.g. oil spills, change in fishing intensity, other pollution events, tourism development).

Introduction

The analyses of factors influencing distribution of individuals are essential for understanding spatial variation in fish assemblages. Our ability to isolate changes induced by anthropogenic stress will improve as we increase our knowledge of natural factors shaping natural communities. One challenge to environmental studies on fishes is that subtle responses due to human impact can fall within the range of performance variability associated with natural environmental stressors (Munkittrick et al., 2000; Baird and Burton, 2001).

Habitat type has been found to be one of the most important factors determining spatial variation in the structure of coastal fish assemblages (Letourneur et al., 2003; Aguilar et al., 2004; Gratwicke and Speight, 2005; Gratwicke et al., 2006). Núñez-Lara et al. (2005) found that geomorphologic

and anthropogenic factors indeed influenced reef fish community composition. Feary et al. (2007) presented evidence suggesting that habitat health may play an important role in structuring coral-associated fish assemblages.

Current methodology for quantitative research on fish assemblages and their relationships with the environment include two main kinds of techniques. Canonical methods allow the investigation of quantitative relationships among species' abundance data and environmental variables (e.g. canonical correspondence analysis, redundancy analysis). Main limitations of these methods are that the resemblance measures (chi-squared, Euclidean distance) are not the best choices for ecological work and that a response model (unimodal, linear) of species on environmental variables is assumed (Legendre and Legendre, 1998). Alternatives to canonical methods are cluster analysis and MDS ordination, which use a much better resemblance measure (Bray-Curtis Index) and are not restricted by any model assumptions. They are more limited, however, in making good, direct analyses of species–environment relationships (Clarke and Warwick, 2001).

Fish assemblages and habitats of northwestern Cuba have been investigated for more than a decade (González-Díaz et al., 2003; Aguilar et al., 2004, 2007, 2008; González-Sansón et al., 2009). This is the first detailed study along the northwestern coast of Cuba that focuses on highly territorial fish assemblages and natural and human-induced factors causing variations in the composition of these assemblages. The main goal of the study was to investigate changes in species' abundance and their correlation with selected environmental variables. Three main questions guided our analyses: (i) Do the analytical methods have a significant influence on the results; (ii) What are the main assemblage variation axes; and (iii) What are the factors correlating best with assemblage composition. Results of this research could be used as a baseline reference for future analyses of the impact of human actions in the region (e.g. oil spills, change in fishing intensity, other pollution events, tourism development). This research also provides input for a more comprehensive understanding of the fish community status in the Gulf of Mexico basin.

Materials and methods

Study area

Three reefs along the northwestern coast of Cuba were selected for the study (Table 1; Fig. 1). At Havana City in the east, a frontal fringing reef develops mainly in the 12–15 m deep terrace, at 200–300 m offshore. The area between the shore

Table 1
Geographical position, habitats sampled, sampling dates and sample sizes of the studied reefs

Site	Reference coordinates	Habitats sampled	Sampling dates	Censuses
HA1	23°08.549′N 82°22.012′W	Echinometra bed Rocky plain Terrace	February–March 2000 June 2000	96 96
HA2	23°08.250′N 82°24.565′W	Echinometra bed Rocky plain Terrace	February–March 2000 June 2000	64 64
HA3	23°07.359′N 82°26.087′W	Echinometra bed Rocky plain Terrace	February–March 2000 June 2000	80 80
HE	23°01.481′N 82°55.014′W	Gorgonians shallow Gorgonians deep Coral heads Acropora + Millepora Wall	March 1996 October 1996	108 109
CO1	22°23.023′N 84°36.589′W	Crest Terrace Spur & grooves	March 2006	30
CO2	22°18.320′N 84°40.235′W	Crest Terrace Spur & grooves	March 2006	30
CO3	22°13.970′N 84°44.091′W	Crest Terrace Spur & grooves	March 2006	30
CO4	22°09.451′N 84°46.373′W	Crest Terrace Spur & grooves	March 2006	30

Site labels: HA = Havana reef; HE = Herradura reef; CO = Colorados reef; Numbers indicate zones inside each reef (see also Fig. 1 and text for details).
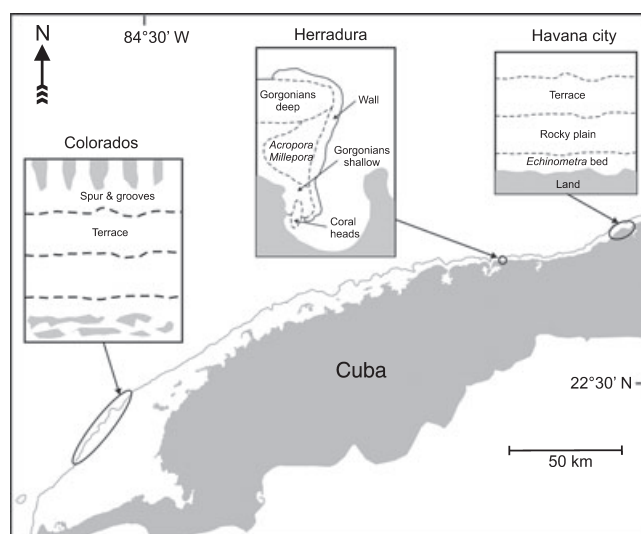

Fig. 1. Northwestern region of Cuban shelf with schematic representation of main habitats sampled in each studied reef (not to the same scale). See Table 1 for more details

and the reef is an almost bare rocky plain with a fringe near the shore where there are large populations of sea urchins (Echinometra spp.). As the impact of pollution emanating from the city varies notably along the coast from the Havana harbor entrance (most polluted area) towards the southwest, the reef was divided into three different sites: HA1 (under direct influence of harbor discharge), HA2 (around the Almendares River, west of the harbor), and HA3 (far from significant land-based pollution sources), and analyzed separately. More details and the rationale for this division can be found in Aguilar et al. (2004, 2007). Herradura (HE) is a fringe reef growing on the west side of a cove of the same name with a

poorly developed crest dominated by A. palmata. In addition, other bottom types were defined for this reef: a rocky bottom covered by shallow and deep gorgonians, coral heads on a shallow sand plain, and the reef wall (de la Guardia and González-Sansón, 1997). The Colorados reef is a large bank-barrier reef of approximately 40 km length with a wide crest area of A. palmata. To be consistent with the spatial scale used for the two other reefs, four sites were defined within the Colorados and treated as separated units (CO1–CO4). Two bottom types were sampled in this reef: terrace, and spur & grooves.

Fish censuses and sessile communities' abundance

The abundance of fish was estimated using the stationary visual census technique of Bohnsack and Bannerot (1986) with some minor modifications. The nominal radius of the observing cylinder was 5 m. We included at least 15 randomly placed censuses (sampling units) in each of the 36 samples (combinations of bottom type, reef and season of the year). Original data included all species observed. For the present analyses, only highly territorial fish were included. Not all species or groups of species (families and/or genera) were selected; nocturnal species were also excluded, as they are cryptic during the day. Species considered for the analyses were butterfly-fishes (Chaetodontidae, genus Chaetodon), damselfishes (Pomacentridae, genera Abudefduf, Chromis and Stegastes) and small wrasses (Labridae, genera Bodianus, Halichoeres and Thalassoma). Depth of each sampling site was recorded. Dates of sampling were classified as pertaining to the rainy season or the dry season.

Colony densities (number of colonies per square meter) of scleractinean corals, gorgonians and sponges were obtained from González-Díaz et al. (2003) for the Havana reef, from de la Guardia and González-Sansón (1997) for the Herradura

reef, and from S.P. González-Díaz (pers. comm.) for the Colorados reef.

Numerical analyses

Comparisons of the mean number of individuals per census among groups of samples were made for each species with 10 or more occurrences using one-way, fixed-effects ANOVA on log transformed values $[x_t = \log_{10}(x + 1)]$. Correlation among pairs of variables was tested with Spearman's rank correlation coefficient. All tests were made with a level of significance equal to 0.05. Analyses were made using STATISTICA 6.0 (Statsoft).

Hierarchical agglomerative cluster analysis was performed using the Bray-Curtis index as a dissimilarity measure on log-transformed counts for sample grouping using the UPGMA clustering algorithm. Non parametric multidimensional scaling (MDS) was employed for ordination of samples based in the same distance matrix as the cluster analysis. The combination of clustering and ordination analyses has been described by Clarke and Warwick (2001) as the most effective way to check the adequacy and mutual consistency of both representations. Analyses were made using PRIMER 5.5 (Clarke and Warwick, 2001).

To select the best method for canonical analysis, a detrended correspondence analysis on species data was made to assess the length of the gradients (ter Braak and Prentice, 2004). These were 2.04 for the first axis and < 2 for the rest of the axes, suggesting a linear response model. Based thereon, species–environment relationship was explored using redundancy analysis (Legendre and Legendre, 1998). Scaling was focused on inter-species correlations, species scores were divided by the standard deviation and data were log transformed and centered by species. Forward selection of environmental variables was performed automatically and statistical signifi-cance determined by unrestricted Monte Carlo permutation tests. Environmental (explanatory) variables included four quantitative (depth and colony density of corals, gorgonians and sponges) and one qualitative (year season) variable, the latter represented by two dummy variables. With the computer program used for calculations it is not necessary to eliminate one of the dummy variables to avoid collinearity because the program does this automatically. This allows representing positions of both classes of the nominal variable in the final ordination diagram. Biplots were used for the representation of ordination results and interpreted using the rules summa-rized by Legendre and Legendre (1998). Analyses were made using CANOCO 4.5 for Windows (ter Braak and Šmilauer, 2002).

Results

A total of 39 701 individuals of 26 species of the selected groups were counted in 817 stationary point censuses (Table 2). Almost 80% of all fish counted belonged to just four species: bluehead (*Thalassoma bifasciatum*), bicolor dam-selfish (*Stegastes partitus*), slippery dick (*Halichoeres bivitta-tus*) and blue chromis (*Chromis cyanea*). Four other species amounted to slightly more than 90% of all individuals: yellowhead wrasse (*Halichoeres garnoti*), sergeant major (*Abudefduf saxatilis*), brown chromis (*Chromis multilineata*) and foureye butterflyfish (*Chaetodon capistratus*). The remain-ing fish, < 10% of the total, were classified into 18 species. Total number of species per sample was correlated with sponge density ($r_s = 0.68$, $P < 0.001$, $n = 36$) but not with coral density ($r_s = -0.02$, $P = 0.920$, $n = 36$), gorgonian density ($r_s = -0.17$, $P = 0.311$, $n = 36$) or depth ($r_s = 0.28$, $P = 0.093$, $n = 36$). There was no dependence of the total number of species on the total number of individuals per count in each sample ($r_s = 0.17$, $P = 0.325$, $n = 36$).

Families & species	N	N %	O	O %	$F_{(5,30)}$	p
Chaetodontidae						
Chaetodon aculeatus	10	< 0.1	4	11.1	-	-
Chaetodon capistratus	967	2.4	36	100.0	6.24	< 0.001
Chaetodon ocellatus	224	0.6	21	58.3	3.60	0.011
Chaetodon sedentarius	176	0.4	18	50.0	4.57	0.003
Chaetodon striatus	435	1.1	31	86.1	2.58	0.047
Pomacentridae						
Abudefduf saxatilis	1429	3.2	24	66.7	16.28	< 0.001
Chromis cyanea	2602	6.6	22	61.1	19.81	< 0.001
Chromis insolata	7	< 0.1	3	8.3	-	-
Chromis multilineata	1133	2.9	22	61.1	18.17	< 0.001
Microspathodon chrysurus	443	1.1	11	30.6	15.40	< 0.001
Stegastes adustus	543	1.4	22	61.1	1.84	0.134
Stegastes diencaeus	44	0.1	15	41.7	8.77	< 0.001
Stegastes leucostictus	490	1.2	33	91.7	1.14	0.361
Stegastes partitus	9236	23.3	35	97.2	32.47	< 0.001
Stegastes planifrons	50	0.1	3	8.3	-	-
Stegastes variabilis	166	0.4	22	61.1	2.58	0.047
Labridae						
Bodianus rufus	337	0.8	19	52.8	19.70	< 0.001
Halichoeres bivittatus	4188	10.5	34	94.4	14.23	< 0.001
Halichoeres cyanocephalus	1	0.0	1	2.8	-	-
Halichoeres garnoti	1281	3.2	27	75.0	41.66	< 0.001
Halichoeres maculipinna	101	0.3	16	44.4	4.45	0.004
Halichoeres poeyi	26	0.1	7	19.4	-	-
Halichoeres radiatus	79	0.2	17	47.2	1.13	0.364
Thalassoma bifasciatum	15656	39.4	36	100.0	3.01	0.026

Table 2
Total number (N) and frequency of occurrence in samples (O) of species included in the analyses

N% and O% = percentages of the total. Also shown are *F*-ratio values and their associated probabilities (p) for 1-way ANOVAs among groups formed by cluster analysis (Fig. 2).

After the numerical classification and multidimensional scaling, samples formed six well-separated groups (Fig. 2). Mean number of individuals per census calculated for groups was significantly different among them for 16 of 19 species tested (Table 2). A graphical representation of species abundance (Fig. 3) makes clear the distribution pattern for each species and allows summarizing main characteristics of groups in terms of species composition. Cluster A included samples from Herradura and Havana City reefs arranged in two well-differentiated subclusters (groups A1 and A2). Group A1 included samples from coral heads, shallow and deep gorgonians from Herradura reef, and samples from the *Echinometra* layer and rocky plain from the highly polluted reef off Havana City; this group was dominated by *Thalassoma bifasciatum* and *Halichoeres bivittatus*. From the dendrogram it is evident that this group could be further divided in a subset containing

Fig. 3. Representation of selected species in groups defined by cluster analysis (see Fig. 2). Diameters of circles proportional to logarithms of mean number of fish per count. Species labels formed by first three letters of genus and specific names combined

Herradura samples and another one containing Havana CH1 reef samples. Group A2 was formed by samples from wall and *Acropora-Millepora* zones in Herradura reef. A higher representation of pomacentrids (mainly *Microspathodon chrysurus*, *Abudefduf saxatilis* and *Chromis cyanea*) is evidently the cause for formation of this subgroup. Cluster B included just two samples from the rocky plain off Havana City in reef zone 3, which is further from port influence. A very low abundance of *H. bivittatus* and high abundance of *Chromis multilineata* are the most evident differences of this group compared to those of Cluster A. Cluster C was formed by most samples from the *Echinometra* layer and rocky plain from zones 2 and 3 of the reef off Havana City. This was the group with fewer species and strongly dominated by *T. bifasciatum*. Cluster D had two well-differentiated subclusters (groups D1 and D2). In both cases *T. bifasciatum* and *S. partitus* were clearly dominant. Group D1 included samples mostly from the terrace of all Havana City's reefs. Pomacentrids and Chaetodontids were well represented and dominated by *H. bivittaus* and *C. cyanea*. Group D2 was formed by almost all sites from Los Colorados reef. The distinctiveness of this group is attributable to high abundance of *Halichoeres garnoti* and *C. cyanea*. In a higher level of dissimilarity, clusters A, B and C form a major cluster including almost all shallow sites, while D can be identified as a cluster grouping deep sites. These two major groups allow identifying depth as a main factor influencing fish assemblage composition.

Redundancy analysis yielded a first canonical ordination axis explaining 35.9% of the variance of species data and 79.9% of the species–environment relationship (Table 3). This axis had a very high species–environment correlation. Joint examination of canonical coefficients and inter-set correlations helped to identify this first axis reflecting a depth gradient (Table 3). The second canonical axis explained much less variation (5.4% of species data and 11.9% of species–environment relation) but had also a high species–environment correlation. This axis can be clearly identified with a gradient of sponge colonies density.

A sufficient subset of the explanatory variables that represents the relation between species and environmental data was obtained based on the significance of conditional effects (Table 4). Considering Bonferoni correction for a
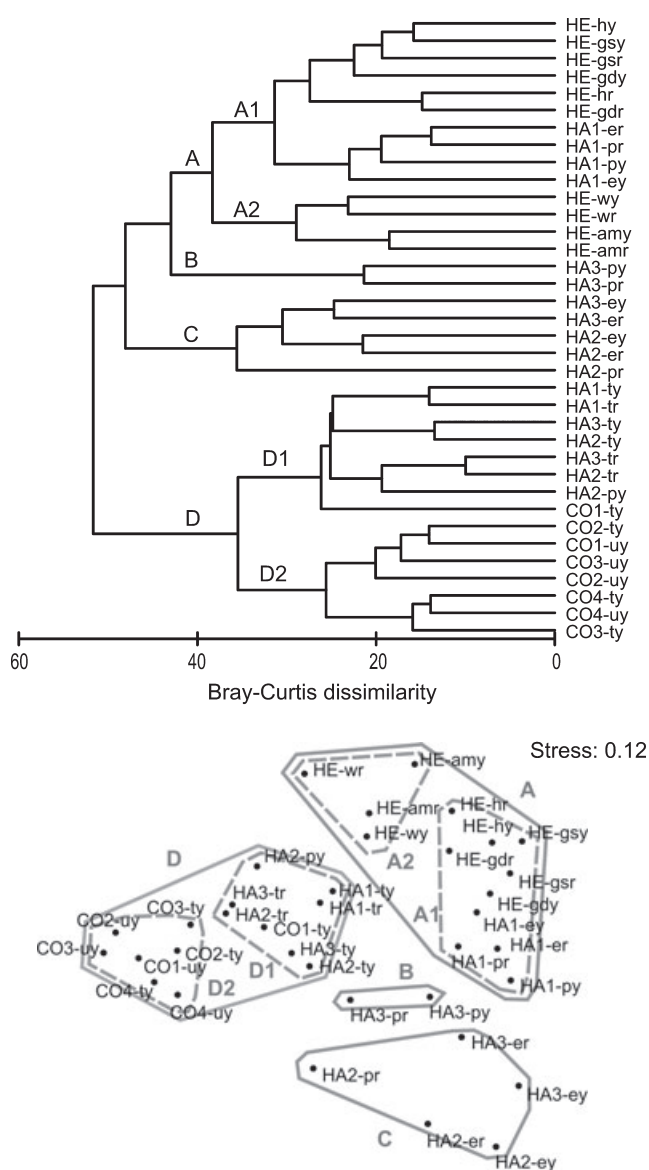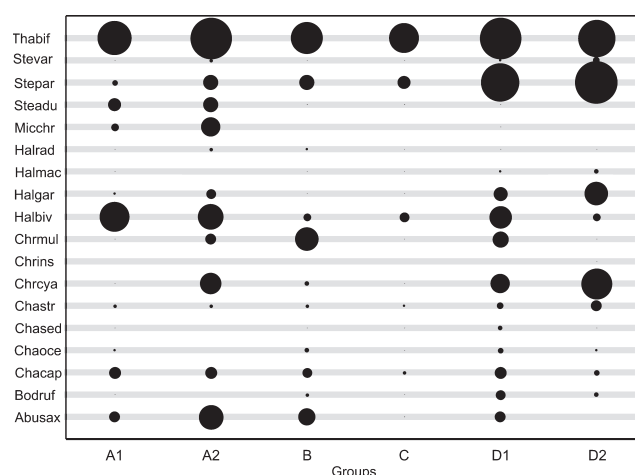

Fig. 2. Classification (upper panel) and MDS ordination (bottom panel) of samples. Each sample is identified by the acronym (defined in Table 1) of the reef area, the habitat sampled (am = *Acropora* + *Millepora*, e = *Echinometra*; gd = gorgonians deep; gs = gorgonian shallow, p = rocky plain, t = terrace, u = spur & grooves, w = wall) and the sampling season (r = rainy, y = dry)

Summary of the ordination axes	1	2	3	4
Eigenvalues	0.359	0.054	0.021	0.012
Species–environment correlations	0.876	0.736	0.452	0.517
Cumulative percentage variance				
of species data	35.9	41.3	43.4	44.6
of species–environment relation	79.9	91.8	96.6	99.2

Canonical coefficients for standardized variables & inter-set correlations of environmental variables with species axes	Canonical coeff.		Inter set correl.	
	Axis 1	Axis 2	Axis 1	Axis 2
Coral colonies density	0.301	−0.396	0.369	−0.358
Gorgonian colonies density	0.036	−0.294	0.473	−0.268
Sponge colonies density	0.148	0.900	0.453	0.590
Depth	0.829	−0.175	0.832	0.031
Year season wet	0.049	−0.122	−0.190	0.085
Year season dry[1]	-	-	0.190	−0.085

Table 3
Summary of redundancy analysis

[1]Canonical coefficient not computed due to collinearity.

Variables	F	p	λ	Vexp	% Vexp
Depth	18.39	0.002	0.33	0.33	73.3
Coral colonies density	3.30	0.006	0.05	0.38	84.4
Sponge colonies density	3.09	0.010	0.05	0.43	95.5
Gorgonian colonies density	0.91	0.508	0.01	0.44	97.7
Year season wet	0.32	0.976	0.01	0.45	100.0

Table 4
Conditional effects of variables in forward stepwise automatic selection procedure (variables ordered after their inclusion sequence)

F and p obtained by partial Monte Carlo permutation tests. λ = additional variance, each variable at the time it was included. Vexp = variance explained by all variables thus far included. Dummy variable 'dry' not included due to collinearity.

preselected significance level $\alpha = 0.05$ and a total of five comparisons during the selection process, only three variables were included in the model: depth, coral density and sponge density.

Although a triplot will be a comprehensive graphical representation of RDA ordination, the number of samples and species makes such a graph difficult to examine. Therefore two separated biplots were drawn (Figs 4 and 6). In both cases the representation of environmental variables is the same. The small angle between the depth arrow and the first canonical ordination axis well-reflect the high positive correlation between them. Coral and gorgonian colonies density are also positively correlated with depth and the first axis. The arrow representing sponge density forms an acute angle with the second ordination axis, reflecting the high correlation between them. On the other hand, the sponge arrow forms an almost right angle with those representing coral and gorgonians colonies density, indicating therefore no correlation with them. Projections of centroids of the nominal variable used to represent season of the year show clearly that this variable has a very low discriminatory value due to the position of the centroids of its classes near the origin of the axes.

In the biplot of samples and environmental variables (Fig. 4) the distance between samples in the graph does not reflect the Euclidean distances between them due to the scaling used (focused on species correlations). However, groups of samples can be arbitrarily delimited based on their distances in graph and groups formed by cluster analysis (Fig. 2). This grouping can be used to help with the interpretation of species correlations. Projection of samples on canonical axes and environmental variables (arrows, including their prolongations in the direction opposite to the arrowhead) is a way to understand main environmental factors associated to each group of samples.

Samples of Colorados reef have the highest colony densities of coral and gorgonians, with a relative low representation of sponges. The positions of samples included in this group in the positive portion of first canonical axis indicate that they are deep sites. Samples of deep sites from zones 2 and 3 of Havana reef have lesser densities of corals and gorgonians and more sponge density than those from the Colorados. Their position in the positive side of the second ordination axis indicates sponge density is a factor explaining the separation of this group of samples from those of Colorados. A small group formed by the two terrace samples from zone 1 of Havana reef showed the highest density of sponges and the lowest density of coral and gorgonians (Fig. 4). In this case, a clear difference in species composition among three Havana reefs (Fig. 5) can be the cause for these two samples to position far from other terrace samples of the same area in the biplot diagram. This subtle but important difference was not detected by cluster analysis. Taken together the three groups just described correspond to groups D1 and D2 from cluster and MDS analyses (Fig. 2).

The shallow Havana reef sites are characterized by low colony densities of corals, gorgonians and sponges (Fig. 4). These samples were classified in groups A1, B and C (80% of samples) by cluster and MDS analyses (Fig. 2). As expected, all samples lay on the negative side of the first axis, which is highly correlated with depth. The Herradura reef stations lay on the negative side of the second axis, in agreement to the lower sponge and higher coral and gorgonians densities compared to those from the Havana reef (Fig. 4). As these stations are predominantly shallow they mostly appear on the
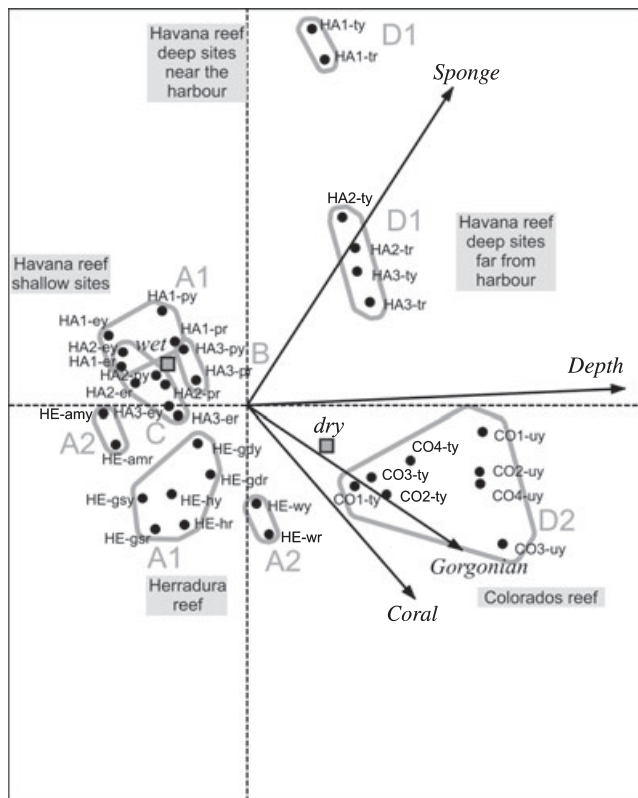
Fig. 4. RDA biplot of samples and environmental variables. Identification key as in Fig. 2. Arrows identify quantitative variables. Squares indicate the centroids of each season class. Thick gray lines identify groups of samples (uppercase letters and numbers) after cluster analysis (Fig. 2)

negative side of the first ordination axis. These samples were classified in groups A1 and A2 by cluster and MDS analyses (Fig. 2). Similar to cluster-MDS results, group A1 appears clearly split into two subgroups (one for samples from Havana reef, the other for samples from Herradura reef). Group A2 also follows the same pattern as in cluster-MDS analysis with shallow *Acropora + Millepora* sites of Herradura reef far on the left side of first axis, and deep wall sites of the same reef on the right side clearly responding to the depth gradient.

Although a detailed description of the species by environmental variables biplot is not provided, it is pertinent to emphasize some of its important features. A group of species is highly correlated among them, and with depth and coral and gorgonian colony densities (Fig. 6). These include, among others, *Stegastes partitus*, *Halichoeres garnoti*, *Chromis cyanea* and *Chaetodon striatus* to mention just the most abundant. The highest ranking sites of these species were those from Colorados reef. Another group of species is negatively correlated with depth, coral and gorgonians, their arrows pointing in the opposite direction of the former group. Some of these species showed a positive correlation with the second axis; *Halichoeres bivittaus*, *Chaetodon capistratus*, and *Abudefduf saxatilis* were included in this group. These species are best represented in the group of samples from shallow sites of Havana reef. Another group of species that were negatively correlated with the first axis were also negatively correlated with the second axis. These were *Stegastes dorsopunicans*, *Microspathodon chrysusrus* and *Halichoeres radiatus*, dominant in the Herradura sites. A third group of highly correlated species is formed by *Chaetodon sedentarius*, *Chromis multilineatus* and *Chaetodon ocellatus*. These species are not correlated with depth, coral or gorgonians, but show a clear, high correlation with sponge density. The respective arrows form sharp acute angles with the second ordination axis. Deep sites from Havana reef have clearly the highest ranks of these species, particularly those from zone 1. Additionally, these sites rank very low on arrows representing *Stegastes partitus*, *Halichoeres garnoti* and *Chromis cyanea*, which are abundant in the rest of the deep sites. A final remark should be made on *Thalassoma bifasciatum*, the most abundant species in the samples. This species was very abundant in almost all groups of samples (Fig. 3) and therefore has a low discriminatory value. This fact is reflected in the short length of the respective arrow.

Discussion

There was a high coincidence between the results obtained by cluster analysis and MDS ordination on one side and redundancy analysis on the other side. Reasons for this conclusion can be summarized as: A primary separation of shallow and deep samples was evident with both methods.
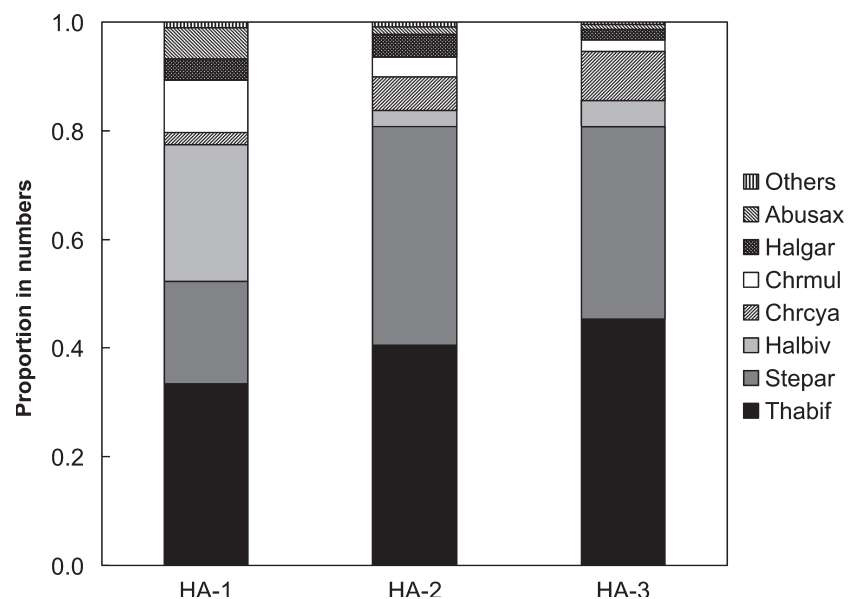

Fig. 5. Species composition of samples taken at Havana reef terrace habitat (year seasons pooled). Species labels formed by first three letters of genus and specific names
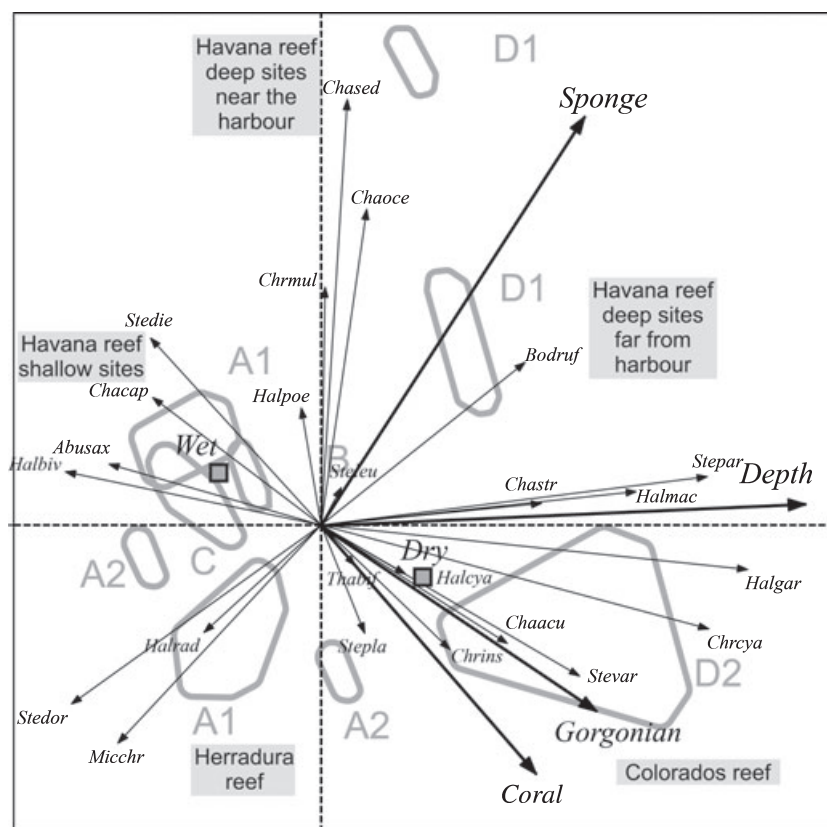
Fig. 6. RDA biplot of species and environmental variables. Species represented by thinner, smaller arrows and their labels formed by first three letters of genus and specific names. Environmental variables symbols as in Fig. 4

Inside deep samples, those from Colorados formed a well differentiated group after the two methods. Samples from shallow sites were grouped slightly differently by both methods, but this difference was highly irrelevant because similar patterns could be extracted from both of them. The only important difference between the results was in the positioning of the Havana reef zone 1 (CH1) deep samples. The constraining nature of RDA allowed sponge density to influence the positioning of these samples, giving a better picture of subtle differences in species composition. The use of both approaches together allow a better interpretation of data in our case.

The main variable explaining variation of fish assemblages in studied reefs is depth. Other authors have also found depth to be an important factor structuring reef fish assemblages (Aguilar et al., 2004; Arias-González et al., 2006; Brokovich et al., 2006). Other ecological factors related to depth and not included in our analyses could have an influence in the distributional patterns observed. Bianchi (1991) pointed out that depth is a spurious variable that integrates many ecological factors (e.g. light intensity, magnitude of wave action, temperature, oxygen concentration). Several authors emphasize main natural factors that can be identified as influencing the fish distribution among habitat types. These factors are water motion (Hilomen and Gomez, 1988) and type and complexity of substrate of the bottom from coral growth and other sessile organisms forming the reef (Chabanet et al., 1997; Lirman, 1999; Floeter et al., 2007). All of these factors are strongly correlated with depth, which is reflected in the zonation of bottom communities as bands running parallel to the shore (Nuñez-Lara and Arias-González, 1998; Aguilar et al., 2004). In our study, we found that colony densities of coral and gorgonians are strongly associated with depth. In spite of its spurious character as an explaining factor, it is

convenient to isolate depth as an important explanatory variable when trying to find which factors influence the composition of reef fish assemblages in a particular region. This is an important fact to keep in mind when designing new sampling and monitoring studies for controlling the effects of natural variation in target assemblages.

We found that sponge density was highly correlated with the second canonical ordination axis and made an additional, significant contribution to the explanatory model. We hypothesize that high sponge density is reflecting high organic pollution. Several authors agree in considering a positive relationship of sponge biomass with organic pollution and high sediment load (Chalker et al., 1985; Rogers, 1990; Wilkinson and Cheshire, 1990; Ward-Paige et al., 2005; Costa et al., 2008). Sponges feed mainly by filtration, targeting mainly ultraplankton. For this reason, land runoff and organic pollution in moderate concentration may benefit sponges by providing nutrients for the increased food bacteria (Rützler, 2004). Concerning the nutrient and sediment increase, sponges and corals can be seen as opposites, with coral biomass decreasing in reefs stressed by pollution and siltation (Aerst and van Soest, 1997; Nughes and Roberts, 2003). Sponge cover was negatively correlated with hard coral cover in the Florida Keys (Maliao et al., 2008). These results and statements from other authors match well with our findings.

Havana Harbor may be the most polluted coastal marine habitat in Cuba, with untreated discharges of crude oil and related substances, sewage, industrial effluents, and heavy metals (UNEP, 2004). Reef site CH1 is under the direct influence of the harbor discharge and presumably receiving large quantities of organic matter and nutrient-enriched waters (Aguilar et al., 2007). The high abundance of sponges and low densities of coral and gorgonians in deep sites (terrace) of this reef could be explained by a potentially high pollution level.

On the other hand, shallower sites of the same reef (*Echinometra* layer and rocky plain) are subject to periodical strong water movements in this unprotected coast. Specially stressing is the wave action produced seasonally by cold fronts (December–April), with strong winds blowing almost perpendicularly to the coastline from sea to land. In this case growth of all sessile animals (i.e. sponges, gorgonians, corals) is depressed in spite of high organic pollution. This is perhaps the most plausible explanation for the different position of the Havana city reef deep sites along the second ordination axis.

In summary, we found that the two different multivariate techniques did not differ significantly in their results when analyzing the same data set. Furthermore, we showed that the combined use of different multivariate techniques enhanced the interpretation of fish assemblage composition changes. The main axis of variation was associated with depth and coral and gorgonian densities. A second source of variation was associated with sponge density.

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