# Spatial and temporal variation of coastal mainland vs. insular amphipod assemblages on *Posidonia oceanica* meadows

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**Abstract** The vagile fauna associated with *Posidonia* oceanica meadows is well studied due to the paramount importance of this Mediterranean habitat, but amphipod assemblages show a paucity of information despite the fact they form a relevant component of seagrass systems and associated food webs. This study analyzed the variability of amphipod assemblages in P. oceanica meadows from mainland vs. insular coastal areas in the central Tyrrhenian Sea during two consecutive summer seasons. Our results showed different spatial and temporal patterns of amphipod assemblages from mainland vs. insular coastal meadows, with the latter characterized by a significant variability across time with respect to the more steady composition shown by the mainland sites. Spatial and temporal heterogeneity is due to fluctuating abundances of a small number of species. Complex mechanisms seem to be involved in generating such heterogeneity, including differences in habitat features, factors related to natural demographic oscillations and co-occurring niche- and dispersal-based processes.

**Keywords** Tyrrhenian Sea · Seagrass · Amphipods · Species distribution · Species diversity · Geographic distance

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## Introduction

Patterns of species distribution and co-existence within ecological communities are usually thought to be largely dependent on the filtering effect of the environment, the degree of resource partitioning and species dispersal abilities (Macarthur and Levins 1967; Gravel et al. 2011). However, recent findings demonstrate how communities are structured by a combination of processes acting at different spatial and temporal scales, thus driving attention on both the geographic and temporal scale of variation (Holyoak et al. 2005; Cavender-Bares et al. 2009; Moritz et al. 2013). Studies taking into account the relative role of spatial and temporal processes in determining community structures are, therefore, needed to better understand patterns of biodiversity and ecosystem functioning (Anderson and Gribble 1998).

The endemic Posidonia oceanica (L.) Delile is the dominant seagrass in the Mediterranean Sea, where it forms extensive meadows in the sub-littoral zone and where it is a widely used biological indicator due to its phenological responses to different types of disturbance (Pergent-Martini 1998; Lopez et al. 2011; Richir and Gobert 2014). P. oceanica sustains highly productive coastal ecosystems (Boudouresque et al. 2006; Montefalcone et al. 2009). The leaf canopy and the network of rhizomes and roots stabilize the sediment and reduce irradiance, producing an array of microhabitats supporting high biodiversity. In addition, its threedimensional structure creates hiding places to avoid predation, and hosts a number of preys as well (Pranovi et al. 2000; Nakamura and Sano 2005). These characteristics make P. oceanica a priority habitat in the Mediterranean Sea (Habitats Directive 92/43/EEC), able to define much of the structure of local communities. It influences indeed the distribution of macrozoobenthic organisms, including amphipod crustaceans that are an important component of the P. oceanica-



associated fauna (Attrill et al. 2000; Sànchez-Jerez et al. 2000; Como et al. 2008; González et al. 2008; Personnic et al. 2014). The variety of available microhabitats allows amphipods to reach a high level of diversity in the meadows in terms of both abundance and species richness (Gambi et al. 1992; Zakhama-Sraieb et al. 2006). Furthermore, they constitute an important link in trophic webs from producers to higher consumers, playing a crucial role both in the recycling of dead organic matter and as trophic resources for fish populations (Carrasco and Arcos 1984; Zakhama-Sraieb et al. 2011).

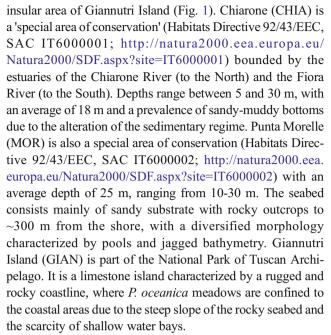
Species richness, abundance and distribution of invertebrate fauna in seagrasses are intimately linked to specific attributes of the meadows, especially in P. oceanica where the functional compartments populated by amphipods are strongly influenced by the spatial heterogeneity of meadows (Stoner 1980; Parker et al. 2001). Some studies have been recently carried out with the aim of clarifying the relationship between seagrass and amphipods in P. oceanica under different levels of protection and at different spatial scales (Sturaro et al. 2014). This evidenced complex interactive effects of protection levels, amphipods ecological traits and, to a minor extent, the phenological and lepidocronological features of the meadows. However, the extent to which spatial features may have a direct or indirect control on amphipod assemblages still remains partially unexplored, although it may provide valuable information on the underlying mechanisms explaining the complex patterns of association with seagrasses (Sturaro et al. 2015).

In this work, we analyzed the spatial and temporal variability of amphipod assemblages in *P. oceanica* meadows from mainland *vs.* insular coastal areas in the central Tyrrhenian Sea. Three sampling localities, known to have different biotic (e.g., seagrass meadows structure) and abiotic characteristics (e.g., substrate composition, human disturbance; Paganelli et al. 2013), were chosen at different spatial scales aimed at maximizing the effects of space and environment on community composition. Analyses were carried out to test for differences in community composition within and between localities in two consecutive summer seasons. Our results provide useful information on amphipod assemblages in the central Tyrrhenian Sea, highlighting the possible role of direct and indirect effects of space in the patterns of amphipod distribution within seagrasses.

### Materials and methods

#### Study area

Organisms were collected in *P. oceanica* meadows from three sampling localities of the central Tyrrhenian Sea: two were located along the mainland coastal area of Montalto di Castro (Chiarone and Punta Morelle) and one was located in the



Sampling was carried out in August 2012 and 2013 at a depth of 15-20 m, as depth gradient and correlated factors are known to play a crucial role in defining amphipod assemblages (Scipione et al. 1983; Mazzella et al. 1989). Each sample was collected by scuba diving in a 40×40 cm quadrant using an airlift sampler (500-um mesh size), originally described in Bussers et al. (1983). Three sampling sites for each locality, delimiting a total surface of 0.48 m<sup>2</sup>, were sucked up by the air-lift during 2 minutes of constant airflow. Samples were sieved on a 500-um mesh and fixed in a 70-% ethanol solution as soon as possible and then sorted under a dissecting microscope. Amphipods were separated, identified to the species level and then counted. The identification was carried out using the taxonomic key of Bellan-Santini et al. (1982, 1989, 1993, 1998), with taxa nomenclature following the World Register of Marine Species (WoRMS 2014; http://www.marinespecies.org).

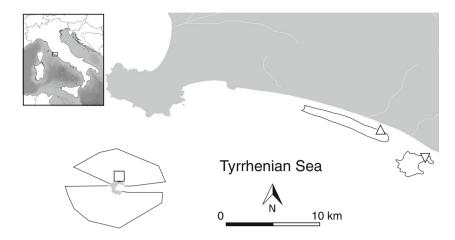
### Statistical analyses

Mean values ( $\pm$  standard deviation (SD)) of total abundance (n), species richness (S), Shannon-Wiener diversity index (H) and Pielou's evenness (J) were measured for each locality. Two-way ANOVA was used to test for differences of these indices with respect to the factors localities (L, fixed factor with three levels corresponding to each locality) and years (Y, fixed and orthogonal to L, with two levels corresponding to different summer seasons). Prior to analysis, homogeneity of variances was checked using Levene's test and transformations were applied when necessary.

The structure of amphipod assemblages between localities and sampling dates was compared by a two-way permutational multi-variate analysis of variance (PERMANOVA, Anderson 2001), factors years (*Y*, two levels fixed) and localities (*L*,



Fig. 1 Study area and sampling localities. *Square*, *upwards* and *downwards triangles* are for Giannutri Island (GIAN), Chiarone (CHIA) and Punta Morelle (MOR), respectively. *Solid lines* indicate the boundaries of protected areas



three levels fixed and orthogonal) with 9999 permutations. A non-metric multidimensional scaling analysis (nMDS) was performed to display similarities in amphipod assemblages and the Kruskal stress value tested the goodness of fit in the nMDS ordination diagram. A stress value<0.2 is considered to provide a reliable ordination. Analyses were based on the Bray-Curtis similarity matrices calculated from the square root transformation of abundance data to overcome the contribution from the rarest species. A similarity percentage analysis (SIMPER) was used to identify species that most contributed to dissimilarity among localities in each year and within each locality between years.

# Results

Two-way ANOVA showed no significant differences between localities and sampling seasons in terms of species richness (Fig. 2 and Table 1), while a significant difference in terms of

total abundances was observed between localities (Fig. 2 and Table 1). Neither the diversity (H') nor the evenness (J) showed significant differences between localities and years (Table 1), although GIAN exhibited substantially higher values in the second sampling season (Fig. 2).

The samples collected in summer 2012 provided a total of 569 individuals, belonging to 37 species, 29 genera and 20 families (Table 2). The most abundant species were *Caprella acanthifera* (99 individuals), *Phtisica marina* (73 individuals) and *Apolochus neapolitanus* (69 individuals). The number of species (*S*) showed similar values across all sampling localities (Fig. 2), while the number of individuals (*n*) showed the highest value at GIAN, followed by CHIA and MOR (Fig. 2). CHIA showed the highest value of Shannon diversity (*H*'), while GIAN was characterized by the lowest values of *H*' and *J*, probably due to the presence of a few species (e.g., *C. acanthifera*, *P. marina* and *A. neapolitanus*) with a high number of individuals (Table 2).

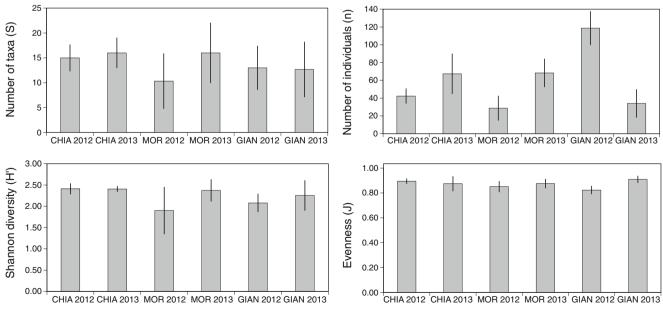


Fig. 2 Average values of diversity indices calculated for the different localities in the two sampling periods



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**Table 1** Results of the two-factor ANOVA for species richness (S), total abundance (n), Shannon-Wiener diversity (H) and Pielou's evenness (J). L and Y stand for factors localities and years, respectively.

		S		n		H'		J	
Factors	df	F	p	F	p	F	p	F	p
L	2	0.577	0.576	4.811	0.029	1.460	0.271	0.573	0.578
Y	1	0.914	0.358	0.754	0.402	2.271	0.158	2.911	0.114
$L \times Y$	2	0.679	0.526	26.09	< 0.001	0.952	0.413	3.068	0.084

In the summer of 2013, the overall number of individuals was 509, belonging to 46 species, sub-divided in 34 genera and 23 families (Table 2). *Apolochus picadurus* (63 individuals), *Gitana sarsi* (59 individuals) and *A. neapolitanus* (57 individuals) were the most abundant species. As in the previous year, the three localities showed quite similar numbers of species, although GIAN was characterized by a substantial decrease in terms of total abundance. Shannon diversity and evenness were quite similar in all sampled localities, although GIAN showed a higher evenness than in 2012 (Fig. 2).

The nMDS ordination plots evidenced a temporal heterogeneity between assemblages in different years (Fig. 3). The congruence in the pattern of ordination was confirmed by the two-way PERMANOVA, which showed how the dissimilarity in assemblages was influenced by locality (F=2.617, p<0.01) and years (F=3.499, p<0.01) and interaction terms (F=3.456, p=0.01). Pairwise comparisons showed that GIAN amphipod assemblages were significantly different from those of CHIA and MOR (2012, p<0.025 after Bonferroni correction) or CHIA alone (2013, p<0.023 after Bonferroni correction), whilst CHIA and MOR always showed similar assemblages (p>0.13 in 2012 and 2013, after Bonferroni correction). SIM-PER analysis showed a greater variability in dissimilarity between localities in 2013 (from 47.53 to 64.6) than in 2012 (from 52.86 to 59.92).

Dissimilarities between localities in 2012 were mainly due to *C. acanthifera* and *A. neapolitanus* (Table 3), whilst, in 2013, the dissimilarity observed involved more species: *A. neapolitanus*, *A. picadurus*, *Gammaropsis maculata* and *Microjassa cumbrensis*. Between-years dissimilarity was greater in GIAN than at the CHIA and MOR mainland sites (Table 3), where *C. acanthifera*, *M. cumbrensis* and *A. neapolitanus* accounted for most of the variation, due to their decrease in abundance or even disappearance (Fig. 4).

#### **Discussion**

The amphipod assemblages analyzed in three central Tyrrhenian Sea *P. oceanica* meadows show a relatively high number of species (more than 40 in both years), most of them with low frequency and abundance. Despite the relatively

small sample size, the observed abundances are in agreement with the observations from other Mediterranean seagrass meadows studied at similar depths, in the same period of the year and with the same sampling techniques (Scipione 1998; Zakhama-Sraieb et al. 2011; Sturaro et al. 2014). Our results show different spatial and temporal distribution patterns of amphipods in P. oceanica meadows when considering the assemblages from the mainland (i.e., CHIA and MOR) vs. insular (i.e., GIAN) coastal meadows, the latter being the most differentiated and characterized by a significant variability in time that contrasts with the constant composition shown by the two mainland sites. This pattern is evidenced by the multivariate analysis, while both species diversity and evenness are ineffective in highlighting substantial differences between localities and years. This poor resolution is due to the degree of functional redundancy found in many marine communities where an array of different species may occupy the same functional role, as in amphipod assemblages (Sanchez-Jerez and Ramos-Esplà 1996; Micheli and Halpern 2005; Sturaro et al. 2014).

The pattern of differentiation observed is likely related to geographic distance, which influences the connectivity (i.e., the degree to which a "landscape" facilitates or impedes the movement of genes, individuals and species), recognised as one of the main driving forces in structuring marine communities (Kinlan and Gaines 2003; Cowen et al. 2007). Accordingly, closely located communities are more similar than those located further apart; this so-called 'distance decay effect' (Soininen et al. 2007) is likely amplified by the low dispersal ability of amphipod species lacking in pelagic larval forms (Thomas 1993). This reduces their chance to disperse and colonize distant areas, thus enhancing insularity and the establishment of local self-recruiting populations (Sànchez-Jerez et al. 2000). Moreover, geographic distance has also a role in determining specific characteristics of habitats, so that closer localities are more likely to be environmentally similar and, thus, suitable for a pool of species that may exhibit the same functional responses to common environmental conditions (Meynard et al. 2011). Accordingly, the insular meadow is characterized by a rocky substrate and its differentiation from coastal-mainland localities, having a sandy-muddy bottom with local rocky outcrops, is linked to species whose distribution (both in terms of presence and abundance) is mainly related with hard bottoms (e.g., C. acanthifera; Kroeker et al. 2011). Also, the closer mainland study localities (i.e., CHIA, MOR) are seagrass meadows equally exposed to the effects of human activities. They are both characterized by the same amount of organic load given by the external input of two main rivers, the Chiarone to the north and the Fiora to the south, influencing both the sedimentological regime and water turbidity (Paganelli et al. 2013). This can indirectly influence community composition (Ben Brahim et al. 2010), by altering



**Table 2** Abundance of amphipod species (total number of individuals per 0.48 m²) identified in *P. oceanica* meadows from different localities and years. *S*=number of species; *n*=total number of individuals; *H'*=Shannon's diversity index; *J*=Pielou's evenness index

		2012			2013		
Family	Species	CHIA	MOR	GIAN	CHIA	MOR	GIAN
Ampeliscidae	Ampelisca dalmatina Karaman, 1975	0	0	0	0	0	1
•	Ampelisca diadema (Costa, 1853)	1	0	0	1	0	0
	Ampelisca serraticaudata Chevreux, 1888	0	0	0	0	1	0
	Ampelisca spinipes Boeck, 1861	0	0	0	0	3	0
	Ampelisca tenuicornis Liljeborg, 1855	0	0	0	1	0	0
	Ampelisca unidentata Schellenberg, 1936	0	0	0	0	1	0
Amphilochidae	Amphilochus brunneus Della Valle, 1893	0	2	0	2	0	0
•	Apolochus neapolitanus Della Valle, 1893	7	0	62	5	44	8
	Apolochus picadurus J. L. Barnard, 1962	16	13	32	20	37	6
	Gitana sarsi Boeck, 1871	17	5	9	27	16	16
Atylidae	Atylus massiliensis Bellan-Santini, 1975	0	0	1	1	0	0
Cressidae	Cressa cristata Myers, 1969	0	3	1	0	0	1
	Cressa mediterranea Ruffo, 1979	0	2	4	0	2	4
Cyprodeidae	Peltocoxa gibbosa (Schiecke, 1977)	0	0	2	0	0	0
	Peltocoxa mediterranea Schiecke, 1977	2	0	1	3	6	0
Dexaminidae	Dexamine spinosa (Montagu, 1813)	4	3	21	3	5	2
Iphimediidae	Coboldus nitior Krapp-Schickel, 1974	0	0	2	0	0	0
•	Iphimedia minuta G. O. Sars, 1882	0	0	0	13	7	4
	Iphimedia serratipes Ruffo & Schiecke, 1979	1	0	0	0	0	0
Leucothoidae	Leucothoe euryonyx (Walker, 1901)	1	0	0	0	0	0
	Leucothoe spinicarpa (Abildgaard, 1789)	3	1	2	0	0	2
Liljeborgidae	Liljeborgia dellavallei Stebbing, 1906	9	1	2	12	13	4
Lysianassidae	Lysianassa costae (Milne-Edwards, 1830)	1	0	0	0	0	0
	Lysianassina longicornis (Lucas, 1846)	0	0	0	0	1	0
	Orchomene humilis (Costa, 1853)	3	3	1	0	1	1
	Orchomene similis (Chevreux, 1912)	1	2	0	0	5	3
Oedicerotidae	Deflexilodes gibbosus (Chevreux, 1888)	2	0	0	0	0	0
	Deflexilodes subnudus (Norman, 1889)	0	2	0	1	2	0
	Monoculodes carinatus (Bate, 1857)	0	0	0	0	0	1
	Perioculodes aequimanus (Korssman, 1980)	0	0	0	5	0	0
	Perioculodes longimanus longimanus (Bate & Westwood, 1868)	1	0	0	2	0	0
	Synchelidium longidigitatum Ruffo, 1947	0	0	1	1	1	0
Phoxocephalidae	Harpinia crenulata (Boeck, 1871)	0	0	0	1	0	0
1	Metaphoxus fultoni (Scott, 1890)	1	0	0	0	1	0
	Phoxocephalus aquosus Karaman, 1985	1	0	0	2	4	0
Stenothoidae	Stenothoe monoculoides (Montagu, 1815)	0	1	0	0	0	2
Aoridae	Aora spinicornis Afonso, 1976	1	1	22	4	1	0
	Autonoe spiniventris Della Valle, 1893	1	0	0	0	0	0
Ampithoidae	Ampithoe ramondi Audouin, 1826	0	0	0	0	1	0
Calliopiidae	Apherusa chiereghini Giordani-Soika, 1949	14	19	13	9	23	19
Caprellidae	Caprella acanthifera Leach, 1814	0	1	98	0	0	0
	Caprella grandimana (Mayer, 1882)	3	0	0	0	0	0
	Pariambus typicus (Krøyer, 1884)	0	0	0	2	0	0
	Phtisica marina Slabber, 1769	15	20	38	6	13	11
	Pseudoprotella phasma Montagu, 1804	0	0	1	0	0	1
Corophiidae	Leptocheirus guttatus (Grube, 1864)	0	0	0	10	3	0
- г	Leptocheirus pilosus Zaddach, 1844	1	0	0	0	0	0



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Table 2 (continued)

		2012			2013	2013		
Ischyroceridae	Ericthonius punctatus (Bate, 1857)	0	0	0	4	3	1	
	Microjassa cumbrensis (Stebbing & Robertson, 1891)	5	3	39	35	8	0	
	Siphonoecetes (Centraloecetes) dellavallei Stebbing, 1899	0	0	0	0	0	5	
Maeridae	Animoceradocus semiserratus (Bate, 1862)	0	0	0	0	0 1		
Melitidae	Abludomelita gladiosa (Bate, 1862)	0	0	0	0	0	2	
Nuuanuidae	Gammarella fucicola (Leach, 1814)	0	0	0	0	0	6	
Phliantidae	Pereionotus testudo (Montagu, 1808)	0	1	0	0	0	0	
Photidae	Gammaropsis maculata (Johnston, 1828)	0	0	0	28	1	1	
	Gammaropsis palmata (Stebbing & Robertson, 1891)	16	3	4	4	1	0	

the structural properties of *P. oceanica* meadows (Alcoverro et al. 1997; Erftemeijer and Lewis 2006; Castejón-Silvo et al. 2012), as well as by directly impacting the abundance and distribution of specific groups of organisms associated with seagrasses (Blake and Duffy 2010; Korpinen and Westerbom 2010). In other words, the persistence of species sharing common responses to similar environmental conditions should decrease the spatial and temporal variability of local assemblages in coastal mainland meadows.

Although limited in time, our study shows a temporal variability of assemblages in insular meadows, which is probably influenced by factors related to natural demographic oscillations, irregularity in recruitment and variation in predation pressure (Nelson 1979; Sturaro et al. 2015). The geographic position of the meadow studied in Giannutri makes this site more vulnerable in terms of species recruitment when subjected to extreme and unpredictable weather events, likely having an impact on assemblage composition. For example, the recorded species depletion observed in Giannutri could be related to the exceptional storm surge that occurred on the 29th and 30th of October 2013 (so, in between the two sampling seasons), as

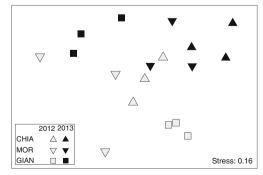
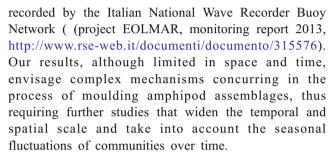


Fig. 3 Non-metric multidimensional scaling ordination (nMDS) based on the Bray-Curtis distance measured on abundance data (three replicates)



The diversity of assemblages in our study area is mainly due to a small number of species with varying abundances. Different species are responsible for the differentiation between coastal mainland vs. insular localities: A. neapolitanus and C. acanthifera in 2012 and M. cumbrensis, G. maculata, A. picadurus and A. neapolitanus in 2013. When comparing temporal data within the same site, different species contribute to the heterogeneity of assemblages for each study site. The assemblages from Giannutri Island appear the most heterogeneous, with most of the differentiation given by a small number of species present with high abundances during the first year of study and almost completely disappearing in the second year, as, for example, C. acanthifera (Fig. 4). This between-years variation in abundance was probably related to complex mechanisms involving not only spatial patterns (e.g., distance from other source populations) and meteorological events but also species-specific features such as differences in recruitment, maturation and reproduction periods. Accordingly, the same species, C. acanthifera, and others such as A. neapolitanus exhibit large demographic fluctuations in the Mediterranean, often related to variability in food resources, natural dynamics or predation pressure (Francour 2000; Leite 2002).

Our results beget questions about the role of co-occurring local (e.g., niche-based) and/or regional (e.g., dispersal-based) processes in the structuring of amphipod assemblages (Leibold et al. 2004; Holyoak et al. 2005). Indeed, the



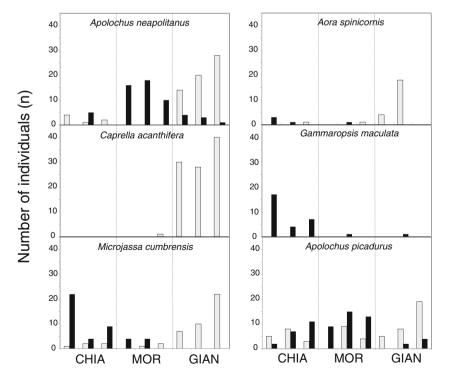
Table 3 SIMPER analysis indicating dissimilarities in amphipod composition between localities and among years

2012			2013			2012/20	013	
	S	Contrib (%)		S	Contrib (%)		S	Contrib (%)
CHIA vs. MOR	G. palmata	8.921	CHIA vs. MOR	A. neapolitanus	10.58	CHIA	G. maculata	10.41
53.49	A.neapolitanus	7.285	47.53	G. maculata	9.227	52.22	I. minuta	7.453
	L. dellavallei	7.159		M.cumbrensis	6.587		M. cumbrensis	6.749
	G. sarsi	6.519		A. chiereghini	5.108		P. marina	4.905
GIAN vs. CHIA	C. acanthifera	18.87	GIAN vs. CHIA	M. cumbrensis	10.12	MOR	A. neapolitanus	14.54
52.86	A.neapolitanus	10.11	64.6	G. maculata	8.02	59.1	A. picadurus	7.598
	M. cumbrensis	7.397		I. minuta	5.01		L. dellavallei	6.895
	A. spinicornis	6.732		A. picadurus	4.986		P.mediterranea	5.471
GIAN vs. MOR	C. acanthifera	18.36	GIAN vs. MOR	A.picadurus	9.425	GIAN	C. acanthifera	17.36
59.92	A.neapolitanus	15.49	53.25	A. neapolitanus	8.442	62.42	M. cumbrensis	10.72
	M. cumbrensis	9.477		P.mediterranea	5.574		A. neapolitanus	8.84
	A. spinicornis	7.038		M. cumbrensis	5.12		A. spinicornis	6.588

relatively temporal stability of assemblages in mainland coastal meadows suggests the possible role for nichebased processes (e.g., species sorting), which allow the coexistence of species sharing functional responses but enables them to differentiate their niche requirements (e.g., microhabitat choice; Logue et al. 2011; Michel et al. 2014). By contrast, species turnover may be involved in the temporal variation of insular assemblages, due to the limited dispersal and the geographic isolation of the meadows (i.e., insularization). Boundaries

between local vs. regional processes in structuring ecological communities are still uncertain (Cottenie 2005; McCauley et al. 2008), varying with the spatial extent and the peculiarity of assemblages. Given their biological features and the high variability over multiple spatial scales (Sturaro et al. 2014, 2015), amphipods from seagrass meadows represent a well-suited tool to test for metacommunity theory and disentangle the role of different processes in determining marine biodiversity and ecosystem functioning (Personnic et al. 2014).

Fig. 4 Number of sampled individuals primarily contributing to the dissimilarity among localities (CHIA, MOR and GIAN) and years 2012 (*gray*) and 2013 (*black*)





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