

RESEARCH ARTICLE

Environmental heterogeneity and benthic macroinvertebrate guilds in Italian lagoons

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Abstract

- 1 - Lagoons are ecotones between freshwater, marine and terrestrial biotopes, characterized by internal ecosystem heterogeneity, due to patchy spatial and temporal distribution of biotic and abiotic components, and inter-ecosystem heterogeneity, due to the various terrestrial-freshwater and freshwater-marine interfaces.
- 2 - Here, we carried out an analysis of environmental heterogeneity and benthic macro-invertebrate guilds in a sample of 26 Italian lagoons based on literature produced over a 25 year period..
- 3 - In all, 944 taxonomic units, belonging to 13 phyla, 106 orders and 343 families, were recorded. Most species had a very restricted geographic distribution range. 75% of the macroinvertebrate taxa were observed in less than three of the twenty-six lagoons considered.
- 4 - Similarity among macroinvertebrate guilds in lagoon ecosystems was remarkably low, ranging from $10.5\% \pm 7.5\%$ to $34.2\% \pm 14.4\%$ depending on the level of taxonomic resolution.
- 5 - Taxonomic heterogeneity was due to both differences in species richness and to differences in species composition: width of seaward outlet, lagoon surface area and water salinity were the most important factors affecting species richness, together accounting for up to 75% of observed inter-lagoon heterogeneity, while distance between lagoons was the most significant factor affecting similarity of species composition.
- 6 - Both environmental filtering and passive diffusion were found to be influential processes in shaping macroinvertebrate guilds in lagoon ecosystems.

Keywords: Lagoons, macro-invertebrates, community assembly rules, niche filtering

Introduction

Community and guild structure are known to be shaped by processes occurring at very different spatial and temporal scales: from speciation events and biogeography, to small-scale biotic interactions, through diffusion processes and abiotic filtering (Zobel, 1997).

At a regional scale, historical processes shaping the species pool can be assumed to be homogeneously distributed and the relative importance of diffusion processes and niche filtering, including both abiotic and competitive filters, can be assessed. Even at this scale,

historical processes shaping the species pool can easily be identified in relation to human activities, which were particularly effective in shaping the landscape of the Mediterranean coasts. The local extinction of species and introduction of others as a consequence of human activities has shaped the regional species pool over the last 15,000 years, being spatially explicit in many cases. However, these are probably better classified as components of environmental filtering, rather than true 'historical processes'.

Transitional water ecosystems represent an ideal study environment in which to evaluate the

significance of various potential drivers of community and guild structure at the local, ecosystem, level. This is due to some features which, when combined together, make transitional waters very distinctive ecosystems in the coastal landscape. Here, we will focus on coastal lagoons, but most of the features outlined below can be generalized to other transitional water body types (Basset *et al.*, 2006; Elliott and McLusky, 2006). Coastal lagoons are habitat islands, whose boundaries and surface area can be identified in relation to tides. They are known to be harsh ecosystems for both plants and animal guilds due to their strong gradients of salinity, temperature and dissolved oxygen in space and time. High water exchange rates and heterogeneity of deposition and erosion processes are additional limiting factors for many species. Because of these two features, niche filtering can be expected to be very significant in lagoon ecosystems, selecting very similar species according to a few well known traits, of which osmoregulation (Hauxwell, *et al.*, 1998), resistance to hypoxia (Smale and Rabeni, 1995), temperature variability adaptation (Nair and Anger, 1972) are the most studied. As habitat islands, lagoons have very little endemism, if any; colonizers come directly from the surrounding freshwater and marine ecosystems, which are the source habitats of lagoons of most lagoon species, with the notable exception of many migratory birds. Since lagoons are surrounded by adequate habitats, rather than inhospitable habitats, dispersal and diffusion are expected to be relevant processes in coastal lagoons for many species and indeed entire guilds. Therefore, relative homogeneity of guild composition among lagoons could be an expected consequence of the strong filtering and dispersion influences. On the other hand, since physiographic and hydrological factors are known to differentiate lagoons into classes according to geomorphology (Kjerfve, 1994), salinity (Battaglia, 1959) and degree of confinement (Guelorget and Perthuisot, 1983; Guelorget *et al.*, 1983), strong niche filtering could also be expected to result in some degree of heterogeneity of species composition among

lagoon types. However, the relative roles of niche filtering and dispersion processes in guild and community assembly in lagoon ecosystems are still poorly investigated.

In the Mediterranean region, lagoon species and ecosystems have traditionally received much attention, mainly following either a species-centred approach, focusing on adaptations (Cognetti and Maltagliati, 2000), or a perturbation-centred approach, focusing on responses and indicators (Reizopoulou and Nicolaidou, 2004; Mouillot, *et al.*, 2006). On the other hand, only a few guild- and community-level studies have considered groups of ecosystems, searching for patterns of fish (Perez-Ruzafa, 2005) and macroinvertebrate (Reizopoulou and Nicolaidou, 2004; Sabetta *et al.*, 2007) guilds linked to environmental factors.

Here, we performed a comparative analysis of macroinvertebrate guild structure in Italian lagoons in order to make a quantitative assessment of macroinvertebrate guild heterogeneity among lagoons. Therefore, the paper assesses the contrasting hypotheses of the relative homogeneity vs. heterogeneity of lagoon guilds/communities, arising from the role of niche filtering and passive diffusion processes in structuring lagoon communities. Differences in the taxonomic structures of benthic macroinvertebrate guilds may be due to different species richness, different taxonomic composition or different species-abundance distributions. The first two components, which tend to be more conservative than the third, were directly addressed in this study.

Material and methods

Data sources

This paper is based on data-mining activity of the taxonomic composition of benthic macroinvertebrate guilds in Italian lagoons. The data used in the present study were gleaned from published sources, including international journals retrieved from electronic databases (ASFA, WebSpirs, Biological Abstracts, Current Contents and Zoological Records), Italian journals covering the fields of ecology

and zoology (*Accademia Peloritana, Il naturalista siciliano, Oebalia, Rendiconti del Seminario della Facoltà di Scienze dell'Università di Cagliari, Thalassia Salentina*) and proceedings of Italian scientific societies covering the field of aquatic ecology and zoology (*Associazione Italiana di Oceanografia e Limnologia, Società Italiana di Biologia Marina, Società Italiana di Ecologia, Società Sarda di Scienze Naturali*). The search was restricted to papers published in the last 25 years.

The electronic search was performed through a three-way factorial combination of the following groups of keywords: a) Italy, Italian; b) lagoon, coastal lake, coastal pond, saltmarsh, saltern, brackish; c) benthos, macrobenthos, macroinvertebrate, benthic invertebrates, benthic fauna. Three unpublished reports to which one of the authors directly contributed were also taken into consideration.

The dataset

In total the search produced 205 papers containing taxonomic lists of benthic macroinvertebrates in Italian lagoons; most papers focused on a single lagoon but comparative studies of different lagoons were also collected in this way. The 205 papers were screened according to three main criteria: a) taxonomic resolution (most taxa classified down to the genus or species level); b) taxonomic completeness (the taxonomic list of a lagoon, resulting from one or more papers, cannot be limited to a few selected phyla); c) sampling design (samplings carried out at a seasonal or higher resolution). According to these criteria, 169 papers were selected for the analysis, referring to 26 lagoon ecosystems. A list of the considered ecosystems, with their key structural abiotic features, is presented in Table 1. In the dataset obtained by applying these criteria, the number of articles referring to each of the 26 transitional aquatic ecosystems ranges from 1 (Massaciuccoli coastal lake, Torre Guaceto brackish wetland, Marsala saltern and Piallassa Baiona lagoon) to 22 (Venice lagoon).

For each lagoon, fifteen physiographic and hydrological parameters were collected from the

published papers as well as from published satellite images and the "Tide tables of Italy" (Istituto Idrografico della Marina, Genova 1999). The parameters are surface area, perimeter and sinuosity of the water body, maximum axis and minimum axis, length and width (and length/width ratio) of its seaward outlet(s), mean depth, maximum and minimum tide, tidal range, maximum and minimum salinity and salinity range.

Study sites

The 26 Italian coastal lagoons for which published species lists of benthic macroinvertebrate taxa were collected are distributed among 15 provinces belonging to 7 regions (Fig. 1), with 6 coastal lagoons in the region of Lazio, 5 in the region of Puglia, 4 in the regions of Sicilia and Emilia Romagna, 3 in the regions of Veneto and Toscana and 1 in the region of Friuli Venezia Giulia. In total, the 26 selected lagoons cover a coastal area of 1133.43 km², which represents 69.6% of the overall surface of Italian transitional waters.

Data analysis

The data were organized into two matrices: a presence/absence matrix with benthic macroinvertebrate data organized into 26 columns (representing the selected lagoons) and 944 rows (the macroinvertebrate taxa); and a rectangular matrix with 26 rows (representing the selected lagoons) and 17 columns, two of which describing the benthic macroinvertebrate guilds (taxonomic richness and standard body length of the largest species), nine describing the physiographic characteristics of the water bodies (surface area, perimeter, sinuosity, length of min. axis, length of max. axis, seaward outlet length, outlet width, outlet length/width ratio, average water depth), and three describing the tidal regime (i.e., minimum and maximum tides and tidal range) and the salinity regime (i.e., minimum, maximum and range of salinity).

The taxonomic composition similarity between lagoon pairs was measured using the Jaccard similarity index, as follows:

$$SJ = a/(a+b+c) \times 100$$

where

SJ = Jaccard similarity coefficient,

a = number of taxa shared by two lagoons,

b = number of taxa unique to the first lagoon, and

c = number of taxa unique to the second lagoon.

The species area-relationships in the selected sample of Italian lagoons were analysed utilising the well-known Arrhenius power function (Arrhenius, 1921) as a descriptive model for species accumulation patterns:

$$S = cAZ^z, \text{ or } \log S = \log C + z \log A,$$

where A is the surface area of the lagoon, S is taxonomic richness expressed as total number of species found, and c and z are regression coefficients. Specifically, z indicates the rate of species number increasing with area and c is a fitting coefficient, or estimated number of species per "unit" area.

Multiple regression was used to evaluate the relative influence and the cumulative importance of surface area and other abiotic structural factors to macro-invertebrate taxonomic richness in the studied Italian lagoons

Results

Abiotic niche dimensions and species list

The sample of lagoons considered in this study covers most of the range of variation in Italy. The lagoon list (Table 1a) geographically includes ecosystems from both northern and southern regions, with the exception of Sardinia; in terms of surface area, tidal range, connection with the sea (outlet length and width) and water salinity, the two largest lagoon complexes, and some of the smallest lagoons, micro-tidal and non-tidal ecosystems, as well as oligohaline and polyhaline ecosystems were included. On the basis of the abiotic structural parameters considered, the 26 lagoons are clustered into 3 groups (Figure 1).

Lagoon surface, width and length of outlets and tidal range were the structural abiotic parameters which statistically differentiated the three groups (Table 1b; ordinary t-statistics, $P < 0.05$); specifically, group B, including most

of the Northern Adriatic lagoons and two enclosed sea gulfs, was characterised by the widest outlets, largest surface areas and the greatest tidal ranges.

Overall, 944 taxa were reported to colonise the whole sample of lagoons, including 343 families, 106 orders, 31 classes and 13 phyla. Mollusca, Annelida and Arthropoda were the three most common phyla. A complete taxonomic list is reported as Annex 1.

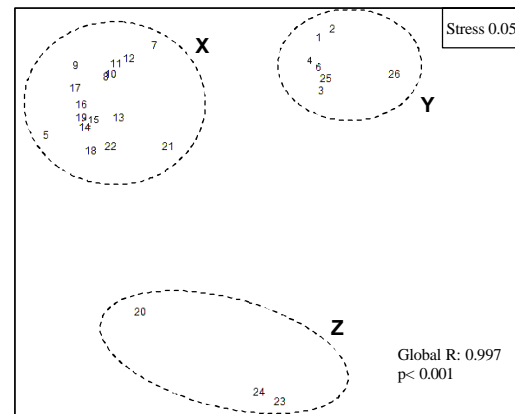


Figure 1 MDS of structural abiotic similarity among lagoon ecosystems. The spatial distribution of clusters of lagoon ecosystems at a significance level $\alpha = 0.05$ is reported. Lagoons are reported with their ID number listed in Table 1

Among the Mollusca, the most common taxa in the Italian lagoons are *Cerastoderma glaucum* (Poiret, 1789), *Abra segmentum* (Récluz, 1843) and *Mytilus galloprovincialis* (Lamarck, 1819) in the Class of Bivalvia, and *Cyclope neritea* (Linné, 1758), *Bittium reticulatum* (da Costa, 1778) and *Hydrobia stagnalis* (Baster, 1765) in the Class of Gastropoda. Among the Annelida, *Polydora ciliate* (Johnston, 1838), *Capitella capitata* (Fabricius, 1780), *Ficopomatus enigmaticus* (Fauvel, 1923), *Nereis diversicolor* (O.F. Müller, 1776), *Perinereis cultrifera* (Grube, 1840) and *Malacoceros fuliginosus* (Claparède, 1868) are the most commonly reported taxa. Finally, among the Arthropoda, the most widespread species are *Gammarus aequicauda* (Martyinov, 1931), *Corophium insidiosum* (Crawford, 1937), *Carcinus aestuarii* (Nardo, 1847), *Microdeutopus gryllotalpa* (Costa, 1853), *Gammarus insensibilis* (Stock, 1966) and *Melita palmata* (Montagu, 1804).

Table 1 – Main structural abiotic features of the 26 lagoons considered for the study (a) and of the 3 groups shown by the MDS (b). The P values of pairwise comparisons of parameter averages between groups are reported for every abiotic feature (Student's t-test)

(a)

ID	Lagoon Name	Abiotic factors								
		A	B	C	D	E	F	G	H	I
1	Grado Marano	160	2	2	485,0	2732,6	0,596	17,05	27,5	15,85
2	Venezia	549	2	1,5	1635,0	8992,5	0,576	26,3	19,4	22,5
3	Sacca Canarin	8,9	1,5	1	365,0	871,6	0,411	14,5	29	14,9
4	Scardovari	38	1,3	1,5	318,0	1011,9	0,411	18,65	29,3	14
5	Nazioni	1	2,1	2	2655,2	8,3	0,411	25	12	16,65
6	Goro	32	1,6	1,5	483,0	1705,1	0,411	21,75	26,3	16,2
7	Comacchio	115	1,2	0,8	441,1	286,7	0,411	23,1	26,2	16
8	Pialassa Baiona	11,8	1,4	0,8	1984,5	132,3	0,411	23	26	16,5
9	Massaciuccoli	7	1,6	3	4276,0	117,2	0,204	8,7	14,6	17,5
10	Orbetello	25,5	2,3	1	1838,0	92,9	0,234	34,35	15,5	17,3
11	Lesina	51	2	0,8	985,0	34,0	0,156	22,5	23	16,5
12	Varano	64	1,2	4	450,1	30,0	0,156	24,86	26,2	19,15
13	Fogliano	4	1,8	0,9	356,0	57,0	0,261	33	30	20
14	Monaci	0,95	1	0,8	818,4	27,3	0,261	27,5	21	19
15	Caprolace	2,3	1	1	974,0	23,6	0,261	41,5	17	20
16	Sabaudia	3,7	3,9	4	980,0	15,2	0,261	22,25	21,5	16,2
17	Fondi	3,9	3,9	9	2349,5	76,9	0,261	20	14	19
18	Lungo	0,47	1,3	4	213,6	17,1	0,261	20	26	20,5
19	Fusaro	1	1,2	3	630,3	39,4	0,246	37,15	8,7	18,65
20	Torre Guaceto	1,2	1,6	0,4	10,0	0,4	0,195	19	28	16
21	Acquatina	0,45	2,94	1	66,8	267,1	0,195	25	30	18
22	Alimini	1,37	2,29	1,5	146,7	19,6	0,195	29	22	19
23	Oliveri-Tindari	0,19	2,7	3	0,0	0,0	0,124	25,5	21	21,15
24	Saline di Marsala	0,89	1,4	0,6	0,0	0,0	0,156	55	30	21
25	Stagnone Marsala	24	1,8	1	314,0	1794,6	0,156	39,3	12,4	19,77
26	Rada di Augusta	23,5	1,4	14,9	235,0	1512,7	0,187	38,15	0,1	24,77

A= surface area (km²); B= sinuosity; C= mean depth (m); D= length of seaward outlet (m); E= width of seaward outlet (m); F= tidal range (m); G= mean salinity (PSU); H= range of salinity (PSU); I= mean water temperature (°C)

(b)

Group name	Parameter average								
	A	B	C	D	E	F	G	H	I
X	18,34	1,95	2,35	1197,82	77,78	0,26	26,06	20,86	18,12
Y	119,34	1,66	3,34	547,86	2660,14	0,39	25,10	20,57	18,28
Z	0,76	1,90	1,33	3,33	0,13	0,16	33,17	26,33	19,38

	P values								
	A	B	C	D	E	F	G	H	I
X,Y	0,005	0,573	0,766	0,280	0,000	0,025	0,750	0,363	0,899
X,Z	0,126	0,964	0,336	0,000	0,000	0,044	0,440	0,215	0,307
Y,Z	0,003	0,487	0,414	0,000	0,000	0,047	0,446	0,461	0,632

Heterogeneity of macroinvertebrate guilds in lagoon ecosystems

Most of the macroinvertebrate taxa which were found to colonise the sample of 26 Italian lagoons were actually reported for a very restricted number of lagoons. 60.6% of taxa were reported for a single lagoon, and only 5.9% of taxa (i.e., 56 taxa) were recorded for at least 8 lagoons (see Annex 1). These most widespread taxa included 20 species of Annelida, 18 species of Arthropoda and 15 species of Mollusca. In the data-base utilised for

the study, the number of taxa recorded in a fixed number of lagoons was inversely related to the number of lagoons (Figure 2).

Species richness varied by more than one order of magnitude between lagoons. Venice lagoon and the Stagnone di Marsala had the highest taxonomic richness at every level of taxonomic resolution considered in the study (S=285 and S=220 at the lowest level of taxonomic resolution, respectively). On the other hand, Lago Nazioni and Torre Guaceto had the lowest species richness at every level of taxonomic

resolution considered in the study (S= 21 and S=22 at the lowest level of taxonomic resolution, respectively).

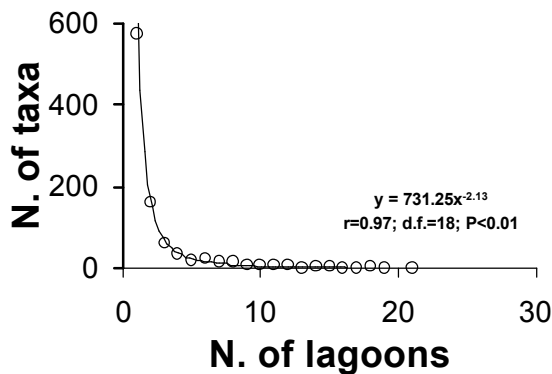


Figure 2 – Width of the distribution of benthic macroinvertebrates within the considered sample of Italian lagoons, as expressed by the number of lagoons colonised by the 944 taxa.

Average similarity in the taxonomic composition of benthic macroinvertebrate guilds was low between lagoons at every level of taxonomic resolution considered, being 0.105 ± 0.008 at the taxon level, 0.217 ± 0.013 at the family level and 0.346 ± 0.016 at the order level. Average similarity between lagoon pairs ranged from 0 to 0.345 at the taxon level, being highest for the spatially neighbouring Fogliano and Monaci lagoons; it ranged from 0 to 0.55 at the family level, being highest for the spatially neighbouring Goro and Sacca del Canarin lagoons, and from 0 to 0.69 at the order level, being highest again for the Goro and Sacca del Canarin lagoons. Taxonomic similarity linearly increased when species composition was progressively restricted to species/taxa with increasingly wider distribution (i.e., removing progressively the species/taxa occurring in an increasingly higher number of lagoons, from 1 to eighteen) (Figure 3a). However, even when almost 95% of species were removed, considering only those species occurring in at least 8 lagoon ecosystems, average similarity in the taxonomic composition of benthic macroinvertebrates among lagoons was still lower than 30% (Figure 3a; $J=0.26 \pm 0.014$). The removal of the rarest species had the most significant effect on taxonomic similarity among lagoons (Figure 3b); however, highly

significant effects were also observed at the thresholds of species occurring in at least 10, 12 and 15 lagoons (black dots in Figure 3b).

Determinants of macro-invertebrate guild heterogeneity

A significant component of the variability of both species richness and taxonomic similarity among lagoons was found to be related to some key physiographic, hydrological and physical-chemical factors.

Outlet width and surface area of coastal lagoons were the only two structural factors considered in the study to which species richness was directly related. The species-area relationship had a slope of 0.18 and explained more than 25% of variability in species richness among the considered lagoons (Figure 4). At the multivariate level, the integration of either outlet width or surface area with average water salinity explained respectively 70% and 48% of species richness variability among lagoons.

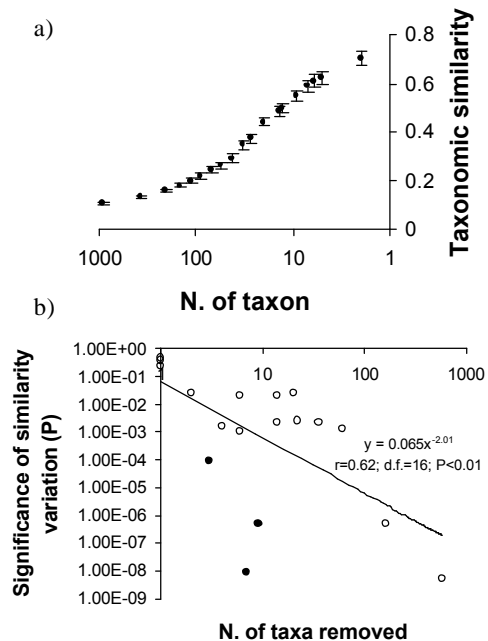


Figure 3 – (a) Relationship between taxonomic similarity and number of taxa. Error bars represent \pm SD of mean. (b) Relationship between significance of taxonomic similarity variation and number of taxa removed.

Distance between lagoons and average water salinity were the two factors with which taxonomic dissimilarity of macroinvertebrate species

composition at every level of taxonomic resolution and at every threshold of species spatial niche (as quantified by the number of lagoons colonised) showed the strongest and most consistent relationships (Figure 5). At the multivariate level, four factors (distance between lagoons, surface area, water salinity and water depth) were the most important factors affecting dissimilarity between taxonomic composition of benthic

macroinvertebrates at every level or condition considered (Table 2). When a threshold is imposed on the spatial niche of a species, hydrodynamic factors, such as outlet length and width and tidal range also had statistical relevance (Table 2). The variance explained by the significant factors listed in Table 2 range from 21 %, when order level was considered, to 44 %, when taxa occurring in at least 15 lagoons were considered.

Table 2 Multiple regression analysis of the relationship between structural abiotic characteristics of the considered lagoons and taxonomic composition of benthic macro-invertebrate guilds. Dissimilarity between lagoons in the two sets of data were compared for the different levels of taxonomic resolution and for the taxa occurring in a number of lagoons larger than some threshold level (taxa=all taxa considered; T12=only taxa occurring in at least 12 lagoons; T15= only taxa occurring in at least 15 lagoons). Beta values and significance levels are also shown (Stepwise multiple regression; ***= P<0.001; **= P<0.01).

	1	2	3	4	5	6	7
taxa	0,44 ***	0,22 ***	-0,2 ***	0,11 **			
family	0,32 ***	0,18 ***	-0,25 ***	0,17 ***			
order	0,23 ***	0,17 **	-0,19 ***	0,15 **			
T12	0,44 ***		-0,29 ***	0,17 **	-0,25 ***		
T15	0,59 ***	0,1 **	-0,23 ***	0,11 **	-0,32 ***	0,14 **	-0,25 ***

1= Distance (km); 2=Mean Salinity (PSU); 3=Surface (Km²); 4=Mean Depth (m); 5=Length out. (m); 6=Width out. (m); 7=Tidal range (m)

Discussion

A central aim of community ecology has been, and remains, to decode patterns of species abundance into mechanisms of guild and community assembly. Here, using lagoons as model ecosystems, we have searched for patterns of species abundance and species association in a sample of Italian lagoons, looking for the influence of niche filtering as a mechanism underpinning community organization. The 26 considered lagoons were likely to be a representative sample of Italian lagoons, accounting for 14.8% of lagoon numbers and 69.6% of lagoon surface area in Italy (Basset and Sabetta, 2005).

The results of this study completely rejected any hypothesis of relative homogeneity of the taxonomic composition of macroinvertebrate guilds in lagoon ecosystems, either due to strong and directional niche filtering and/or to passive diffusion of colonising species.

Taxonomic composition of macroinvertebrate guilds was extremely heterogeneous among lagoons at every level of taxonomic resolution and selection considered.

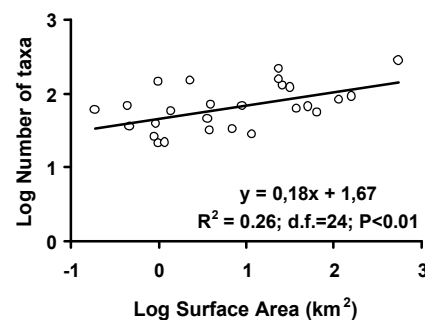


Figure 4 Species- area relationships in lagoon ecosystems.

This was highlighted at the species level, since almost 95% of the 944 species detected overall were recorded in less than 8 lagoons, and at the guild level, as shown by the low similarity between lagoons. Even neighbouring lagoons of similar surface area, which would be expected

to share a common potential species pool, such as Lesina and Varano in the Puglia region or Caprolace and Monaci in the Lazio region, had very different taxonomic composition of macroinvertebrate guilds (Jaccard similarity index; $J = 0.174$ and $J = 0.154$, respectively). In principle, the diversity of macro-invertebrate guilds could result from stochastic, ecological and evolutionary processes on the local (e.g.,

community level) and regional (e.g., meta-community level) scale (Hubbell, 2001), or from dispersal and recruitment limitations on macro-invertebrate taxa (Hurtt & Pacala, 1995), or from the structural heterogeneity of the transitional waters (Basset & Abbiati, 2004) and the consequent selection of macroinvertebrate taxa according to their functional traits and niche requirements (MacArthur, 1970).

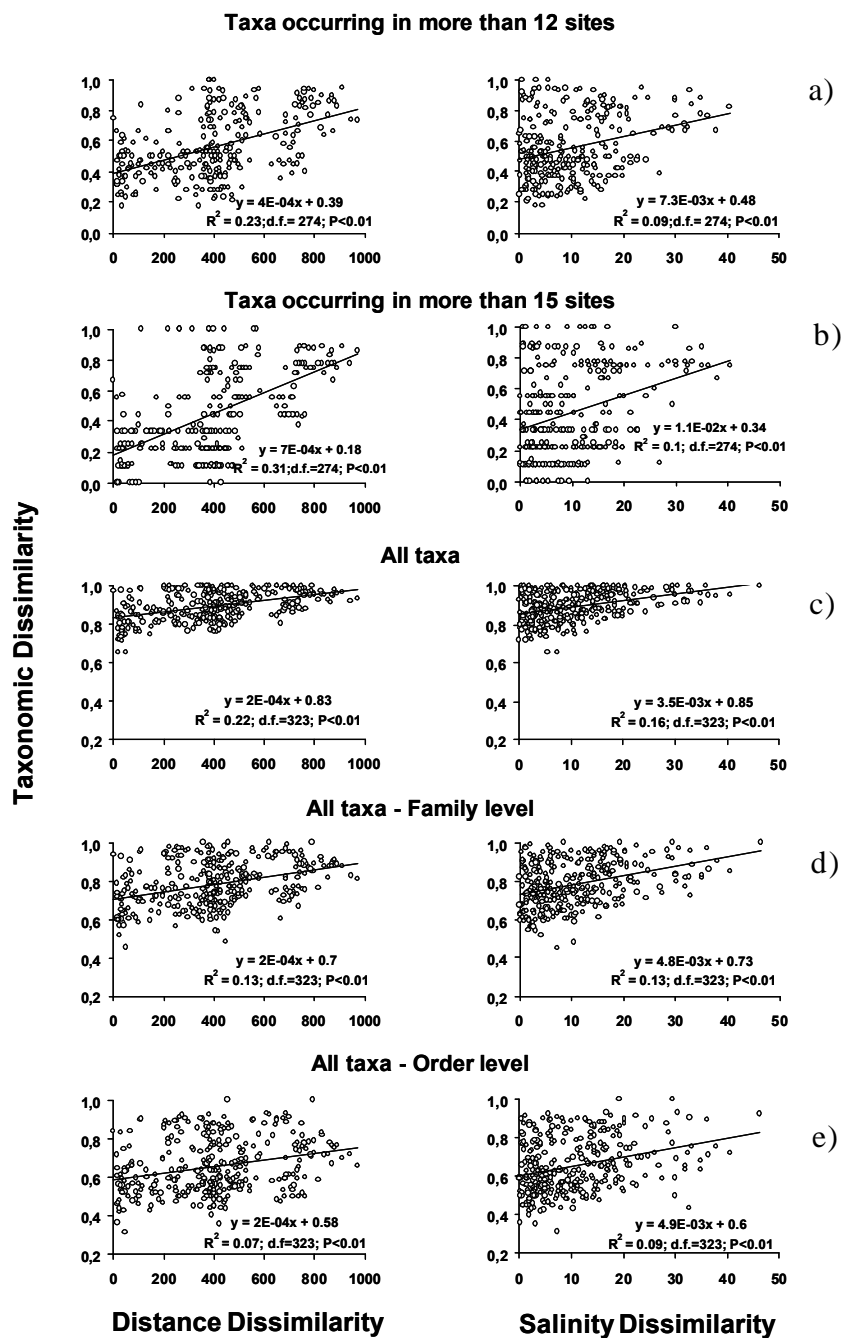


Figure 5 Relationships between taxonomic dissimilarity and distance dissimilarity / salinity dissimilarity for taxa occurring in a number of lagoons considered (a, b) and at each of the different levels of taxonomic resolution (c, d, e).

The results of this study showed that in Mediterranean lagoons, niche filtering of species traits along the main axes of structural heterogeneity of lagoon ecosystems has an important role in the assembly of macroinvertebrate guilds. However, the heterogeneity of macro-invertebrate guilds among the Italian lagoons is much larger than that explained by niche filtering. Therefore, the observed results suggest that other processes, either stochastic, such as diffusion and colonisation, or deterministic, such as competitive selection, or an integration of stochastic and deterministic processes in a competitive lottery must have an important effect on niche filtering in the assembly of benthic macro-invertebrate guilds.

The deterministic influence of some niche dimensions of lagoon ecosystems, such as surface area, water salinity, outlet width and length and water depth, on taxonomic abundance and taxa distribution among lagoons of benthic macro-invertebrates supports the role of niche filtering. Within and among habitats, structural heterogeneity is a common feature of lagoons and coastal lakes, which are ecotones between terrestrial, freshwater and marine ecosystems (e.g., Basset and Abbiati, 2004), whose relative influence varies over time and determines characteristic scales of temporal variability inside transitional aquatic ecosystems (Comin *et al.*, 2004). The observation of significant co-variations of taxonomic richness and taxonomic composition of benthic macro-invertebrates along gradients of surface area, water salinity, outlet width and length and water depth, agree with various classifications already proposed to account for the heterogeneity of transitional Mediterranean waters, based on geomorphology (Kjerfve, 1994), salinity (Battaglia, 1959), degree of confinement (Guelorget and Perthuisot, 1983; Guelorget *et al.*, 1983) and physiographic characteristics, such as surface area and outlet length (Basset *et al.*, 2006). Physiographic characteristics have recently been proposed as major factors determining lagoon type across a very large geographical range from the Mediterranean (Basset *et al.*, 2005) to French

Polynesia (Andrefouet *et al.*, 2001). Consequently, surface area, water salinity, and outlet width and length, which are likely to be descriptors of water exchange and confinement of the lagoon ecosystems, can actually be considered the key limiting, dimensions defining the environmental niche space for benthic macroinvertebrates in lagoon ecosystems. Physiographic and hydrological differences among lagoons set different environmental niche conditions, within which there is ground for niche partitioning among species. Niche differences among species with respect to the physical environment could potentially account for the heterogeneity observed in the taxonomic composition of macro-invertebrate guilds in the 26 Italian lagoons considered, particularly as regards species richness. It is supported by the observation of significant species/area relationships, which have already been demonstrated for lagoon ecosystems (Sabetta *et al.*, 2007). Species/area relationships in lagoon ecosystems are held to be consistent with a deterministic integration of the capacity rule (*sensu* Brown, 1981) set by energy availability, according to the More Individual Hypothesis (MIH, Wright, 1983), and the allocation rule arising from species interactions and niche partitioning (Sabetta *et al.*, 2007).

On the other hand, while up to 75% of taxonomic richness variability among Italian lagoons was explained by outlet width, surface area and average salinity of Italian lagoons, only 44% of the heterogeneity in taxonomic composition was explained. Moreover, distance between lagoons was the most important source of variation of taxonomic composition, even though the above-mentioned structural niche dimensions were also significant sources of variation. Observations of exponential decline in taxonomic similarity with increasing geographic distance are common for many different guilds, including fossil plant communities (Enquist *et al.*, 2002), different terrestrial guilds of the Canary Islands (Fernandes-Palacios and Andersson, 1993) and aquatic parasites (Poulin, 2003); in all cases, dispersal was considered a main factor

determining the observed patterns of taxonomic similarity decline with increasing geographic distance. Therefore, dispersal is likely to be influential in the assembly of macroinvertebrate guilds in the studied Italian lagoons. However, the patterns of taxonomic composition similarity among lagoons do not appear to be accounted for completely by potential limitations on the dispersal and recruitment of macro-invertebrate taxa. Indeed, even though neighbouring lagoons, which would be expected to share common hydrology and recruitment from marine and freshwater environments, tend to have more similar taxonomic composition than lagoons which are geographically distant, this similarity is in any case very low, even when comparing neighbouring lagoons of similar surface area, such as Lesina and Varano or Caprolace and Monaci. Dispersal and recruitment limitation could explain the meta-community level heterogeneity and could have a role in the geographical clustering of Italian lagoons (Sabetta *et al.*, 2004), but they do not seem to account for the variations observed at a smaller spatial geographical scale. Therefore, the observed heterogeneity of macroinvertebrate guilds supports the view that some complementarities among dispersal and recruitment, differences in the freshwater and marine fluxes of both abiotic components among lagoons, and directional or neutral (He, 2005) species interactions have determined over time such a large gradient of environmental conditions that each lagoon has its own specific features, implying an individualistic approach to lagoon ecology.

In conclusion, the observed results exclude any hypothesis of large scale homogeneity of macro-invertebrate guilds of Mediterranean lagoons, due to expected strong filtering selection and dispersal. Moreover, both niche filtering and dispersal and recruitment were found to have an important role in the assembly of macro-invertebrate guilds, even though the presence of some unexplained variations suggest species interaction at the local level.

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Phylum	Taxon	N. sites	Phylum	Taxon	N. sites	Phylum	Taxon	N. sites
Mollusca	<i>Rissoa paradoxa</i>	1	Bryozoa	<i>Valkeria vva</i>	1	Porifera	<i>Toposentia genitrix</i>	1
Mollusca	<i>Rissoa pulchella</i>	1	Mollusca	<i>Tapes rhomboides</i>	1	Arthropoda	<i>Heterotanais oerstedii</i>	1
Mollusca	<i>Rissoa similis</i>	1	Mollusca	<i>Venerupis sp.</i>	1	Arthropoda	<i>Echinogammarus pungentoides</i>	1
Mollusca	<i>Rissoella opalina</i>	1	Porifera	<i>Aplysina aerophoba</i>	1	Arthropoda	<i>Gammarus crinicornis</i>	1
Nematoda	<i>Sabatieria pulchra</i>	1	Porifera	<i>Verongia sp.</i>	1	Arthropoda	<i>Jassa sp.</i>	1
Anellida	<i>Sabella sp.</i>	1	Arthropoda	<i>Veruca stroemia</i>	1	Arthropoda	<i>Liocarcinus bolivari</i>	1
Anellida	<i>Sabellides octocirrata</i>	1	Arthropoda	<i>Xestoleberis aurantia</i>	1	Tunicata	<i>Phallusia ingeria</i>	1
Cnidaria	<i>Sarsia sp.</i>	1	Anellida	<i>Orbinia foetida</i>	1	Arthropoda	<i>Janopsis sp.</i>	1
Bryozoa	<i>Schizomavella auriculata</i>	1	Mollusca	<i>Diplodonta rotundata</i>	1	Arthropoda	<i>Microdeutopus anomalous</i>	1
Bryozoa	<i>Schizoporella longirostris</i>	1	Anellida	<i>Eunice torquata</i>	1	Arthropoda	<i>Ampithoe sp.</i>	1
Bryozoa	<i>Schizoporella sp.</i>	1	Arthropoda	<i>Jassa falcata</i>	1	Cnidaria	<i>Obelia sp.</i>	1
Anellida	<i>Scaloria typica</i>	1	Mollusca	<i>Odosstomia conoidea</i>	1	Cnidaria	<i>Cordylophora sp.</i>	1
Anellida	<i>Serpula sp.</i>	1	Echinodermata	<i>Ophiactis virens</i>	1	Mollusca	<i>Xenostobus sp.</i>	1
Bryozoa	<i>Sertella couchii</i>	1	Mollusca	<i>Paludinella littorina</i>	1	Anellida	<i>Polydora ligni</i>	1
Cnidaria	<i>Sertularella ellisi</i>	1	Arthropoda	<i>Parapseudes latifrons</i>	1	Anellida	<i>Marephya sp.</i>	1
Cnidaria	<i>Sertularia nemusilla</i>	1	Bryozoa	<i>Parasmitina sp.</i>	1	Arthropoda	<i>Sphaeroma sp.</i>	1
Mollusca	<i>Setia semistriata</i>	1	Mollusca	<i>Pirina nobilis</i>	1	Mollusca	<i>Abra sp.</i>	1
Mollusca	<i>Sinezona cingulata</i>	1	Mollusca	<i>Polycera dubia</i>	1	Mollusca	<i>Teredo navalis</i>	1
Arthropoda	<i>Sirrus zariaeivi</i>	1	Bryozoa	<i>Schizobrachiella sanguinea</i>	1	Tunicata	<i>Didemnum sp.</i>	1
Mollusca	<i>Salpa marginatus</i>	1	Bryozoa	<i>Smittoides reticulata</i>	1	Arthropoda	<i>Gnathia sp.</i>	1
Anellida	<i>Sphaerosyllis hystrix</i>	1	Bryozoa	<i>Watersipora subovoidea</i>	1	Mollusca	<i>Haminoea sp.</i>	1
Anellida	<i>Janua corrugatus</i>	1	Arthropoda	<i>Xantho incisus</i>	1	Mollusca	<i>Bitium latreillii</i>	1
Porifera	<i>Spongia officinalis</i>	1	Mollusca	<i>Diodora graeca</i>	1	Mollusca	<i>Rissoella globularis</i>	1
Porifera	<i>Spongia virgulosa</i>	1	Arthropoda	<i>Elasmopus affinis</i>	1	Mollusca	<i>Rudolphoseia turriculata</i>	1
Arthropoda	<i>Stenoboe valida</i>	1	Arthropoda	<i>Ammothella longipes</i>	1	Mollusca	<i>Runcina sp.</i>	1
Arthropoda	<i>Stenoboe tergestina</i>	1	Arthropoda	<i>Ischnura elegans</i>	1	Mollusca	<i>Calliostoma laugierii</i>	1
Anellida	<i>Sthenelais boa</i>	1	Arthropoda	<i>Cercion lindeli</i>	1	Mollusca	<i>Mansella costulata</i>	1
Porifera	<i>Sycon ciliatum</i>	1	Arthropoda	<i>Hoplodonta sp.</i>	1	Arthropoda	<i>Anseudes sp.</i>	1
Porifera	<i>Sycon raphanus</i>	1	Arthropoda	<i>Cloaca sp.</i>	1	Arthropoda	<i>Parasynsira helleri</i>	1
Anellida	<i>Syllides edentula</i>	1	Arthropoda	<i>Gerris sp.</i>	1	Arthropoda	<i>Leucon mediterraneus</i>	1
Anellida	<i>Syllis cirropunctata</i>	1	Arthropoda	<i>Notonecta glauca</i>	1	Porifera	<i>Siphonocalina coriacea</i>	1
Mollusca	<i>Tellina fabula</i>	1	Arthropoda	<i>Plea minutissima</i>	1	Mollusca	<i>Setia amabilis</i>	1
Mollusca	<i>Tellina incarnata</i>	1	Arthropoda	<i>Naucoris cimicoides</i>	1	Mollusca	<i>Alvania mamillata</i>	1
Mollusca	<i>Tellina planata</i>	1	Arthropoda	<i>Aeschna mista</i>	1	Mollusca	<i>Pusillina sp.</i>	1
Mollusca	<i>Tellina pulchella</i>	1	Arthropoda	<i>Lentocerus fineiformis</i>	1	Bryozoa	<i>Beania robusta</i>	1
Nematoda	<i>Terschellingia communis</i>	1	Arthropoda	<i>Aeravlea sexmaculata</i>	1	Anellida	<i>Pseudoleiocapitella fauveli</i>	1
Nematoda	<i>Terschellingia longicaudata</i>	1	Arthropoda	<i>Argyroseta caudata</i>	1	Anellida	<i>Cirratulus filiformis</i>	1
Mollusca	<i>Thais haemastoma</i>	1	Arthropoda	<i>Corixa affinis</i>	1	Anellida	<i>Brania pusilla</i>	1
Mollusca	<i>Thracia carbuloides</i>	1	Arthropoda	<i>Smptetrum sp.</i>	1	Anellida	<i>Marephya bellii</i>	1
Mollusca	<i>Thyasira flexuosa</i>	1	Arthropoda	<i>Chaoborus plumicornis</i>	1	Mollusca	<i>Bitismella sp.</i>	1
Arthropoda	<i>Titanethes albus</i>	1	Bryozoa	<i>Chelostomata anasca</i>	1	Mollusca	<i>Retusa sp.</i>	1
Mollusca	<i>Turbonilla delicata</i>	1	Bryozoa	<i>Chelostomata ascanphora</i>	1	Platyhelminthes	<i>Syriacus nillidum</i>	1
Mollusca	<i>Turbonilla lactea</i>	1	Bryozoa	<i>Tubulipora flabellaris</i>	1	Arthropoda	<i>Eriphia spinifrons</i>	1
Mollusca	<i>Turbonilla obliquata</i>	1	Mollusca	<i>Gibbula richardi</i>	1	Arthropoda	<i>Callinassa candida</i>	1
Mollusca	<i>Turbonilla striatula</i>	1	Echinodermata	<i>Holothuria bolii</i>	1	Arthropoda	<i>Saccalina sp.</i>	1
Mollusca	<i>Turritella turbona</i>	1	Anellida	<i>Sireblosio dekhuzeni</i>	1			