

Effects of habitat and substrate complexity on shallow sublittoral fish assemblages in the Cyclades Archipelago, North-eastern Mediterranean sea

S. GIAKOUMI^{1,2} and G. D. KOKKORIS¹

¹ Department of Marine Sciences, University of the Aegean, University Hill, Mytilene, Lesvos Island 81100 Greece

² Institute of Marine Biological Resources and Inner Waters, Hellenic Centre for Marine Research, Ag. Kosmas, Greece

Corresponding author: sylvaine@aegean.gr

Received: 4 January 2012; Accepted: 29 October 2012; Published on line: 21 February 2013

Abstract

This is the first study to explore fish community structure and its relations to habitat and topographic complexity in the shallow coastal waters of the Cyclades Archipelago, North-eastern Mediterranean Sea. *In situ* visual surveys were carried out at 233 sampling sites in 26 islands of the Cyclades Archipelago. Fish community parameters and biomass were estimated across seven substrate types: sand, seagrass, vertical walls, boulders, horizontal/subhorizontal continuous rock, rocky substrate with patches of sand, and rocky substrate with patches of sand and *Posidonia oceanica*. Topographic complexity and percentage of algal cover were estimated on hard substrate. Substrate type was found to be a determining factor affecting the structure and composition of fish assemblages. Species number, abundance and biomass were significantly lower in sandy areas and always higher on hard substrates, with seagrass habitats presenting intermediate values. Topographic complexity in rocky bottoms did not seem to affect species richness, density or biomass. This study provides a baseline for future evaluation of changes produced by potential management actions such as the creation of marine protected areas in the study region.

Keywords: canopy algae, fish assemblages, North-eastern Mediterranean, Cyclades Archipelago, substrate type, topographic complexity.

Introduction

Spatial and temporal variation in fish community structure are influenced both by biological and environmental factors. Such biological factors include predation (Heinlein *et al.*, 2010), competition (Bonin *et al.*, 2009), larval dynamics (Leis & McCormick, 2002) and recruitment variability (Booth & Brosnan, 1995). At the same time, physical parameters, such as light and nutrient availability (Emery, 1978), habitat structure and substrate complexity (Luckhurst & Luckhurst, 1978), variations in depth (Harmelin, 1990; Dufour *et al.*, 1995; García-Charón & Pérez-Ruzafa, 1998), climatic differences (Holbrook *et al.*, 1997), and current flow and exposure (Williams, 1982), have been reported to influence directly or indirectly community structure. Apart from these natural features human exploitation of fish populations is considered a major determinant of their abundance and, consequently, of their spatial and temporal distribution (García-Rubies & Zabala, 1990; Friedlander & De Martini, 2002; De Martini *et al.*, 2008).

Habitat structure and topographic complexity resulting in differential availability of food and shelter are important factors in structuring fish assemblages (e.g. Pollard, 1984; Bonin *et al.*, 2009). Most reef fishes have

two-phase life histories, one mobile pelagic phase as larvae and one sedentary juvenile and adult phase in the vicinity of the bottom. Habitat structure plays a significant role in fish distribution affecting recruitment (e.g. providing microhabitat requirements for settlement) and post-recruitment (e.g. providing shelter from predation) processes (Connell & Jones, 1991; Harmelin-Vivien *et al.*, 1995; Juanes, 2007).

The relationship between fish and substrate type has been studied both in coral (e.g. Holbrook *et al.*, 2000; McClanahan & Arthur, 2001; Messmer *et al.*, 2011) and temperate regions (e.g. Jenkins & Wheatley, 1998; Tuya *et al.*, 2009). These studies reveal that fish species richness and density differ among substrate types. Habitats with increased complexity, such as seagrass and rocky reefs, tend to have higher values. Moreover, some species are found to inhabit one specific habitat exclusively or predominantly. Other species are found in more than one habitat, and some can change habitats depending on the phase of their life cycle (Francour, 1997). Such evidence have management implications, suggesting that protection actions should consider all inshore habitats in order to maintain fish biodiversity (Guidetti, 2000; Tunessi *et al.*, 2006).

There is also abundant literature reporting that in tropical reefs, habitat structure and topographic complexity affect species density and richness in many marine invertebrates and fishes (e.g. Risk, 1972; Luckhurst & Luckhurst, 1978; Freidlander *et al.* 2003; Gratwicke & Speight, 2005). In temperate seas, the effect of topographic complexity is less documented. However, in different temperate regions, this factor appears to be important in shaping fish assemblages by influencing both density and species richness (e.g. Leum & Choat, 1980; Aburto-Oropeza, 2001; Harman *et al.*, 2003).

In the Mediterranean Sea, different inshore habitats present dissimilarities in fish species composition, richness and abundance, with some species demonstrating different habitat preferences (Francour, 1994; Guidetti, 2000; Tunesi *et al.*, 2006, La Mesa *et al.*, 2011). Moreover, evidence from the western basin reveals a positive relation between topographic complexity and fish species richness (Harmelin, 1987; Macpherson, 1994, Reñones *et al.*, 1997; García-Charton & Pérez-Ruzafa, 1998; García-Charton & Pérez-Ruzafa, 2001, García-Charton *et al.*, 2004), while the relation between topographic complexity and fish density is less consistent (Ruitton *et al.*, 2000).

With the present study, we aim to describe shallow sublittoral fish assemblages in an Eastern Mediterranean archipelago and explore their relations to substrate type and topographic complexity. Only a few studies

have been conducted on the composition and structure of sublittoral fish assemblages in the Eastern Mediterranean (Harmelin-Vivien *et al.*, 2005). Moreover, this study, being the first large-scale quantitative survey on shallow sublittoral fish communities in the Central Aegean Sea, provides a baseline for future evaluation of the changes that will be produced by potential management measures, such as the establishment of marine protected areas (Giakoumi *et al.*, 2011).

Materials and methods

Study area

The study area was located in the Cyclades Archipelago, Central Aegean, North-eastern Mediterranean Sea. Morphologically, the Central Aegean Plateau (Cyclades Plateau) represents a shallow platform of about 200 m mean depth. The region is characterized as oligotrophic ($\text{Chl a} < 0.10 \text{ mg m}^{-3}$) with low continental influence (SOHELME, 2005). We conducted surveys around 13 islands in July and August 2007 and another 13 islands in June and July 2008, covering a total of 233 sites (Fig. 1). Sampling sites were situated at ~5km (4.5-5.5 km) intervals along the coastline of each island, although sampling at some of the initially selected sites was not possible due to lack of accessibility.

Small-scale coastal fishing has always occurred in the Cyclades, where much of the catch is not reported

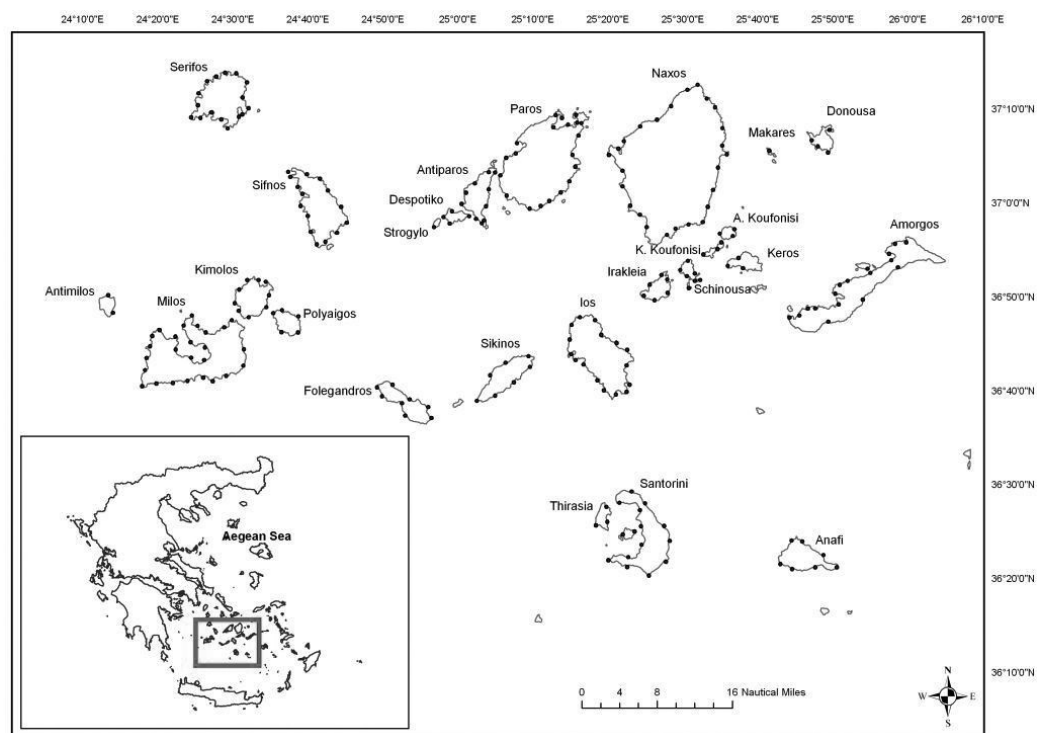


Fig. 1: Study area in the Cyclades Archipelago (Central Aegean Sea, Greece). Points represent the 233 sampling sites where we conducted visual census surveys.

to the authorities but directly sold in local markets (Stergiou *et al.*, 2002). Coastal fishers' primary target fishes are red mullet (*Mullus surmuletus*), common sea bream (*Pagrus pagrus*), bogue (*Boops boops*), red scorpionfish (*Scorpaena scrofa*) and common pandora (*Pagellus erythrinus*).

Fish counts

At each site, we conducted standard underwater surveys of the abundance and size of fishes along visual transects. Counts were conducted along a 75m x 5m transect line, placed parallel to the shore at approximately 3m depth. At the beginning of each transect, an observer would estimate visually a 5m distance perpendicular to the transect line and then snorkel at constant speed, identifying and counting individuals 2.5m either side of the observer. The transect line was released gradually while fish counting to avoid disturbance of fish. On the way back, the observer would do a second swim spirally within the range of 5m from the transect line in order to record cryptic species (e.g. scorpionfish).

Fish biomass calculations

Length estimates of fish from surveys were converted to wet weight by using the allometric length–weight conversion equation: $W = aL^b$, where W is weight in grams and L is total length in cm. Parameters a and b are constants obtained for each species from Fishbase (www.fishbase.org) and Moutopoulos & Stergiou (2002). Whenever values for a and b were unavailable, the parameters from a congeneric species with similar shape and maximum total length were used. We chose the parameter values corresponding to our study area or the closest geographical area.

Substrate classification, rugosity and algae coverage estimation

At each site, we identified and estimated the percentage coverage of substrate type along the transect line. The main substrate categories were: 1) hard substrate, which included boulders, horizontal and subhorizontal continuous rock, and vertical wall; 2) unvegetated sand; and 3) seagrass (*Posidonia oceanica* and *Cymodocea nodosa*). Rocky boulders were classified by the size of their major length: B1- small (less than 1m), B2 - medium (between 1 and 2m) and B3- large (more than 2m). Continuous rock substrate types were categorized in the following groups: CR1: continuous rock horizontal, CR2: continuous rock sub-horizontal 30–60°, CR3: vertical continuous rock (slope greater than 60°). Due to habitat heterogeneity and discontinuity along the transects, substrate was classified in the following seven substrate categories: sand, seagrass, vertical walls, boulders, horizontal/subhorizontal continuous rock, rocky substrate with patches of sand and rocky substrate with patches of sand and *Posidonia oceanica*.

At each site we estimated rugosity using a classical method (Luckhurst & Luckhurst, 1978). Using a 5-m chain with links 1 cm in length, the contoured distance was estimated by serially laying the chain across the substratum, following every topographical high and low underneath the transect line. Chain-transect rugosity is the ratio of the contoured distance to the linear distance.

At each site with hard substrate, we estimated the cover of different algal taxa/group using ten replicate photoquadrats per site, haphazardly situated along each transect line. A Canon G7 camera was mounted on a 50 x 50 cm frame with a custom-built camera setup. We estimated the percentage coverage of the algal groups using the software Photogrid 1.0 beta (Preskitt *et al.*, 2004). The algae identified in the field were attributed to the following groups: crustose coralline algae (CCA), turf (small filamentous algae), *Sargassum* spp., *Cystoseira* spp., Dictyotales, *Caulerpa prolifera*, and alien species including *Caulerpa racemosa* var. *cylindracea*, *Stypopodium schimperi* and *Asparagopsis taxiformis*. In addition to algae, we included some other categories in the photo analysis: bare rock, sand, pebbles, seagrass *Posidonia oceanica*, seagrass *Cymodocea nodosa* and macroinvertebrates (e.g. sponges, bryozoans, tunicates) (see Giakoumi *et al.* 2012).

Statistical analysis

Community indices such as species richness (number of species), diversity (Shannon – Wiener H'), evenness (Pielou's J) as well as biomass (g m^{-2}) were calculated for each site and compared among habitat types using one-way ANOVA. Post-hoc Scheffe test was applied to account for unequal group sizes. Homogeneity of variances was tested with Levene's test. Community indices were calculated with the software Species Diversity and Richness Version 4 (Seaby & Henderson, 2006), while one-way ANOVA was carried out with SPSS 17.0.

To explore the structure of the fish community across the main physical habitat types (sand, seagrass and rock), we conducted Redundancy analysis (RDA) on abundances of most common fish species with occurrence frequency >20% (24 species). RDA is, in principle, an extension of multiple regression when there is more than one response (species) variables (Legendre & Legendre, 1998). RDA generates ordination axes that are linear combinations of descriptor (environmental) variables. Furthermore, we conducted RDA on abundances of most common fish species in rocky sites (17 species) in order to explore the structure of the reef fish community across the major biological habitat types: crustose coralline algae (CCA), turf (small filamentous algae), *Cystoseira* spp., Dictyotales, and bare rock. The RDAs were applied to the correlation matrix and carried out with the software Ecological Community Analysis II (Henderson & Seaby, 2007).

To detect correlations between substrate rugosity and

fish biomass, rugosity and density, and rugosity and species richness, we used Spearman rank of order coefficient (SPSS 17.0). Those correlations were tested for all sites (all substrate types) and exclusively for rocky sites.

Results

Composition and structure of fish assemblages

Overall, we counted 50406 individuals and estimated their length. We identified 54 species belonging to 21 families, while individuals belonging to the 5 families Mugilidae, Atherinidae, Blenniidae, Gobiidae, and Tripterygiidae were identified to family level (Table 1). In all habitat types, the most abundant family was the Atherinidae, followed by the Pomacentridae (comprised of the single species *Chromis chromis*), which was absent only in sand habitats. In sandy bottoms, the Mullidae family, represented by the species *Mullus surmuletus*, was the second most abundant. In seagrass meadows, *Oblada melanura* was the third most abundant species (after the Atherinidae and *Chromis chromis*). Fish assemblages in seagrass beds and rocky habitats had many species in common, in contrast to sandy bottoms which had less overlap in species composition with other habitats. The species *Pagellus acarne*, *Pseudocaranx dentex*, *Syngnathus typhle typhle* were recorded exclusively over seagrass meadows, whereas *Bothus podas*, *Dasyatis pastinaca*, *Trachinus draco* and *Xyrichtys novacula* were censused only in unvegetated sand habitats.

For all rocky habitats, the families with most species were the Labridae (14 species) and the Sparidae (12 species). In boulder habitats and vertical walls, the most abundant representative species of these families were *Thalassoma pavo* and *Sarpa salpa* respectively. Regarding the other substrate types, in continuous rock bottoms *T. pavo* and *Diplodus vulgaris* displayed the highest abundances, whereas in rocky habitats with patches of sand or *Poceanica* and sand, *Coris julis* and *S. salpa* were the most abundant species.

Fish community parameters

Rocky habitats with patches of sand and *P. oceanica* displayed the highest diversity and evenness (Figs. 2, 3), whereas substrates with boulders had the highest species richness (Fig. 4). The lowest values for all indices were found in sandy bottoms. Community indices were compared among habitats using one-way ANOVA, which indicated an overall significant effect of the habitat type on diversity ($F_{6, 228} = 11.55, p < 0.001$), evenness ($F_{6, 228} = 6.48, p < 0.001$) and species richness ($F_{6, 228} = 31.91, p < 0.001$). Regarding diversity, Scheffe post-hoc test revealed that sandy bottoms were significantly different from all other substrate types ($p < 0.05$) except for seagrass meadows. In terms of evenness, sandy bottoms significantly differed from all other substrate types

Table 1. Fish species and families recorded in the shallow sublittoral of the Cyclades Archipelago.

Family - Species	Family - Species
Apogonidae	<i>Epinephelus costae</i>
<i>Apogon imberbis</i>	<i>Epinephelus marginatus</i>
Atherinidae	<i>Mycteroperca rubra</i>
Belonidae	<i>Serranus cabrilla</i>
<i>Belone belone</i>	<i>Serranus scriba</i>
Blennidae	Labridae
Sparidae	<i>Labrus bergylta</i>
<i>Boops boops</i>	<i>Labrus merula</i>
<i>Dentex dentex</i>	<i>Labrus viridis</i>
<i>Diplodus annularis</i>	<i>Symphodus cinereus</i>
<i>Diplodus puntazzo</i>	<i>Symphodus doderleini</i>
<i>Diplodus sargus</i>	<i>Symphodus mediterraneus</i>
<i>Diplodus vulgaris</i>	<i>Symphodus melanocercus</i>
<i>Oblada melanura</i>	<i>Symphodus ocellatus</i>
<i>Pagrus pagrus</i>	<i>Symphodus roissali</i>
<i>Pagellus acarne</i>	<i>Symphodus rostratus</i>
<i>Sarpa salpa</i>	<i>Symphodus tinca</i>
<i>Spondylusoma cantharus</i>	<i>Xyrichtys novacula</i>
<i>Lithognathus mormyrus</i>	<i>Thalassoma pavo</i>
Engraulidae	<i>Coris julis</i>
<i>Engraulis encrasicolus</i>	Mugilidae
Bothidae	Mullidae
<i>Bothus podas</i>	<i>Mullus surmuletus</i>
Pomacentridae	Muraenidae
<i>Chromis chromis</i>	<i>Muraena helena</i>
Dasyatidae	Sciaenidae
<i>Dasyatis pastinaca</i>	<i>Sciaena umbra</i>
Carangidae	Scorpaenidae
<i>Pseudocaranx dentex</i>	<i>Scorpaena porcus</i>
<i>Seriola dumerili</i>	<i>Scorpaena scrofa</i>
<i>Trachinotus ovatus</i>	Siganidae
<i>Trachurus mediterraneus</i>	<i>Siganus luridus</i>
Clupeidae	Sphyraenidae
<i>Sardina pilchardus</i>	<i>Sphyraena sphyraena</i>
Centracanthidae	Syngnathidae
<i>Spicara maena</i>	<i>Syngnathus typhle typhle</i>
<i>Spicara smaris</i>	Trachinidae
Gobiidae	<i>Trachinus draco</i>
Scaridae	Tripterygiidae
<i>Sparisoma cretense</i>	
Serranidae	

($p < 0.05$). Regarding species richness, sandy bottoms and seagrass were significantly different from other habitats ($p < 0.05$). Indices were also estimated for the different boulder (B1, B2, B3) and continuous rock (CR1, CR2, CR3) categories, but no significant differences were found.

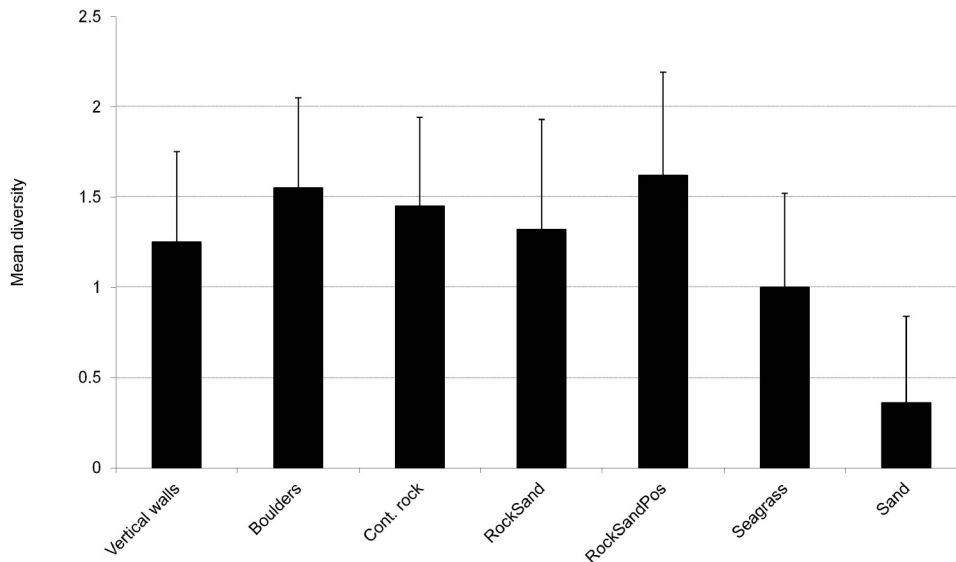


Fig. 2: Mean diversity (Shannon-Wiener H'). Bars indicate standard deviations.

The highest fish biomass was recorded in rocky bottoms with patches of sand and *P. oceanica*, however, in bottoms with continuous rock, the average biomass was higher. The lowest values were recorded in sandy bottoms. One-way ANOVA and Scheffe post-hoc test showed that sandy and seagrass bottoms were significantly different from all other substrate types ($p < 0.05$) (Fig. 5).

To examine the interrelations with environmental factors (Fig. 6), we conducted a Redundancy analysis (RDA) on the abundances of 24 fish species with occurrence frequency $>20\%$, which were: *Apogon imberbis*, *Boops boops*, *Bothus podas*, *Chromis chromis*, *Coris julis*, *Diplodus annularis*, *Diplodus puntazzo*, *Diplodus sargus*, *Diplodus vulgaris*, *Epinephelus marginatus*, *Lithog-*

nathus mormyrus, *Mullus surmuletus*, *Oblada melanura*, *Sarpa salpa*, *Serranus cabrilla*, *Serranus scriba*, *Siganus luridus*, *Sparisoma cretense*, *Symphodus mediterraneus*, *Symphodus roissali*, *Symphodus tinca*, *Thalassoma pavo* and *Xyrichthys novacula*, *Atherina* spp. were excluded from the analysis due to their wide habitat range and high abundance. Such gregarious planktonic species with patchy distributions can obscure the variation of necto-benthic fish species (Ferrell & Bell, 1991). The RDA regarding physical factors indicated that the presence of hard substrate was the most important physical factor that determined the species composition and distribution of fishes (Fig. 6). The first two axes explained 15.5% of the variance and the first two species-environment cor-

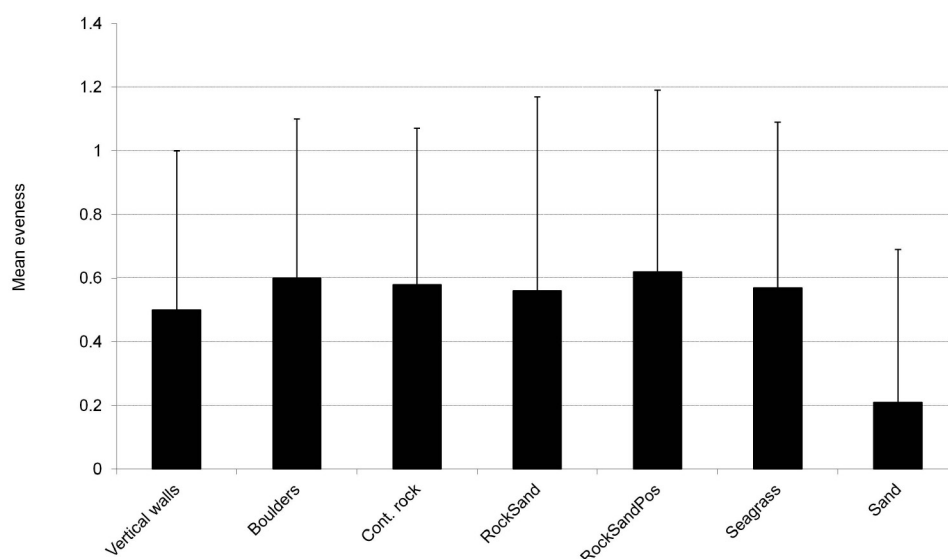


Fig. 3: Mean evenness (Pielou's J). Bars indicate standard deviations.

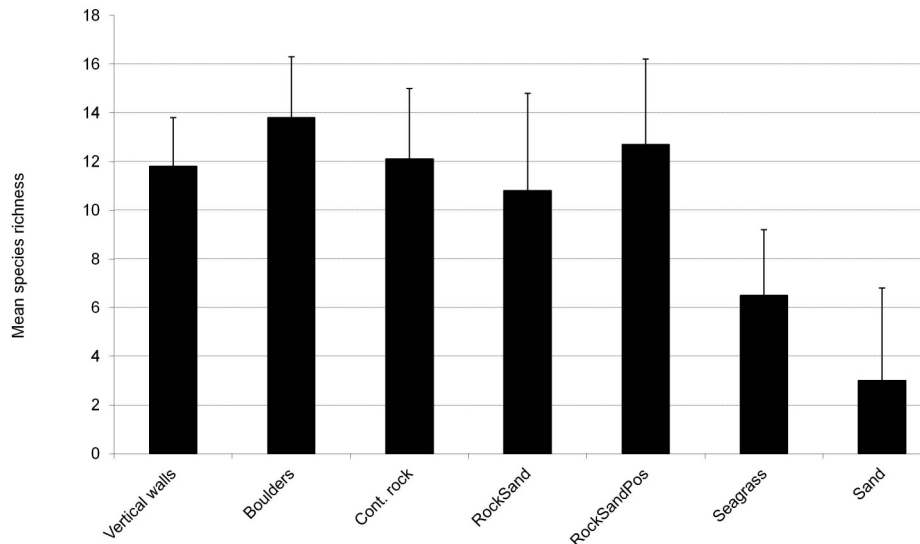


Fig. 4: Mean species richness (species number). Bars indicate standard deviations.

relations were 0.77 and 0.50. Most species recorded were strongly related to the presence of rocky habitats.

We also conducted a RDA on the abundances of the most common reef fish species – *Apogon imberbis*, *Coris julis*, *Diplodus puntazzo*, *Diplodus sargus*, *Diplodus vulgaris*, *Epinephelus marginatus*, *Oblada melanura*, *Sarpa salpa*, *Serranus cabrilla*, *Serranus scriba*, *Siganus luridus*, *Sparisoma cretense*, *Symphodus mediterraneus*, *Symphodus ocellatus*, *Symphodus roissali*, *Symphodus tinca*, and *Thalassoma pavo* – in order to detect their interrelations to the benthic seascape (Fig. 7). On most islands, the dominant benthic group was turf algae. However, in islands situated in the eastern part of our study area, around 50% of the substrate was barren (bare rock

with calcareous algae), while in the islands Kimolos, Stroglylo and Donousa, the dominant group was *Cystoseira* spp. (see Giakoumi *et al.*, 2012). The first two axes of the RDA explained only 5% of the variance and the first two species-environment correlations were 0.43 and 0.38. Evidence showed that most common species are not associated with the benthic seascape. However, Labridae species, like *Symphodus tinca*, *Symphodus mediterraneus*, and *Coris julis* were found to be highly associated with *Cystoseira* spp. coverage. Furthermore, the herbivore species *Sparisoma cretense* appeared to be associated with CCA while the alien herbivore species *Siganus luridus* was associated with bare rock.

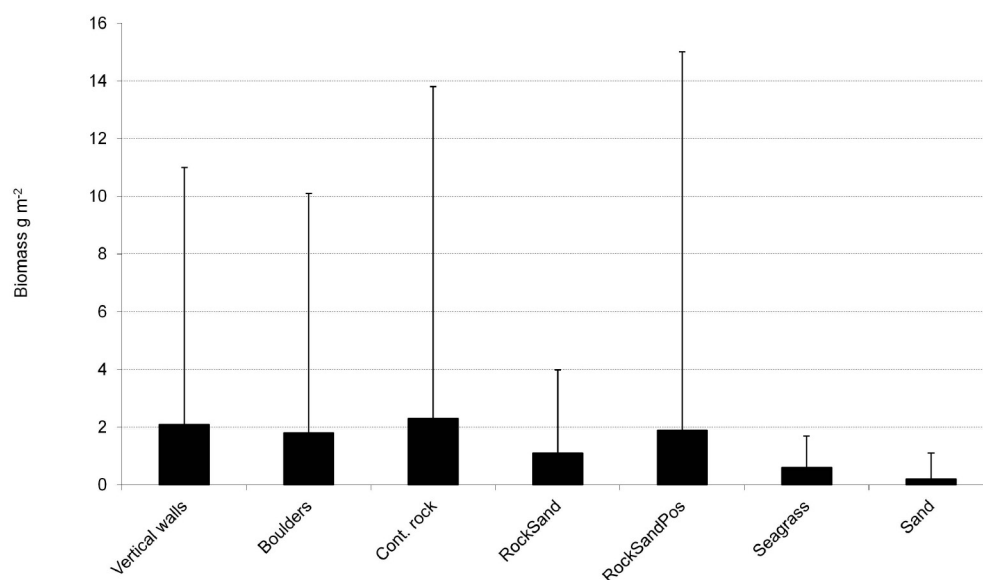


Fig. 5: Mean fish biomass. Bars indicate standard deviations.

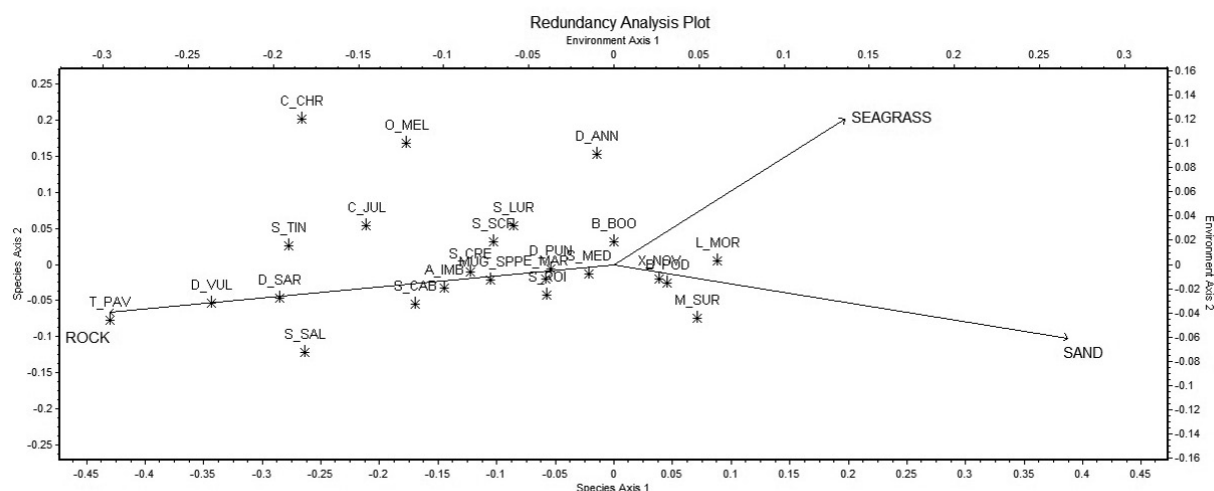


Fig. 6: Redundancy analysis (RDA) diagram of the 24 most common fish species abundances: *Apogon imberbis* (A_IMB), *Boops boops* (B_BOO), *Bothus podas* (B_POD), *Chromis chromis* (C_CHR), *Coris julis* (C_JUL), *Diplodus annularis* (D_ANN), *Diplodus puntazzo* (D_PUN), *Diplodus sargus* (D_SAR), *Diplodus vulgaris* (D_VUL), *Epinephelus marginatus* (E_MAR), *Lithognathus mormyrus* (L_MOR), *Mullus surmuletus* (M_SUR), *Oblada melanura* (O_MEL), *Sarpa salpa* (S_SAL), *Serranus cabrilla* (S_CAB), *Serranus scriba* (S_SCR), *Siganus luridus* (S_LUR), *Sparisoma cretense* (S_CRE), *Symphodus mediterraneus* (S_MED), *Symphodus roissali* (S_ROI), *Symphodus tinca* (S_TIN), *Thalassoma pavo* (T_PAV) and *Xyrichtys novacula* (X_NOV), versus physical habitat represented by arrows.

Correlation to rugosity

Rugosity ranged from 1 to 1.4, with mean value 1.28. We found that substrate complexity was positively correlated to species richness ($r=0.356$, $p<0.01$), but no significant correlation was detected with fish biomass, density or diversity. These results refer to all sites, including those with soft sediment. When only rocky bottoms were taken into account, no statistically significant correlation was detected among rugosity and community parameters.

Discussion

We used visual census techniques to explore and study the shallow sublittoral fish community of the Cyclades Archipelago, North-eastern Mediterranean, and its relation to habitat and substrate complexity. We found similar species richness, in terms of species number, to other areas of the Eastern Mediterranean, but fish species composition differed (Harmelin-Vivien *et al.*, 2005). In the shallow sublittoral of the Central Aegean Sea, all but one species recorded (*Siganus luridus*) were native, in

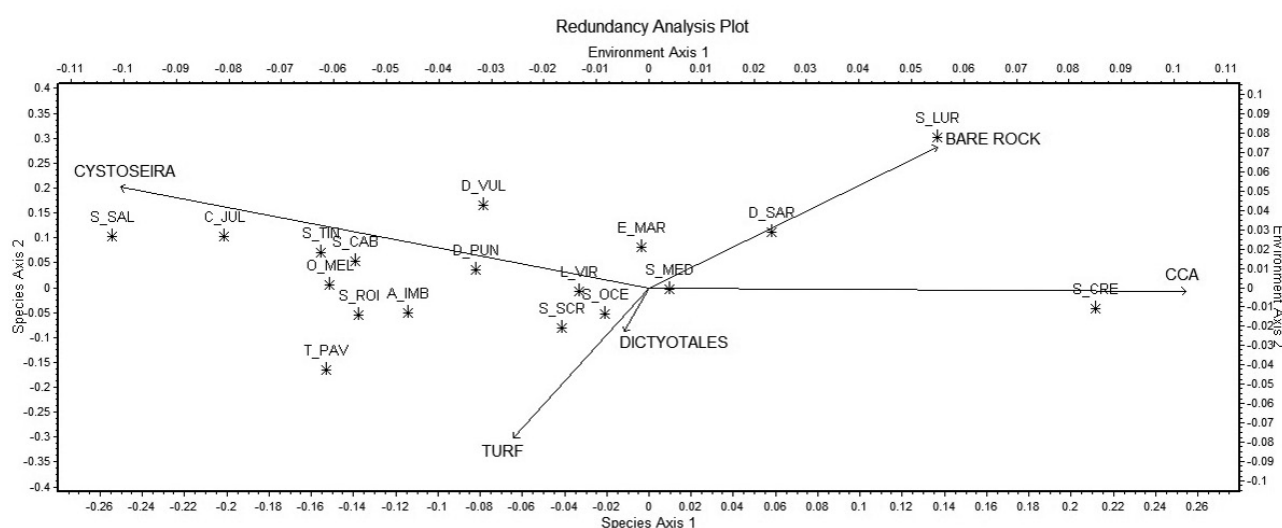


Fig. 7: Redundancy analysis (RDA) diagram of the 17 reef fish abundances: *Apogon imberbis* (A_IMB), *Coris julis* (C_JUL), *Diplodus puntazzo* (D_PUN), *Diplodus sargus* (D_SAR), *Diplodus vulgaris* (D_VUL), *Epinephelus marginatus* (E_MAR), *Oblada melanura* (O_MEL), *Sarpa salpa* (S_SAL), *Serranus cabrilla* (S_CAB), *Serranus scriba* (S_SCR), *Siganus luridus* (S_LUR), *Sparisoma cretense* (S_CRE), *Symphodus mediterraneus* (S_MED), *Symphodus ocellatus* (S_OCE), *Symphodus roissali* (S_ROI), *Symphodus tinca* (S_TIN), *Thalassoma pavo* (T_PAV), versus biological habitat.

contrast to the Levantine basin, South-eastern Mediterranean, where alien species (originating from the Red Sea) are abundant (Hassan *et al.*, 2003). Rocky habitats displayed a species composition more similar to regions of the Western and Central Mediterranean (Harmelin, 1987; Harmelin *et al.*, 1995; Dufour *et al.*, 1995; Reñones *et al.*, 1997; García-Charton & Perez-Ruzafa, 1998; Ruitton *et al.*, 2000; Macpherson *et al.*, 2002; Micheli *et al.*, 2005), but the main difference was the presence of two herbivores, *Sparisoma cretense* (native) and *Siganus luridus* (exotic) in addition to *Sarpa salpa* (native species, encountered in the entire Mediterranean).

Worldwide, different substrate types in marine ecosystems have been found to support fish assemblages of different composition, richness and density (Gray *et al.*, 1996; Jenkins & Wheatley, 1998; Jackson *et al.*, 2001; Curley *et al.*, 2002; Anderson & Millar, 2004; Chittaro, 2004). In the Mediterranean Sea, few studies have been conducted to investigate dissimilarities in spatial patterns of fish assemblages among rocky *P. oceanica* beds and unvegetated sand habitats (Francour, 1994; Guidetti, 2000; Tunesi *et al.*, 2006; La Mesa, 2011). Those studies support the important effect of substrate type on fish community characteristics. In the present study, the type of habitat was significant in determining the distribution of fish species and their abundances. Fish assemblages associated with sand were clearly distinct from other substrate types, probably due to the presence of many exclusive species in that habitat. The highest diversity and evenness were found in habitats characterized by high heterogeneity, i.e. hard bottoms with patches of sand and *Posidonia oceanica*. Species number, abundance and biomass were significantly lower in sandy areas and always higher on hard substrates, with seagrass habitats presenting intermediate values. The lower complexity of unvegetated sandy bottoms is a possible explanation for the low values in all indices (Gratwicke & Speight, 2005; Harmelin-Vivien *et al.*, 2005). On the other hand, rocky habitats, with higher mean complexity, provide numerous microhabitats and abundance of prey, resulting in greater diversity of fish assemblages (Bonaca & Lipej, 2005). These results are concordant with evidence from the North-western and South-eastern Mediterranean (Harmelin-Vivien *et al.*, 2005; Tunesi *et al.*, 2006; La Mesa *et al.*, 2011). However, in the Adriatic Sea, Central Mediterranean, Guidetti (2000) recorded higher species richness in *P. oceanica* meadows than in rocky bottoms.

Among rocky habitats, boulders displayed the highest species number. Macpherson (1994) argued that more species are found where boulders are present because the topographic complexity is higher, offering more cover from predators. Density was higher in vertical walls, a fact that can be explained by the large numbers of zooplanktivores (mainly damselfishes, *Chromis chromis*) present in that habitat. In other Mediterranean and temperate regions, zooplanktivores were also dominant in

vertical walls, possibly because these species are associated with strong currents for feeding purposes (Aburto-Oropeza & Balart, 2001; Bussotti & Guidetti, 2009). Apex predators displayed lower values in density and biomass in all habitats. Fishing practices that target high trophic level species (Pauly *et al.*, 1998; Macpherson, 2000), the shallow depth of the sampling (Tunesi *et al.*, 2006) and the low detectability of apex predators during visual census (Kruschel & Schultz, 2011) could be considered responsible for the observed scarcity of their occurrence.

Topographic complexity of the substratum is more or less a determining factor for fish communities in the tropics as well as in temperate latitudes (e.g. Luckhurst & Luckhurst 1978, Leum & Choat 1980). Regarding the Mediterranean Sea, there are evidences supporting such argument. Harmelin (1987), describing a rocky fish assemblage in the North-western Mediterranean, observed an increase in species richness related to topographic complexity. Reñones *et al.* (1997) found that in the Balearic Islands, abundance of both species and individuals increase with rugosity. Similar results were obtained by García-Charton & Perez-Ruzafa (1998, 2001) in the South-western Mediterranean. However, Ruitton *et al.* (2000) found that in the French Mediterranean coast, there is a positive impact of topographic complexity on the number of species but not on their abundances. In the rocky sublittoral of the Cyclades Archipelago, rugosity did not seem to be an important factor in structuring fish assemblages. All sampling sites with hard substrates, which were situated in fished areas, exhibited very low fish abundances compared to other regions of the Western Mediterranean (Harmelin-Vivien *et al.* 2008). These low densities could be a result of the interaction of human activities (intense fishing pressure) and natural processes (e.g. low productivity resulting in limited larvae survival and abundance). With such low values of density, below the carrying capacity of the habitat, topographic complexity and competition for space may not act as driving forces in shaping fish assemblages. Although the hydrodynamic conditions did not differ significantly among our sites, this factor may have partly masked the influence of topographic complexity in determining fish abundances across the study area. However, our results are consistent with Sala *et al.* (2012) who found no influence of rugosity on fish biomass or the structure of the benthic and fish community at the Mediterranean Basin scale. According to the authors, the level of protection of a marine area and not local habitat characteristics is the most important factor in determining total fish biomass and community structure in the Mediterranean Sea.

Visual sampling techniques have been associated with a number of biases related to the observer (e.g. speed, experience, presence) and behaviour of fishes (e.g. response to observer's presence, cryptic behaviour) (Cheal & Thompson 1997; De Girolamo & Mazzoldi

2001; and references therein). However, a visual census permits an estimate of the density of one or more species with relatively little expenditure of field time and without the undesired disturbances caused by destructive sampling processes. There is evidence that some fish species, e.g. fast-swimming necto-benthic fishes, are much better estimated visually than by trawling (Harmelin-Vivien & Francour 1992). Furthermore, such methods are necessary when sampling fish assemblages from sensitive habitats and marine protected areas (Edgar *et al.* 2004). Fish abundances may appear lower in habitats that are highly complex due to restricted detectability (e.g. Bozec *et al.* 2011). Yet, there are studies indicating that fish densities among different habitats are unrelated to detectability (e.g. Pelletier *et al.* 2011). To address some aspects of bias, the observers were well trained. At the same time the clear waters of the Cyclades Archipelago, which allows for greater visibility, the shallow depth at which the surveys were conducted, and the relatively low density of fishes all contributed in reducing potential biases in detectability.

The present work is the first attempt in investigating the effects of habitat and topographic complexity on fish assemblages in the Aegean Sea. Our results indicate that substrate type influences the composition and structure of fish assemblages. Fish density and biomass reached their highest values in rocky bottoms. However, fish community structure does not seem to differ among rocky habitats in relation to topographic complexity. In future studies, more detailed descriptors of habitat structure should be taken into account, e.g. specific numbers of small boulders and size of cavity aperture between them. Moreover, variability of fish assemblages across habitat structure should be explored at different spatial scales before evidences can be generalized.

Acknowledgements

We would like to thank Dr. E. Sala for his help in designing the field methodology and Dr. Enric Ballersteros for helping us with the algae species identification. Special thanks to M. Sini, A. Spyropoulou, A. Pantazis, I. Vlachou and A. Gomez Gomez for their invaluable efforts during the underwater surveys. Funding for material and field expenses was provided by the Prefecture of the Cyclades. S. Giakoumi was supported by a Hellenic State Postgraduate Scholarship (IKY).

References

Aburto-Oropeza, O., Balart, E.F., 2001. Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. *P.S.Z.N.I.: Marine Ecology*, 22 (4), 283-305.
Anderson, M.J., Millar, R.B., 2004. Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand. *Journal of Experimental Ma-*

rine Biology & Ecology, 305 (2), 191-221.
Bonaca, M.O., Lipej, L., 2005. Factors affecting habitat occupancy of fish assemblages in the Gulf of Trieste (Northern Adriatic Sea). *Marine Ecology*, 26 (1), 42-53.
Bonin, M.C., Srinivasan, M., Almany, G.R., Jones, G.P., 2009. Interactive effects of interspecific competition and micro-habitat on early post-settlement survival in a coral reef fish. *Coral reef*, 28 (1), 265-274.
Booth, D.J., Brosnan, D.M., 1995. The role of recruitment dynamics in rocky shores and coral reef fish communities. *Advances in Ecological Research*, 26, 309-385.
Bozec, Y.-M., Kulbicki, M., Laloë, F., Mou-Tham, G., Gascuel, D., 2011. Factors affecting the detection distances of reef fish: implications for visual counts. *Marine Biology*, 158 (5), 969-981.
Bussotti, S., Guidetti, P., 2009. Do Mediterranean fish assemblages associated with marine caves and rocky cliffs differ? *Estuarine, Coastal & Shelf Science*, 81, 65-73.
Cheal, A.J., Tompson, A.A., 1997. Comparing visual counts of coral reef fish: implications of transect width and species selection. *Marine Ecology Progress Series*, 158, 241-248.
Chittaro, P.M., 2004. Fish-habitat associations across multiple spatial scales. *Coral Reefs*, 23 (2), 235-244.
Connell, S.D., Jones, G.P., 1991. The influence of habitat complexity on post-recruitment processes in a temperate reef fish population. *Journal of Experimental Marine Biology & Ecology*, 151, 271-294.
Curley, B.G., Kingsford, M.J., Gillanders, B.M., 2002. Spatial and habitat-related patterns of temperate reef fish assemblages: implications for the design of Marine Protected Areas. *Marine & Freshwater Research*, 53, 1197-1210.
De Girolamo, M., Mazzoldi, C., 2001. The application of visual census on Mediterranean rocky habitats. *Marine Environmental Research*, 51 (1), 1-16.
De Martini, E.E., Friedlander, A.M., Sandin, S.A., Sala, E., 2008. Differences in fish assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Marine Ecology Progress Series*, 365, 199-215.
Dufour, V., Jouvenel, J.-Y., Galzin, R., 1995. Study of a reef fish assemblage: comparison of population distributions between depths in protected and unprotected areas over one decade. *Aquatic Living Resources*, 8, 17-25.
Edgar, G.J., Barrett, N.S., Morton, A.J., 2004. Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. *Journal of Experimental Marine Biology & Ecology*, 308 (2), 269-290.
Emery, A.R., 1978. The basis of fish community structure: marine and freshwater comparisons. *Environmental Biology of Fishes*, 3 (1), 33-47.
Ferrell, D.J., Bell, J.D., 1991. Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. *Marine Ecology Progress Series*, 72, 15-24.
Francour, P., 1994. Pluriannual analysis of the reserve effect on ichthyofauna in the Scandola natural reserve (Corsica, Northwestern Mediterranean). *Oceanologica Acta*, 17 (3), 309-317.
Francour, P., 1997. Fish assemblages of *Posidonia oceanica* beds at Port-Cros (France, NW Mediterranean): assessment of composition and long-term fluctuations by visual census. *P.S.Z.N.I.: Marine Ecology*, 18 (2), 157-173.

- Friedlander, A.M., De Martini, E.E., 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: the effects of fishing down apex predators. *Marine Ecology Progress Series*, 230, 253-264.
- Froese, R., Pauly, D., 2010. *Fishbase World Wide Web electronic publication*. www.fishbase.org (Accessed in March 2010).
- García-Charton, J.A., Pérez-Ruzafa, A., 1998. Correlation between habitat structure and a rocky reef fish assemblage in the southwest Mediterranean. *P.S.Z.N.I.: Marine Ecology*, 19 (2), 111-128.
- García-Charton, J.A., Pérez-Ruzafa, A., 2001. Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. *Marine Biology*, 138 (5), 917-934.
- García-Charton, J.A., Pérez-Ruzafa, A., Sánchez-Jerez, P., Bayle-Sempere, J.T., Reñones, O. *et al.*, 2004. Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. *Marine Biology*, 144, 161-182.
- García-Rubies, A., Zabala, M., 1990. Effects of total fishing prohibition on the rocky fish assemblages of Medes Islands Marine Reserve (NW Mediterranean). *Scientia Marina*, 54 (4), 317-328.
- Gratwicke, B., Speight, M.R., 2005. Effects of habitat complexity on Caribbean marine fish assemblages. *Marine Ecology Progress Series*, 292, 301-310.
- Gray, C.A., McElligott, D.J., Chick, R.C., 1996. Intra- and interestuary differences in assemblages of fishes associated with shallow seagrass and bare sand. *Marine & Freshwater Research*, 47 (5), 723-735.
- Giakoumi, S., Cebrian, E., Kokkoris, G.D., Ballesteros, E., Sala, E., 2012. Relationships between fish, sea urchins and macroalgae: The structure of shallow sublittoral communities in the Cyclades, Eastern Mediterranean. *Estuarine, Coastal & Shelf Science*, 109, 1-10.
- Giakoumi, S., Grantham, H.S., Kokkoris, G.D., Possingham, H.P., 2011. Designing a network of marine reserves in the Mediterranean Sea with limited socio-economic data. *Biological Conservation*, 144 (2), 753-763.
- Guidetti, P., 2000. Differences among fish assemblages associated with nearshore *Posidonia oceanica* beds, rocky-algal reefs and unvegetated sand habitats in the Adriatic Sea. *Estuarine, Coastal & Shelf Science*, 50 (4), 515-529.
- Harman, N., Harvey, E.S., Kendrick, G.A., 2003. Differences in fish assemblages from different reef habitats at Hamelin Bay, south-western Australia. *Marine & Freshwater Research*, 54 (2), 177-184.
- Harmelin, J.-G., 1987. Structure and variability of the ichthyofauna in a Mediterranean protected rocky area (National Park of Port Cros, France). *P.S.Z.N.I.: Marine Ecology*, 8 (3), 263-284.
- Harmelin, J.-G., 1990. *Ichtyofaune des fonds rocheux de Méditerranée: structure du peuplement du coralligène de l'île de Port-Cros (Parc national, France)*. *Mésogée*, 50, 23-30.
- Harmelin, J.-G., Bacht, F., Garcia, F., 1995. Mediterranean marine reserves: Fish indices as tests of protection efficiency. *P.S.Z.N.I.: Marine Ecology*, 16 (3), 233-250.
- Harmelin-Vivien, M.L., Bitar, G., Harmelin, J.-G., Monestiez, P., 2005. The littoral fish community of the Lebanese rocky coast (eastern Mediterranean Sea) with emphasis on Red Sea immigrants. *Biological Invasions*, 7 (4), 625-637.
- Harmelin-Vivien, M.L., Francour, P., 1992. Trawling or visual censuses? Methodological bias in the assessment of fish population in seagrass beds. *P.S.Z.N.I.: Marine Ecology*, 13 (1), 41-51.
- Harmelin-Vivien, M.L., Harmelin, J.-G., Lebourleux, V., 1995. Micro-habitat requirements for settlement of juvenile sparid fishes on Mediterranean rocky shores. *Hydrobiologia*, 300-301 (1), 309-320.
- Harmelin-Vivien, M.L., Le Diréach, L., Bayle-Sempere, J., Charbonnel, E., García-Charton, J.A. *et al.*, 2008. Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: Evidence of fish spillover? *Biological Conservation*, 141 (7), 1829-1839.
- Hassan, M., Harmelin-Vivien, M., Bonhomme, F., 2003. Les-sepsian invasion without bottleneck: example of two rabbitfish species (*Siganus rivulatus* and *Siganus luridus*). *Journal of Experimental Marine Biology & Ecology*, 291 (2), 219-232.
- Heinlein, J.M., Stier, A.C., Steele, M.A., 2010. Predators reduce abundance and species richness of coral reef fish recruits via non-selective predation. *Coral Reefs*, 29 (2), 527-532.
- Henderson, P.A., Seaby, R.M.H., 2007. *Environmental Community Analysis 2.1*. Pisces Conservation Ltd, Lymington, UK.
- Holbrook, S.J., Forrester, G.E., Schmitt, R.J., 2000. Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. *Oecologia*, 122, 109-120.
- Holbrook, S.J., Schmitt, R.J., Stephens, J.S. 1997. Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecological Applications*, 7 (4), 1299-1310.
- Jackson, E.L., Rowden, A.A., Atrill, M.J., Bossey, S.J., Jones, M.B. 2001. The importance of seagrass beds as a habitat for fishery species. *Oceanography & Marine Biology*, 39, 269-303.
- Jenkins, G.P., Wheatley, M.J., 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. *Journal of Experimental Marine Biology & Ecology*, 221, 147-172.
- Juanes, F., 2007. Role of habitat in mediating mortality during the post-settlement transition phase of temperate marine fishes. *Journal of Fish Biology*, 70 (3), 661-677.
- Kruschel, C., Schultz, S.T., 2011. Use of a lure in visual census significantly improves probability of detecting wait-ambushing and fast cruising predatory fish. *Fisheries Research*, 123-124, 70-77. doi:10.1016/j.fishres.2011.11.015.
- La Mesa, G., Molinari, A., Gambaccini, S., Tunesi, L., 2011. Spatial pattern of coastal fish assemblages in different habitats in North-western Mediterranean. *P.S.Z.N.I.: Marine Ecology*, 32 (1), 104-114.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. 2nd edition. Elsevier, Amsterdam, 853 pp.
- Leis, J.M., McCormick, M.I., 2002. The biology, behavior and ecology of the pelagic larval stage of coral reef fishes. p. 171-199. In: *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Sale, P.F. (Ed.). Academic Press, San Diego.
- Leum, L.L., Choat, J.H., 1980. Density and distribution patterns of the temperate marine fish *Cheilodactylus spectabilis* (Cheilodactylidae) in the reef environment. *Marine Biology*, 57 (4), 327-337.
- Luckhurst, B.E., Luckhurst, K., 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Ma-*

- rine Biology, 49 (4), 317-323.
- Macpherson, E., 1994. Substrate utilization in a Mediterranean littoral fish community. *Marine Ecology Progress Series*, 114, 211-218.
- Macpherson, E., 2000. Fishing effects on trophic structure of rocky littoral fish assemblages. p. 43-44. In: *Fishing down the Mediterranean food webs? Kerkyra, Greece, 26-30 July 2000. CIESM Workshop Series, No.12*. CIESM, Monaco.
- Macpherson, E., Gordo, A., García-Rubies, A., 2002. Biomass size spectra in littoral fishes in protected and unprotected areas in the NW Mediterranean. *Estuarine Coastal & Shelf Science*, 55 (5), 777-788.
- McClanahan, T.R., Arthur, R., 2001. The effect of marine reserves and habitat on populations of East African coral reef fishes. *Ecological Applications*, 11 (2), 559-569.
- Messmer, V., Jones, G.P., Munday, P.L., Holbrook, S.J., Schmitt, R.J. *et al.*, 2011. Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology*, 92 (12), 2285-2298.
- Micheli, F., Benedetti-Cecchi, L., Gambaccini, S., Bertocci, I., Borsini, C. *et al.*, 2005. Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages. *Ecological Monographs*, 75 (1), 81-102.
- Moutopoulos, D.K., Stergiou, K.I., 2002. Length-weight and length-length relationships of fish species from the Aegean Sea (Greece). *Journal of Applied Ichthyology*, 18 (3), 200-203.
- Papathanassiou, E., Zenetos, A. (Eds.), 2005. *State of the Hellenic marine environment (SOHELME)*. HCMR Publications, Athens, 360 pp.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998. Fishing down marine food webs. *Science*, 279 (5352), 860-863.
- Pelletier, D., Leleu, K., Mou-Tham, G., Guillemot, N., Chabonet, P., 2011. Comparison of visual census and high definition video transects for monitoring coral reef fish assemblages. *Fisheries Research*, 107 (1-3), 84-93.
- Preskitt, L.B., Vroom, P.S., Smith, C.M., 2004. A Rapid Ecological Assessment (REA). quantitative survey method for benthic algae using photoquadrats with scuba. *Pacific Science*, 58 (2), 201-209.
- Pollard, D.A., 1984. A review of ecological studies on sea-grass-fish communities, with particular reference to recent studies in Australia. *Aquatic Botany*, 18 (1-2), 3-42.
- Reñones, O., Moranta, J., Coll, J., Morales-Nin, B., 1997. Rocky bottom fish communities of Cabrera Archipelago National Park (Mallorca, Western Mediterranean). *Scientia Marina*, 61 (4), 495-506.
- Risk, M.J., 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bulletin*, 153, 1-6.
- Ruitton, S., Francour, P., Boudouresque, C.F., 2000. Relationships between algae, benthic herbivorous invertebrates and fishes in rocky sublittoral communities of a temperate sea (Mediterranean). *Estuarine, Coastal & Shelf Science*, 50 (2), 217-230.
- Sala, E., Ballesteros, E., Dendrinos, P., Di Franco, A., Ferretti F. *et al.*, 2012. The structure of Mediterranean rocky reef ecosystems across environmental and human gradients and conservation implications. *PloS ONE*, 7 (2), e32742. doi:10.1371/journal.pone.0032742.
- Seaby, R.M., Henderson, P.A., 2006. *Species Diversity & Richness. Version 4*. Pisces Conservation Ltd., Lymington.
- Stergiou, K.I., Moutopoulos, D.K., Erzini, K., 2002. Gill net and longlines fisheries in Cyclades waters (Aegean Sea): species composition and gear competition. *Fisheries Research*, 57 (1), 25-37.
- Tunesi, L., Molinari, A., Salvati, E., Mori, M., 2006. Depth and substrate type driven patterns in the infralittoral fish assemblage of the NW Mediterranean Sea. *Cybium*, 30, 151-159.
- Tuya, F., Wernberg, T., Thomsen, M.S., 2009. Habitat structure affect abundances of labrid fishes across temperate reefs in south-western Australia. *Environmental Biology of Fishes*, 86 (2), 311-319.
- Williams, D.McB., 1982. Patterns in distribution of fish communities across the central Great Barrier Reef. *Coral Reefs*, 1 (1), 35-43.