# Micro- and macroscale factors affecting fish assemblage structure in the rocky intertidal zone

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ABSTRACT: Intertidal fish are adapted to live in a fluctuating environment and are considered suitable bioindicators of environmental change. Understanding the relationship between fish species distribution and environmental variables is fundamental for comparative analysis among geographical locations and identification of long-term trends predicted by global warming. Here we analysed a combination of the main micro- and macroscale factors that affect the distribution and abundance of rocky intertidal fish communities. Monthly sampling of fish assemblages at 3 sites in the rocky intertidal zone of the Gulf of Cadiz was conducted from 2008 to 2014. Fish assemblage descriptions were based on relative abundance, biomass, diversity and evenness. A canonical correspondence analysis was performed to evaluate the relationship between pool characteristics (substratum type, depth and surface area) and the abundance of fish assemblages in tidepools. The results showed differences between protected and unprotected sites, which may indicate that human pressure induces changes at all assemblage levels. At all sites, the lowest abundance was observed in the year with the greatest wave energy. The diversity at the 3 sites showed interannual variation correlated with pool complexity, wave energy and air temperature. These findings increase our understanding of the mechanisms that regulate the distribution of fish assemblages in shallow coastal waters and provide a useful baseline for future management and conservation of these areas.

KEY WORDS: Intertidal fishes  $\cdot$  Community structure  $\cdot$  Interannual variability  $\cdot$  Microhabitat preferences  $\cdot$  Environmental parameters  $\cdot$  Gulf of Cadiz

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# 1. INTRODUCTION

Biogeographic transition zones in marine temperate ecosystems are often hotspots of biodiversity, with high levels of resilience to short-term climate shifts as a result of naturally occurring, cyclic oscillations of oceanographic conditions (Horta e Costa et al. 2014). Given that the relationships between fish populations and their environment or habitat are seasonally and spatially dynamic (Koutrakis et al. 2000, Morrison et al. 2002), fish assemblage composition and species distribution in temperate areas will vary depending on species life-history strategies and habitat requirements. However, although habitat connectivity exerts a significant effect on the structure of biological communities (Vega Fernández et al. 2008), not all temperate fish species respond similarly to every type of habitat variable, and different species may react in a specific way to some environmental variables but not others (Wellenreuther et al. 2007).

Shifts in the structure of fish assemblages on rocky shores have been reported both across tidal zones (Faria & Almada 2006, 2008) and among seasons (Drake & Arias 1991, Faria & Almada 2006). However, because the abundance of fish species with a short lifespan depends on annual recruitment, it is necessary to determine the inter-annual variability in their abundance to achieve a better understanding of their population dynamics and community structure. Such information is fundamental to allow comparative analysis among geographical locations and to distinguish between inter-annual fluctuations and long-term trends, such as those predicted by global warming (Gonçalves et al. 2002).

On rocky shores, the main factors that have considerable influence at the microscale level on the fish assemblage composition or structure are substratum type (Nemeth 1998) and its complexity (De Raedemaecker et al. 2010), biocover (Kovačić et al. 2012) and rock pool size (Bennett & Griffiths 1984). In addition to micro-habitat availability, several environmental factors contribute to fish assemblage structure at different spatial and temporal scales. The major macroscale factors defining the fish community structure are seasonal oscillations in temperature (Horn et al. 1999), wave exposure (Arreola-Robles & Elorduy-Garay 2002), wind stress and currents (Horta e Costa et al. 2014). In the Gulf of Cadiz, Spain, and most notably along our study area on the coast of Cadiz, wind speed may be a major factor affecting hydrodynamic conditions (Benavente 2000) and marine processes that shape the coastline (Del Río et al. 2008). Apart from abiotic factors, changes in fish assemblage structure can be affected by biotic factors such as predation and intra- and interspecific competition. On the other hand, in addition to natural processes, fish assemblage composition also responds to human pressures (McKinley & Johnston 2010 and references therein) and the establishment of protected areas (Willis & Anderson 2003).

Understanding the relationship between species distribution and environmental variables allows the identification of the ecological processes that regulate different populations and communities (Chaudhuri et al. 2013). Therefore, the overall goal of this study was to investigate how the combination of microhabitat characteristics, air and water temperature, wind speed and wave energy conditions will affect the distribution and abundance of rocky intertidal fish. Our specific objectives were to (1) characterise the structure of a fish assemblage in the Gulf of Cadiz, (2) assess its inter-annual variability and (3) analyse the relation between fish assemblage composition and the type of substratum and other physical environmental variables. This information is useful to improve our understanding of the mechanisms regulating the distribution of a fish assemblage in shallow coastal areas, providing a useful baseline for future management and conservation.

# 2. MATERIALS AND METHODS

## 2.1. Study area and general sampling protocol

Fish assemblages were surveyed at 3 rocky intertidal sites along the coast of the Gulf of Cadiz (Fig. 1). Sampling was carried out during low spring tide, and from 1 to 6 tidal pools were randomly chosen for each monthly collection, starting from January 2008 for El Chato (36° 28' N, 6° 15' W), April 2008 for Caños de Meca (36°11'N, 6°01'W) and July 2008 for Torregorda (36° 26' N, 6° 14' W), and ending at all sites in December 2014. The number of pools sampled each month varied according to pool size and the duration of low tide that allowed the sampling process. Yearly numbers of sampled pools at each site are given in Table 1. Torregorda is a restricted, military area, while the other 2 sites allow public access. The subtidal slope at Caños de Meca is steeper than at the other 2 sampling sites, such that a depth of 30 m is reached closer to shore at this site than at the others (Fig. 1). This depth indicates the lower limit of distribution for some resident species (Quignard & Pras 1986, Baensch & Debelius 1997, Kovačić & Golani 2007). All specimens were caught using natural clove essential oil as an anaesthetic at a concentration of  $40 \text{ mg } l^{-1}$  (Griffiths 2000). The water in the pools was stirred with hand nets, and after a short time to allow the anaesthetic to take effect, the boulders were removed to avoid losses, given that some species may remain hidden in deep holes, crevices and under stones (Faria & Almada 1999). Boulders were replaced in the same position after sampling. The use of different techniques other than visual census should be considered whenever cryptobenthic fish species are studied, since all or most of them cannot be recorded by the visual census method (Willis 2001, La Mesa et al. 2004), and hence, both the abundance of these small and highly sedentary species (La Mesa et al. 2006) and their role in the ecosystem

| Site          | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | Surface area (m <sup>2</sup> ) | Depth (m)       | Volume (l)      |  |
|---------------|------|------|------|------|------|------|------|--------------------------------|-----------------|-----------------|--|
| Torregorda    | 14   | 25   | 27   | 29   | 24   | 22   | 22   | $7.47 \pm 6.41$                | $0.19 \pm 0.06$ | $1392 \pm 1168$ |  |
| El Chato      | 35   | 25   | 28   | 24   | 23   | 24   | 22   | $8.29 \pm 5.67$                | $0.19 \pm 0.05$ | $1635 \pm 1207$ |  |
| Caños de Meca | 22   | 27   | 26   | 25   | 23   | 24   | 22   | $15.16 \pm 9.77$               | $0.11 \pm 0.04$ | $1680 \pm 1048$ |  |

Table 1. Number of pools sampled annually, and mean ± SD surface area, depth and volume at each of the 3 study sites

function could be underestimated (Willis 2001). As demonstrated in intertidal rocky pools, the use of anaesthetic (which requires just 2–3 min to sedate the fish) in censuses of fish assemblages has also been reported as the best technique to obtain a complete census of fishes in the sample quadrats (Beldade & Gonçalves 2007, Kovačić et al. 2012).

Given the importance of habitat complexity and characteristics in the distribution of fish species in rocky shores (Faria & Almada 2001), each pool was measured and its physiographic characteristics recorded. The intertidal sampling locations along the coast of Cadiz are composed of cemented Pleistocene deposits formed by alternating laminated



Fig. 1. Study area in the eastern Gulf of Cadiz, Spain. Points indicate the sampling sites, and isolines represent the bathymetry (only bathymetric depths of -30, -20 and -10 m are depicted) according to Sandwell et al. (2001)

sandstones and quartzitic conglomerate (Gracia et al. 2006). Pools are mainly produced by abrasion, because the wave energy and currents drag boulders along the bedrock (Trenhaile 1997). Despite the different shapes, pools generally deepen from the edges towards the centre. Consequently, maximum depth of the pool was recorded, and the surface area of the pool was approximated by multiplying the maximum length by the width perpendicular to the midpoint of the length-axis. Pool volume was then determined by approximating the shape to a triangular prism. Physiographic features were recorded by visual census (presence or absence of sand, rock, boulders, sea urchins and algae cover) and ascribed to 5 categories: pools with a sandy bottom (SB), with or without algae or boulders; and pools with a rocky bottom. This latter group was divided into rocky pools with boulders (RB), with algae (RA), with sea urchins Paracentrotus lividus (RSU) and with both boulders and algae (RBA). The level of preference of species for the different types of cover was evaluated using Jacobs' (1974) modification of Ivlev's electivity index (D):

$$D = \frac{(r-p)}{(r+p-2rp)} \tag{1}$$

where *r* is the proportion of substratum used, and *p* is the proportion of substratum available in the environment. The index *D* ranges between -1.0 and 1.0, corresponding to total avoidance and total preference for a given environmental variable, respectively (Jacobs 1974). Following Atienza (1994), selection exists when the absolute value of *D* is >0.6. There is no relationship with the substratum when *D* ranges between -0.1 and 0.1. The electivity values were determined for each location when a particular substratum represented more than 5% of total pools.

The meteorological data analysed were air temperature and wind speed, obtained from nearby terrestrial weather stations. Data for Torregorda and El Chato came from the station located in Cadiz ( $36^{\circ}30'$  N,  $6^{\circ}16'$  W), and for Caños de Meca, data were obtained from the station located in Vejer de la Frontera ( $36^{\circ}17'$  N,  $5^{\circ}50'$  W). This regional information was obtained from the Regional Council for the Environment and Spatial Planning of the Autonomous Government of Andalucia. Mean monthly values were determined from daily values. The gridded maps of sea surface temperature were obtained from the US National Oceanic and Atmospheric Administration (NOAA). The maps have a spatial resolution of  $1^{\circ} \times 1^{\circ}$  (latitude/longitude). They are obtained by optimal linear interpolation, calculated as the monthly average of daily values (obtained via in situ measurements from ships and moored and drifting buoys, and from satellites) (Reynolds et al. 2002). Wave information was obtained from the Spanish Puertos del Estado records. The data for Torregorda and El Chato were obtained from a coastal buoy, Cadiz-1320 (36° 30' N, 6° 20' W). In Caños de Meca, the wave data were instead retrieved from WANA point 1055045 (36°15'N, 6°15'W), which can be considered the most representative of the sea climate for this location, and is a time series derived from a numerical model. Both datasets have a monthly temporal resolution, and values of significant wave height  $(H_{\rm S})$  and peak period  $(T_{\rm P})$  were obtained, finding a positive correlation (p < 0.025) between them. For this purpose, the wave energy equation (E)(Komar 1998) was used:

$$E = \left(\frac{1}{8}\rho g H_{\rm S}^2\right) \left(\frac{g T_p}{2\pi}\right) \tag{2}$$

where  $\rho$  is the water density and g is gravity.

## 2.2. Study species

A total of 15425 resident fishes of 16 species were collected at the 3 study sites. To analyse the community structure, fish species were grouped into families: Gobiidae (Gobius incognitus [previously known as G. bucchichi, and mentioned as such in Compaire et al. 2016, 2018], G. cobitis, G. paganellus, Zebrus zebrus) and Blenniidae (Coryphoblennius galerita, Lipophrys pholis, L. trigloides, Microlipophrys dalmatinus, Parablennius incognitus, P. sanguinolentus, Salaria pavo), which accounted for over 80% of the total relative abundance at all sites, while the remaining species were designated as 'Other residents': Clinitrachus argentatus (Clinidae), Lepadogaster lepadogaster (Gobiesocidae), Symphodus roissali (Labridae), Scorpaena porcus (Scorpaenidae) and Tripterygion tartessicum (Tripterygiidae).

The fish relative abundance was calculated as the number of fish caught m<sup>-2</sup>. The relative biomass was calculated as the relationship between relative abundance and average weight,  $W_{\rm M}$ , of each species (Bio-

mass = Relative abundance ×  $W_{\rm M}$ ). The fish community structure was calculated for each location using the Shannon-Wiener diversity index (H') and Pielou's evenness index (J'). To estimate the interannual stability of species, the coefficient of variation (CV) was calculated as:

$$CV = \frac{\sigma}{|\overline{x}|} 100$$
(3)

where  $\sigma$  is the standard deviation and  $\overline{x}$  is the average relative abundance.

# 2.3. Data analysis

Regarding pool characteristics and environmental variables, 1-way ANOVA was used to test for differences between pool size variables (surface, depth, volume) and sites. A chi-squared analysis was done to test the physiographic differences among sites, and a non-parametric Kruskal-Wallis test was used to test the differences between the pool size variables and physiography at each site. Regarding the structure of the fish assemblages, we analysed differences between fish length and weight among sites using a Kruskal-Wallis test. This test was also used to evaluate both the pool size effect on the presence or absence of fish, and the interannual differences in relative abundance, biomass, diversity and evenness.

A canonical correspondence analysis (CCA) was performed to elucidate the possible relationships between species abundance and microhabitat characteristics (physiography, depth and pool surface area). The physiographic data were used as a quantitative variable indicating which substratum was present (1) or absent (0). Prior to analysis, environmental variables and fish abundance were transformed to ln(x+1) to achieve normality and homogeneity of variance. Substrata that represented less than 5% of total pools at each site, and species that were not found in at least 10% of the pools were eliminated in the CCA. This analysis was carried out on the whole fish assemblage and for each site separately using the 'vegan' package implemented in R (Oksanen et al. 2017). An unrestricted random permutation (n = 9999) was used to assess the statistical significance of the canonical axes and of the environmental variables. A more acute angle between vectors  $(0^{\circ})$  indicates a strong positive correlation (+1), those at right angles  $(90^\circ)$  indicate no correlation (0), while arrows pointing in opposite directions (180°) have a strong negative correlation (-1). In order to test for spatial and temporal differences in commu-



Fig. 2. Percentage of each physiographic feature by site. SB: pools with sand bottom with or without algae or boulders; RA: pools with rocky bottom and algae; RB: pools with rocky bottom and boulders; RSU: pools with rocky bottom and sea urchins; RBA: pools with rocky bottom, boulders and algae

nity structure among sites, a cluster analysis (based on Bray-Curtis distance) was performed using the interannual variation both in the proportion and biomass of the different species. Lastly, Pearson's correlation coefficient *r* values were used to determine the strength of the correlations between interannual variations in biotic variables (fish abundance, diversity and evenness) and environmental variables (air and water temperatures, wave energy, wind speed and physiography).

#### 3. RESULTS

#### 3.1. Pool and environmental features

Although the 3 sampling sites were similar in terms of exposure time during low tide, pool sizes and physiography (Table 1, Fig. 2) varied among sites. There was a significant difference between the average surface area (ANOVA,  $F_{2.510} = 56.26$ , p < 0.005) and depth (ANOVA,  $F_{2,510} = 129.50$ , p < 0.005) of the pools at Caños de Meca with respect to the other sites, but not for volume (ANOVA,  $F_{2,510}$  = 3.02, p > 0.050). Torregorda was characterised by RSU pools and El Chato and Caños de Meca by SB pools, which in turn differed because Caños de Meca showed the highest proportion of RBA pools (Fig. 2). The boulders observed in Caños de Meca were frequently much larger than those in El Chato. These physiographic differences among sites were significant  $(\chi^2 = 309.52, df = 8, p < 0.005)$ . However, there were no significant differences between size variables and



Fig. 3. Interannual variation in (a) diversity and (b) evenness of the intertidal fish community at the 3 study sites (T: Torregorda; CH: El Chato; CM: Caños de Meca)

physiographic features at each site (Kruskal-Wallis test, p > 0.050).

## 3.2. Interannual changes in diversity and evenness

Diversity and evenness indices (mean  $\pm$  SD) were positively correlated (p < 0.050) and were slightly higher at El Chato ( $H' = 2.53 \pm 0.13$ ;  $J' = 0.66 \pm 0.04$ ) than at Caños de Meca ( $H' = 2.50 \pm 0.28$ ;  $J' = 0.65 \pm$ 0.07) and Torregorda ( $H' = 2.42 \pm 0.29$ ,  $J' = 0.65 \pm$ 0.09). However, these small variations in both parameters were not significant among sites (Kruskal-Wallis test, p > 0.050) or years (Kruskal-Wallis test, p > 0.050). Over the years, diversity in El Chato showed a declining trend, while it oscillated in Torregorda and Caños de Meca (Fig. 3a). Evenness showed a similar pattern to diversity (Fig. 3b). The lowest diversity value in Torregorda in 2011 occurred because only 2 species, Gobius paganellus and Parablennius incognitus, accounted for 80.8% of the total abundance. There was a negative linear correlation between diversity and the annual percentage of SB pools at the 3 sites (Torregorda:  $R^2$  = 0.76, p < 0.050; El Chato: R<sup>2</sup> = 0.90, p < 0.005; Caños de Meca:  $R^2 = 0.61$ , p < 0.005), whereas there was a



Fig. 4. Mean + SD (a) relative abundance and (b) estimated biomass of different intertidal fish groups at the 3 study sites

positive correlation between diversity and RBA pools in El Chato ( $R^2 = 0.72$ , p < 0.050) and Caños de Meca ( $R^2 = 0.66$ , p < 0.005). There was a negative correlation between diversity and previous year values of wave energy at Torregorda (p < 0.050), and of air temperature both at El Chato (p < 0.010) and Caños de Meca (p < 0.025).

## 3.3. Structure of the fish assemblage

The family Gobiidae was the best represented at all study sites (Fig. 4a); however, whereas Blennidae was the second most abundant family in Torregorda and El Chato, at Caños de Meca, the 'Other residents' group was the second most abundant. The highest biomass values for all groups were recorded in Caños de Meca, followed by El Chato (Fig. 4b). Fig. 5a shows the results of the species-specific analysis of relative abundance at each site. G. paganellus was the dominant species at all sites, whereas G. incognitus and G. cobitis were scarce in Torregorda and El Chato, respectively, and the 3 species coexisted in Caños de Meca. Within the Blennidae, P. incognitus followed by Lipophrys trigloides were the dominant species in Torregorda and El Chato, whereas P. sanguinolentus was followed by Salaria pavo at Caños de Meca. With respect to the 'Other species' group, Symphodus roissali was well represented at all sites, Lepadogaster lepadogaster was more abundant at Caños de Meca and Torregorda, and Tripterygion tartessicum was more abundant in Caños de Meca and El Chato. There were also species that were characterised by their abundance at only 1 site, e.g. Coryphoblennius galerita in Torregorda, Clinitrachus argentatus in El Chato and Scorpaena porcus in Caños de Meca; these species were rare at the other sites.

With respect to biomass, *G. paganellus* was the dominant species at all study sites (Fig. 5b). However, the other species that made the greatest contri-



Fig. 5. Species-specific composition of fish in intertidal pools in terms of (a) abundance and (b) biomass at each of the 3 study sites. Full species names are given in Table 2



Fig. 6. Interannual variation in the abundance of resident fish species at the 3 study sites. Dotted lines separate the families Gobiidae, Blenniidae and 'Other residents'. Full species names are given in Table 2

bution to the biomass differed among sites: *G. cobitis*, *S. roissali*, *L. trigloides*, *P. incognitus* and *P. sanguinolentus* were dominant in terms of biomass at Torregorda; *S. roissali*, *L. trigloides*, *S. porcus* and *P. incognitus* at El Chato; and *S. porcus*, *G. cobitis* and *P. sanguinolentus* at Caños de Meca. These last 3 species are the largest sizes of their respective groups. There were significant differences between length and weight of both *S. porcus* and *G. cobitis* among sites (Kruskal-Wallis test, p < 0.025).

Interannual variability in the relative abundance at Torregorda and El Chato showed a very similar temporal distribution pattern, which differed at Caños de Meca (Fig. 6). There were significant differences in the relative abundance among sites (Kruskal-Wallis test, p < 0.005) but not among years (Kruskal-Wallis test, p > 0.050). The Gobiidae were the best represented group at all sites (except at Torregorda for the years 2011-2013), followed by Blenniidae at Torregorda and El Chato, and 'Other residents' at Caños de Meca. The variability of these groups over the years was evaluated according to environmental conditions. Variability in Gobiidae at Torregorda showed a positive correlation with average wind speed of the year of capture and the previous year (p < 0.005), and that of Blenniidae showed a negative relationship with wave energy both at Torregorda (p < 0.025) and El Chato (p < 0.005). The abundance of both families at Caños de Meca was negatively correlated with average wind speed (Gobiidae: p < 0.005, Blenniidae: p < 0.025). The 'Other residents' group showed a negative relationship with the air

temperature of the previous year (p < 0.025) both at Torregorda and Caños de Meca. The analysis with sea surface temperature did not show any detectable correlation. Regarding the stability of the relative abundance, at Torregorda the most stable species (which accounted for 49% of the total abundance) were *G. paganellus*, *S. roissali*, *Zebrus zebrus* and *G. incognitus*, the latter 2 species showing a lower abundance, while in El Chato the most stable species were *G. paganellus*, *S. roissali*, *P. incognitus*, *P. trigloides* and *C. argentatus* (81% of the total fish abundance). Lastly, in Caños de Meca, the most stable species were *G. paganellus*, *G. incognitus*, *S. porcus*, *S. roissali* and *L. lepadogaster*, which collectively contributed 76% of the total abundance.

Interannual variability in the biomass (mean  $\pm$  SD) ranged between  $4.9 \pm 0.7$  g m<sup>-2</sup> (2011) and  $7.3 \pm 0.7$  g  $m^{-2}$  (2012) at Torregorda; between 7.8 ± 0.9 g  $m^{-2}$ (2013) and 14.3  $\pm$  1.7 g m<sup>-2</sup> (2009) at El Chato; and between 11.6  $\pm$  1.2 g m<sup>-2</sup> (2014) and 20.9  $\pm$  2.5 g m<sup>-2</sup> (2012) at Caños de Meca. As in the case of relative abundance, there were significant differences among sites (Kruskal-Wallis test, p < 0.005) but not among years (Kruskal-Wallis test, p > 0.050). When expressed as percentages (Fig. 7), it became apparent that at Torregorda, G. paganellus, the most abundant species, did not always contribute the greatest biomass, and S. roissali, G. cobitis, P. incognitus and P. trigloides made an important contribution (up to 57%) to the total fish biomass. G. paganellus, followed by S. roissali and L. trigloides, contributed most in terms of biomass (up to 62%) throughout the study period



Fig. 7. Interannual variation in the percentage of the biomass of resident fish species at the 3 study sites. Dotted lines separate the families Gobiidae, Blenniidae and 'Other residents'. Full species names are given in Table 2

in El Chato. The species that most contributed to biomass in Caños de Meca (up to 78%) were *G. paganellus*, *G. cobitis*, *P. sanguinolentus* and *S. porcus*. Cluster analysis of the interannual variation in the proportion of different species (Fig. 8a) showed that Caños de Meca exhibited a more homogeneous species composition than the other locations, where the survey results were intermingled, especially in the more recent years. Hierarchical clustering analysis of the interannual biomass variation for different species shows even greater differences among locations (Fig. 8b).

#### 3.4. Habitat preferences

The presence/absence of species captured in >10% of the pools in relation to pool surface area and depth is analysed in Table 2. In Torregorda, the dominant blennies (*P. incognitus* and *L. trigloides*) and *L. lepadogaster* were the only species that were not affected by the pool surface area. *G. incognitus, C. argentatus, S. roissali, S. porcus* and *T. tartessicum* were associated with pools of greater surface area in El Chato, whereas this relationship was observed for *G. incognitus, Microlipophrys* 



Fig. 8. Cluster dendrograms of the interannual variation in the (a) proportion of different fish species and (b) in the biomass of different species. Each survey is designated by location (T: Torregorda; CH: El Chato; CM: Caños de Meca) and year (from 2008 to 2014)

| Species                   | Torregorda |         |        |         | El Chato |         |         |         | ———— Caños de Meca——— |         |        |         |
|---------------------------|------------|---------|--------|---------|----------|---------|---------|---------|-----------------------|---------|--------|---------|
|                           | Surface    |         | Depth  |         | Surface  |         | Depth   |         | Surface               |         | Depth  |         |
|                           | Η          | р       | Н      | р       | Н        | р       | Н       | р       | Н                     | р       | Η      | р       |
| Gobius cobitis            | 28.949     | < 0.005 | 3.214  | 0.073   |          |         |         |         | 0.077                 | 0.781   | 1.283  | 0.257   |
| G. incognitus             | 14.100     | < 0.005 | 1.894  | 0.169   | 6.272    | < 0.025 | 7.575   | < 0.025 | 8.149                 | < 0.005 | 0.726  | 0.394   |
| G. paganellus             | 11.361     | < 0.005 | 0.868  | 0.352   | 2.286    | 0.131   | 0.079   | 0.779   | 1.324                 | 0.250   | 0.299  | 0.585   |
| Zebrus zebrus             | 5.099      | < 0.025 | 0.328  | 0.567   | 0.611    | 0.434   | 2.127   | 0.145   | 0.545                 | 0.460   | 2.379  | 0.123   |
| Lipophrys trigloides      | 0.924      | 0.336   | 4.023  | < 0.050 | 0.135    | 0.714   | 0.774   | 0.379   | 3.548                 | 0.060   | 0.106  | 0.744   |
| Microlipophrys dalmatinus |            |         |        |         | 0.396    | 0.529   | 0.105   | 0.746   | 4.890                 | < 0.050 | 0.032  | 0.858   |
| Parablennius incognitus   | 0.616      | 0.433   | 11.556 | < 0.005 | 3.433    | 0.064   | 16.584  | < 0.005 |                       |         |        |         |
| P. sanguinolentus         | 9.518      | < 0.005 | 3.573  | 0.059   |          |         |         |         | 10.873                | < 0.005 | 0.063  | 0.802   |
| Salaria pavo              | 6.586      | < 0.010 | 0.065  | 0.799   | 0.376    | 0.540   | < 0.001 | 0.986   | 2.972                 | 0.085   | 0.783  | 0.376   |
| Clinitrachus argentatus   |            |         |        |         | 9.014    | < 0.005 | 6.040   | < 0.025 | 0.832                 | 0.362   | 0.268  | 0.605   |
| Lepadogaster lepadogaster | 3.191      | 0.074   | 0.624  | 0.430   |          |         |         |         | 0.568                 | 0.451   | 5.135  | < 0.025 |
| Symphodus roissali        | 19.160     | < 0.005 | 10.317 | < 0.005 | 7.786    | 0.005   | 2.797   | 0.094   | 0.182                 | 0.669   | 4.699  | < 0.050 |
| Scorpaena porcus          |            |         |        |         | 14.038   | < 0.005 | 9.414   | < 0.005 | 4.336                 | < 0.050 | 11.567 | < 0.005 |
| Tripterygium tartessicum  |            |         |        |         | 5.363    | < 0.025 | 5.451   | < 0.025 | 0.164                 | 0.685   | 11.615 | < 0.005 |

Table 2. Kruskal-Wallis test results between pool size (surface area and depth) and the presence of resident fish that were caught in more than 10% the pools at each site. Blank spaces indicate that species were found in <10% of the pools. Significant (p < 0.05) values are highlighted in **bold** 

dalmatinus, P. sanguinolentus and S. porcus in Caños de Meca. Regarding depth, several species showed a preference for the deepest pools at more than 1 site: P. incognitus in Torregorda and El Chato, S. roissali in Torregorda and Caños de Meca, and S. porcus and T. tartessicum in El Chato and Caños de Meca.

CCA based on species abundance was performed on the whole fish assemblage (Fig. 9a); the figure shows only axes 1 and 2, which account for 92.3% of the total variance. The species-microhabitat correlations of each axis were 0.74 and 0.52 (axis 1 and 2, respectively). The first axis was mostly correlated (>0.7) with depth and a lesser extent with RSU pools and surface area. The second axis was strongly correlated (>0.7) with RSU pools, and moderately with SB pools. P. incognitus, L. trigloides and L. lepadogaster were associated with the deepest pools and the presence of sea urchins. On the other hand, the larger goby and blenny, G. cobitis and P. sanguino*lentus*, were associated with larger pools. Because there were both physiographic and pool size differences among sites, and to avoid the masking effect of analysing all datasets together, the CCA was carried out for each area separately. Fig. 9b shows the CCA ordination plot for the Torregorda assemblage. The species-microhabitat correlations of the first 2 axis were 0.74 (axis 1) and 0.62 (axis 2), and they account for 87.9% of the total variance. The first axis was mainly correlated (>0.8) with RSU pools and to a lesser extent with SB pools and surface area. The second axis was more correlated (>0.7) with RBA pools, and moderately with surface area and RSU pools. L.

lepadogaster was also associated with this physiography, while P. sanguinolentus, S. pavo, G. incognitus, G. cobitis avoided it. On the other hand, T. tartessicum and C. argentatus were associated with RBA pools. The ordination plot of the El Chato assemblage using CCA (Fig. 9c), whose species-microhabitat correlations of each axis were 0.59 (axis 1) and 0.37 (axis 2) and accounted for 85.1% of the total variance, showed that the 4 environmental variables analysed made a similar contribution to axis 1 (> 0.5), whereas the main correlation (>0.7) in axis 2 was obtained for depth. T. tartessicum was the only species that showed any kind of preference at this site, in particular, towards more complex pools (i.e. RBA pools). The CCA performed at Caños de Meca (Fig. 9d), where axis 1 and 2 accounted for 83.4% of the total variance and the species-microhabitat correlations of each axis were 0.61 (axis 1) and 0.52 (axis 2), showed that the first axis was principally correlated (>0.8) with depth and to a lesser extent with both physiographies (i.e. RBA and SB). Axis 2 was strongly correlated (>0.9) with surface area. At this site, no species presented a preference for a particular physiography. The permutation procedure in the CCA was highly significant (p < 0.050) for the first axis and for the sum of all constrained eigenvalues in all analyses.

The electivity index evaluated for each species is shown in Fig. 10. The smallest values were observed for *G. paganellus* and *S. roissali*, suggesting that there was no relationship between the presence of these species in the pools and their different type of cover. Despite the rare presence of *G. cobitis*, *P.* 



Fig. 9. Canonical correlation analysis ordination diagram based on species abundances, with environmental factors represented by vectors on (a) the whole fish assemblage, (b) Torregorda, (c) El Chato and (d) Caños de Meca. Pool types are defined in Fig. 2

sanguinolentus and L. lepadogaster in El Chato, these species showed a preference for SB pools, avoiding the RBA pools. In Torregorda, P. sanguinolentus and S. pavo avoided RSU pools, whereas L. lepadogaster was the only species showing preference for this physiography. T. tartessicum and L. lepadogaster showed avoidance of SB pools at this site. The latter species also avoided the complex pools. The habitat preference values obtained for the other species did not define their microhabitat selection. Unfortunately, the scarcity of C. galerita and Lipophrys pholis did not allow exploration of their habitat requirements.

# 4. DISCUSSION

Habitat complexity, which increases access to shelter, has been used traditionally to explain the differences in the abundance (Macpherson 1994, De Raedemaecker et al. 2010) and diversity of fish species in temperate waters (Macpherson 1994, Charton & Ruzafa 1998), whereas in pools with sandy bottoms, both parameters decrease. Torregorda, the site with a greater fraction of complex pools, showed the lowest abundance and average diversity, whereas at El Chato, the site with a greater number of SB pools, these parameters were higher. This might be



Fig. 10. Ivlev's modified electivity index (*D*) for different substrata that are represented in >5% of pools at each study site (T: Torregorda; CH: El Chato; CM: Caños de Meca). \*Indicates that species were found in <10% of the pools. Pool types are defined in Fig. 2; full species names are given in Table 2

explained by the so-called 'reserve effect' that causes an abundance and/or diversity decrease in cryptic fish within marine reserves in comparison with nearby unprotected areas (Sasal et al. 1996, Willis & Anderson 2003). This effect may also be responsible for the low abundance of Scorpaena porcus in Torregorda, since it has been reported that the competition for food or habitat with other subtidal piscivorous species could have a detrimental effect on the distribution or abundance of this species (La Mesa et al. 2006). A larger number of stones and small boulders result in a greater availability of shelter, whereas sites with predominantly rocky habitat and >1 m boulders provide a reduced range of niches resulting in lower species diversity (De Raedemaecker et al. 2010). Therefore, the slightly lower diversity at Caños de Meca could be due to the greatest proportion of rocky bottom pools and the presence of larger boulders at this location than at El Chato. The interannual changes in diversity are also explained by the positive correlation of diversity with habitat complexity, since as mentioned above, less complex pools showed a lower diversity at all 3 sites.

Cluster analysis based on the interannual variation in species proportions showed that in the last years, Torregorda clustered with El Chato, due to the greatest abundance of Parablennius incognitus in 2011 and 2014 at the protected site. The lower abundance of blennies in Caños de Meca may be related to the fact that most blennies preferentially inhabit a very shallow depth range (Macpherson 1994), and at this site, the slope of the subtidal zone is steeper. The effects of wave exposure are one of the main factors that influence the distribution patterns of fish associated with coral reefs (Bellwood et al. 2002). In the present study, the 3 sites exhibited their lowest abundance in 2010, the year with the greatest wave energy. The higher biomass at Caños de Meca can be explained because the species that reach a larger size for each group, namely, Gobius cobitis, P. sanguinolentus and S. porcus, are more abundant and exhibit a greater biomass at this site. Faria & Almada (2001) noted that when G. cobitis reaches about 7-8cm, it tends to disappear from these high level pools, moving to deeper channels that are usually permanently connected to the sea. However, in our study area, larger fish of these 3 species are more numerous in Caños de Meca. It may be hypothesized that the steeper subtidal slope in Caños de Meca is the reason that the abundance and biomass of these species are greater, as the reduced extent of their ecological niche at this site could increase the migration of larger fish coming from the subtidal zone.

In addition to habitat complexity, physical factors that are known to affect the structure of the fish assemblages in shallow reef habitats include currents, wind stress (Horta e Costa et al. 2014), wave exposure (De Raedemaecker et al. 2010) and temperature (Ritter 2009). The interannual changes in diversity showed that diversity is typically related to environmental conditions occurring during the previous year. This pattern seems to confirm that the increase in diversity is not only related to the substratum but is also linked to environmental factors that enhance the development of Blenniidae in Torregorda and El Chato, and the group 'Other residents' in Caños de Meca. Almada & Santos (1995) argued that for fishes of the family Blenniidae, adaptations to the turbulent conditions of the intertidal zone involve behavioural modifications that minimize movement in the water column and loss of contact with the substratum. However, our results on interannual variation in the abundance of Blenniidae suggest that harsh conditions, strong wind and waves are not favourable for this family. This relationship with wave energy was not observed for the Gobiidae, which could be related to the fact that species in this family are characterised by fusion of their pelvic fins forming a disc to function as a sucker with which gobies can attach to the bottom and withstand high stream flows (Zander 2011).

Historically, sea urchins have been a primary target of human harvesting along the coastline of Cadiz. The great presence of sea urchins at the protected site compared to the other locations suggests the importance of these voracious grazers in shaping the intertidal ecosystem. According to the CCA, the main factors affecting fish species abundance varied among sites. Specifically, fish species caught at the 2 unprotected areas showed a lesser correlation with both physiography and pool size, which seems to indicate that human pressure induces changes at all assemblage levels, and highlights the importance of separate analysis even in near zones. Previous studies on hard substrates influenced by human disturbances have demonstrated that marine fish assemblages react to anthropogenic pressures (Henriques et al. 2013 and references therein). The discrepancies in habitat preference documented within the same species or families may be explained by the differences in analysed microhabitats and coastal dynamics at each study location. It also must be highlighted that censuses of fish assemblages are often limited to the collected quadrats, which are not chosen randomly, but according to habitat types (Willis 2001), substrate types, inclination or depth categories

(Kovačić et al. 2012), and consequently, might not be representative of the entire cryptobenthic fish community (Kovačić et al. 2012). The results of habitat preferences of *G. paganellus* and *Symphodus roissali* showed that these species did not select for any specific physiography. Gibson (1972) noted that the microhabitats associated with *G. paganellus* in tidepools were weedier. On the other hand, and through information obtained from visual censuses, the preference of wrasses for shallow rocky substratum colonized by macroalgae is well documented (Bonaca & Lipej 2005).

Results of the present study on the habitat preferences of G. cobitis, P. sanguinolentus and Lepadogaster lepadogaster in El Chato should be treated with caution because these species were found in <10% of the pools at this site. *G. cobitis* has been described in bare pools where the cover consists of stones and boulders (Gibson 1972), which would serve as their spawning sites (Faria & Almada 1995). References on microhabitat selection by P. sanguino*lentus* according to visual censuses are contradictory. Bonaca & Lipej (2005) observed selection of areas with turf cover and boulders, and La Mesa et al. (2006) noted that these fish inhabit bare rock. Lepadogaster spp. have been previously found in association with sea urchins (Fischer et al. 2007). Among the species with a nearly significant relationship, G. incognitus would avoid RSU pools at Torregorda, whereas Salaria pavo, Clinitrachus argentatus and Tripterygion tartessicum appear to indicate a preference for SB pools for the first species, and RBA pools for the latter 2 species. This agrees with visual census results indicating that tripterygiids are associated with a complex habitat of cobbles and boulders (La Mesa et al. 2004) and with turf cover (Bonaca & Lipej 2005). The electivity results for the other species did not show any significant relationship with the physiography at our study sites. According to the literature based on visual census, in the case of Z. zebrus, Fischer et al. (2007) described their presence under stones, in small crevices, in holes and in association with the sea urchins. Microlipophrys dalmatinus has been detected on flat rocks and boulders and pebbles (La Mesa & Vacchi 2005), between algae on rounded stones in shallow waters (Fischer et al. 2007) and also in the smallest holes made by sponges and bivalves (Orlando-Bonaca & Lipej 2007). P. incognitus has been found in areas with turf cover (Bonaca & Lipej 2005), and Lipophrys trigloides has been associated with rocky cliffs (La Mesa et al. 2006). There is no available information about the habitat preference of S. porcus in shallow waters, but the density of scorpionfish has been described as positively influenced by substratum complexity on temperate rocky reefs (Willis & Anderson 2003).

As mentioned in Section 1, the composition of fish assemblages is also influenced by biotic factors, and therefore, intra- or interspecific resource partitioning might affect assemblage structure. A high diet overlap among species could encourage competition for limited resources that would affect the stability of their populations. However, the diet for most of these species, both at Torregorda and El Chato (Velasco et al. 2010), and Caños de Meca (Compaire et al. 2016), has already been described, highlighting their lack of competition and maintenance of an adequate distribution of resources. In Caños de Meca, a temporal segregation of the reproductive cycles, which reduces reproductive competition, has been noted in their spawning as well as recruitment and ensures high survival during the early life cycle stages of most of these species (Compaire et al. 2018). Thus, diet and reproductive interspecific competition are unlikely to explain the patterns of microhabitat segregation.

In conclusion, the overall results of this study on the relationships between interannual changes in abundance and diversity with macroscale factors show that air temperature, wind stress and wave energy are the major physical features that define fish community structure. Although the pool surface is the main microscale factor affecting the fish presence at all sites, the apparent discrepancy in habitat selection results among sites seems to indicate that human disturbances affect fish distribution patterns in tidepools. To augment our results about habitat preference, future studies should assess the degree of bedrock covered by the different microhabitats in such a way as to achieve a greater understanding of their distribution patterns. Other physical, biological or chemical variables that were not incorporated in the present study could likely account for the unexplained variation in the structure of the fish assemblages at the study sites. Nevertheless, these overall results are useful to improve our understanding of the complex mechanisms through which these factors operate. They may also stimulate future ecological investigations to corroborate our findings on relationships between the distribution of fish species and environmental variables.

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