SPATIAL AND TEMPORAL PATTERNS OF DIVERSITY IN MEDITERRANEAN ROCKY REEF FISH ASSEMBLAGES

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ALPHA DIVERSITY BETA DIVERSITY DEPTH ROCKY REEF FISH ASSEMBLAGES MEDITERRANEAN SEA

ABSTRACT. – The present study aimed at evaluating spatial and temporal patterns of diversity in Mediterranean rocky reef fish assemblages. With this objective, we tested the following hypotheses: i) assemblages of different depth ranges differed in terms of species composition and patterns of diversity, ii) within each depth range, patterns of diversity varied depending on the spatial scale examined and iii) they followed seasonal and inter-annual dynamics. Three habitats related to different intervals of depths were studied within a rocky coastal area during a year one period using visual census techniques. Alpha diversity, at different spatial and temporal scales, and beta diversity, between and within different habitats, were evaluated. 65 valid taxa were determined during the study period, 33 in 25-30 m deep assemblages, 38 in 10-15 m deep assemblages and 35 in 0-5 m deep assemblages, such as their seasonal dynamics, significantly changed in relation to depth and that these differences remained constant between years.

INTRODUCTION

The knowledge of patterns of biodiversity and causes of its variations represents one of the main goals for ecologists (Walker 1992, 1995, Sax & Gaines 2003). In fact, diversity is considered as a main characteristic of ecosystems for environmental conservation and management. There is an important need for the knowledge of diversity spatial patterns and temporal dynamics (Gray 1997). Diversity of an ecological system may be considered under several aspects. Thus, a punctual assessment of alpha diversity, considered as the number of species in a community and/or the number of species and the relative abundance of individuals, may be not enough to understand patterns of biodiversity at the ecosystem level. In fact, diversity may change at different spatial and temporal scales (Whittaker 1972) and the correspondence between values of diversity at small and large spatial scales is not always evident because patterns of diversity are related to the spatial variability of each system (Gray 2000, Gering & Crist 2002). Moreover, temporal dynamics of assemblages can influence patterns of diversity, which may change following the cycles of the organisms, the evolution of the ecosystems, and stochastic events. Finally, beta diversity is also considered as a key concept for understanding the functioning of ecosystems and for their conservation and management (Gray 1997, 2000, Legendre et al. 2005). Beta diversity may be evaluated at two different levels: between habitats, normally referring to turnover diversity, or within each habitat as the measure of the heterogeneity of assemblages (Gray 2000).

A simultaneous evaluation of alpha and beta diversity and the assessment of their spatial and temporal variability are considered to be the most useful approaches to determine patterns of diversity of ecosystems (Mokany *et al.* 2011).

Fish assemblages have a key role in coastal habitats due to their economic value and ecological importance. The knowledge of their patterns of diversity is fundamental for the management of coastal ecosystems (Smith et al. 1999). The most part of knowledge of marine fish assemblage diversity is related to studies carried out by trawl surveys, mainly on the continental shelf, while coastal fish assemblages are less investigated. Richness is the most commonly used method to determine the diversity of fish assemblages but it is a weak indicator of effects of anthropogenic pressures (Azzurro et al. 2010). Different aspects of diversity should be considered in order to understand causes of erosion of diversity and to develop appropriate programs of maintenance management. In this contest, beta diversity may be useful even if it has been less investigated for fish assemblages (Lorance et al. 2002, Arias-Gonzales et al. 2008). Moreover, it is important to evaluate temporal patterns of diversity during periods long enough to separate different causes of assemblage variability; in fact, fish assemblages may change their structure following temporal dynamics related both to seasonal cycles and to inter-annual variations (Dulčić et al. 1997; Matić-Skoko et al. 2007).

In subtidal marine systems, depth represents a valid proxy to measure beta diversity along a gradient (Balata & Piazzi 2008); many physical and biotic factors, such as light, water movement, temperature, food availability, biotic interactions and human disturbance, are also structured following gradients related to depth (Garrabou *et al.* 2002). Depth, together with morphological characteristics of the bottom, is considered an important factor to determine beta diversity of fish assemblages (Lorance *et al.* 2002, Arias-Gonzales *et al.* 2008). In the Mediterranean Sea, this aspect has been scarcely evaluated, even if patterns related to depth have been widely described (Bell 1983, Dufour *et al.* 1995, Cecchi *et al.* 2007, Milazzo *et al.* 2011).

The aims of the present study are to evaluate spatial and temporal patterns of diversity in Mediterranean rocky reef fish assemblages through the concurrent use of different diversity aspects. Richness was particularly determined at different spatial scales and beta diversity was evaluated along a depth gradient and within each depth range. Moreover, temporal variability of patterns of diversity was evaluated for three years throughout a five years period. The following hypotheses were tested: i) assemblages of different depth ranges differed in terms of species composition and patterns of diversity, ii) within each depth range, diversity varied depending on the spatial scale examined and iii) diversity followed seasonal and interannual dynamics.

MATERIAL AND METHODS

The study was carried out along a rocky coast situated at the south of Leghorn (north western Mediterranean Sea, Italy) (43°28'24"N and 10°19'42"E). The study area is characterized by rocky cliffs that end on a sandy bottom at 40 m depth. From the surface to about 25 m deep, photophilous macroalgal assemblages colonize the bottom; below this depth, benthic assemblages were characterized by a typical coralligenous habitat (*sensu* Ballesteros 2006) constituted by calcareous structures built by Corallinales. Both commercial and recreational (mostly spearfishing) fishing activities are permitted in the area; no quantitative data about fishing pressure are available for the area, even if the pressure is to be considered quite similar during the year (personal observation).

Three habitats related to different intervals of depths were studied: from the surface to 5 meters (shallow), between 10 and 15 meters (intermediate), between 25 and 30 meters (deep). The study was performed in three different years within a 5-years period (2003, 2005, 2007). For each year, 2 random dates were sampled both in Spring and in Autumn. For each habitat, two sites standing some km apart from each other were randomly selected for each sampling date. In each site and for each sampling date, two replicate samples distant about 100 m from each other were carried out in the early morning, to

Table I. – Fish taxa list showing presence	(x) or absence (-) regarding ha	ıbi
tat (S: Shallow, I: Intermediate, D: Deep	p) and season (Spr: Spring, A	ut
Autumn)		

	SEASON		HABITAT		
ΤΑΧΑ	Spr	Aut	s	Т	D
	•				
Congridae					
Conger conger (Linnaeus, 1758)	х	_	_	_	х
Muraenidae					
<i>Muraena helena</i> Linnaeus, 1758	х	х	-	х	х
BELONIFORMES					
Belonidae					
Belone belone (Linnaeus, 1761)	-	Х	х	-	-
PERCIFORMAE					
Serranidae					
Epinephelus marginatus (Lowe, 1834)	х	Х	-	Х	Х
Serranus cabrilla (Linnaeus, 1758)	Х	Х	Х	х	Х
Serranus scriba (Linnaeus, 1758)	х	Х	х	х	х
Dicentrarchus Jahrax (Linnacus, 1759)		v	v		
Apogonidae	-	~	^	-	-
Apogon imberbis (Linnaeus, 1758)	v	v	v	v	v
Carangidae	~	~	~	^	^
Trachinotus ovatus (Linnaeus, 1758)	_	x	x	_	_
Seriola dumerili (Bisso, 1810)	_	x	_	х	х
Trachurus spp.	_	x	_	_	х
Sciaenidae					
<i>Sciaena umbra</i> (Linnaeus, 1758)	х	х	-	х	х
Mullidae					
Mullus surmuletus Linnaeus, 1758	х	х	х	х	х
Sparidae					
Boops boops (Linnaeus, 1758)	-	Х	-	х	-
Dentex dentex (Linnaeus, 1758)	х	Х	-	-	Х
<i>Diplodus annularis</i> (Linnaeus, 1758)	х	Х	-	х	-
Diplodus puntazzo (Walbaum, 1972)	х	Х	-	Х	Х
Diplodus sargus (Linnaeus, 1758)	х	Х	-	х	Х
Diplodus vulgaris (Geoffroy Saint-Hilaire, 1817)	х	Х	х	Х	Х
Oblada melanura (Linnaeus, 1758)	Х	Х	Х	х	_
Sarpa salpa (Linnaeus, 1758)	X	X	х	X	Х
Sparus aurata (Linnaeus, 1758)	X	X	-	X	-
Maenidae	~	~	-	~	-
Spicara maena (Linnaeus, 1758)	x	_	_	x	x
Pomacentridae	~			~	~
Chromis chromis (Linnaeus, 1758)	х	х	х	х	х
Labridae					
Coris julis (Linnaeus, 1758)	х	х	х	х	х
Labrus merula Linnaeus, 1758	х	х	х	х	х
Labrus mixtus Linnaeus, 1758	х	х	-	-	х
Labrus viridis Linnaeus, 1758	х	х	-	х	х
Symphodus cinereus (Bonnaterre, 1788)	х	Х	-	х	-
Symphodus doderlenii Jordan, 1891	х	Х	-	х	-
Symphodus mediterraneus (Linnaeus, 1758)	х	Х	х	х	Х
Symphodus melanocercus (Risso, 1810)	х	Х	х	Х	Х
Symphodus ocellatus Forsskål, 1775	х	Х	-	Х	-
Symphodus roissali (Risso, 1810)	х	Х	х	х	-
Symphodus rostratus (Forsskål, 1775)	х	Х	х	Х	Х
Sympnodus tinca Linnaeus, 1758	X	X	X	х	-
<i>i nalassoma pavo</i> (Linnaeus, 1758)	х	х	х	-	-
	Y	×			
Convohoblennius gelerita (Linnacus, 1030)	×	×	x	_	_
Lipophrys canevae (Vinciguerra, 1880)	×	A Y	×	_	_
	^	^	^		

Table I. - Continued.

ТАХА		SEASON		HABITAT		
		Aut	S	I	D	
Parablennius gattorugine (Linnaeus, 1758)	х	х	х	х	х	
Parablennius incognitus (Bath, 1968)	-	х	х	-	-	
Parablennius pilicornis (Cuvier, 1829)	х	х	х	-	-	
Parablennius rouxi (Cocco, 1833)	х	х	-	х	х	
Parablennius sanguinolentus (Pallas, 1814)	х	х	х	-	-	
Parablennius zvonimiri (Kolombatovic, 1892)	х	х	х	-	-	
Paralipophrys trigloides (Valenciennes, 1836)	х	-	х	-	-	
Tripterygiidae						
Tripterygion delaisi Cadenat & Blache, 1971	х	х	х	-	-	
Tripterygion melanurus Guichenot, 1845	х	-	х	-		
Tripterygion tripteronotus (Risso, 1810)	х	х	х	-	-	
Scombridae						
Sarda sarda (Bloch, 1793)	-	х	-	-	х	
Gobiidae						
Gobius auratus Risso, 1810	х	х	-	-	х	
Gobius bucchichii (Steindachner, 1870)	х	х	-	х	-	
Gobius cobitis Pallas, 1811	-	х	х	-	-	
Gobius cruentatus Linnaeus, 1758	-	х	-	-	х	
Gobius paganellus Linnaeus, 1758	х	-	-	х	-	
SCORPAENIFORMES						
Scorpaenidae						
Scorpaena notata Rafinesque, 1810	х	х	-	х	х	
Scorpaena porcus Linnaeus, 1758	х	х	-	х	х	
Scorpaena scrofa Linnaeus, 1758	х	х	-	х	х	
SYNGNATHIFORMES						
Syngnathidae						
Sygnathus typhle Linnaeus, 1758	х	-	-	х	-	
MUGILIFORMES						
Sphyraenidae						
Sphyraena spp.	-	Х	-	-	х	
Mugilidae						
Chelon labrosus (Risso, 1827)	-	х	х	-	-	
Liza spp.	х	х	х	-	-	
ATHERINIFORMES						
Atherinidae						
Atherina spp.	-	Х	х	-	-	

avoid - disturbance. Each sample consisted of a belt transect 50 m long and 5 m wide (Garcia-Rubies & Zabala 1990). A total of 144 replicate samples were considered. The presence of each species was recorded while swimming slowly along the transect at about 1 m from the bottom. Data were expressed in presence/ absence of each species in the transect: the combination of species richness and composition dissimilarity is considered useful to assess spatial variability of community diversity (Mokany *et al.* 2011).

Alpha diversity was evaluated using species richness at 3 different spatial scales for each habitat: sample diversity (referred to the sample surface), site diversity (referred to sites within one km of coastline where more sample surfaces were present), location diversity (referred to the whole trait of coast) (Gray 2000). The number of species per sample was analyzed by 4-way analysis of variance (ANOVA). Factors and levels of analysis were the same for multivariate analysis. Homogeneity of variance was tested with Cochran C-test (Underwood 1997). Beta diversity within each habitat was estimated as the contribution to alpha diversity due to differences between sample points (Gray 2000): $\beta s = NH/\lambda$, where NH = species richness in habitat H, λ = average sample species richness in habitat H.

Beta diversity along the depth gradient (turnover diversity) was evaluated both through the β_D index (Lorance *et al.* 2002) and through multivariate analyses (Permutation analysis of variance, PER-MANOVA) and SIMPER procedure (Gray 2000).

 β_D index was calculated as $\beta_D = (G + L) / N_1 + N_2$ where G = number of species gained along the gradient, L = number of species lost along a gradient, N₁ and N₂ = the species richness in the habitats 1 and 2, respectively.

PERMANOVA was used to test the hypothesis that species composition of fish assemblages differed between habitats, years and seasons, to detect interactions among these factors and to evaluate the spatial variability within each habitat (Anderson 2001). To quantify turnover diversity of the system, Jaccard measures of dissimilarity were used to calculate a matrix of distances between pairs of samples. The Jaccard index is considered as the proportion of species shared amongst levels of each factor (Jaccard 1900) and it is one of the most frequently used ecological measures of compositional dissimilarity (Anderson et al. 2006). The analysis consisted of a 5-way model with Habitat (shallow vs. intermediate vs. deep) as fixed factor, Years (3 levels) as random and crossed factor, Season (Spring vs. Autumn) as fixed and orthogonal factor, Date (2 levels) as random factors nested in Season, and Site (2 levels) as random factor nested in the interaction Habitat x Date. Pairwise test was conducted to discriminate among levels of significant factors. The SIMPER test was used to evaluate the average dissimilarity among habitats and to determine the most

heavily contributing species to dissimilarity. A Venn diagram was used to show exclusive and common species among habitats.

RESULTS

A total of 65 valid taxa were determined during the study period (Table I): 33 in deep assemblages, 38 in intermediate assemblages and 35 in shallow assemblages. The mean number of species per belt transect was 13.0 \pm 9.3 (mean \pm SE, n = 48), 16.1 \pm 0.3 and 14.4 \pm 0.3, in deep, intermediate and shallow habitat, respectively. Species number was higher in intermediate assemblages for all the spatial scales examined (Fig. 1). ANOVA detected significant differences in values of species number per sample in relation to habitat and season; SNK test showed



Fig. 1. – Mean number of species calculated for sample, site and location in the three habitats.

Table II. – Result of ANOVA analysis on species richness per sample (df: degree of freedom, MS: mean square, F: ratio-values and P: probability). Significant effects are in bold.

Source	df	MS	F	Р	
Habitat = H	2	115.770	38.46	0.002	
Year = Y	2	0.395	0.19	0.828	
Season = S	1	47.840	22.89	0.041	
Date(YxS) = D(YxS)	6	2.034	0.31	0.921	
Area(HxD(YxS))	12	6.618	1.11	0.362	
HxY	4	3.010	0.77	0.565	
HxS	2	5.673	5.94	0.063	
Hx D(YxS)	12	3.909	0.77	0.676	
HxA(D(YxS))	24	5.097	0.86	0.653	
YxS	2	2.090	1.03	0.413	
HxYxS	4	0.954	0.24	0.907	
Residual	72	5.937			
Total	143				
Cochran's Test	C = 0.0573				



Fig. 2. - Values of Beta Diversity in the three years studied.

that values were higher in intermediate assemblages than in shallow assemblages and in this latter than in deep assemblages (Table II).

Values of β s index were higher for deep assemblages in the three years of study (Fig. 2).

The Venn diagram showed that 19, 10 and 8 taxa were exclusive of shallow, intermediate and deep assemblages, respectively; 25 taxa were common between deep and intermediate assemblages, 16 taxa were common between intermediate and shallow assemblages and 13 taxa were common between deep and shallow assemblages (Fig. 3).



Fig. 3. – Venn diagram showing number of exclusive and common species among habitats. Names are given in Table I.

Table III. – Result of PERMANOVA analyses (df: degrees of	٥t
freedom, MS: mean square, F: ratio-values and P(perm): permu	1-
tation probability). Significant effects are in bold.	

Source	df	MS	Pseudo-F	P(perm)
Habitat = H	2	60411 118.24		0.001
Year = Y	2	360.21 0.36831		1
Season = S	1	4132	8.7466	0.001
HxY	4	510.92	0.57311	0.997
HxS	2	3575	6.7931	0.001
YxS	2	472.41	0.48304	0.989
Date(YxS) = D(YxS)	6	977.99	0.73392	0.986
HxYxS	4	526.27	0.59033	0.997
Hx D(YxS)	12	891.49	0.669	1
Area(Hx D(YxS))	36	1332.6	0.70109	1
Residual	72	1900.7		
Total	143			
PAIRWISE TESTS (H x	S)			
Spring	P(perm)	Deep		P(perm)
Deep, Intermediate	0.001	Spring, Autumn		0.072
Deep, Shallow	0.001			
Intermediate, Shallow	0.001	Intermediate		
		Spring, Autumn		0.001
Autumn				
Deep, Intermediate	0.001	Shallow		
Deep, Shallow	0.001	Spring, Autumn		0.001
Intermediate, Shallow	0.001			

Values of β_D index were 0.39 between shallow and intermediate assemblages, 0.25 between intermediate and deep assemblages and 0.40 between shallow and deep assemblages.

PERMANOVA analysis detected a significant interaction between Habitat and Season. Pairwise test showed that differences among depths were significant in both seasons and differences between seasons were significant

Tava	Mean presence per sample	Contrib%	
Idxa	Deep assemblages	Interm. assemblages	Av. dissim. 48.5
Symphodus tinca	0.00	0.90	6.52
Diplodus annularis	0.00	0.54	3.94
Sarpa salpa	0.46	0.90	3.91
Symphodus melanocercus	0.27	0.58	3.90
Symphodus mediterraneus	0.44	0.67	3.83
Labrus merula	0.31	0.58	3.83
Epinephelus marginatus	0.54	0.21	3.75
Muraena helena	0.46	0.13	3.40
Diplodus puntazzo	0.25	0.42	3.36
Parablennius rouxi	0.42	0.13	3.15
Labrus mixtus	0.40	0.00	2.81
Sciaena umbra	0.33	0.17	2.76
	Assemblages	Shallow assemblages	Av. dissim. 69.2
Diplodus sargus	0.79	0.00	5.37
Oblada melanura	0.00	0.85	4.56
Tripterygion tripteronotus	0.00	0.79	4.25
Chelon labrosus	0.00	0.77	4.08
Atherina spp.	0.00	0.75	3.98
Serranus cabrilla	0.90	0.21	3.95
Aidablennius sphynx	0.00	0.63	3.36
Apogon imberbis	0.58	0.04	3.03
Epinephelus marginatus	0.54	0.00	2.83
Thalassoma pavo	0.00	0.54	2.80
Belone belone	0.00	0.50	2.59
Coryphoblennius galerita	0.00	0.50	2.55
Paralipophrys trigloides	0.00	0.46	2.49
Muraena helena	0.46	0.00	2.45
Labrus mixtus	0.40	0.00	2.07
	Interm. assemblages	Shallow assemblages	Av. dissim. 61.1
Diplodus sargus	0.79	0.00	4.28
Chelon labrosus	0.00	0.77	4.12
Tripterygion tripteronotus	0.08	0.79	4.03
Atherina spp.	0.00	0.75	4.01
Serranus cabrilla	0.85	0.21	3.8
Mullus surmuletus	0.83	0.21	3.76
Symphodus tinca	0.90	0.29	3.61
Aidablennius sphynx	0.00	0.63	3.39
Symphodus mediterraneus	0.67	0.17	3.30
Oblada melanura	0.38	0.85	3.25
Diplodus annularis	0.54	0.00	2.93
Serranus scriba	0.83	0.46	2.88
Labrus merula	0.58	0.29	2.87

Thalassoma pavo

Belone belone

Table IV. – Result of Simper test showing species that mostly contribute to determine differences among assemblages.

0.54

0.50

2.84

2.62

0.00

0.00

for intermediate and shallow assemblages but not for deep assemblages; no significant differences resulted among years, dates and areas (Table III).

The SIMPER test detected the following dissimilarity values: 48.5 between deep and intermediate assemblages, 61.1 between intermediate and shallow assemblages and 89.2 between deep and shallow assemblages. Chromis chromis, Coris julis, Serranus scriba and Diplodus vulgaris were common in all habitats surveyed. The species characterizing shallow assemblages were Oblada melanura, Thalassoma pavo, Atherina spp., Chelon labrosus, Tripterygion tripteronotus, Belone belone, Coryphoblennius galerita, Aidablennius sphynx and Paralipophrys trigloides. The most abundant species in the intermediate assemblages were Sarpa salpa, Diplodus sargus, Mullus surmuletus, Symphodus tinca and S. mediterraneus. The species characterizing the deep assemblages were Serranus cabrilla, Epinephelus marginatus, Muraena helena, Sciaena umbra and Labrus mixtus. Diplodus sargus was common in intermediate and deep assemblages (Table IV).

DISCUSSION

The present study showed that patterns of alpha and beta diversity of the studied fish assemblages, such as their seasonal dynamics, have significantly changed in relation to depth and that these differences remained constant among years.

The results of this study confirm the role of rocky habitat for the diversity of coastal fish assemblages; in fact, rocky bottoms show high habitat complexity related to topographic features and the presence of macroalgae and sessile invertebrates (Guidetti & Bussotti 2000, Guidetti & Boero 2004); moreover they act as feeding and nursery areas supplying food and refuge to many adult and juvenile fish (Guidetti 2000).

The present paper shows the importance of depth to determine beta diversity for Mediterranean rocky reef fish assemblages, confirming patterns observed in other geographical regions (Arias-Gonzales *et al.* 2008).

Differences in species composition between depth ranges were related both to natural patterns of fish distribution and to human induced patterns. On the one hand, several species distributions were strictly related to habitat, especially in shallow (*Thalassoma pavo*, *Coryphoblennius galerita*, *Aidablennius sphynx*, *Paralipophrys trigloides*) and deep assemblages (*Labrus mixtus*, *Gobius auratus*, *Gobius cruentatus*); on the other hand, deep assemblages were also characterized by several species targeted by fishing. These latter, normally distributed along a wider depth range, appeared confined to deeper habitats in areas subjected to fishing activities, especially when exposed to spearfishing, such as in the studied area. This pattern is widely documented in the Mediterranean Sea (Harmelin 1987, Garcia-Rubies & Zabala 1990, Dufour *et al.* 1995, Pelaprat 1999). Human activities may change fish behavior (Vacchi & La Mesa 1999, Jouvenel & Pollard 2001, Micheli *et al.* 2005) and different patterns of vertical distribution may be detected in areas with different levels of disturbance (Cecchi *et al.* 2007).

Coastal fish assemblages vary at different spatial scales (La Mesa *et al.* 2011) due to biotic interactions and in relation to physical gradients (De Raedemaecker *et al.* 2010). In the present study, differences between sites within each depth range were not significant, showing a homogeneity of assemblages at the spatial scale examined. However, the size of the studied area did not allow to infer patterns of beta diversity along horizontal gradients within each depth range. This aspect is important to be considered in the management of fish assemblages and deserves further investigations.

Alpha and beta diversity within each habitat showed different patterns in relation to depth. Alpha diversity remains higher in the intermediate assemblages at all the spatial scales examined, probably in relation to the presence of low-specialized organisms. Deep assemblages, despite the low values of alpha diversity, showed higher values of beta diversity than other habitats. This result could be related with the morphological traits of the bottom. Indeed, bioconstructions characterizing coralligenous habitat enhance the heterogeneity of bottom with possible consequences on organism distribution (Garcia-Charton & Pérez-Ruzafa 2001). The influence of tropical bioconstructions on fish assemblages is well known (Arias-Gonzales et al. 2008, Lecchini & Tsuchiya 2008), while this aspect has been less investigated in the Mediterranean Sea and further investigations would be necessary to confirm this model. Moreover, the characteristics of species constituting deep assemblages could also influence patterns of beta diversity. In fact, the presence of large carnivorous animals with territorial behavior could contribute to determine a higher heterogeneity in fish distribution.

Temporal dynamics of assemblages showed different patterns in relation to the scale examined. In fact, the species composition of assemblages much as their diversity patterns remained steady throughout different years, while seasonal changes were detected at least in shallower habitats. The lack of significant differences among years is an interesting result; in fact, fishes may change their abundance in relation to fishing pressure, food availability, change in their behavior and migrations (Harmelin 1987, Francour 1994, Dufour et al. 1995, Pelaprat 1999) and inter-annual variations in assemblages could be hypothesized. The stability of the structure of fish assemblages throughout long periods improves their value as bioindicator (Guidetti et al. 2002, 2003). Results also showed seasonal dynamics in intermediate and shallow assemblages, while deep assemblages appeared steady during the year. Temporal variations in shallower assemblages

were more related to the seasonal presence of pelagic species (e.g. *Belone belone, Trachinotus ovatus, Atherina* spp., Table I) in coastal waters (D'Anna *et al.* 1999) than to changes in the abundance of resident fishes.

The simultaneous evaluation of different aspects of diversity in coastal fish assemblages may be a suitable approach to understand potential drivers of diversity. The present investigation tested this approach within one restricted area. Larger scales of investigations are needed to detect other scales of variation in diversity patterns, to evaluate turnover diversity along a larger horizontal gradient and to compare the gamma diversity among different Mediterranean areas; this knowledge is important in order to design suitable conservation plans of coastal systems (Malcom *et al.* 2007, Arias-Gonzales *et al.* 2008, Wilson *et al.* 2009).

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REFERENCES

- Anderson MJ 2001. A new method for a non-parametric multivariate analysis of variance. *Aust Ecol* 26: 32-46.
- Anderson MJ, Ellingsen KE, McArdle BH 2006. Multivariate dispersion as a measure of beta diversity. *Ecol Lett* 9: 683-693.
- Arias-Gonzales JE, Legendre P, Rodriguez-Zaragoza FA 2008. Scaling up beta diversity on Caribbean coral reefs. *J Exp Mar Biol Ecol* 366: 28-36.
- Azzurro E, Matiddi M, Fanelli E, Guidetti P, La Mesa G, Scarpato A, Axiak V 2010. Sewage pollution impact on Mediterranean rocky-reef fish assemblages. *Mar Environ Res* 69: 390-397.
- Balata D, Piazzi L 2008. Patterns of diversity in rocky subtidal macroalgal assemblages in relation to depth. *Bot Mar* 51: 464-471.
- Ballesteros E 2006. Mediterranean coralligenous assemblages: a synthesis of present knowledge. *Oceanogr Mar Biol Ann Rev* 44: 123-195.
- Bell JD 1983. Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the north-western Mediterranean Sea. *J Appl Ecol* 20: 357-369.
- Cecchi E, Piazzi L, Balata D 2007. Interaction between depth and protection in determining the structure of Mediterranean coastal fish assemblages. *Aquat Living Resour* 20: 123-129.
- D'Anna G, Badalamenti F, Riggio S 1999. Traditional and experimental floating fish aggregating devices in the Gulf of Castellammare (NW Sicily): results from catches and visual observation. *Sci Mar* 63: 209-218.
- De Raedemaecker F, Miliou A, Perkins R 2010. Fish community structure on littoral rocky shores in the Eastern Aegean Sea: Effects of exposure and substratum. *Estuar Coast Shelf Sci* 90: 35-44.
- Dufour V, Jouvenel J, Galzin R 1995. Study of a Mediterranean reef fish assemblage. Comparison of population distributions between depths in protected and unprotected areas over one decade. *Aquat Living Resour* 8: 17-25.

- Dulčić J, Kraljević M, Grbec B, Pallaoro A 1997. Composition and temporal fluctuations of inshore juvenile fish populations in the Kornati Archipelago, eastern middle Adriatic. *Mar Biol* 129: 267-277.
- Francour P 1994. Pluriannual analysis of the reserve effect on ichtyofauna in the Scandola natural reserve. *Oceanol Acta* 17: 309-317.
- Garcia-Charton JA, Pérez-Ruzafa A 2001. Spatial patterns and the habitat structure of a Mediterranean rocky reef fish local assemblage. *Mar Biol* 138: 917-934.
- Garcia-Rubies A, Zabala M 1990. Effects of total fishing prohibition on a rocky fish assemblages of Medes Islands marine reserve (NW Mediterranean). *Sci Mar* 54: 317-328.
- Garrabou J., Ballesteros E., Zabala M 2002. Structure and dynamics of north-western Mediterranean rocky benthic communities along a depth gradient. *Estuar Coast Shelf Sci* 55: 493-508.
- Gering JC, Crist TO 2002. The alpha-beta-regional relationship: providing new insights into local-regional patterns of species richness and scale-dependence of diversity components. *Ecol Lett* 5: 433-444.
- Gray JS 1997. Marine Biodiversity: patterns, threats and conservation needs. *Biodiv Conserv* 6: 153-175.
- Gray JS 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. *J Exp Mar Biol Ecol* 250: 23-49
- Guidetti P 2000. Differences among fish assemblages associated with nearshore *Posidonia oceanica* seagrass beds, rockyalgal reefs and unvegetated sand habitats in the Adriatic Sea. *Estuar Coast Shelf Sci* 50: 515-529.
- Guidetti P, Bussotti S 2000. Near shore fish assemblages associated with shallow rocky habitats along the southern Croatian coast (eastern Adriatic Sea). *Vie Milieu* 50: 171-176.
- Guidetti P, Boero F 2004. Desertification of Mediterranean rocky reefs caused by date-mussel, *Lithophaga lithophaga* (Mollusca: Bivalvia), fishery: effects on adult and juvenile abundance of a temperate fish. *Mar Poll Bull* 48: 978-982.
- Guidetti P, Fanelli G, Fraschetti S, Terlizzi A, Boero F 2002. Coastal fish indicate human-induced changes in the Mediterranean littoral. *Mar Environ Res* 53: 77-94.
- Guidetti P, Terlizzi A, Fraschetti S, Boero F 2003. Changes in Mediterranean rocky-reef fish assemblages exposed to sewage pollution. *Mar Ecol Prog Ser* 253: 269-278.
- Harmelin JG 1987. Structure and variability of the ichthyofauna in a Mediterranean protected area (National Park of Port-Cros, France). *Mar Ecol* 8: 263-284.
- Jaccard P 1900. Contribution au problème de l'immigration post-glaciare de la flore alpine. *Bull Soc Vaudoise Sci Nat* 36: 87-130.
- Jouvenel JY, Pollard DA 2001 Some effects of marine reserve protection on the population structure of two spearfishing target-fish species, *Dicentratus labrax* (Moronidae) and *Sparus aurata* (Sparidae), in shallow inshore waters, along a rocky coast in the nortwestern Mediterranean Sea. *Aquat Conserv Mar Freshw Ecosyst* 11: 1-9.
- La Mesa G, Molinari A, Gambaccini S, Tunesi L 2011. Spatial pattern of coastal fish assemblages in different habitats in North-western Mediterranean. *Mar Ecol* 32: 104-114.
- Lecchini D, Tsuchiya M 2008. Spatial structure of coral reef fish communities at Kudaka Island (Ryukyu Archipelago), Japan. *Ichthyol Res* 55: 321-327.
- Legendre P, Borcard D, Peres-Neto PR 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol Monogr* 75: 435-450.

- Lorance P, Souissi S, Uiblein F 2002. Point, alpha and beta diversity of carnivorous fish along a depth gradient. *Aquat Living Resour* 15: 283-271.
- Malcom HA, Gladstone W, Lindfield S, Wraith J, Lynch TP 2007. Spatial and temporal variation in reef fish assemblages of marine parks in New South Wales, Australia baited video observations. *Mar Ecol Prog Ser* 350: 277-290.
- Matić-Skoko S, Peharda M, Pallaoro A, Cukrov M, Baždarić B 2007. Infralittoral fish assemblages in the Zrmanja estuary, Adriatic Sea. *Acta Adriat* 48: 45-55.
- Micheli F, Benedetti-Cecchi L, Gambaccini S, Bertocci I, Borsini C, Osio CG, Romano F 2005. Cascading human impacts, marine protected areas and the structure of Mediterranean rocky-reef assemblages. *Ecol Monogr* 75: 81-102.
- Milazzo M, Palmeri A, Falco JM, Badalamenti F, Garcia-Charton JA, Sinopoli M, Chemello R, Brito A 2011. Vertical distribution of two sympatric labrid fishes in the Western Mediterranean and Eastern Atlantic rocky subtidal: local shore topography does matter. *Mar Ecol* 32: 521-531.
- Mokany K, Harwoord TD, Overton MC, Barker GM, Ferrier S 2011. Combining α and β -diversity models to fill gaps in our knowledge of biodiversity. *Ecol Lett* 14: 1043-1051.
- Pelaprat C 1999. Influence of protection measures on the seasonal and annual variations of densities and biomasses within the no invigilated fishing reserve of Calvi. *Nat Sicil* 23: 223-242.

- Sax DV, Gaines SD 2003. Species diversity: from global decreases to local increases. *Trends Ecol Evol* 18: 561-556.
- Smith AK, Ajani PA, Roberts DE 1999. Spatial and temporal variation in fish assemblages exposed to sewage and implications for management. *Mar Environ Res* 47: 241-260.
- Underwood AJ 1997. Experiments in ecology. Their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge.
- Vacchi M, La Mesa G 1999. Fish visual census in Italian Marine Protected Areas: experiences and perspectives. *Nat Sicil* 23: 105-121.
- Walker BH 1992. Biodiversity and ecological redundancy. Conserv Biol 6: 18-23
- Walker BH 1995. Conserving Biological diversity through ecosystem resilience. Conserv Biol 9: 747-752.
- Whittaker RH 1972. Evolution and measurement of species diversity. *Taxon* 21: 213-251.
- Wilson SK, Dolman AM, Cheal AJ, Emslie MJ, Pratchett MS, Sweatman HPA 2009. Maintenance of fish diversity on disturbed coral reefs. *Coral Reefs* 28: 3-14.

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