

Spatial persistence of megazoobenthic assemblages in the Adriatic Sea

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ABSTRACT: The Adriatic Sea plays a central role in the economies of both European and non-European countries. As such, it is subject to impacts from a large number of human activities, including fishing. In a basin characterized by high biodiversity and complex ecosystem processes, such as the Adriatic Sea, habitat conservation and protection measures rely on detailed information on the composition and structure of benthic assemblages. The present study describes the composition, spatial distribution and persistence of invertebrate megazoobenthic assemblages in the Adriatic Sea. Samples were collected during rapido trawl surveys performed from 2007 to 2012. A total of 4 main megazoobenthic assemblages were identified and were designated as A, B, C and D. Group A assemblages were detected in the northern and central offshore area, Group B assemblages occupied the northernmost part of the basin, Group C assemblages were predominantly found along the western coast and Group D assemblages were detected in the deepest parts of the northern and central basin. A degree of spatial overlap in the northern Adriatic was probably due to the physical and chemical characteristics of the area, which is characterized by strong river runoff, hence by changes in sediment composition from sandy mud to muddy sand. The present findings may help to devise integrated management strategies of fishing activities, especially trawling, in view of the implementation of the Ecosystem Approach to Fisheries Management, and may help to define some descriptors of the Marine Strategy Framework Directive.

KEY WORDS: Megafauna · Adriatic Sea · Persistence · Distribution · Fisheries management · Fish ecology · Marine Strategy Framework Directive · Habitat

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INTRODUCTION

The marine environment is an invaluable heritage that provides a range of ecosystem services that are essential for human life and wellbeing. However, as marine ecosystems are under pressure from a variety of sources, protection efforts need to be increased. The European Union (EU) Marine Strategy Framework Directive (MSFD; EC 2008) is a significant step in this direction.

The Mediterranean Sea is subject to strong anthropogenic impacts from a variety of sources that include coastal development, urbanization, tourism, invasion of alien species, global warming, overfishing, aquaculture, point-source pollution and commercial ship traffic (Jennings & Kaiser 1998, Halpern et al. 2008, Coll et al. 2010, Micheli et al. 2013, Halpern et al. 2015). Fishing exerts direct impacts on target and bycatch species, and on the marine ecosystem as a whole. In particular, bottom trawling for

species living on, within, or close to the seabed—a century-old activity in many areas of the Mediterranean Sea (Botter et al. 2006, Coll et al. 2010)—involves direct physical contact of the gear with the substratum and consequently the direct removal, displacement and/or death of benthic animal and plant species. Trawling can also induce sediment re-suspension and fragmentation of biogenic substrata, thus affecting habitat complexity, and the structure and diversity of benthic communities (Kaiser et al. 1998, Kaiser et al. 2001, Gislason 2002). The composition and status of resident fish species may also be affected by such modifications. The conservation and protection of marine habitats is therefore critical for the sustainable, long-term management of fisheries resources (Colloca et al. 2003). The ecosystem approach envisages the analysis of marine resources and of the potential impacts suffered by them on a wide spatial scale, as well as a multispecies strategy that considers the overall community (Colloca et al. 2003). By providing insight into interspecies relationships and into how they influence species distribution, the approach also helps to improve resource management (Pitcher 2000, Pranovi et al. 2001, Coll et al. 2007).

With regard to the Mediterranean Sea, most of the available literature on the management of biological resources focuses on the distribution of highly valuable species, e.g. *Solea solea*, *Engraulis encrasicolus*, *Merluccius merluccius* and *Squilla mantis* (Tudela et al. 2002, Maynou et al. 2003, 2004, Grati et al. 2013, Scarcella et al. 2014b, Colloca et al. 2015). Where macrobenthic assemblages are concerned, the majority of studies consider the local scale or a small number of taxa or sets of interacting species (e.g. De Biasi 2004, Frascchetti et al. 2005, Tecchio et al. 2011, El Lakhrech et al. 2012). A similar situation is found for the Adriatic Sea, the widest continental shelf in the Mediterranean Sea (Pinardi et al. 2006) and a highly important fishing area for Italy and the EU (Bombace 1992). The Adriatic hosts a broad variety of benthic communities, especially due to the marked geophysical differences existing between the eastern and western coast, and between the central and northern basins and the southern basin (Bombace 1992). In addition to anthropogenic pressure, natural and extreme events such as red tides and mucilage (and the consequent anoxic crises) have caused mass mortality of benthic organisms and modifications of benthic assemblages (Boero 2001). In particular, mass mortality of benthic macrofauna induced by repeated hypoxia and anoxia events in the 1970s and 1980s is reported (Giani et al. 2012).

The distribution of benthic taxa has also been investigated at the local scale or in a limited number of species (Froglia 1978, Pozar-Domac 1978, Šimunović & Grubelić 1998, Hall-Spencer et al. 1999, Šimunović et al. 2000, Panfili et al. 2003a, 2003b, Despalatović et al. 2007, 2009, 2010, Salvalaggio et al. 2014). Moreover, data on the distribution of benthic biocoenoses in the Adriatic come from dated studies. In particular, Vatova (1949) described zoocoenoses in the northern and central Adriatic considering the biomass and abundance of various species; Gamulin-Brida (1967, 1974) reviewed biome diversity and provided a detailed map of biocoenoses; Fedra et al. (1976) studied the distribution and composition of benthic communities in the Gulf of Trieste (northern Adriatic Sea). The latest study of the distribution of soft-bottom benthic communities in the Adriatic Sea dates from the late 1990s (Šimunović 1997).

In the light of the above considerations, the present study was devised to (1) investigate the structure and composition of megazoobenthic invertebrate assemblages in the northern and central Adriatic Sea, (2) gain information on their spatial distribution and persistence over a 6 yr period, and (3) contribute data for a more effective sustainable management of fisheries resources.

MATERIALS AND METHODS

Study area and sampling methods

The Adriatic Sea is an elongated basin in the central Mediterranean Sea, between the Italian peninsula and the Balkans, whose major axis lies in a NW–SE direction. Its northern section is characterized by shallow bottoms and gentle slopes (average depth ~35 m), whereas in the central section the 2 Pomo depressions reach a depth of 260 m (average depth 140 m). While the eastern coast is largely deep and rocky, the western side is shallow and mostly sandy. The numerous river estuaries in the northern and central areas on the Italian side, especially the Po River, significantly affect seawater circulation (Artegiani et al. 1997).

The study was carried out in the northern and central Adriatic Sea, in Geographical Sub-Area (GSA) 17, as defined by the General Fisheries Commission for the Mediterranean (GFCM 2009). The study area measured 36 742 km² and extended from the Italian coast to 12 and 6 nautical miles from the Croatian and Slovenian coasts, respectively; its maximum depth was 100 m (Fig. 1).

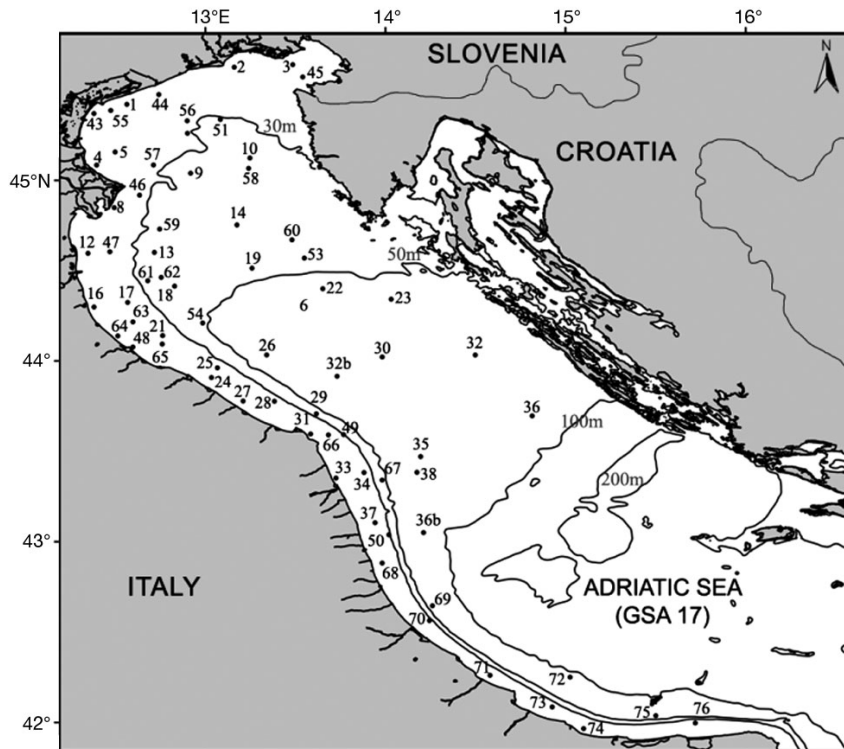


Fig. 1. Study area (GSA 17) and stations sampled during the 6 rapido trawl surveys (2007 to 2012)

From 2007 to 2012, 6 yearly surveys were conducted in November or December by a team consisting of researchers from the National Research Council (CNR-ISMAR UOS, Ancona, Italy) in co-operation with researchers from the National Institute for Environmental Protection and Research (ISPRA, Chioggia, Italy), the Institute of Oceanography and Fisheries (IOF, Split, Croatia) and the Fisheries Research Institute of Slovenia (FRIS, Ljubljana-Šmartno, Slovenia), in the framework of the SoleMon project; an exhaustive description of the project objective, survey strategy and sampling procedure is reported in Grati et al. (2013) and Scarcella et al. (2014b). Each year, samples were collected at 69 stations, whenever possible at the same geographical coordinates (Fig. 1, Table 1). Megazoobenthic fauna was collected using a rapido trawl, a modified beam trawl commonly used by Italian fishermen to catch flatfish and other benthic species. The sampling gear consisted of a stiff iron frame provided with 4 skids and bearing 46 iron teeth along the lower leading edge. The net was a polyamide net bag whose lower side was reinforced with rubber diamond-mesh net. An inclined wooden board on the front of the iron frame acted as a spoiler, keeping the gear in contact with the seabed. The codend had 40 mm mesh size (stretched) and was 2.7 m long. In this study, the term

'megazoobenthos' refers to all the benthic animal species collected using this gear.

Two rapido trawls were towed simultaneously during each haul. Average speed was 5.5 knots ($\sim 10.5 \text{ km h}^{-1}$) and average haul duration was 30 min; at a small number of stations, haul duration had to be modified due to seabed texture and to the accumulation of excessive weight in the net.

At the end of each haul, the total catch was weighed with an electronic dynamometer (Dynafor LLX2; accuracy $\pm 3.2 \text{ kg}$). After the commercial catch was sorted, biological samples of megazoobenthos, which amounted to 15 to 80 kg (in line with the SoleMon protocol; Grati et al. 2013), depending on the weight of the fraction of epibenthic/benthic species and of debris in the catch, were randomly collected from the total discard and immediately classified on board. Each specimen was identified to the lowest possible taxonomic level. Standard identification guidelines (Tortonese 1965, Riedel 1991, Cossignani et al. 1992, Falciai & Minervini 1992) and recent nomenclature according to the World Register of Marine Species (WoRMS Editorial Board 2016) were applied. The specimens of each species were counted and weighed (g). Unidentified organisms were preserved in ethanol (70%) for subsequent identification in the laboratory.

In 2009, sediment samples for grain size analysis were also collected at each station using a box-corer. After the description of macroscopic sediment features, the upper portion of each sample was extracted, homogenized and preserved at 4°C. Samples were classified according to Folk (1954) based on percent composition of gravel, sand and mud (silt and clay).

Data analysis

Data regarding the abundance and biomass of each species, haul duration and haul geographical coordinates were stored in the AdriaMed Trawl Surveys Information System (ATrIS) database (Gramolini et al. 2005), which allowed standardization of these parameters to the swept area (km^2).

The average biomass of each species at each station was estimated based on the standardized biomass values recorded in each yearly sample (2007 to

Table 1. Geographical coordinates and depth of the stations sampled during the 6 rapido trawl surveys (2007 to 2012)

Station	Latitude (N)	Longitude (E)	Depth (m)	Station	Latitude (N)	Longitude (E)	Depth (m)
1	45° 24' 18.07"	12° 29' 37.78"	19.3	38	43° 22' 38.56"	14° 09' 19.51"	69.4
2	45° 36' 35.27"	13° 06' 31.86"	15.7	43	45° 21' 52.45"	12° 22' 29.2"	12.6
3	45° 40' 02.71"	13° 31' 02.53"	16.1	44	45° 27' 16.74"	12° 40' 13.07"	21.6
4	45° 07' 02.53"	12° 22' 06.88"	16.6	45	45° 41' 17.23"	13° 39' 19.87"	24.8
5	45° 07' 148.18"	12° 29' 13.48"	27.0	46	44° 54' 14.65"	12° 35' 24.46"	29.0
6	45° 15' 8.89"	12° 51' 8.78"	32.1	47	44° 35' 25.61"	12° 24' 55.08"	24.6
8	44° 47' 58.12"	12° 27' 48.24"	11.8	48	44° 03' 7.3"	12° 37' 11.92"	10.6
9	45° 01' 39"	12° 55' 23.33"	34.5	49	43° 35' 49.38"	13° 45' 17.74"	31.0
10	45° 07' 18.01"	13° 14' 55.13"	30.2	50	43° 04' 38.35"	14° 00' 33.76"	26.7
12	44° 36' 5.4"	12° 21' 7.3"	14.8	51	45° 20' 3.01"	13° 05' 19.93"	32.7
13	44° 35' 53.41"	12° 42' 48.31"	34.9	53	44° 33' 58.39"	13° 33' 10.8"	41.5
14	44° 45' 39.95"	13° 05' 2.93"	38.3	54	44° 13' 8.14"	12° 57' 50.94"	49.0
16	44° 15' 44.63"	12° 28' 41.51"	10.9	55	45° 22' 45.94"	12° 25' 36.91"	18.2
17	44° 17' 47.65"	12° 28' 55.84"	22.6	56	45° 19' 49.69"	12° 54' 16.92"	29.9
18	44° 22' 45.37"	12° 50' 49.66"	41.4	57	45° 04' 2.29"	12° 44' 55.31"	29.9
19	44° 28' 44.21"	13° 09' 30.06"	44.4	58	45° 01' 23.8"	13° 14' 36.67"	34.0
21	44° 08' 7.69"	12° 46' 11.17"	20.6	59	44° 41' 20.5"	12° 47' 35.26"	34.7
22	44° 24' 56.08"	13° 38' 48.11"	52.5	60	44° 41' 6.64"	13° 28' 52.57"	39.8
23	44° 20' 14.02"	14° 01' 34.78"	54.7	61	44° 25' 50.44"	12° 35' 53.62"	34.1
24	43° 57' 19.69"	12° 58' 27.37"	16.4	62	44° 28' 35.29"	12° 45' 37.9"	37.5
25	43° 59' 26.26"	13° 04' 5.15"	22.0	63	44° 12' 43.92"	12° 35' 36.34"	17.1
26	44° 01' 3.43"	13° 20' 35.87"	59.1	64	44° 11' 33.89"	12° 31' 46.56"	10.6
27	43° 46' 30.46"	13° 14' 1.96"	15.2	65	44° 03' 25.3"	12° 45' 20.95"	16.9
28	43° 46' 18.73"	13° 23' 13.3"	23.7	66	43° 36' 54.61"	13° 40' 14.26"	20.1
29	43° 43' 11.17"	13° 36' 33.76"	37.4	67	43° 21' 49.06"	13° 59' 13.45"	40.0
30	43° 58' 48.46"	14° 01' 14.51"	64.7	68	42° 52' 33.31"	13° 58' 7.06"	16.3
31	43° 33' 57.7"	13° 37' 48.25"	13.7	69	42° 40' 17.22"	14° 15' 18.82"	62.9
32	44° 02' 27.13"	14° 27' 50.29"	66.9	70	42° 36' 9.9"	14° 12' 58.42"	26.2
32b	43° 31' 25.56"	13° 47' 22.919"	54.3	71	42° 16' 3.97"	14° 34' 23.98"	16.9
33	43° 20' 37.42"	13° 43' 59.69"	8.4	72	42° 15' 5.21"	15° 0' 56.59"	91.6
34	43° 20' 9.41"	13° 55' 55.81"	18.7	73	42° 05' 13.45"	14° 54' 24.19"	21.3
35	43° 28' 11.17"	14° 12' 3.88"	75.8	74	41° 59' 3.76"	15° 04' 38.53"	13.8
36	43° 41' 18.34"	14° 49' 23.44"	84.1	75	42° 02' 19.42"	15° 28' 54.04"	68.7
36b	43° 43' 31.8"	13° 43' 24.959"	59.8	76	41° 59' 44.44"	15° 41' 21.83"	19.6
37	43° 08' 43.51"	13° 53' 6.35"	19.3				

2012) and used to identify the main megazoobenthic assemblages by means of multivariate analysis. The use of biomass data for this purpose was prompted by the presence of colonial species such as bryozoans (e.g. *Amathia semiconvoluta*) and cnidarians (e.g. *Virgularia mirabilis*, *Funiculina quadrangularis*), whose number of individuals could not be estimated with accuracy.

Species that were found in a single year and those whose frequency of occurrence was less than 5% of the overall sample were considered sporadic and excluded from the analyses.

Multivariate analyses were performed based on the matrix of species biomass of each sample after $\log(x + 1)$ transformation using Primer 6 (Clarke & Gorley 2006).

The similarities in species composition shared by the 69 sampling stations were calculated using the quantitative Bray-Curtis coefficient. An unconstrained approach, principal coordinates analysis (PCO), was

applied to highlight patterns in multivariate data. The PCO plot was based on Bray-Curtis dissimilarities; a projection biplot drawn onto the PCO axes was used to examine relationships with (1) sediment variables of sampling sites and (2) taxa abundance (Anderson et al. 2004). Average linkage cluster analysis was then performed to identify the main groups of megazoobenthic assemblages *a posteriori*. One-way permutational multivariate analysis of variance (PERMANOVA) using assemblage as a fixed factor and the Bray-Curtis similarity index, and post hoc pairwise tests (Anderson 2001) were applied to test differences between the assemblages identified.

A multivariate multiple permutations test (SIMPER, similarity percentage analysis; Clarke 1993) was used to determine the contribution of each species to the differentiation of the assemblages identified by PERMANOVA.

Synthetic indices of diversity as mean species richness (S_m), Shannon diversity (H' ; Pielou 1974) and

Simpson index (λ ; Simpson 1949) were calculated for each station in each year. The last 2 indices were computed using biomass unit as basic data; such an approach is formally accepted due to the fact that diversity indices H' and λ are dimensionless and thus the choice of biomass units will not influence the results (McIntosh 1967, Wilhm 1968, Hill 1973). A 2-way ANOVA was conducted for each diversity index considering group (as defined in the multivariate analyses) and year as fixed factors. In the case of significant interactions, a 1-way ANOVA was employed for each year factor level to compare the group. Prior to performing statistical analyses, normal distribution and heterogeneity of variances were evaluated through the Kolmogorov-Smirnov and Bartlett tests, respectively (Lindman 1992). When the latter was significant, the relationship between means and the respective standard deviations was analysed to check whether the ANOVA assumptions were met. Tukey's HSD test for unbalanced samples was used to make comparisons across all pairs of group means when corresponding ANOVA tests were significant. Tukey's HSD test for balanced samples was, instead, used to make comparisons across all pairs of year means when corresponding ANOVA tests were significant. Results were considered highly significant at $p < 0.01$ and significant at $p < 0.05$.

Grain size analysis disclosed sand and mud fractions, but no gravel (i.e. grain size >2 mm) at any of the sampling sites. The percentage of sand in sediment samples in each assemblage was thus compared by applying a 1-way non-parametric Kruskal-Wallis ANOVA (Zar 1984). Post hoc pairwise comparisons were carried out using the Mann-Whitney U -test (Zar 1984).

A Spearman's rank correlation test showed a significant negative correlation ($p < 0.05$; $r = -0.68$) between sediment grain size (% of sand) measured in the box-corer samples and the sediment data (ϕ) derived from a detailed sedimentological map obtained by kriging interpolation of raw data (dbSEABED; Jenkins 2008). This result validated the sedimentological map and allowed its use in spatial modelling.

The significance level was set at $\alpha = 0.05$ for all statistical comparisons.

Spatial modelling

Exploratory analyses using generalized linear models/generalized linear mixed models (GLM/GLMM) and generalized additive models (GAM) (not shown) were conducted to determine the percent of

total variance explained by the models for each group identified by multivariate analysis. However, the percent of total variance explained by the models was not satisfactory, possibly due to the large amount of zero catches in the data matrix. A zero inflated generalized additive model (ZIGAM; Liu & Chan 2010, Yu et al. 2012) was therefore applied to define the spatial distribution of each group of species. The model assumes that the response variable follows a probabilistic mixture distribution of a zero atom and a continuous distribution belonging to the exponential family (Lambert 1992, Hall 2000, Yu et al. 2012), thus providing a better performance in the presence of zero-inflated data.

Data were modelled in 2 steps. First, the probability (p) of finding a density >0 was modelled with GAM, where the dependent variable had a binomial distribution and the link function was the logit (logarithm of the probability of finding a positive catch relative to the probability of finding a zero; Liu & Chan 2010).

Subsequently, a GAM was fitted to the positive catch data using a Gaussian family model and the identity link function. In this case, the dependent variable, distributed as a normal random variable, was $\log[y(v,t)]$.

The log-transformed data were assumed to be independent, and the outcomes of the 2 models were crossed to obtain biomass predictions using year (as a factor, y), latitude and longitude (v), and grain size (ϕ , t) from the sedimentological map as covariates.

As in the exploratory analyses of the GLM and GAM, we checked for spatial autocorrelation in the residuals (Zuur et al. 2009); however, in the present ZIGAM analyses, kriging was not required to interpolate residual variation to be incorporated into the model as random effects.

Annual biomass hotspots were then identified for each species assemblage. The Getis G -statistic (Getis & Ord 1992), with a radius of 2.5 to 5.0 km and a 0.95 level of significance, was selected among the local methods for spatial biomass hotspot identification to test differences in the high-density clusters of the 4 assemblages.

Finally, the index of persistence (I_i) was calculated in each 1 km^2 cell to measure the relative persistence of each cell as an annual biomass hotspot (Fiorentino et al. 2003, Colloca et al. 2009). The index ranges from 0 (cell i never included in an annual biomass hotspot) to 1 (cell i always included in an annual biomass hotspot). Results were plotted in the persistence maps; only class 0.81 to 1 data are reported.

All analyses were performed using R software (version 2.8.2) and libraries `mgcv`, `maps`, `mapdata`,

akima, fields, COZIGAM, numDeriv and gstat. These packages also produced the shape files, which were subsequently processed with GIS software (ArcView 3.2 and Manifold) to visualize the results on spatial georeferenced maps. Finally, a georeferenced map was drawn up to display the persistence of species groups and grain size characteristics (Jenkins 2008) in the whole study area.

RESULTS

Faunal composition

A total of 101 taxa were collected and identified in the course of the study (2007 to 2012). Of these, 39 were sporadic or had a frequency <5%; most of the other 62 taxa belonged to echinoderms (23), molluscs (11), or crustaceans (11). These data are reported in Table 2.

Cluster analysis (33% similarity) split the sampling stations into 4 groups that were designated A, B, C and D. They included, respectively, 7, 14, 27 and 21 stations (Fig. 2). The PCO plot (Fig. 3) accounted for 51.2% of total variation when the PCO1 and the PCO2 axes were both considered, and provided a clear visualization of station distribution along the grain size gradient from mud to sand on the PCO1 axis, whereas the PCO2 axis showed the coast-wide distribution. The plot highlighted the separation among groups; the difference was especially marked between C and A, as confirmed by PERMANOVA (pseudo- $F = 23.1$; $p < 0.001$; permutation number = 9999; pairwise test: $A \neq B \neq C \neq D$).

According to SIMPER analysis (Table 3), the similarity among Group A stations was 57.96%. This assemblage was characterized by *Holothuria (Panningothuria) forskali* (17.36%) followed by *Amathia semiconvoluta* (12.63%), *Parastichopus regalis* (10.48%), *Phallusia mammillata* (9.21%) and *H. tubulosa* (7.66%).

Table 2. Species collected during the survey period. x: present; s: sporadic (species found in a single year and/or species whose frequency of occurrence accounted for <5% of the sample). nd: not determined

Taxon	2007	2008	2009	2010	2011	2012
Porifera						
<i>Aptos aaptos</i>					s	
<i>Acanthella</i> sp.				s		
<i>Aplysina</i> spp.					s	s
<i>Cliona celata</i>		s		s	s	s
<i>Polymastia mamillaris</i>	s			s		
<i>Suberites carnosus</i>					x	x
<i>Suberites domuncula</i>	x	x	x	x	x	x
<i>Tethya aurantium</i>	x		x	x	x	x
Porifera ndd	x	x	x	x	x	x
Hydrozoa						
<i>Nemertesia</i> spp.	s		s		s	s
Anthozoa						
<i>Alcyonium palmatum</i>	x	x	x	x	x	x
<i>Calliactis parasitica</i>	s			s	s	s
<i>Cereus pedunculatus</i>						s
<i>Funiculina quadrangularis</i>					x	x
<i>Pennatulula rubra</i>	x					x
<i>Pteroides spinosum</i>		s				
<i>Virgularia mirabilis</i>	x	x	x	x	x	x
Gastropoda						
<i>Diodora italica</i>		s			s	
<i>Nassarius nitidus</i>	s		s	s		
<i>Turritella communis</i>	x	x	x	x	x	x
Bivalvia						
<i>Acanthocardia aculeata</i>	s			s	s	
<i>Acanthocardia paucicostata</i>	x		x	x	x	x
<i>Acanthocardia tuberculata</i>	x		x	x	x	x
<i>Anadara transversa</i>	x	x	x	x	x	x
<i>Anadara kagoschimensis</i>	x	x	x	x	x	x
<i>Atrina fragilis</i>	x	x	x	x	x	x
<i>Flexopecten flexuosus</i>	x	x	x	x	x	x
<i>Flexopecten glaber</i>	x	x	x	x	x	x
<i>Callista chione</i>		s	s	s		s
<i>Glycymeris insubrica</i>				s		
<i>Glossus humanus</i>	x	x		x	x	x
<i>Laevicardium oblongum</i>		s	s	s		s
<i>Lutraria</i> sp.	s				s	
<i>Mactra stultorum</i>						s
<i>Mimachlamys varia</i>	x	x	x	x	x	x
<i>Neopycnodonte cochlear</i>		x				
<i>Paphia</i> sp.	s					
<i>Pharus legumen</i>					s	s
<i>Pteria hirundo</i>		s		s	s	
<i>Thracia pubescens</i>						s
Polychaeta						
<i>Aphrodita aculeata</i>	x	x	x	x	x	x
Decapoda						
<i>Carcinus aestuarii</i>	s			s	s	s
<i>Dromia personata</i>	x		x	x	x	x
<i>Eriphia verrucosa</i>						s
<i>Ethusa mascarone</i>	x				x	x
<i>Galathea dispersa</i>			x		x	x
<i>Goneplax rhomboides</i>	x	x	x	x	x	x
<i>Illia nucleus</i>	x	x	x	x	x	
<i>Jaxea nocturna</i>				s	s	
<i>Liocarcinus vernalis</i>	x	x	x	x	x	x

Table 2 (continued)

Taxon	2007	2008	2009	2010	2011	2012
<i>Liocarcinus depurator</i>	x	x	x	x	x	x
<i>Macropodia</i> spp.	s		s		s	s
<i>Medorippe lanata</i>	x	x	x	x	x	x
<i>Munida</i> spp.	s		s	s	s	
<i>Palemon serratus</i>			s			
<i>Parthenope</i> sp.		s	s	s	s	s
<i>Pilumnus hirtellus</i>	x	x	x	x		
<i>Pilumnus spinifer</i>	x	x	x		x	x
<i>Pisa</i> spp.		s		s	s	s
<i>Pisidia</i> spp.	s				s	s
<i>Processa</i> spp.						s
<i>Scyllarus arctus</i>				x	x	x
<i>Xantho</i> spp.					s	s
Bryozoa						
<i>Amathia semiconvoluta</i>	x	x	x	x	x	x
Bryozoa nd	x	x	x	x	x	x
<i>Cellaria salicornoides</i>	x		x	x	x	x
<i>Schizobrachiella sanguinea</i>			s		s	s
Crinoidea						
<i>Antedon mediterranea</i>				x	x	
Holothuroidea						
<i>Holothuria (Panningothuria) forskali</i>	x	x	x	x	x	x
<i>Holothuria tubulosa</i>	x	x	x	x	x	x
<i>Oestergrenia digitata</i>	s			s	s	s
<i>Ocnus planci</i>	x	x	x	x	x	x
<i>Parastichopus regalis</i>	x	x	x	x	x	x
<i>Thyone fusus</i>	x		x	x	x	x
<i>Leptopentacta elongata</i>	x		x	x	x	x
<i>Leptopentacta tergestina</i>	x		x	x	x	x
Echinoidea						
<i>Brissopsis atlantica mediterranea</i>	x		x	x	x	x
<i>Cidaris cidaris</i>	x	x	x	x	x	x
<i>Echinocardium cordatum</i>	x		x		x	x
<i>Echinus acutus</i>				x	x	x
<i>Paracentrotus lividus</i>	x		x	x	x	x
<i>Psammechinus microtuberculatus</i>	x	x	x	x	x	x
<i>Ova canaliferus</i>	x	x	x	x	x	x
<i>Sphaerechinus granularis</i>	x	x	x	x	x	x
Asteroidea						
<i>Anseropoda placenta</i>	x	x	x	x	x	x
<i>Astropecten irregularis</i>	x	x	x	x	x	x
<i>Chaetaster longipes</i>	s					
<i>Echinaster (Echinaster)sepositus</i>	x	x	x	x	x	x
<i>Marthasterias glacialis</i>	x	x	x	x	x	x
<i>Peltaster placenta</i>	s					
Ophiuroidea						
<i>Amphiura chiajei</i>	s				s	
<i>Ophiura albida</i>	x	x	x	x	x	x
<i>Ophiothryx fragilis</i>	x	x	x	x	x	x
<i>Ophiura ophiura</i>	x	x	x	x	x	x
Ascidacea						
<i>Aplidium conicum</i>					s	s
<i>Ascidia mentula</i>		x		x	x	x
<i>Ascidia virginea</i>		x			x	x
<i>Halocynthia papillosa</i>	s				s	
<i>Microcosmus</i> sp.	x	x	x	x	x	x
<i>Microcosmus vulgaris</i>	x			x	x	x
<i>Phallusia mammillata</i>	x	x	x	x	x	x

The similarity among Group B stations was 49.18%; the major contributors were *Ocnus planci* (22.32%), *Astropecten irregularis* (21.70%) and *Suberites domuncula* (9.57%).

Group C stations showed a similarity of 50.23%; the 3 main species were *A. irregularis* (30.59%), *Anadara kagoshimensis* (23.79%) and *Anadara transversa* (12.93%),

Group D stations showed a similarity of 51.77%, the main species being *Liocarcinus depurator* (48.67%) and, to a lesser extent, *A. irregularis* (13.23%).

Dissimilarity was greatest between Groups C and A (93.30%), as also shown by PCO analysis, and lowest between Groups C and D (71.60%). Regarding C and A, the dissimilarity was mainly due to the absence of *H. (Panningothuria) forskali* and *P. regalis* in C, the absence of *A. kagoshimensis* and *A. transversa* in A, and the higher biomass of *A. semiconvoluta*, *P. mammillata* and *P. tubulosa* in A. The dissimilarity between C and D was mainly due to the high biomass of *L. depurator* and the low biomass of *A. kagoshimensis* and *A. transversa* in Group D.

The highest values of the analysed biotic indices were observed in Groups A and B (Fig. 4, Table A1 in the Appendix), and ANOVA showed significant differences among groups and years, highlighting spatial and temporal variations of these indices (Table 4).

In particular, S_m showed a significant interaction between the 2 main factors. One-way ANOVA carried out to compare the groups showed significant differences between Group A and the others. Highly significant differences were also observed between Group B and Groups C and D. Statistical analysis also showed significant variations among groups in each year separately. In the first 3 yr, S_m of Group A was significantly higher than that of Groups C and/or D, while in 2010, S_m of Group B was significantly higher than that of Group C. In

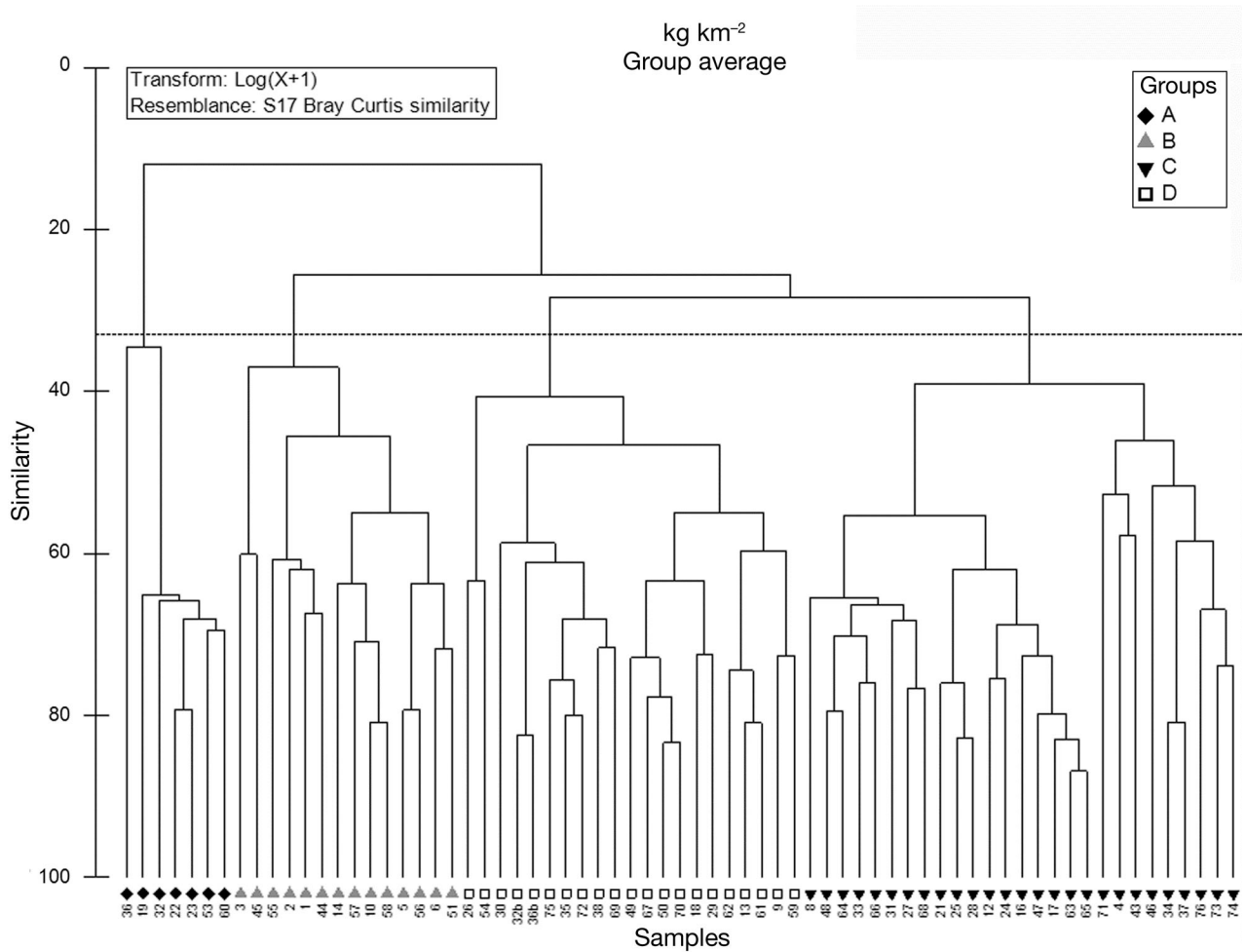
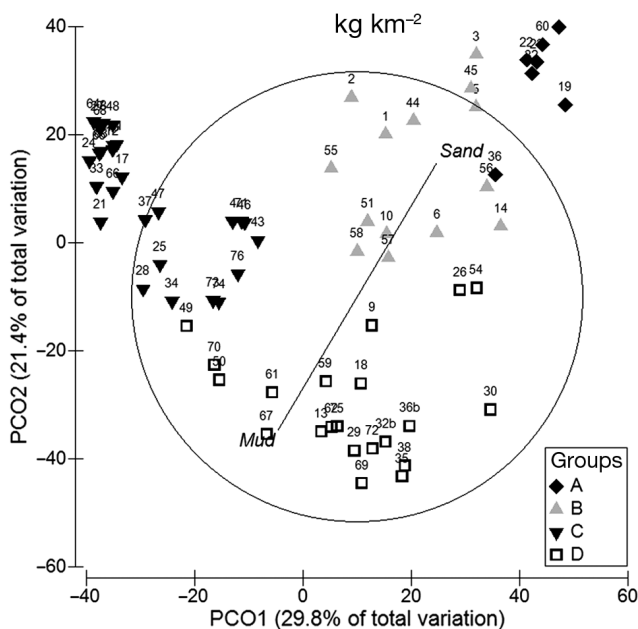


Fig. 2. Dendrogram obtained from cluster analysis (average linkage) applied to the biomass data (kg km^{-2}) of the megazoobenthic species collected during the 6 yearly surveys (2007 to 2012) with specification of the 4 assemblage groups (A to D). The horizontal dotted line represents the similarity (33 %)



2011 and 2012, highly significant values of S_m were recorded in Group A in comparison to the others.

The highest values of H' were observed in Groups A and B, and ANOVA showed significant differences between these groups and the others (Fig. 4, Tables 4 & A1). The low values recorded in C and D stations were probably due to the high dominance of *A. irregularis* and *L. depurator*, respectively. In the sampling period, this index showed low values in 2008 and 2009, with significant differences between these years and 2011 and 2012.

Accordingly, λ index followed an opposite trend with respect to H' (Fig. 4, Tables 4 & A1).

Fig. 3. Principal coordinates analysis (PCO) plot of the biomass of megazoobenthic assemblages with the line showing grain size texture. Numbers above symbols are stations

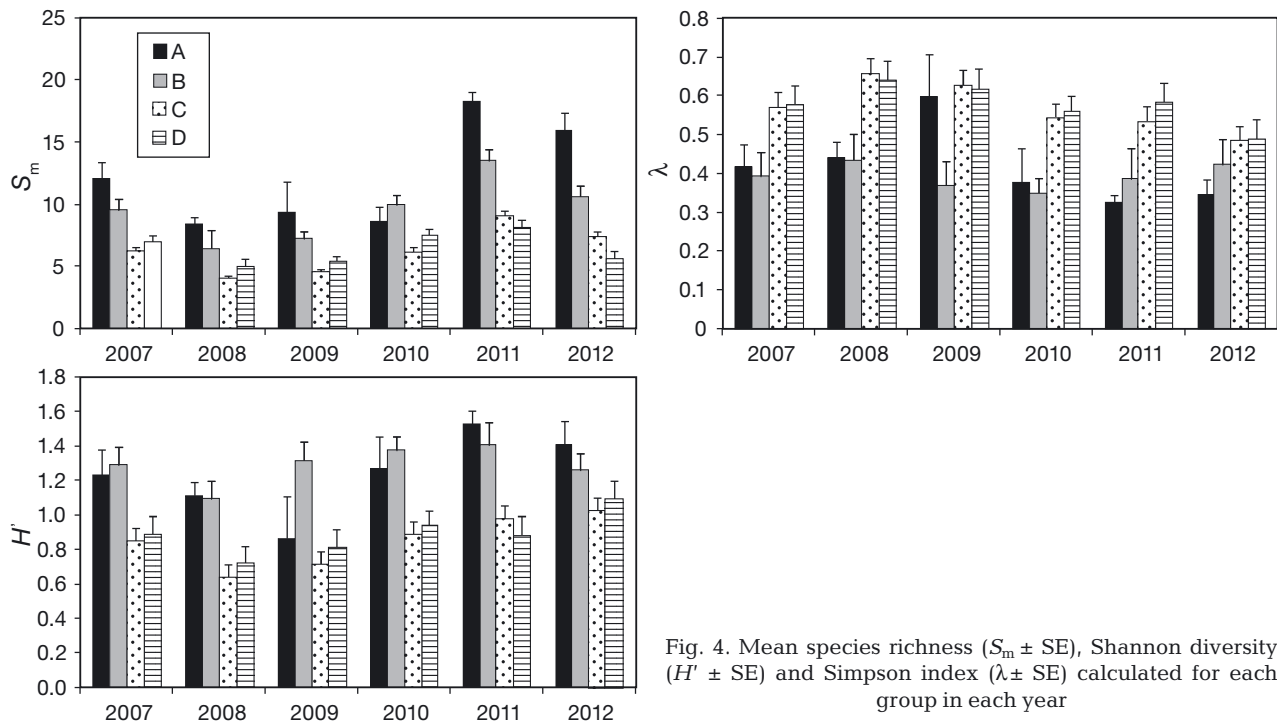


Fig. 4. Mean species richness ($S_m \pm SE$), Shannon diversity ($H' \pm SE$) and Simpson index ($\lambda \pm SE$) calculated for each group in each year

Table 3. Summary of SIMPER analysis. Cumulative contribution (cum. %) of each species to average similarity (only species reaching a cumulative contribution of about 85% are reported)

Group	Cum. %	Group	Cum. %
Group A		<i>Ophiura ophiura</i>	81.05
Similarity: 57.96%		<i>Aphrodita aculeata</i>	84.36
<i>Holothuria (Panningothuria) forskali</i>	17.36	<i>Microcosmus vulgaris</i>	86.8
<i>Amathia semiconvoluta</i>	29.99		
<i>Parastichopus regalis</i>	40.47	Group C	
<i>Phallusia mammillata</i>	49.68	Similarity: 50.23%	
<i>Holothuria tubulosa</i>	57.34	<i>Astropecten irregularis</i>	30.59
<i>Marthasterias glacialis</i>	63.82	<i>Anadara kagoschimensis</i>	54.38
<i>Alcyonum palmatum</i>	70.1	<i>Anadara transversa</i>	67.31
<i>Ascidia mentula</i>	75.02	<i>Liocarcinus vernalis</i>	74.44
<i>Echinaster (Echinaster) sepositus</i>	78.7	<i>Goneplax rhomboides</i>	80.36
<i>Echinus acutus</i>	81.97	<i>Ova canaliferus</i>	86.14
<i>Ascidia virginea</i>	85.15		
Group B		Group D	
Similarity: 49.18%		Similarity: 51.77%	
<i>Ocnus planci</i>	22.32	<i>Liocarcinus depurator</i>	48.67
<i>Astropecten irregularis</i>	44.03	<i>Astropecten irregularis</i>	61.89
<i>Suberites domuncula</i>	53.6	<i>Goneplax rhomboides</i>	69.9
<i>Liocarcinus depurator</i>	62.56	<i>Turritella communis</i>	77.06
<i>Phallusia mammillata</i>	70.12	<i>Leptopentacta tergestina</i>	82.85
<i>Psammechinus microtuberculatus</i>	77.54	<i>Medorippe lanata</i>	86.63

Analysis of sediment grain size

Seabed sediments ranged from mud to sandy mud and muddy sand, with a prevalence of small grain sizes. The grain size composition associated with the 4 megazoobenthic assemblages showed a significant

pattern (1-way Kruskal-Wallis ANOVA: $H(3, N = 69) = 27.99, p < 0.001$), with a decreasing percentage of sand and a shift from muddy sand to sandy mud and mud from Group A to Group D (Fig. 5). In particular, group D stations were characterized by a significantly lower percentage of sand compared with

Table 4. Summary of statistical analyses applied to values of mean species richness (S_m), Shannon diversity (H') and Simpson index (λ). >: significant ($p < 0.05$); >>: highly significant ($p < 0.01$)

Source	df	S_m			H'				λ			
		MS	F	p-value	MS	F	p-value	Tukey test	MS	F	p-value	Tukey test
2-way ANOVA												
Year (Y)	5	372.46	44.158	0.000	0.998	5.214	0.000	2011,2012>>2008; 2011,2012>2009	0.129	2.933	0.021	2009>2012
Group (G)	3	425.10	50.397	0.000	3.825	19.983	0.000	B>>C,D; A>>C; A>D	0.627	14.220	0.000	C,D>>B; D>A
Y × G	15	26.46	3.137	0.000	0.149	0.779	0.672		0.036	0.811	0.639	
Source	df	MS	F	p-value	Tukey test							
1-way ANOVA on S_m												
Group	3	444.25	33.260	0.000	A,B>>C,D; A>B							
2007	3	110.734	12.49	0.000	A>>C,D							
2008	3	46.582	4.755	0.005	A>C							
2009	3	56.024	7.186	0.000	A>>C; A>D							
2010	3	48.600	6.561	0.000	B>>C							
2011	3	247.809	27.221	0.000	A,B>>C,D; A>B							
2012	3	154.701	16.826	0.000	A>>B,C,D; B>C							

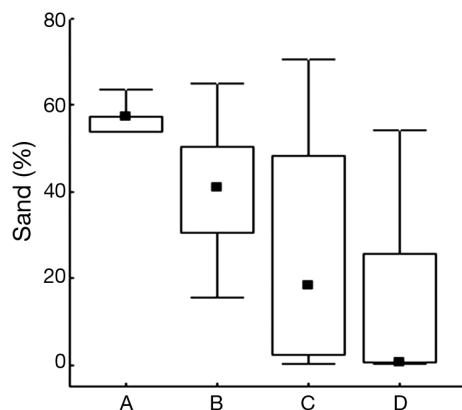


Fig. 5. Sediment grain size composition (% sand) at the stations corresponding to the 4 main megazoobenthic assemblages (A to D). Median: ■; box: 25 to 75th percentiles; bars: minimum to maximum values

Groups A, B and C ($p < 0.001$ vs. A and B; $p < 0.05$ vs. C). Group C stations also showed a significantly lower percentage of sand compared with Group A ($p < 0.05$). It is worth noting that whereas Group A stations were characterized by muddy sand, the other groups showed a broad range of sediment types, with a predominance of sandy mud in Group B, mud/sandy mud in Group C and mud in Group D.

Spatial distribution of the megazoobenthic assemblages

Biomass hotspots were grouped as follows:

Group A: a biomass hotspot (Fig. 6a) extending

from the Croatian territorial waters to about 40 km off the Italian coast was detected in the central portion of GSA 17 (depth 30 to 50 m) and remained virtually constant throughout the study.

Group B: concentrated in the northern part of GSA 17 (Fig. 6b). It formed a large biomass hotspot (depth 5 to 50 m), whose extension showed some changes in the southern portion and in front of the Po delta; in particular, it shrank in 2008, expanded again until 2011 to the size that was recorded in 2007, and slightly shrank again in 2012.

Group C: mainly found along the western side of GSA 17 (Fig. 6c) and in a portion of open waters off the Po River delta, forming a single, unvarying biomass hotspot (depth 5 to 30–50 m) that was detected every year.

Group D: showing 2 separate biomass hotspots (Fig. 6d) in the deeper parts of the northern and central portions of GSA 17, close to areas occupied by Group A assemblages. The former hotspot was found at a depth >30 m and remained almost constant throughout the study, whereas the latter was recorded at a depth >50 m and began to shrink in 2010, its southern edge splitting into separate patches.

Persistence

The persistence of each species group was established by superimposing their annual biomass hotspots (Fig. 7). It indicates the areas that, according to the modelling approach, show a stable presence of the areas occupied by each assemblage at the sampling

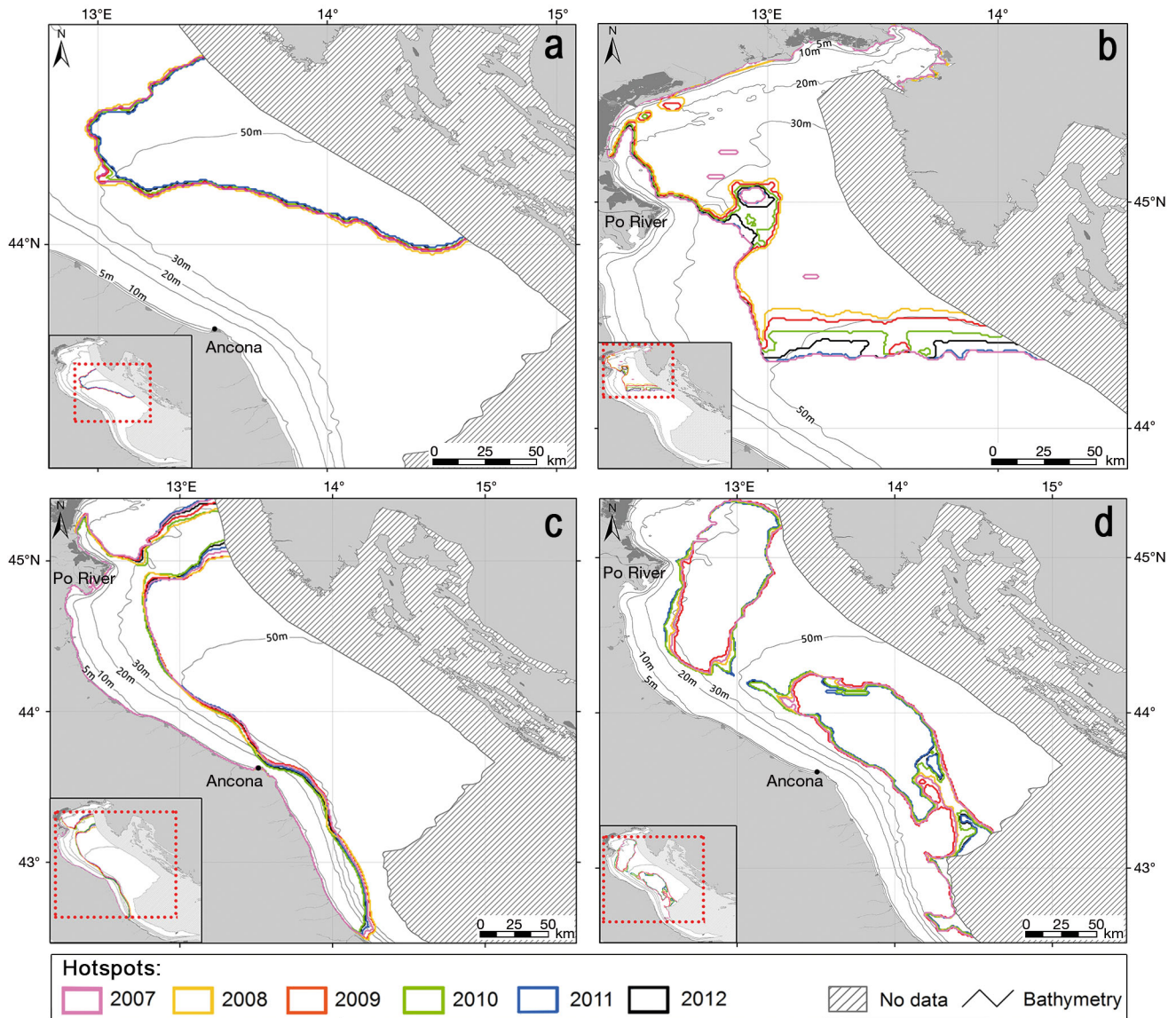


Fig. 6. Yearly biomass hotspots of (a) A, (b) B, (c) C and (d) D megazoobenthic assemblages

stations. The area of persistence of Group A was largely characterized by muddy sand, whereas those of Groups C and D were predominantly located on muddy bottoms. In contrast, the area of persistence of Group B species was chiefly characterized by a variable sediment composition. The data show that the central part of the northern portion of the Adriatic Sea, off the Po River delta, was characterized by the greatest overlap of different areas of persistence, i.e. the northeastern portion of Group C, the central portion of Group B and the northern portion of Group D assemblages. Moreover, the southern portion of the area of persistence of Group B overlapped with the northern part of Group A. Only the areas of persistence of Groups A and C never overlapped with one another.

DISCUSSION

Benthic invertebrate communities play a large role in the spatial distribution of several finfish species in their different life stages. Detailed knowledge of the structure of benthic populations and of their changes over time is therefore critical to gain a thorough understanding of energy pathways and population dynamics, as well as to devise ecosystem-based fishery management strategies (Bussotti et al. 2006, Pubill et al. 2011). Trawl surveys are a useful tool, providing efficient sampling and accurate quantitative description of benthic communities, especially the megazoobenthic fraction, and valuable data for resource management (Brind'Amour et al. 2014).

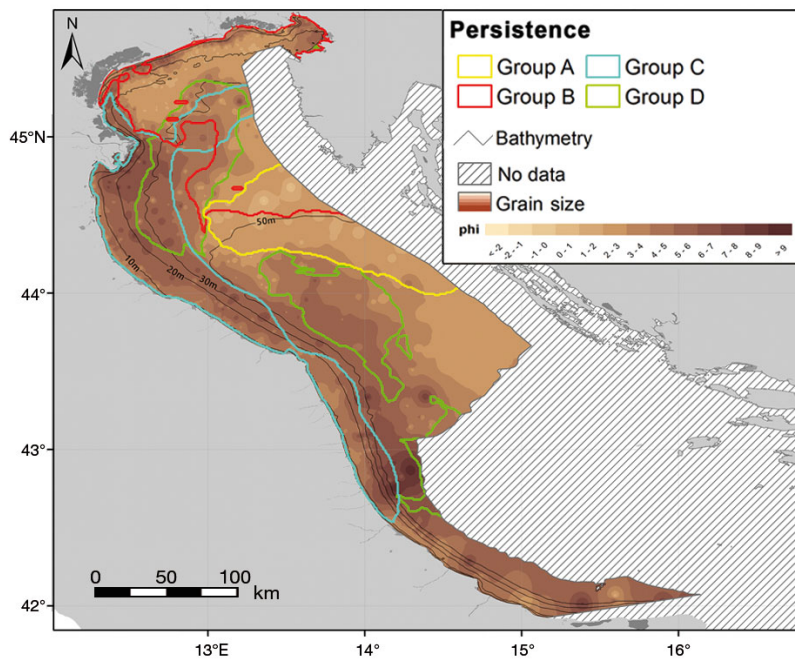


Fig. 7. Grain size map and persistence of the 4 megazoobenthic assemblages from 2007 to 2012

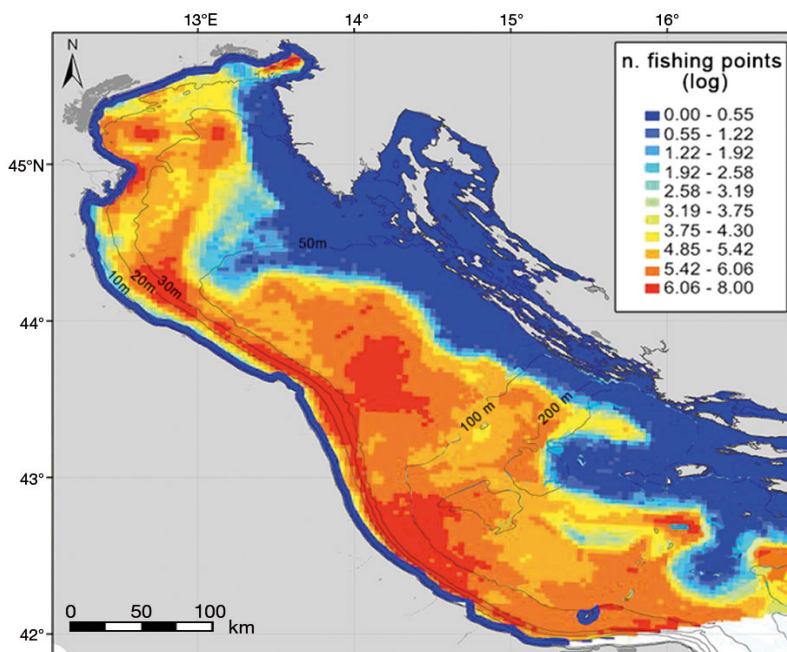


Fig. 8. Spatial distribution (3×3 km grid) of otter trawling relative fishing pressure (LOA [length overall] > 15 m; mean 2007 to 2010) based on vessel monitoring system data (modified from ISPRA 2013)

In the present study, multivariate analysis identified 4 main assemblages of megazoobenthic invertebrates, and spatial modelling of these associations allowed description of their distribution. Combining geostatistical methods with GAMs is reported to be a useful method to describe and model the spatial distribution

of benthic organisms and to gain information on their spatial dependence on environmental factors (Freire et al. 1992, Maynou 1998, Rufino et al. 2004, Rufino & Maynou 2006). However, a common problem encountered when analysing ecological and biological data collected during experimental trawl surveys is the presence of large numbers of zeros (zero inflation) that may result from various mechanisms (e.g. biological processes, sampling limitations and observer effects; Martin et al. 2005). For these types of survey data, zero-inflated distributions may be more appropriate (Lambert 1992, Hall 2000) than the commonly used GLMs.

The study showed that the offshore waters of the northern and central Adriatic, which are characterized by muddy sand sediments, are dominated by holothurians, bryozoans and ascidians, especially *Holothuria (Panningothuria) forskali*, *Amathia semiconvoluta*, *Parastichopus regalis* and *Phallusia mammillata* (Group A).

The distribution of *H. (Panningothuria) forskali* agrees with that reported by Šimunović et al. (2000), who found it mainly at depths between 50 and 100 m in relict sand bottoms; the holothurian *P. regalis* generally inhabits sandy substrates too, although it may also be found on other types of substrata (Šimunović 1997), as confirmed by our data. A characteristic of many holothurians is that physical or chemical stress causes their evisceration (Mosher 1965, Tortonese 1965, Brusca & Brusca 1996), which results in damage to the catch, reducing its market value. The bryozoan *A. semiconvoluta* clogs the nets, reducing their efficiency (Salvalaggio et al. 2014). As a result, the areas in the northern and central Adriatic characterized by the presence of these species are accurately avoided by trawlers (Fig. 8). As this part of the Adriatic is an important reproduction area for *Solea solea* (Grati et al. 2013), it might function as a refugium area for adults, ensuring the reproduction of this resource despite its intense exploitation (Scarcella et al. 2014a). Investigation of the spatial distribution of *H. (Panningothuria) forskali*, *P. regalis* and *A. semiconvoluta* over time

may thus supply useful information for the integrated management of Adriatic sole stocks based on an ecosystem approach.

Astropecten irregularis, *Anadara kagoshimensis* and *Anadara transversa* (Group C) were the predominant species along most of the western coast. The presence of *A. irregularis* nearly everywhere in the sampling area, especially in Groups B and D, confirmed the broad distribution of this sea star, which is reported by Despalatović et al. (2010) on the basis of otter trawl surveys conducted from 1985 to 1994 in the area. The authors described its common occurrence on the soft bottoms of the Adriatic Sea, the highest biomass and abundance being detected in some areas of the northernmost part of the basin and along the western coast (corresponding to Groups B, C, and D of the present study) at depths of 10 to 50 m. As in our study, they found *A. irregularis* at depths greater than 50 m on relict sand (corresponding to our Group A), although its low density at these sites suggests a preference for sediments with smaller grain sizes. Interestingly, trawling activities may actually be beneficial for the sea star because they increase food availability for this opportunistic species, while its strong regeneration capacity, burrowing behaviour and fast population growth make it highly resilient to trawling (de Juan et al. 2007). These features may explain its abundance in fishing grounds.

The other predominant species found along the western coast were *A. kagoshimensis* and *A. transversa*, 2 invasive taxa that have gradually colonized the Adriatic Sea. The former species has been recorded in the Adriatic Sea since the 1970s and was first described off Ravenna (Rinaldi 1972), whereas the latter has been reported in the Adriatic since 2000 and has been detected between Ancona and Porto Recanati (Morello & Solustri 2001). These opportunistic species have become quite common along the western Adriatic coast, which is characterized by sandy silt sediments (Froglia et al. 1998, Morello et al. 2004), but they were recently also recorded in the deepest bottoms of the northern Adriatic (Despalatović et al. 2013). Our findings confirm their presence in the central part of the northern Adriatic. *Ocnus planici* (Group B) was also abundant in this area, even though it was also detected in the other groups, as previously reported by Šimunović (1997). Another highly abundant species, besides *A. irregularis*, was *Liocarcinus depurator*, which was the main species of Group D but was also found in the other assemblages. This decapod lives on several types of substratum, especially muddy and sandy mud bottoms (Falciai &

Minervini 1992, Rufino et al. 2004), but along the western Adriatic coast it is replaced by *Liocarcinus vernalis*, which inhabits shallow sandy bottoms (Minervini et al. 1982, Falciai & Minervini 1992). The 2 decapods are the chief prey of reef-dwelling fish such as the brown meagre *Sciaena umbra* and the striped seabream *Lithognathus mormyrus*, thus playing an important ecological role (Fabi et al. 1998, Fabi et al. 2006, Šantić et al. 2010, Santelli et al. 2013).

The persistence data showed a degree of overlap of all assemblages (except A with C) in the northern area of the basin. This can probably be ascribed to the physical and chemical features of the area, where sediment composition ranges from sandy mud to muddy sand. Such granulometric structure was confirmed by the statistical analyses, which showed a marked grain size variability in the areas occupied by Groups B, C and D. In the area where the assemblages overlapped, most of the fine sediment, e.g. silt and clay, was supplied by river runoff (Wang & Pinardi 2002). These sediments are transported in suspension by the rivers and then spread by the seawater circulation, which is strongly influenced by atmospheric forces, mainly Bora and Scirocco winds. These forces, together with the Po River plume and surface waves, are the main factors in sediment transport, and significantly contribute to the sediment distribution and flux features in the area (Wang & Pinardi 2002). Such complex sediment distribution underpins the diverse assemblages of benthic fauna described in the study, which are closely related to sediment texture.

The strong river runoff in this region is an important source of nutrients, favouring primary and secondary production (Gilmartin et al. 1990, Grilli et al. 2005) up through the higher levels of the food chain and, ultimately, fishing activities (Nixon & Buckley 2002).

Interestingly, some specimens of the sea pens *Virgularia mirabilis* and *Funiculina quadrangularis* were found during the 6 surveys, the former chiefly in shallow waters along the Italian coast and the latter mainly at greater depths in the central Adriatic (Salvalaggio et al. 2016). These species have recently been included in the IUCN Red List of Italian corals as a Vulnerable and a Critically Endangered species, respectively (Salvati et al. 2014). More detailed studies of their spatial distribution are thus needed to include their conservation in sustainable fisheries management strategies.

The present study can provide useful data for the definition of Good Environmental Status (GES) in the framework of the MSFD, contributing to a greater understanding of the spatial distribution and status of

benthic species and habitats, especially in relation to Descriptors 1 (Biodiversity) and 6 (Sea-floor integrity), and to the achievement of the relevant environmental targets.

Indeed, according to the assessment of the first stage of MSFD implementation in relation to Descriptor 6, 'Member states appear to have undertaken specific new studies to map and quantify the distribution and extent of pressures; however, this was rarely assessed in relation to each type of seabed habitat' (EC 2014, p. 46). The lack of detailed habitat maps and data on the spatial distribution of key species is a common reason for such failure. In this connection, groundfish surveys such as the SoleMon project have provided valuable information, especially for assessing the impacts of commercial fisheries, e.g. on benthic communities by certain types of gear (Zampoukas et al. 2014).

With regard to MSFD implementation, Italy has defined, among others, the GES for Descriptor 6 as the 'absence of significant alteration on seabed due to fishing', and its target as the 'prevention of trawling from at least 10% of currently trawlable fishing grounds' (Italian Ministry Decree of 17th October 2014¹). However, the lack of detailed information has prevented the definition of quantitative thresholds for the GES and of a suitable set of indicators for its assessment. According to Van Hoey et al. (2013), the determination of ecological quality status of soft-sediment benthic habitats requires habitat assignment of the samples, the definition of reference or target conditions for the benthic parameters and the selection of indicator tools to assess habitat quality status. The considerable stability of the benthic assemblages recorded over the 6 yr of the study and the description of their spatial distribution provides information on habitats that can contribute to define reference/target conditions. The present findings, combined with spatialized pressure data including trawling and other sources of stress, can help define areas subject to low disturbance within each habitat type. Such data can then be used to set reference conditions and ultimately enable testing and validation of the most appropriate metrics (e.g. size-based, diversity) to assess the presence of significant adverse impacts on seafloor integrity (Rice et al. 2012).

In the context of the Ecosystem Approach to Fisheries (EAF), the habitat is defined as the chemical

and biophysical environment where an organism resides, the basic units being pelagic (the water column) and benthic (the seafloor structure, including the attached flora and invertebrate fauna) habitats. Areas subject to intensive fishing are likely to experience a permanently altered state and are inhabited by fauna adapted to frequent physical disturbance (Kaiser et al. 2001). Such effects are more clearly apparent in stable types of habitat that contain structural biogenic components, and presumably take longer to recover compared with less stable substrata. Yet, data for these habitats are especially scant (Kaiser et al. 2000). The present study describes for the first time the features of structural habitats in the northern and central Adriatic Sea in terms of megazoobenthic assemblages. Some assemblages are clearly characterized by high species richness and diversity (Groups A and B), and some organisms (such as bryozoans, holothuroideans and sponges) form complex substrata characterized by marked 3-dimensional complexity and by some large-bodied, slow-growing, associated species (e.g. *Echinus acutus*, *Marthasterias glacialis*). Such habitats play important roles also for commercial fish species (e.g. common sole).

Habitats are also crucial for maintaining the productivity of fishery resources and are a key component of ecosystem-oriented management approaches. For instance, habitats characterized by structural relief and increased fractal dimensions on an otherwise featureless bottom provide important areas for fish feeding, reproduction and shelter from predators (Bradbury et al. 1984, Schmid 2000, Caddy 2008). As bottom trawl fishing gear also has the potential to disturb structural habitats, regulations should be adopted to protect the areas where they occur.

As in the oceans, where vast areas are permanently closed to groundfish trawling to reduce potential adverse impacts on sensitive habitats and to protect benthic invertebrates, a spatial-based management should be implemented for the northern Adriatic Sea, taking into account the spatial distribution of the assemblages examined in the present study.

In some regions, such as Alaska, where fishery management is considered particularly efficient, management plans include a description and identification of essential fish habitats, adverse impacts, and actions for habitat conservation and enhancement (Witherell et al. 2000). The results of the present study can thus provide one of the pillars for integrated fishery management according to the EAF, as envisaged by the new Common Fisheries Policy (EU 2013).

¹ Italian Ministry Decree of 17th October (2014) Determinazione del buono stato ambientale e definizione dei traguardi ambientali. Ministero dell'Ambiente e della Tutela del Territorio e del Mare. GU 10 novembre 2014 no. 261

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Appendix

Table A1. Synthetic indices of diversity \pm SE calculated for each group in each year. S_m : mean species richness; H' : Shannon diversity; λ : Simpson index

Index	Group			
	A	B	C	D
S_m				
2007	12.1 \pm 1.3	9.5 \pm 0.9	6.1 \pm 0.4	6.8 \pm 0.6
2008	8.4 \pm 0.6	6.4 \pm 1.4	3.9 \pm 0.3	4.9 \pm 0.6
2009	9.3 \pm 2.5	7.2 \pm 0.6	4.4 \pm 0.3	5.2 \pm 0.3
2010	8.6 \pm 1.2	9.9 \pm 0.8	6.1 \pm 0.5	7.3 \pm 0.5
2011	18.3 \pm 0.8	13.5 \pm 0.9	8.9 \pm 0.5	8.0 \pm 0.5
2012	16.0 \pm 1.3	10.6 \pm 0.9	7.3 \pm 0.5	5.5 \pm 0.5
H'				
2007	1.2 \pm 0.1	1.3 \pm 0.1	0.8 \pm 0.1	0.9 \pm 0.1
2008	1.1 \pm 0.1	1.1 \pm 0.1	0.6 \pm 0.1	0.7 \pm 0.1
2009	0.9 \pm 0.2	1.3 \pm 0.1	0.7 \pm 0.1	0.8 \pm 0.1
2010	1.3 \pm 0.2	1.4 \pm 0.1	0.9 \pm 0.1	0.9 \pm 0.1
2011	1.5 \pm 0.1	1.4 \pm 0.1	1.0 \pm 0.1	0.9 \pm 0.1
2012	1.4 \pm 0.1	1.3 \pm 0.1	1.0 \pm 0.1	1.1 \pm 0.1
λ				
2007	0.42 \pm 0.06	0.39 \pm 0.06	0.57 \pm 0.04	0.57 \pm 0.05
2008	0.44 \pm 0.04	0.44 \pm 0.07	0.65 \pm 0.04	0.64 \pm 0.05
2009	0.60 \pm 0.11	0.37 \pm 0.06	0.62 \pm 0.05	0.61 \pm 0.06
2010	0.38 \pm 0.09	0.35 \pm 0.04	0.54 \pm 0.04	0.56 \pm 0.04
2011	0.33 \pm 0.02	0.39 \pm 0.08	0.53 \pm 0.04	0.58 \pm 0.05
2012	0.35 \pm 0.04	0.42 \pm 0.07	0.48 \pm 0.04	0.49 \pm 0.05

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