**RESEARCH ARTICLE**

Multi-scale spatio-temporal patchiness of macrozoobenthos in the Sacca di Goro lagoon (Po River Delta, Italy)

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Abstract

- 1 - In this study, the macrobenthos from different habitats in the Sacca di Goro lagoon (Po River Delta, Italy) is analysed by following a multi-scale spatio-temporal approach, with the aim of evaluating the spatial patchiness and stability of macroinvertebrate assemblages in the lagoon. The scale similarity is examined by using a taxonomic metrics based on the Kullback-Leibler divergence and a related index of similarity.
- 2 - Data were collected monthly during one year in four dominant habitat types, which were classified on the basis of main physiognomic traits (type of vegetation and anthropogenic impact). Three of the selected habitats were natural (macroalgal beds, bare sediment and *Phragmitetum*) and one anthropogenically modified (the licensed area for Manila clam farming). Each habitat was sampled in a variable number of stations representative of specific microhabitats, with three replicates each.
- 3 - Of the 47 taxa identified, only few species were found exclusively in one habitat type, with low densities. No taxon was dominant in all the considered habitats.
- 4 - The results show that, in spite of the large overlapping of species, the spatio-temporal dissimilarity within each habitat type was higher than expected on the basis of the common physiognomic traits. This suggests that local factors (mainly hydrodynamism, quality and quantity of vegetal matter) play a significant role in determining the structure of the macroinvertebrate assemblages.
- 5 - The dissimilarity between habitats was significant and maintained all over the seasonal progression, indicating that the macroinvertebrate assemblages were steadily different. Each habitat allowed some specific taxa to maintain a significant population size, which is a prerequisite for preserving biodiversity.
- 6 - The variety of vegetation types and hydrodynamic conditions in the lagoon emerges as crucial for sustaining biodiversity and capacity to recover from disturbances.

Keywords: biodiversity, macrozoobenthos, patchiness, coastal lagoons, Mediterranean Eco-region.

Introduction

The coastal lagoons, as habitat islands along the coastal landscape, have their biotic structure forced by immigration and emigration processes, habitat selectivity (Zobel, 1997) and coexistence relationships (Tilman, 2004). The coastal lagoons are also ecotones among freshwater, marine and terrestrial biotopes, and thus their abiotic structure is forced by geomorphological and hydrological processes, as well as by land use in the watershed (Carrada *et al.*, 1988; Rossi and Costantini, 2000).

Coastal communities are under an increasing pressure from multiple stressors, including anthropogenic exploitation, which are determining a progressive loss of habitats worldwide (Carrada, 2007; Halpern *et al.*, 2008), with a consequent loss in biodiversity and ecosystem functionality (Solan *et al.*, 2008; Duffy, 2009).

In Sacca di Goro, the most southern lagoon of the Po River Delta (northern Italy), a progressive worsening of the environmental quality has been observed during the last decades, as a consequence of two main processes, i.e., the increase of eutrophication and the expansion of intensive shellfish culture (Bartoli *et al.*, 2001; Castaldelli *et al.*, 2003; Viaroli *et al.*, 2006). As a consequence, some typical habitats of the River Po Delta, such as the *Ruppium*, have declined and been substituted by nitrophilous macroalgae. In the above scenario of simultaneous and rapid environmental changes, some macrobenthic species, owing to their sensitivity to environmental conditions (Galuppo *et al.*, 2007; Barbone and Basset, 2010; Barbone *et al.*, 2012), are exposed to a high risk of depletion, as well as local extinction.

Since coastal lagoons are ecotones continuously exposed to natural and anthropogenic disturbances, they are sometimes regarded as being composed of a mosaic of transitory patches colonized by

opportunistic species. This view, which could be founded in some cases, has the drawback of spreading the perception that the resilience of these ecosystems is high enough to ensure a recovery from disturbances. The assessment of the strength and stability of the spatial structuring in these ecosystems is therefore necessary in order to give to ecosystem patchiness a proper importance and role in the maintenance of ecosystem functioning and biodiversity. Such a knowledge is also a prerequisite for evaluating ecosystem services and for selecting sustainable policies of ecosystem management, particularly when in presence of a significant anthropogenic exploitation.

The basic aim of the present study is to evaluate the spatial patchiness and stability of macroinvertebrate assemblages in the Sacca di Goro lagoon. To fulfill this task, the similarity among the macrobenthic assemblages found in several stations representative for the main habitats was evaluated, taking also into account the temporal variability.

Materials and methods

Study area

The Sacca di Goro (Fig. 1) is a shallow-water embayment of the Po River Delta (44.78-44.83°N, 2.25-12.33°E), approximately triangular in shape with a surface area of 26 km² and an average depth of 1.5 m. During the sampling period, the lagoon was connected to the Adriatic Sea by two mouths each wide about 0.9 km (Fano *et al.*, 2000). The western area (Valle Giralda) is influenced by freshwater inflow from the canal Po di Volano, whereas the central area is influenced by the sea. The eastern zone (Valle di Gorino) is very shallow (maximum depth 1 m) and accounts for half of the total surface area and a quarter of the water volume (for further information, see the Lagunet Site: <http://www.dsa.unipr.it/lagunet/infosheet/02-goro.pdf>).

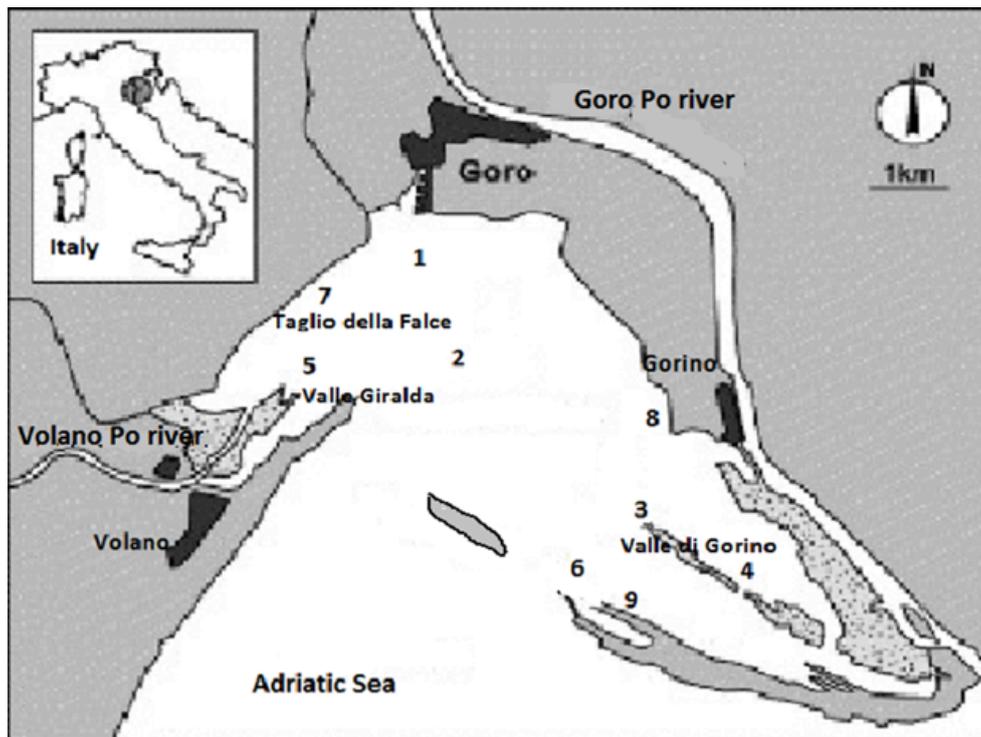


Figure 1. Map of the Sacca di Goro lagoon showing the location of the sampling stations.

The present study is a part of a regional programme aimed to understand the spatio-temporal patterns of variability in macroinvertebrates in Po River Delta (Italy). A common sampling design was adopted for characterizing the biodiversity in the main lagoons of the delta. In each lagoon, the main habitat types were identified on the basis of the vegetation type (Roff and Taylor, 2000; Mistri *et al.*, 2001) and each habitat was sampled in a variable number of stations representative of specific microhabitats, with three replicates each. In the Sacca di Goro lagoon, three of the selected dominant habitats were natural: i.e., the macroalgal beds (MAB), the bare sediment (BAS) and the *Phragmitetum* (*P. australis* (Cav.) Trin. ex Steud.) (PHR), and one anthropogenically modified, i.e., the licensed area for Manila clam farming, called Manila clam beds (*Venerupis philippinarum*

(A. Adams and Reeve, 1850)) (MCB). MAB is the most widespread habitat in the lagoon. To account for the wide variability of hydrological conditions, it was sampled along a gradient of confinement, from the channel connecting the mouths of the lagoon with the port of Goro (Station 1), to the centre of the open lagoon (Station 2), to the edge with the Valle di Gorino (Station 3) and to the Gorino lagoon, the most confined sub-basin (Station 4). In this habitat, both sediment and macroalgal bed were sampled. The BAS habitat was sampled in two opposite conditions: the western corner of the lagoon, corresponding to the inlet of the Po di Volano (Station 5), characterized by low salinity and hydrodynamics and the outer portion of the lagoon, close to the sand bank and exposed to high salinity and hydrodynamism (station 6). The PHR habitat was sampled in two sites having low salinity (a basic requirement

for the survival of a stand of *Phragmites australis*), but different hydrodynamism: the Station 7 (Taglio della Falce), located in the western corner of the lagoon, at the outlet of the Po di Volano, characterised by and high hydrodynamism and the Station 8, which is located in the Valle di Gorino, characterised by a low hydrodynamism. The habitat MCB was selected within the most intensively farmed area of the lagoon, behind the outer sand bank (Station 9).

Sampling methods

The selected stations were sampled monthly from March 1997 to February 1998 (Stations 1 – 8) and from March 1998 to February 1999 (Station 9). The four considered habitats were sampled using the standard methods for the specific features of the sites. The sediment at MAB and MCB stations was sampled in triplicate using a Van Veen grab (surface area 0.06 m²) with a penetration depth of 12 cm. When present, the macroalgae were collected in triplicate, using a benthic hand grab net (mesh size 500 µm, mouth size 0.4 m), pulled for 1 m to cover an area of 0.4 m². Filtered sediment samples were stored in 1 L polyethylene bottles and fixed using buffered 8% formaldehyde. Macroalgal samples, mainly represented by pleustophytes *Ulva* sp. and *Gracilaria verrucosa* (Hudson) Papenfuss, and more rarely by *Cladophora* sp. (Fano *et al.*, 2000), were stored in plastic bags, within refrigerated containers and sorted when reaching the laboratory, in a few hours. The macroalgal biomass was evaluated as Ash Free Dry Weight in the oven for 48 h at 80°C and after in the muffle furnace at 400°C for 4 h. BAS stations were sampled in triplicate, using plexiglass core liners (8 cm i.d.). PHR stations were sampled in triplicate using steel squares (20X20 cm) mounting a 500 µm mesh net, randomly positioned on the sediment after the removal of reed stems and inserted in the sediment to a 20 cm depth. To collect the sample, roots underneath were

cut using a shovel. The collected samples were filtered (500 µm) in situ and then stored in 1 L polyethylene bottles, using 8% buffered formaldehyde. At the first sampling of the campaign, sediment samples were taken in triplicate at each station, dried in a ventilated oven at 60° C for three days and sieved on a granulometric column analyser (Fritsch GmbH). Water quality variables were measured as follows. Water transparency was measured by Secchi Disk. Depth, temperature, salinity, dissolved oxygen concentration and saturation were measured with a multiparametric probe (Ocean Seven, 316, Idronaut, Brugherio, MI, Italy). Water samples were taken from the middle of the water column, filtered in the field (Whatman GF/C), and stored at -20°C until analysed. Inorganic nitrogen was calculated as sum of ammonia (Bower and Holm-Hansen, 1980), nitrite and nitrate (Armstrong *et al.*, 1967). Dissolved orthophosphate was measured according to Valderrama (1977). Chlorophyll *a* was determined according to Lorenzen (1967).

Analysis of biodiversity

The variability of macroinvertebrate assemblages was analysed at different spatial and ecological scales by using a similarity index proposed by Ludovisi and Taticchi (2006):

$$s_j = 1 - \frac{\hat{J}(P : Q)}{\hat{J}(P : Q)_{max}}$$

$$(0 \leq s_j \leq 1) \tag{1}$$

where

$$\hat{J}(P : Q) = \sum_{i=1}^{\hat{S}} (p'_{iP} - p'_{iQ}) \ln \frac{p'_{iP}}{p'_{iQ}}$$

$$\hat{J}(P : Q) \geq 0 \tag{2}$$

is the Kullback-Leibler divergence and $\hat{J}(P:Q)_{max}$ is the maximum value allowed to $\hat{J}(P:Q)$. In Eq. 2, p'_{iP} and p'_{iQ} are the proportions of the i -th species in the assemblages under comparison (P and Q), \hat{S} is the total number of species found in the two assemblages. The proportion of each species was adjusted for sample coverage by using the estimator proposed by Turing (see Good, 1953), which is based on the proportion of singletons in a sample:

$$C = 1 - f_i/N \quad (0 \leq C \leq 1), \quad [3]$$

where N is the total number of counts in a sample and f_i the number of taxa found with one specimen (when no singletons were found, f_i was assumed equal to 0.5).

The similarity index s_j was calculated for each month of sampling, by comparing samples collected in the three replicates of each station (within-station similarity), samples collected in different stations of the same habitat (within-habitat similarity), and samples collected in stations of different habitats (between-habitats similarity). Within-habitat and between-habitats similarities were calculated using count data integrated over replicates. In order to obtain an integrated picture of the spatio-temporal variability in the macrobenthic assemblages, the monthly values of s_j obtained in any single comparisons were averaged, and the monthly averages examined for distribution using a box-plot representation.

The use of the above measures of similarity is advantageous, because the examination of the terms of the summation $\hat{J}(P:Q)$ allow us to identify the taxa that mostly contributes to the dissimilarity between samples. In addition, since the Kullback-Leibler information measures are strictly linked with thermodynamics (Ludovisi, 2009, 2013; Ludovisi and Jørgensen, 2009; Jørgensen *et al.*, 2010; Ludovisi *et al.*, 2012), they allow us to frame the analysis of biodiversity

within a broader ecological context.

Results

The environmental data collected during the sampling survey are summarised in Table 1. Bottom sediment was quite homogeneous in the lagoon, and mostly represented by granulometric classes of a small size (mud). Only in the stations 6 and 9 higher granulometric classes were detected. The main water quality variables were similar within each habitat type and also among the habitat types. This is likely due to the water movement, relatively high and favoured by the amplitude of the two mouths to the sea, by the ramification of the network of submerged channels and by the shallowness of the waters. Salinity characterized all stations as mesohaline. Oxygen saturation showed a general oversaturation in the MAB and a slight tendency to undersaturation in the other considered habitats, but markedly hypoxic values were never detected. Reactive nutrients showed high values in all stations, typical of eu-hypertrophic environments. The relatively low chlorophyll *a* concentration found in all stations indicates the dominance of macroalgae as primary producers in the whole lagoon (Table 1).

The macroinvertebrates found in the Sacca di Goro lagoon are listed in Table 2. Overall, the sample coverage (Eq. 3) was highly satisfactory ($C > 0.95$) in all stations and months, except in few cases in winter when a low number of individuals was gathered. Only few taxa were found exclusively in one habitat type: *Bittium reticulatum*, *Doris bicolor*, *Heteromastus filiformis*, *Mytilaster minimus*, *Ostrea edulis*, *Spio decoratus*, *Venerupis decussata*, and *Turritella communis* were found only in the habitat MAB; *Ensis minor* was found only in the habitat MCB. These species showed low densities, with the exceptions of *V. decussata*, which reached 12,900 Ind. m⁻² at Station 8 in May 1997. No taxon was dominant in all the considered

Table 1 - Geographical location and main environmental features of the sampling stations in the Sacca di Goro lagoon. A = Sediment composition; B = Hydrodynamics; C = Water transparency (% of total depth); D = Water temperature (°C); E = Salinity; F = Dissolved oxygen (% sat.); G = Inorganic nitrogen ($\mu\text{g N L}^{-1}$) H = Phosphorous orthophosphate ($\mu\text{g P L}^{-1}$); I = Chlorophyll *a* ($\mu\text{g L}^{-1}$); L= Total macroalgal biomass (AFDW, g m^{-2}).

Habitat	Station	GIS coordinates	A	B	C	D	E	F	G	H	I	L
						mean	mean	mean	mean	mean	mean	mean
							$\pm\text{SD}$	$\pm\text{SD}$	$\pm\text{SD}$	$\pm\text{SD}$	$\pm\text{SD}$	$\pm\text{SD}$
Macroalgal beds (MAB)	1	44°50'02.35"N 12°17'39.59"E	mud	Medium	66	15.8 ± 7.7	26.8 ± 4.1	115.1 ± 10.6	299.2 ± 218.4	44.4 ± 12.8	7.92 ± 6.54	12.03 ± 2.98
	2	44°49'15.87"N 12°18'26.58"E	mud	High	73	15.9 ± 7.7	28.3 ± 4.2	107.3 ± 18.2	464.8 ± 265.7	42.6 ± 17.1	6.89 ± 3.22	9.41 ± 3.41
	3	44°48'23.74"N 12°20'02.71"E	mud	Medium	82	15.2 ± 8.2	20.8 ± 5.8	106.3 ± 11.8	433.3 ± 249.0	34.3 ± 12.8	8.06 ± 3.94	7.89 ± 1.88
	4	44°47'52.64"N 12°21'06.04"E	mud	Low	87	15.4 ± 8.3	16.3 ± 3.2	107.8 ± 12.7	468.6 ± 204.6	64.5 ± 21.5	4.89 ± 2.54	7.52 ± 2.02
Bare sediment (BAS)	5	44°49'09.22"N 12°16'36.31"E	mud	Low	87	16.0 ± 7.2	26.3 ± 4.4	93.4 ± 3.8	423.8 ± 282.6	48.1 ± 18.3	11.03 ± 4.85	-
	6	44°47'47.92"N 12°19'13.57"E	mud- very fine sand	High	85	16.1 ± 8.1	28.6 ± 3.3	99.7 ± 5.9	478.4 ± 254.1	37.7 ± 14.2	5.48 ± 1.65	-
Phragmitetum (PHR)	7	44°49'45.97"N 12°16'35.38"E	mud	Low	70	15.4 ± 7.5	16.1 ± 5.1	97.4 ± 9.7	413.2 ± 208.7	35.1 ± 12.5	7.91 ± 3.11	-
	8	44°49'08.98"N 12°20'14.22"E	mud	Medium	93	15.3 8.4	17.1 ± 5.8	98.2 ± 7.8	452.7 ± 198.8	35.6 ± 14.1	9.74 ± 2.28	-
Manila clam beds (MCB)	9	44°47'49.81"N 12°19'59.62"E	fine sand	High	83	16.3 ± 7.4	25.7 ± 3.9	95.6 ± 4.8	493.11 ± 225.6	37.4 ± 13.2	5.88 ± 2.04	-

habitats (Table 2). However, *Capitella capitata* and *Streblospio shrubsolii* appear among the dominant taxa in the habitats PHR, BAS and MCB, whereas *Chironomus salinarius* and *Gammarus aequicauda* were dominant in both the habitats MAB and PHR. Within-station similarities were quite high in all habitats and months (Fig. 2a), indicating that the replicates can be considered homogeneous in most cases. However, although the annual range of variation of s_j is similar in the different habitats, s_j shows a lower mean value and a higher dispersion in the MAB habitat, suggesting that the

small scale patchiness in this habitat is more variable during the year in comparison with the other habitats. In contrast, the habitat characterized by clams (MCB) shows a very high median value and a low dispersion, which testify for a low spatio-temporal variability at a local scale.

The similarity declines drastically (Fig. 2b) when comparing the macroinvertebrate assemblages collected in a given habitat but in different stations (within-habitat similarity). BAS and MAB habitats showed a very high spatio-temporal variability, with a clear seasonal progression (in general,

Table 2 - List of the macrobenthos taxa found in the four habitat types investigated in Sacca di Goro lagoon. The presence of a taxon is marked by a single asterisk and the dominant taxa (the ones appearing with the highest relative abundance in at least one sampling occasion) are marked by a double asterisk. The figures in brackets indicate the overall percentage of occurrence in the samples.

TAXON ^a	HABITAT TYPE ^b			
	MAB	PHR	BAS	MCB
<i>Abra segmentum</i> (Récluz, 1843)	* (5.6)		* (6.9)	
Actiniaria	* (9.7)	* (2.8)		* (1.4)
<i>Ampelisca</i> sp.			* (11.1)	** (77.8)
<i>Anadara inaequalis</i> (Bruguière, 1789)	* (20.5)		* (9.7)	
<i>Arcuatula senhousia</i> (Benson in Cantor, 1842)	** (62.5)	* (54.2)	* (29.2)	* (2.8)
Asciacea	* (4.9)			
Balanidae	* (2.4)	* (27.1)		* (4.2)
<i>Bittium reticulatum</i> (da Costa, 1778)	* (5.2)			
<i>Brachynotus sexdentatus</i> (Risso, 1827)	* (8.3)		* (13.9)	* (19.4)
<i>Capitella capitata</i> (Fabricius, 1780)	* (39.2)	** (26.4)	** (94.4)	** (93.1)
<i>Carcinus aestuarii</i> (Nardo, 1847)	* (6.9)		* (2.8)	
<i>Cerastoderma glaucum</i> (Bruguière, 1789)	* (24.3)	* (14.6)	* (20.8)	* (58.3)
<i>Chironomus salinarius</i> (Kieffer, 1915)	** (52.4)	** (29.2)	* (23.6)	
<i>Cyclope neritea</i> (Linnaeus, 1758)	* (0.7)		* (6.9)	* (30.6)
<i>Doris bicolor</i> (Bergh, 1884)	* (2.4)			
<i>Ensis minor</i> (Chenu, 1843)				* (8.3)
<i>Ficopomatus enigmaticus</i> (Fauvel, 1923)	* (24.7)		* (9.7)	* (2.8)
<i>Gammarus aequicauda</i> (Martinov, 1931)	** (54.2)	** (54.9)	* (33.3)	* (37.5)
<i>Haminoea hydatis</i> (Linnaeus, 1758)	* (21.2)		* (22.2)	
<i>Heteromastus filiformis</i> (Claparède, 1864)	* (3.8)			
<i>Hydrobia</i> sp.	* (40.3)	* (4.2)	* (8.3)	
<i>Hydroides dianthus</i> (Verrill, 1873)	* (4.2)			* (2.8)
<i>Idotea balthica</i> (Pallas, 1772)	* (12.8)	* (1.4)	* (5.6)	* (1.4)
<i>Lekanesphaera hookeri</i> (Leach, 1814)	* (3.5)	* (27.1)		
<i>Lentidium mediterraneum</i> (O.G. Costa, 1829)	* (0.7)		* (4.2)	
<i>Microdeutopus gryllotalpa</i> (Costa, 1853)	* (47.6)	* (11.8)	* (31.9)	* (59.7)
<i>Monocorophium insidiosum</i> (Crawford, 1937)	* (16)	* (1.0)	* (30.6)	
<i>Mytilaster minimus</i> (Poli, 1795)	* (2.8)			
<i>Mytilus galloprovincialis</i> (Lamarck, 1819)	* (5.9)	* (2.8)	* (16.7)	
<i>Nassarius reticulatus</i> (Linnaeus, 1758)	* (7.6)		* (19.4)	
<i>Neanthes succinea</i> (Leuckart, 1847)	* (53.1)	* (54.9)	* (65.3)	* (77.8)
<i>Nephtys hombergii</i> (Savigny in Lamarck, 1818)	* (13.2)			* (2.8)
Oligochaeta	* (10.4)	* (18.1)	* (20.8)	* (23.6)
<i>Ostrea edulis</i> (Linnaeus, 1758)	* (0.7)			
<i>Palaemon elegans</i> (Rachte, 1837)	* (5.6)			* (1.4)
Pectinidae	* (0.7)			
<i>Phyllodoce lineata</i> (Claparède, 1870)	* (3.5)		* (6.9)	
<i>Polydora ciliata</i> (Johnston, 1838)	** (45.5)	* (17.4)	* (43.1)	** (44.4)
<i>Prionospio multibranchiata</i> (Berkeley, 1927)	* (9.4)		* (40.3)	** (90.3)
<i>Sphaeroma serratum</i> (Fabricius, 1787)	* (1.0)	* (3.5)		
<i>Spio decoratus</i> (Bobretzky, 1870)	* (1.7)			
<i>Streblospio shrubsolii</i> (Buchanan, 1890)	* (25.3)	** (52.1)	** (90.3)	** (81.9)
<i>Tellina</i> sp.	* (2.4)			* (1.4)
Turbellaria	* (3.5)		* (2.8)	* (8.3)
<i>Turritella communis</i> (Risso, 1826)	* (2.4)			
<i>Venerupis decussata</i> (Linnaeus, 1758)	** (3.5)			
<i>Venerupis philippinarum</i> (A. Adams & Reeve, 1850)	* (11.1)		* (33.3)	* (77.8)
No. STATIONS	4	2	2	1
No. SPECIES	45	18	28	24

^aAccording to the World Register of Marine Species (Appeltans et al., 2012).

^bHabitat types: macroalgal beds (MAB); bare sediment (BAS); *Phragmitetum* (PHR); Manila clam beds (MCB).

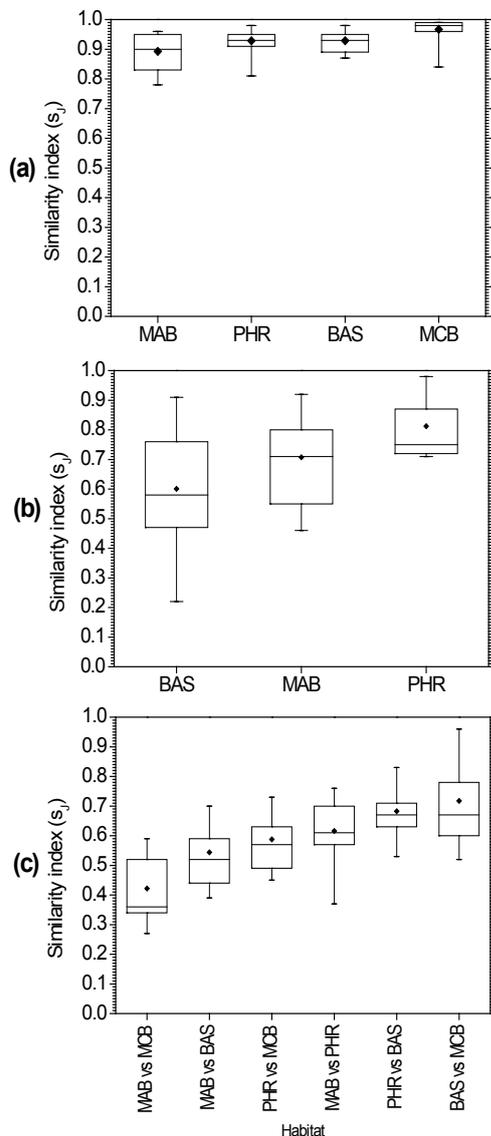


Figure 2. Boxplots showing the similarity at different ecological scales in the Sacca di Goro lagoon: a) within-station similarity; b) within-habitat similarity, c) between-habitats similarity. The plot summarises the distribution of monthly average values of the index of similarity s_j . The box represents the interval that includes 50% of the data and shows the annual mean (diamond) and median (line); the whiskers represent the annual minima and maxima. Habitat types: macroalgal beds (MAB); bare sediment (BAS); *Phragmitetum* (PHR); Manila clam beds (MCB).

summer months showed a lower similarity). In the PHR habitat, seasonal changes are less significant and the similarity is relatively high (50% of data in the range $0.72 \leq s_j \leq 0.87$).

The examination of the terms of the summation of $\hat{J}(P:Q)$ (Eq. 2) allow us to identify the taxa that mostly contributed to the within-habitat diversity. The lists in Table 3 include the taxa whose relative abundance changed significantly (e.g., shifting a taxon from dominant to rare) in the different habitats. Although the heading taxa are different, a common set of species (*Arcuatula senhousia*, *Streblospio shrubsolii*, *Chironomus salinarius*, *Gammarus aequicauda* and *Capitella capitata*) appear in the lists of all the considered habitats. Since the above species are also among the most dominant and widespread ones (see Table 2), it can be concluded that most of the spatio-temporal variability of macroinvertebrates within the main habitats of Sacca di Goro is related to a shift of dominance among prevailing and ubiquitous species. However, a significant contribution to the within-habitat variability is also provided by non-ubiquitous and/or non-dominant species, such as *V. decussata* and *Nephtys hombergii* in the habitat MAB, and Balanidae in PHR.

The similarity between macroinvertebrate assemblages from different habitats is fairly low ($0.42 \leq s_j \leq 0.72$ on average), whatever is the pair of habitats under comparison (Fig. 2c). The low dispersion of s_j around the means indicate that the dissimilarity is maintained all over the year. The examination of the terms of the summation of $\hat{J}(P:Q)$ (Eq. 2) shows that (Table 4):

- the shift in dominance between *A. senhousia* and *S. shrubsolii* is the main source of dissimilarity between MAB and the other habitats;
- the abundance of Balanidae in the PHR habitat significantly contributes to

Table 3 - List of the main taxa (ordered by decreasing importance) contributing to the within-habitat diversity in the investigated habitats^a. The percentage gives a measure of the contribution of the taxa to the overall within-habitat dissimilarity (as $\hat{J}(P:Q)$).

MAB	%	PHR	%	BAS	%
<i>Arcuatula senhousia</i>	24.3	Balanidae	27.0	<i>Streblospio shrubsolii</i>	27.0
<i>Venerupis decussata</i>	10.7	<i>Chironomus salinarius</i>	15.9	<i>Polydora ciliata</i>	22.5
<i>Streblospio shrubsolii</i>	9.9	<i>Streblospio shrubsolii</i>	14.6	<i>Arcuatula senhousia</i>	14.7
<i>Nephtys hombergii</i>	8.1	<i>Gammarus aequicauda</i>	13.4	<i>Microdeutopus gryllotalpa</i>	6.4
<i>Neanthes succinea</i>	7.5	<i>Capitella capitata</i>	8.3	<i>Gammarus aequicauda</i>	6.2
<i>Chironomus salinarius</i>	4.9	<i>Monocorophium insidiosum</i>	6.2	<i>Prionospio multibranchiata</i>	5.9
<i>Mytilus galloprovincialis</i>	4.7	<i>Arcuatula senhousia</i>	3.8	<i>Capitella capitata</i>	5.9
<i>Capitella capitata</i>	4.0	<i>Neanthes succinea</i>	2.7	<i>Chironomus salinarius</i>	3.6
<i>Gammarus aequicauda</i>	3.7	<i>Lekanesphaera hookeri</i>	1.6	<i>Haminoea hydatis</i>	1.8
	77.9		93.5		94.0

^aHabitat types: macroalgal beds (MAB); bare sediment (BAS); *Phragmitetum* (PHR).

Table 4 - List of the main taxa (ordered by decreasing importance) contributing to the between-habitats dissimilarity^a. The percentage gives a measure of the contribution of the taxa to the between-habitats dissimilarity (as $\hat{J}(P:Q)$) obtained for any specific habitat comparison.

	MAB	%	PHR	%	BAS	%	MCB	%
MAB			<i>S. shrubsolii</i>	26.2	<i>S. shrubsolii</i>	25.8	<i>A. senhousia</i>	21.7
			Balanidae	15.1	<i>A. senhousia</i>	20.8	<i>S. shrubsolii</i>	16.3
			<i>A. senhousia</i>	10.7	<i>C. salinarius</i>	10.0	<i>P. multibranchiata</i>	11.1
PHR	<i>S. shrubsolii</i>	26.2			Balanidae	17.8	<i>P. multibranchiata</i>	17.1
	Balanidae	15.1			<i>S. shrubsolii</i>	15.6	<i>Ampelisca</i> sp.	14.6
	<i>A. senhousia</i>	10.7			<i>G. aequicauda</i>	14.6	Balanidae	14.0
BAS	<i>S. shrubsolii</i>	25.8	Balanidae	17.8			<i>Ampelisca</i> sp.	22.0
	<i>A. senhousia</i>	20.8	<i>S. shrubsolii</i>	15.6			<i>P. multibranchiata</i>	17.5
	<i>C. salinarius</i>	10.0	<i>G. aequicauda</i>	14.6			<i>S. shrubsolii</i>	16.1
MCB	<i>A. senhousia</i>	21.7	<i>P. multibranchiata</i>	17.1	<i>Ampelisca</i> sp.	22.0		
	<i>S. shrubsolii</i>	16.3	<i>Ampelisca</i> sp.	14.6	<i>P. multibranchiata</i>	17.5		
	<i>P. multibranchiata</i>	11.1	Balanidae	14.0	<i>S. shrubsolii</i>	16.1		

^aHabitat types: macroalgal beds (MAB); bare sediment (BAS); *Phragmitetum* (PHR); Manila clam beds (MCB).

distinguish such habitat from the others;

- *Prionospio multibranchiata* and *Ampelisca* sp. are the most distinctive taxa for the MCB habitat;

- in the bare sediment (BAS), no taxon stands out as distinctive and the differences with the other habitats are mostly due to the reasons mentioned to above.

Discussion

As a whole, the results show that, in spite of the large overlapping in species composition, the spatio-temporal variability in macroinvertebrates is very high in Sacca di Goro. In particular, the dissimilarity between habitats was significant and maintained all over the seasonal progression, indicating that the structure of the macroinvertebrate assemblages were steadily different. The physiognomic features seem to play the foremost role in selecting the distinctive species in each habitat type. In particular, the great abundance of *A. senhousia* in the MCB habitat can be explained by considering mechanical, more than food, factors: in fact, macroalgal beds represent an insuperable obstacle for settling larvae, which attach on the bed without reaching the sediment (Mistri *et al.*, 2004). The positive selectivity for hard substrata can explain the preference of Balanidae for PHR habitat. The preference of *P. multibranchiata* and *Ampelisca* sp. for the MCB habitat appears to be linked mainly to the high food availability in the form of clam's feces and pseudofeces (Mantovani *et al.*, 2006; Cinar *et al.*, 2012).

In spite of the common physiognomic traits, a high dissimilarity was also found within each habitat type. This suggests that local factors play a significant role in determining the composition of the macroinvertebrate assemblages. Water quality data did not help us to identify any clear driving factor for the observed within-habitat dissimilarity, as water quality variables, although changing in time, had similar annual averages among

the stations of any given habitat (Table 1). Neither bottom sediment seems to play a significant role, as it is quite homogeneous in the lagoon. Therefore, the determinants of the observed within-habitat heterogeneity likely are other such as hydrodynamics, food availability and disturbance. Hydrodynamism is highly variable in the lagoon and could help to explain the changes in the abundance of sessile taxa, such as Balanidae within the PHR habitat. Hydrodynamism could also be important in determining the shift in dominance among the deposit feeders *A. senhousia*, *S. shrubsolii* and *P. ciliata* in the BAS habitat. Differences in hydrodynamism could also contribute to determine different composition and dynamics of macroalgal beds in the various areas of the lagoon. Thus, different conditions given by different macroalgal species, different density and physiological state, influencing in turn both food availability and water quality in a specific MAB microhabitat, may have exerted a strong conditioning of the macroinvertebrates community composition. This has reasonably contributed to enhance the dissimilarity between the macrobenthic assemblages in the MAB habitat and force species to move from a site, searching for more favourable conditions.

Disturbance events, acting at a local scale with high frequency (e.g., the daily mechanical clam harvesting in the MCB) or with annual periodicity (e.g., the collapse of the macroalgal beds in the MAB, culminating in some occasions with long-lasting anoxia and dystrophy), may have also contributed to sustain the within-habitat, as well as the between-habitats diversity of macrobenthos in the lagoon of Goro. Opportunistic and ubiquitous species, belonging to the trophic group of deposit feeders (*A. senhousia*, *S. shrubsolii*, *C. salinarius* and *C. capitata*) and shredders/scrapers (e.g., *G. aequicauda* in macroalgal beds and *Phragmitetum*), are likely to play

a key role in sustaining biodiversity, as they ensures a rapid recolonization of patches after the occurrence of disturbance (Taghon and Linton, 2000; Mistri *et al.*, 2004).

Conclusion

As a whole, the research show that a highly-structured and persistent patchiness, which is also higher than expected on the basis of the main physiognomic traits, there exists in the macroinvertebrate community of Sacca di Goro. A set of opportunistic and ubiquitous species is responsible for most part of the macrobenthic patchiness, but a significant contribution is also provided by habitat-selective taxa. Each microhabitat allows some specific taxa to maintain a significant population size, which is a prerequisite for ensuring a long-term survival of these species in the lagoon. The variety of vegetal habitat types and hydrodynamic conditions in the lagoon emerges as crucial for sustaining biodiversity and capacity to recover from disturbances.

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