RESEARCH ARTICLE

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Multivariate analysis of the bentho-demersal ichthyofauna along soft bottoms of the Eastern Atlantic: comparison between unvegetated substrates, seagrass meadows and sandy bottoms beneath sea-cage fish farms

Abstract By means of multivariate techniques, we studied: (1) the differences in the structure of bentho-demersal, non-cryptic, fish assemblages associated with unvegetated sandy substrates, vegetated meadows constituted by the seagrass *Cymodocea nodosa* and the bottoms under the influence of sea-cage fish farms; as well as (2) the persistence of these patterns with regard to different scales of spatial variability, across three islands of the Canarian Archipelago (Central East Atlantic). Our sampling strategy (involving three islands, with five locations per island, and two sites within each location) detected significant changes in the composition and structure of the fish assemblages between the three habitats. Fish assemblages associated with the unvegetated and vegetated bottoms were similar among the surveyed islands. In contrast, we observed a significant inter-island variability in the fish populations associated with the sea-cage fish farms. The presence of the sea-cage fish farms increased the overall fish abundance (184.8 ± 49.8 ind 100 m^{-2}) as compared to both the vegetated (38.8 ± 9.7 ind 100 m^{-2}) and unvegetated habitats (1.1 ± 0.4 ind 100 m^{-2}). Differences within and between the habitats were found to be associated with the relative abundance of a few fish species. The most abundant species were *Xyrichthys novacula* in the unvegetated bottoms and *Diplodus annularis*, *Spondyliosoma cantharus* and *Mullus surmuletus* on the seagrass meadows. Finally, we recorded an increase in the abundance of *Heteroconger longissimus*, *Trachinus draco* and *Pagellus acarne* in the bottoms beneath the sea-cage fish farms. These species, in addition to a group of large benthic chondrichthyes, were responsible for the differences between islands in the composition and structure of the demersal ichthyofauna beneath the sea-cage fish farms.

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Introduction

The structural complexity of coastal habitats has been shown to play a major role in structuring fish assemblages (Kingsford and Battershill 1998; Garcia-Charton and Perez-Ruzafa 1999; Kaiser et al. 1999; Guidetti and Bussoti 2002; Mora et al. 2003; Anderson and Millar 2004 and references therein; Garcia-Charton et al. 2004).

Inshore sandy substrata are homogeneous environments that often support fish populations with lower abundance and richness than the nearby substrates with higher structural complexity (Jenkins and Wheatly 1998; Guidetti 2000; Guidetti and Bussoti (2002) and references therein; Pihl and Wennhage 2002). The existence of elements that increase the structural complexity of the substrate contribute to qualitative and quantitative changes in the composition and structure of the fish populations, such as the presence of seagrass beds (Francour 1994; Mcpherson 1994; Guidetti 2000 and references therein; Pihl and Wennhage 2002) or artificial reefs (for a review, see Bohnsack 1989). The installation of offshore fish cages in coastal areas provides a significant increase in the structural complexity of sandy bottoms, as analogous to large fish attraction devices (FADs) (Dempster et al. 2002; Boyra et al. 2004). The floating cages provide structure in the pelagic environment, although the unused portion of the fish feeding pellets that passes through the cages probably enhances

their attractive effect through additional nutrient inputs. In the case of the latter, an extensive research has documented the environmental effects of marine fish farms in inshore waters, as they are a source of organic matter into the system (Iwama 1991; Rönenberg et al. 1992; Karakassis et al. 1999; Ruiz et al. 2001; Alongi et al. 2003).

While numerous studies have analyzed the ichthyofauna associated with specific coastal habitats in temperate soft bottoms, investigations involving the comparison of different habitats across a specific geographical range are lacking (Guidetti 2000). No study has assessed the differences in the fish faunas associated with different shallow habitats throughout the Macaronesian region. Additionally, a key aspect of understanding the spatial distributions of fish in relation to habitat characteristics is to recognize that the observed patterns are dependent on the spatial scale of observation (Underwood and Chapman 1996; Benedetti-Cecchi 2001; Anderson and Millar 2004). It may not be possible to understand the effect of the habitat, which is a spatial phenomenon involving both patchiness and heterogeneity, without an understanding of variability at different spatial scales (Underwood and Chapman 1996; Anderson and Millar 2004).

The purpose of the present investigation was to conduct a mensurative observational experiment (sensu Hulbert 1984; Underwood 1997) to test the hypothesis of whether changes in the habitat complexity may alter the composition and structure of the demersal fish assemblages associated with soft bottoms. Specifically, the goals were: (1) to compare the structure of the ichthyofauna associated with sandy unvegetated substrates with those on vegetated seagrass meadows and on unvegetated sandy bottoms under the influence of marine sea-cage farms; and (2) to assess the effect of different hierarchically organized sources of spatial variability (islands and locations within islands) on those patterns related to the habitat.

Materials and methods

Sampling design and study locations

Our sampling strategy involved the spatial analysis of the fish assemblages associated with three types of habitat: (1) unvegetated sandy substrates with no overlying fish farm; (2) vegetated seagrass beds; and (3) sandy bottoms beneath the sea-cage fish farms, in three islands of the Canarian Archipelago separated between 60 km and 200 km (Gran Canaria, Tenerife and Lanzarote; 28°N; Central East Atlantic; Fig. 1) during March 2003. We selected five locations in each island: an unvegetated substrata beneath a sea-cage fish farm (dedicated to the culture of both *Sparus aurata* and *Dicentrarchus labrax*), two unvegetated sandy substrate locations, and two seagrass meadows consisting of a continuous habitat (100% vegetated coverage) of the

marine phanerogam *Cymodocea nodosa* Ucria (Aschers). Two sites separated by hundreds of meters were sampled in each location. Depth ranged between 15 m and 20 m.

Estimation of fish assemblages abundance

We sampled non-cryptic, diurnally exposed, benthodemersal fish populations (size of individuals > 2 cm) by means of visual census techniques. At each sampling site, in each location, four replicate 25-m transects were haphazardly laid during daylight hours. The abundance of each fish species was recorded on a waterproof paper by a SCUBA diver within 2 m of either side of the transects (100 m^2), according to standard procedures (Brock 1982; Lincoln-Smith 1988, 1989; Kingsford and Battershill 1998; Boyra et al. 2004; Tuya et al. 2004). Although our sampling technique was biased towards large- and slow-swimming individuals, it was selected among the available visual methods as the more appropriate. Fish abundance was estimated based on a modification of the method presented by Harmelin-Vivien et al. (1985). As fishes were grouped in schools larger than 20 individuals, their numbers were estimated according to six abundance classes (20–40, 40–70, 70–150, 150–300, 300–700, > 700).

Statistical analysis

Abundance estimates were highly skewed and contained a great many zero counts, making parametric analysis (which assumes statistical normality) unsuitable. Therefore, we selected non-parametric approaches (Anderson 2001; Anderson and Millar 2004) and applied a mixed analysis technique by combining non-metric multidimensional scaling (MDS) ordination (PRIMER software; Clarke 1993; Clarke and Warwick 1994) and the semi-parametric permutational multivariate analysis of variance (PERMANOVA, Anderson 2004) to test for significant differences between the different habitats and spatial scales.

Differences among the three habitats for the overall multivariate fish dataset were tested by the ANOSIM procedure (Clarke 1993). The PERMANOVA was carried out to test for differences in the structure of the fish assemblages within each habitat with regard to the different spatial scales considered by our sampling design. We selected a two-factor nested design for both unvegetated and vegetated substrates, with "Islands" (three levels corresponding to each island) and "Locations" (two levels and nested within islands). Moreover, we tested for differences among the three islands for the fish assemblages beneath the sea-cage fish farms. In both cases, the data was double square root transformed and the Bray-Curtis dissimilarity index was selected. For the overall multivariate testing techniques, we pooled the data for both sites within each location. The SIMPER procedure (Clarke and Warwick 1994) was additionally
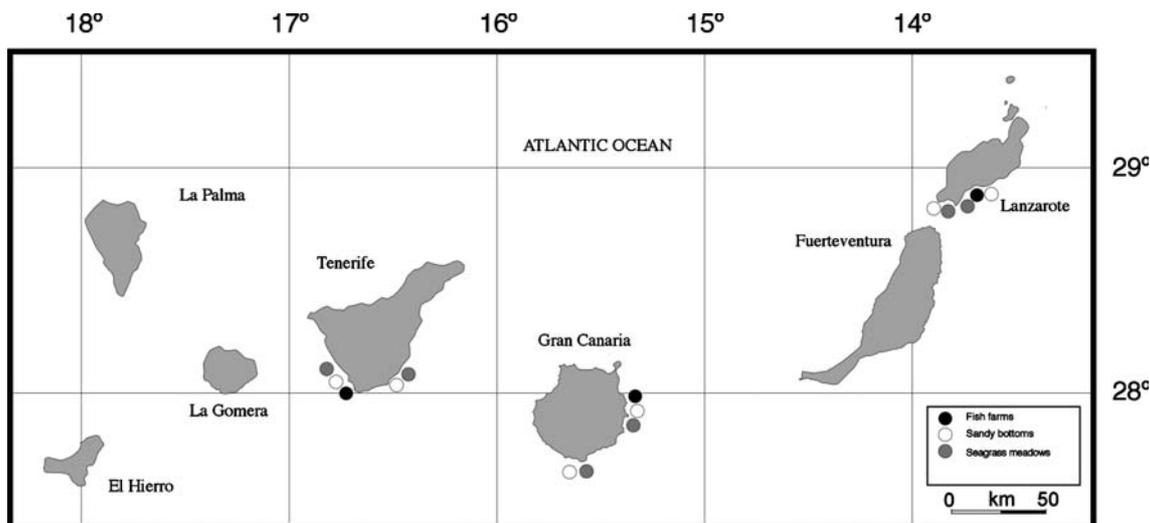
Fig. 1 Map of the study area showing sampled locations within each island

carried out to identify the contribution of each fish species to the differences within and between the studied habitats. The abundance of the prominent species was graphically represented for each habitat and island.

Results

Differences among habitats

The mean total abundance of littoral bentho-demersal fish across the studied soft bottoms of the Canarian Archipelago was four to five times higher under the influence of sea-cage fish farms (184.8 ± 49.8 ind 100 m^{-2}) in comparison with seagrass meadows (38.8 ± 9.7 ind 100 m^{-2}), and about 200 times greater than unvegetated sandy substrates (1.1 ± 0.4 ind 100 m^{-2}) (Fig. 2). However, mean fish richness was

similar between the substrates under the influence of sea-cage fish farms (3.33 ± 1.18 species) and the seagrass beds (2.98 ± 0.53) (Fig. 3), being higher than the mean richness detected at unvegetated bottoms (0.54 ± 0.22). These overall differences have been reflected with the significance of the R statistic associated with the ANOSIM test (Global R-statistic = 0.607, P < 0.01). Thus, the two-dimensional MDS revealed a clear separation of locations along the ordination diagram (Fig. 4).

The SIMPER procedure indicated which species contributed most importantly to the differences within and between habitats for the entire study. *Xyrichthys novacula* was the most common species across unvegetated sandy substrata and accounted 84.67% of the overall similarity (Fig. 5). *Diplodus annularis*, *Spondyliosoma cantharus* and *Mullus surmuletus* were the most abundant species, respectively, over *C. nodosa* meadows (69.94% of accumulated similarity) (Fig. 5). Finally, the abundance of *Heteroconger longissimus*, *Trachinus draco* and *Pagellus acarne* exhibited an increase in the sandy substrata beneath sea-cage fish farms (88.54% of accumulated similarity) (Fig. 5).
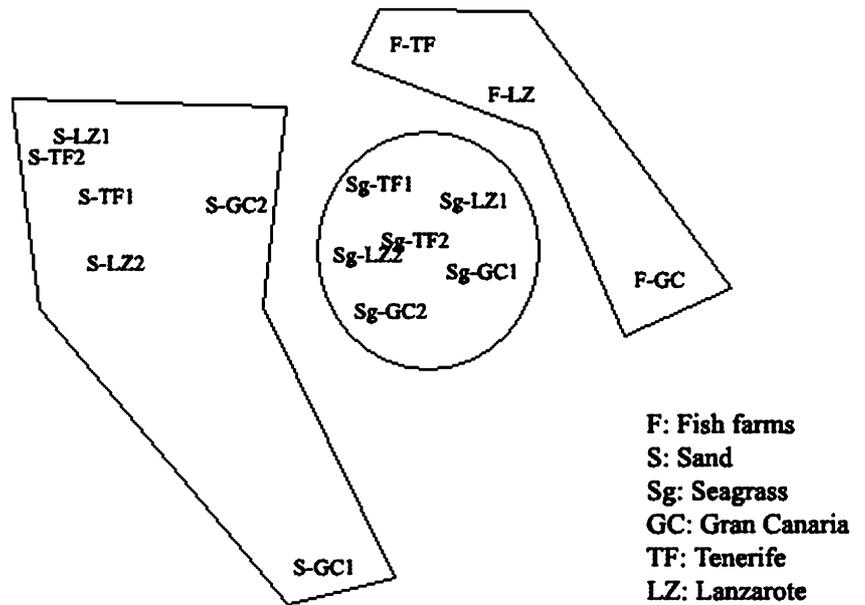
Fig. 2 Mean fish abundance associated to each habitat. *Error bars* indicate standard error of the means
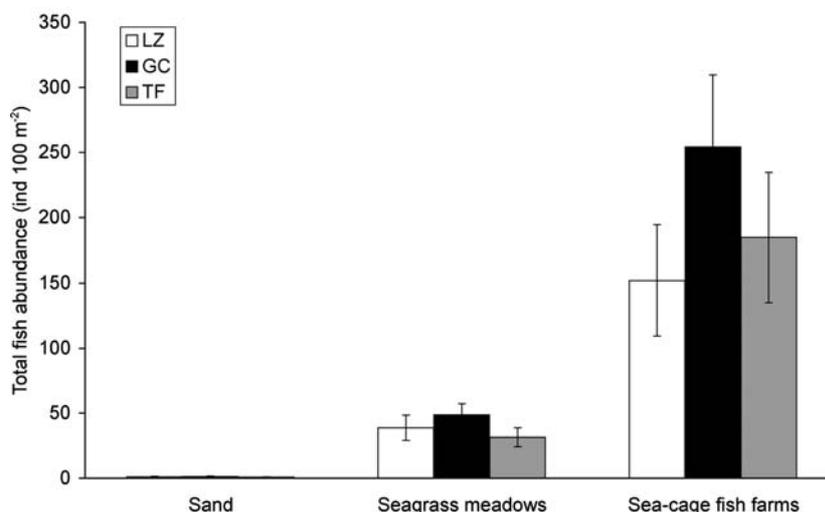
Fig. 3 Mean fish richness associated to each habitat. *Error bars* indicate standard error of the means
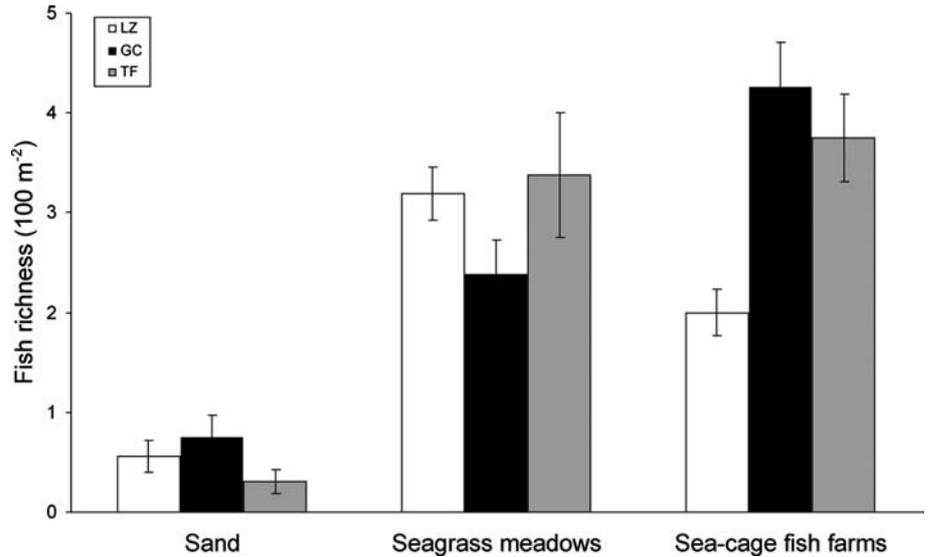
Fig. 4 Bidimensional ordination plot (MDS) of fish species abundance data at each location within each island

The dissimilarity between the species composition over the unvegetated substrates and the sandy substrata beneath the marine farms was 97.73%, compared to a 92.56% between the seagrass beds and the fish farms. In both cases, the high abundance of the species *H. longissimus* and *P. acarne* beneath the sea-cage fish farms were responsible for these dissimilarities, accumulating 58.71% and 43.93 % of the dissimilarity, respectively (Fig. 5). The lack of individuals of *X. novacula*, *D. annularis* and *S. cantharus* in the "fish farm" locations, and the high abundance of these species at both unvegetated and vegetated substrates (Fig. 5), also contributed to the dissimilarity between the demersal fish assemblages associated with the sea-cage fish farms and at the unvegetated and vegetated bottoms. In addition, the sparids *D. annularis* and *S. cantharus* were the spe-

cies that contributed most to the differences between the unvegetated substrates and the seagrass meadows (46.69% of accumulated dissimilarity) (Fig. 5). Finally, we detected the attraction of a group of large-sized benthic chondrichthyes (*Dasyatis* spp., *Taenuria grabata* and *Gymmura altavela*) on the sandy substrata under the influence of the fish farms. However, their low abundances resulted in them making only a small contribution to the dissimilarities within and between the studied habitats.

Differences among islands

As indicated by the PERMANOVA, the composition and structure of the fish assemblages associated with
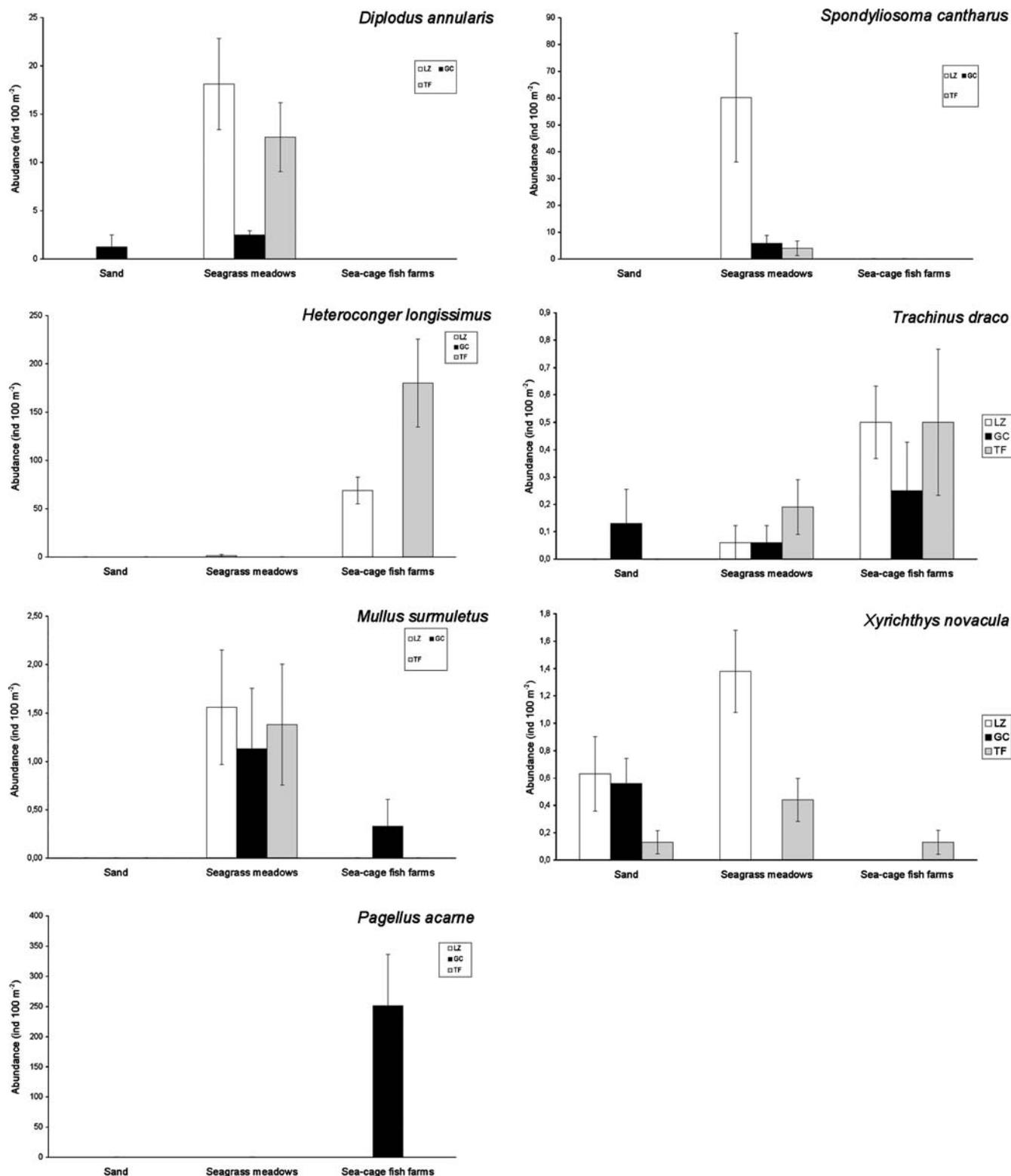
Fig. 5 Abundance of fish species that most contribute to differences between habitats. *Error bars* indicate standard error of the means

both unvegetated and vegetated substrates were similar among the three islands ($P > 0.05$, Table 1). Nevertheless, we detected significant differences between both locations within each island ($P < 0.01$, Table 1) for both unvegetated and vegetated habitats. These results clearly contrast with that obtained for the substrata under the influence of the marine fish farms, as significant differences were found in the structure of the associated ichthyofauna among the islands ($P < 0.01$, Table 1). As indicated by SIMPER, the species

Table 1 PERMANOVA results for each habitat contrasting the null hypothesis of absence of differences in the composition and structure of fish assemblages with regard to islands and sampled locations within each island

Source of variation	Unvegetated substrates			Seagrass meadows			Bottoms beneath sea-cage fish farms		
	df	MS	F	df	MS	F	df	MS	F
Islands	2	5,614.22	0.52	2	10,932.84	1.06	2	19,604.99	12.89*
Locations (Islands)	3	10,763.26	4.44*	3	10,227.88	5.29*	–	–	–
Residual	42	2,423.38		42	1,931.78		21	1,520.71	

*$P < 0.01$

responsible for these differences were: *P. acarne*, *G. altavela* and *Myliobatis aquila* in Gran Canaria, *H. longissimus* in Tenerife, and *H. longissimus* and *T. grabata* in Lanzarote (Fig. 6). Thus, *P. acarne*, *H. longissimus* and *G. altavela* accumulated 58% of dissimilarity between Gran Canaria and Tenerife; *H. longissimus* and *T. grabata*, 44.97% of dissimilarity between Lanzarote and Tenerife; and *H. longissimus*, *P. acarne* and *T. grabata*, 52.11% of dissimilarity between Gran Canaria and Lanzarote.

Fig. 6 Abundance of fish species that most contribute to differences among sea-cage fish farms. *Error bars* indicate standard error of the means
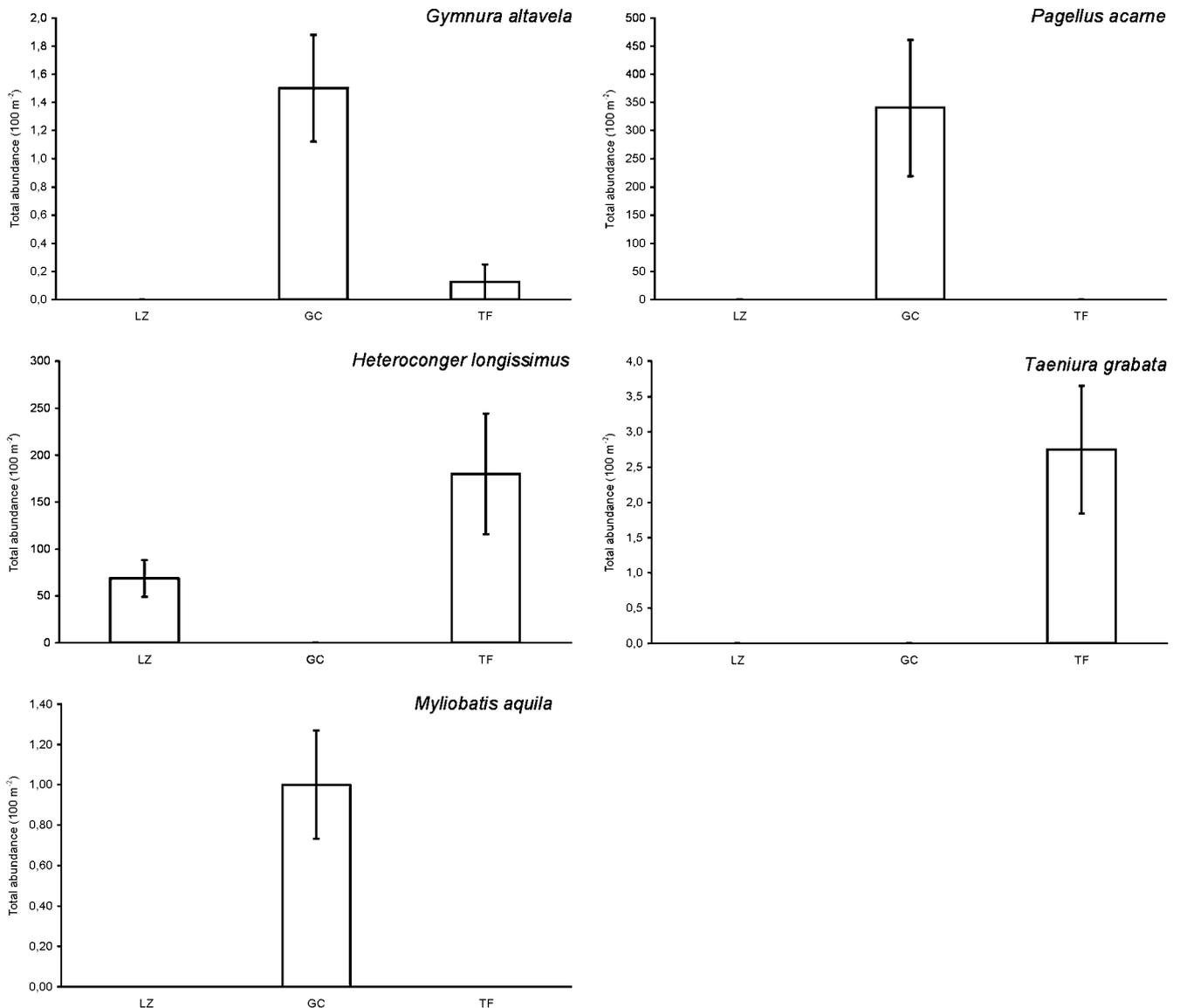
Discussion

Our study has highlighted an important change in the composition and structure on the bentho-demersal, non-cryptic, ichthyofauna exposed to the census-taker associated with each type of habitat, two natural and one human-influenced. Therefore, clear qualitative and quantitative differences in the overall distribution and abundance of fish populations associated with the different types of soft bottoms across the Canarian Archipelago have been found: this supports the hypothesis that physical structure per se is one of the main factors affecting nearshore fish assemblages (Guidetti 2000).

Differences between unvegetated and vegetated substrates

Detection of inter-habitat variability in the composition and structure of fish assemblages between both unvegetated and vegetated systems is widely acknowledged across temperate waters, as for example in the Mediterranean (Guidetti 2000; Guidetti and Bussotti 2000, 2002), or the Australasian regions (Bell and Pollard 1989; Conolly 1994; Gray et al. 1998; Jenkins and Wheatly 1998). The higher species richness and overall fish abundance on soft vegetated bottoms (seagrass beds) compared to unvegetated substrates reported here has been extensively explained elsewhere by a higher degree of structural complexity and productivity (Guidetti 2000 and references therein). Seagrasses supply many niches for fishes, providing a fixed substrate as shelter and favouring the establishment of epiphytic algae and sessile invertebrates that are consumed by higher trophic levels (Bell and Pollard 1989; Klumpp et al. 1989; Jenkins and Wheatly 1998; Guidetti 2000; Guidetti and Bussoti 2002). Moreover, seagrass beds often exert a paramount role as nursery grounds for juveniles of many inshore fish populations (Bell and Pollard 1989; Guidetti and Bussotti 2000).

The habitat-associated distribution patterns of fish detected by our study are consistent with other data reported from the Mediterranean comparing sandy substrates and small-sized seagrasses as *C. nodosa* beds (Guidetti and Bussotti 1997, 2000, 2002). In this sense, our results have shown that in comparison to the unvegetated habitats, the sparids *D. annularis* and *S. cantharus*, as well as *M. surmuletus*, are almost exclusively found and are an important component of the fish assemblages over *C. nodosa* seagrass meadows, as Tuya et al. (2002) observed in the Canary Islands. This fact suggests that these species appear to have specific habitat requirements, since their distribution patterns among habitats did not vary from island to island.

The most conspicuous species across unvegetated sandy substrates was the labrid *X. novacula*, which can be found likewise over seagrass and sandy bottoms beneath sea-cage fish farms. Therefore, this species appears to show a clear ubiquitous pattern across different types of soft bottoms in the islands studied.

Fish assemblages associated with both vegetated (seagrass systems) and unvegetated substrates have shown a homogeneous pattern with regard to the largest spatial scale considered in our sampling strategy: differences among islands. Consequently, it is worth noting that the organization patterns (structure and composition) of the inshore demersal fish fauna appear to be similar across a geographic range from 10s to 100s of kilometres along the Canarian Archipelago. In contrast, multivariate techniques have detected significant differences in the structure of the fish assemblages between locations within islands. Although it could be interpreted as a response to the high power of the multivariate analysis (Anderson 2001), this inter-location variability could indicate the natural patchiness of wild populations across space in response to small-scale habitat heterogeneity (Benedetti-Cecchi et al. 2001 and references cited therein), as well as differences in the environmental context of locations within islands. Thus, differences in the fishing pressure, degree of water turbulence, and especially, the mosaic of marine habitats that surround each location and the connectivity among them (sensu Van Elven et al. 2004) are important determinants of this inter-location variability. Moreover, this patchiness could also be influenced by ecological features of each taxa and/or assemblage. In this sense, these processes could mask the finding of inter-habitat variability in the composition and structure of fish assemblages at extreme situations (e.g., Heck and Thoman 1984).

Attraction of wild fish to sea-cage fish farms

This study has shown the attraction and increase in the abundance of a certain group of bentho-demersal wild fish populations to soft bottoms beneath sea-cage fish farms in the Canarian Archipelago. This result is in agreement with the observations recently reported by Boyra et al. (2004) for the island of Gran Canaria and Dempster et al. (2002) and Machias et al. (2004) in the Mediterranean. The persistent artificial food input and the chemical attraction due to the presence of farmed fish may influence which species of wild fish will be associated with farms (Dempster et al. 2002). Both these factors, in addition to the increase in habitat complexity, have been considered as responsible for the increase in fish abundance relative to nearby sandy bottoms with no overlying fish farm (Dempster et al. 2002; Boyra et al. 2004; Machias et al. 2004) with an effect size quantified in terms of hundreds of fish individuals per 100 m^2.

The overall fish abundance is dominated by the osteichthyes *H. longissimus* and *P. acarne*, as well as to a group of large-sized benthic chondrichthyes (*T. grabata*, *M. aquila* and *G. altavela*): these species are principally responsible for the differences in the composition of the

fish assemblages associated to the benthos beneath each sea-cage fish farm at each island. Consequently, this result reflects the significance of spatial variations with regard to the largest spatial scale considered in our study: differences between islands (10s of kilometres apart), as observed along 10s of kilometres for the western Mediterranean (Dempster et al. 2002). These differences can be attributable to: (1) differences in the input of organic matter into the system; (2) untested physical factors intrinsic to each farm; and particularly (3) the marine habitats that surround each fish farm (Dempster et al. 2002; Boyra et al. 2004). Th e presence and abundance of some species may change the fish assemblage structure around the cages, depending on the species that turn up first (Dempster et al. 2002). This fact has been extensively reviewed in the literature on artificial reefs (e.g., Bohnsack 1989).

Regional authorities have planned future development on the installation of several fish farms along the Canarian Archipelago, but without any scientific support. Consequently, there is an urgent need for baseline information on the fish species that have the potential to associate with sea-cage fish farms. Although the approach used in our study (visual census) enabled us to characterize the associated fish populations around sea-cage fish farms, further research requires an approach based on each particular case. Thus, knowledge of movements of fish around farms, estimates of residency times, as well as feeding behaviour studied through stomach contents may be the key factors to achieve a general idea on their role in the dynamics of coastal fish farms.

References

Alongi DM, Chong VC, Dixon P, Sasekumar A, Tirendi F (2003) The influence of fish cage culture on pelagic carbon flow and water chemistry in tidally dominated mangrove estuaries of Peninsular Malaysia. Mar Environ Res 55:313–333

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance in ecology. Aust Ecol 26:32–46

Anderson MJ (2004) PERMANOVA_2factor: a FORTRAN computer program for permutational multivariate analysis of variance (for any two-factor ANOVA design) using permutation tests. Department of Statistics, University of Auckland, New Zealand

Anderson MJ, Millar RB (2004) Spatial variation and effects of habitat on temperate reef assemblages in north eastern New Zealand. J Exp Mar Biol Ecol 305:191–221

Bell JD, Pollard DA (1989) Ecology of fish assemblages and fisheries associated with seagrasses. In: Larkum AWD, McComb AJ, Shepherd SA (eds) The biology of seagrasses: an Australian perspective. Elsevier, Amsterdam, pp 565–609

Benedetti-Cecchi L (2001) Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. Mar Ecol Prog Ser 215:79–92

Bohnsack J (1989) Are high densities of fishes at artificial reefs the results of habitat limitation or behavioural preference? Bull Mar Sci 44:631–645

Boyra A, Sanchez-Jerez P, Tuya F, Espino F, Haroun RJ (2004) Attraction of wild coastal fishes to cage fish farms on Atlantic subtropical latitude (Gran Canaria, Canary Islands). Environ Biol Fish 70:393–401

Brock RE (1982) A critique of the visual census method for assessing coral reef fish populations. Bull Mar Sci 32:269–276

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, United Kingdom

Conolly RM (1994) A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australian estuary. Aust J Mar Fresh Res 45:1033–1044

Delgado O, Ruiz JM, Perez M, Romero J, Ballesteros E (1999) Effects of fish farming on seagrass (*Posidonia oceanica*) in a Mediterranean Bay: seagrass decline after organic loading cessation. Oceanol Acta 22:109–117

Dempster T, Sanchez-Jerez P, Bayle-Sempere JT, Jimenez F, Valle C (2002) Attraction of wild fish to sea-cage fish farms in the south-western Mediterranean Sea: spatial and short-term temporal variability. Mar Ecol Prog Ser 242:237–252

Francour P (1994) Pluriannual analysis of the reserve effect on fish community in the Scandola natural reserve (Corsica, North-western Mediterranean). Oceanol Acta 17:309–317

Garcia-Charton JA, Perez-Ruzafa A (1999) Ecological heterogeneity and the evaluation of the effects of marine reserves. Fish Res 42:1–20

Garcia-Charton JA, Perez-Ruzafa A, Sanchez-Jerez P, Bayle-Sempere JT, Reñones O, Moreno D (2004) Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. Mar Biol 144:161–182

Gray CA, Chick RC, McElligot DJ (1998) Diel change in assemblages of fishes associated with shallow seagrass and bare sand. Estuar Coast Shelf Sci 46:849–859

Guidetti P (2000) Differences among fish assemblages associated with nearshore *Posidonia oceanica* seagrass beds, rocky-reefs and unvegetated sand habitats in the Adriatic Sea. Estuar Coast Shelf Sci 50:515–529

Guidetti P, Bussotti S (1997) Recruitment of *Diplodus annularis* and *Spondyliosoma cantharus* in shallow seagrass beds along the Italian coasts (Mediterranean Sea). Mar Life 7:47–52

Guidetti P, Bussotti S (2000) Fish fauna of a mixed meadow composed by the seagrass *Cymodocea nodosa* and *Zostera noltii* in the Western Mediterranean. Oceanol Acta 23:759–770

Guidetti P, Bussotti S (2002) Effects of seagrass canopy removal on fish in shallow Mediterranean seagrass (*Cymodocea nodosa* and *Zostera noltii*) meadows: a local-scale approach. Mar Biol 140:445–453

Harmelin-Vivien ML, Harmelin-Vivien JG, Chauvet C, Duval C, Galzin R, Lejeune P, Barnabé G, Blanc F, Chevalier J, Duclerc J, Lasserre G (1985) Evaluation visuelle des peuplements et populations de poissons: méthodes et problèmes. Terre Vie 40:467–539

Heck KL, Thoman TA (1984) The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. Estuaries 7:70–92

Hulbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecol Monogr 54:187–211

Iwama GI (1991) Interactions between aquaculture and the environment. Crit Rev Environ Control 21:177–216

Jenkins GP, Wheatly MJ (1998) The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: comparison of shallow seagrass, reef algal and

unvegetated sand habitats, with emphasis on their importance to recruitment. J Exp Mar Biol Ecol 221:147–172

Kaiser MJ, Rogers SI, Ellis JR (1999) Importance of benthic habitat complexity for demersal fish assemblages. Proc Am Fish Soc 22:212–223

Karakassis I, Hatziyanni E, Tsapakis M, Plaiti W (1999) Benthic recovery following cessation of fish farming: a series of successes and catastrophes. Mar Ecol Prog Ser 184:205–218

Kingsford M, Battershill C (1998) Studying marine temperate environments: a handbook for ecologists. Canterbury University Press, Christchurch

Klumpp DW, Howard RK, Pollard DA (1989) Trophodynamics and nutritional ecology of seagrass communities. In: Larkum AWD, McComb AJ, Shepherd SA (eds) The biology of seagrasses: an Australian perspective. Elsevier, Amsterdam, pp 394–457

Lincoln-Smith MP (1988) Effects of observer swimming speed on sample counts of temperate rocky reef fish assemblages. Mar Ecol Prog Ser 43:223–231

Lincoln-Smith MP (1989) Improving multispecies rocky reef fish censuses by counting different groups of species using different procedures. Environ Biol Fish 26:29–37

Machias A, Karakassis I, Labropoulou M, Somarakis S, Papadopoulou KN, Papaconstantinou C (2004) Changes in wild fish assemblages after the establishment of a fish farming zone in oligotrophic marine ecosystem. Estuar Coast Shelf Sci 60:771–779

McPherson E (1994) Substrate utilization in a Mediterranean littoral fish community. Mar Ecol Prog Ser 114:211–218

Mora C, Chittaro PM, Sale PF, Kritzer JP, Ludsin SA (2003) Patterns and processes in reef fish diversity. Nature 421:933–936

Pihl L, Wennhage H (2002) Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish west coast. J Fish Biol 61:148–166

Rönenberg O, Adjers K, Ruokolahti C, Bondestam M (1992) Effect of fish farming on growth, epiphytes and nutrient contents of *Fucus vesiculosus* L. in the Aland Archipelago, Northern Baltic Sea. Aqua Bot 42:109–120

Ruiz JM, Perez M, Romero J (2001) Effects of fish farm loadings on seagrass (*Posidonia oceanica*) distribution, growth and photosynthesis. Mar Poll Bull 42:749–760

Tuya F, Martin JA, Luque A (2002) Impact of a marina construction on a seagrass bed at Lanzarote (Canary Islands). J Coast Cons 8:157–162

Tuya F, Boyra A, Sanchez-Jerez P, Barbera C, Haroun RJ (2004) Relationships among fishes, the long-spined sea urchin *Diadema antillarum* and algae throughout the Canarian Archipelago. Mar Ecol Prog Ser 278:157–169

Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge

Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution on intertidal invertebrates. Oecologia 107:212–224

Van Elven BR, Lavery PS, Kendrick GA (2004) Reefs as contributors to diversity of epiphytic macroalgae assemblages in seagrass meadows. Mar Ecol Prog Ser 276:71–83