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AMPHIPOD ASSEMBLAGES OF *POSIDONIA OCEANICA* MEADOWS: SPACE, TIME AND METACOMMUNITY STRUCTURE

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1. INTRODUCTION AND OBJECTIVES

Posidonia oceanica meadows represent a key ecosystem in the Mediterranean Sea, being a highly productive system able to supply a number of important ecosystem services. They play also an important role in marine food webs, by transferring organic matters from producers to first order consumers, and contribute to the maintenance of marine biodiversity by providing habitat for a large set of organisms that cannot live in unvegetated bottoms, such as vagile invertebrates. Among all, amphipod crustaceans represent an important component of the fauna associated with *P. oceanica* (Gambi et al., 1992). However, their ecology still remains partially unknown, as well as their impact on the functioning of seagrass meadows ecosystems, their feeding preferences and the role of spatial scales and environmental characteristic of habitats on their assemblage structure over time.

The general goal of this study is to deepen the knowledge of amphipod assemblages living on seagrass meadows by checking for their spatial and temporal variability (both on seasonal and annual basis) and the emergence of metacommunity patterns. To achieve this goal, we studied the amphipod assemblages on *P. oceanica* meadows during two consecutive years from three different localities in central Tyrrhenian Sea at increasing spatial distance. To reach this objective, the research was subdivided in three tasks.

1. The first task was aimed at analyzing the spatial and temporal variability of amphipod assemblages in *P. oceanica* meadows from insular *vs*. mainland coastal areas. Diversity and multivariate analyses were used to investigate the role of direct and

indirect effects of space in the patterns of amphipod distribution within seagrasses. To this end, two sampling localities were chosen in close proximity along the northern coasts of Latium (Central Italy), characterized by high anthropogenic disturbance, which is responsible for eutrophication and turbidity of coastal waters (Paganelli et al., 2013). Amphipod assemblages of these two mainland localities were compared with those from Giannutri Island, a Marine Protected Area belonging to the National Park of Tuscan Archipelago. The temporal variability of assemblages in three study localities was also investigated by analyzing their composition across two years (summer 2012 and 2013).

2. The second task aimed at analyzing the structure and yearly seasonal variability of amphipod communities from two localities of Giannutri Island (Punta Secca and Secca di Punta Secca). Diversity and multivariate patterns of assemblages were used to evaluate the role of spatial *vs*. seasonal factors in structuring *P. oceanica* amphipods during one year of sampling. Further analyses were carried out in order to shed light on the number and identity of species influencing the seasonal dynamics. A further contribution of this task was to deepen the knowledge of the benthic fauna of Giannutri Island, which was previously lacking.

3. The third task was aimed at understanding whether and how the amphipods-*Posidonia* system can be considered as a metacommunity. In particular, we tested for the existence of a spatial scale at which patterns of metacommunity structure emerge, and if these scales are conservative in time. The ultimate aim of this task was to provide a rigorous statistical approach able to measure the geographic extent at which regional, dispersal-based processes surpass the local, niche-based ones in explaining the pattern of biodiversity in amphipods-seagrass systems.

Recent findings in conservation biology showed the need to understand patterns of biodiversity in a spatial context, focusing on the dynamic responses of habitat loss at landscape level (i.e. the secondary loss of biodiversity, Cabeza and Moilanen, 2001). Anthropogenic alterations may indeed act at different spatial scales, ranging from local to regional and global, so that a metacommunity perspective becomes fundamental to assess the relative importance of spatial and environmental components in the variability of community assemblages (Heino, 2013).

Peracarid crustaceans are widely used as sensitive indicator of marine environmental alterations (Bellan-Santini, 1980; Conradi et al., 1997), but their responses may be strongly influenced by the spatial heterogeneity of the meadows (Stoner, 1980a, 1980b; Parker et al., 2001), the spatial scale of observations and the fluctuation of the environmental characteristic of habitats over time. We believe that our approach may be useful to test a series of theoretical and conservation issues, providing an insight into the patterns, scales and processes involved in the responses of the amphipods metacommunity to the main structuring processes.

2. BACKGROUND

2.1 *Posidonia oceanica*

The seagrass *Posidonia oceanica* is a marine phanerogam belonging to the group of angiosperm monocotyledons. The genus *Posidonia* includes about 60 species among which the widespread Mediterranean species *P. oceanica*, *Zostera noltii*, *Cymodocea nodosa*, *Halophila stipulacea* and *Nanozostera noltii*. Being a vascular plant *P. oceanica* maintained characteristics similar to those of terrestrial plants, such as the structure differentiated into roots, rhizome (modified stem) and leaves (Fig. 2.1), and sexual reproduction with flowering.

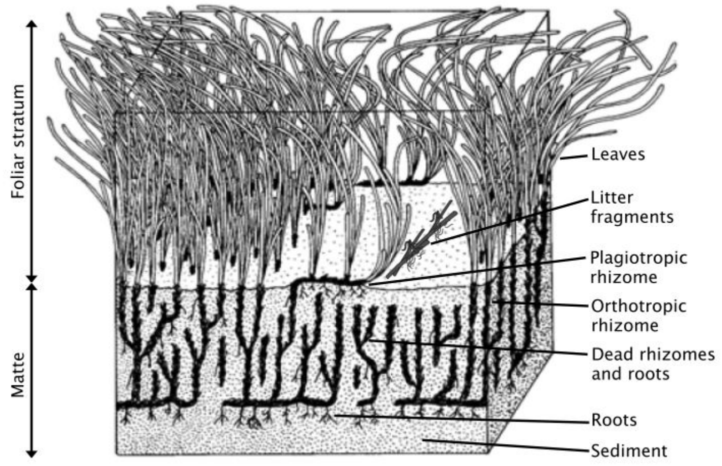


Figure 2.1 - Schematic representation of the structure of a *Posidonia oceanica* meadow).

P. oceanica is the most important seagrass species in the Mediterranean area, where it is almost ubiquitous covering 2% of the seabed and colonizing areas less exposed to hydrodynamism (Garcia and Duarte, 2001; Lipkin et al., 2003; Procaccini et al., 2003). It settles mainly on sandy bottoms, but can also colonize irregular substrates and rocky seabeds at a variable depth between less than 1 m up to a maximum of 40 m. The upper limit depends mainly from the intensity of hydrodynamism, while the lower limit is influenced by both light availability and water transparency (Boudouresque et al., 2006).

Besides its extension, *P. oceanica* meadows represent a key ecosystem and play one of the most important ecological roles in the Mediterranean coastal area, being listed among **priority habitats** (1120*) in the Habitats Directive (92/43/EEC). *P. oceanica* meadows host a high number of species and playing fundamental ecosystem functions, such as providing nursery habitat, refuge from predators and representing a direct or indirect source of food for many species (Fig. 2.2) (Macpherson et al., 1997; Cebriàn and Duarte 2001; Guidetti, 2000).

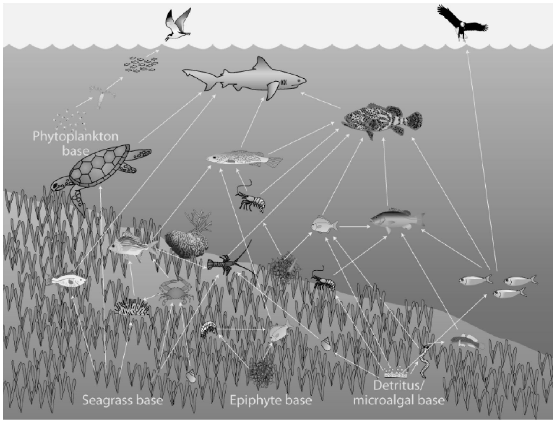
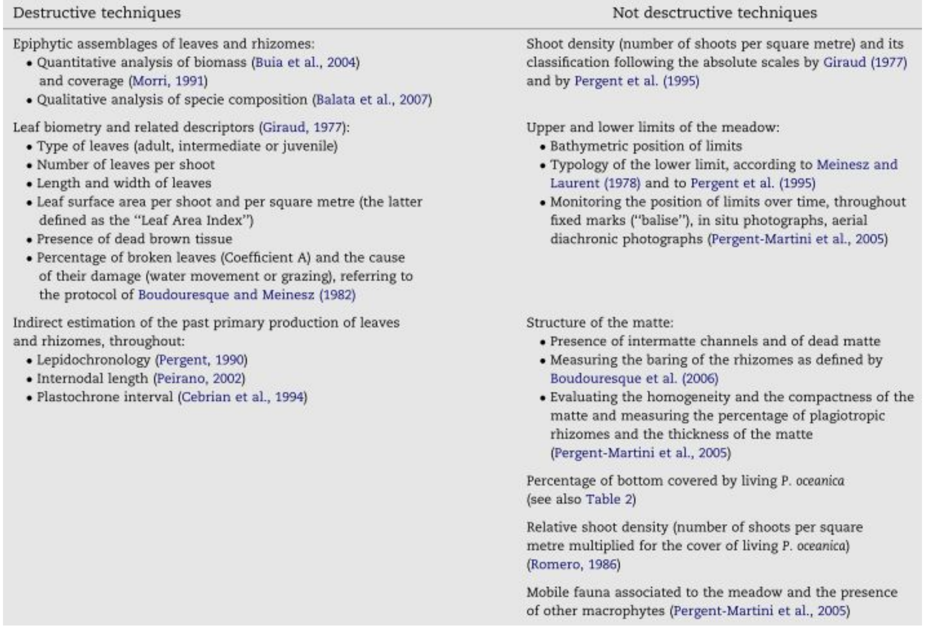


Figure 2.2 - Scheme of a marine trophic web associated with seagrass.

As a consequence, it has a relevant ecological importance as 'foundation species' because it defines much of the structure of local communities by creating locally stable conditions for other species, by modulating and stabilizing fundamental ecosystem processes (Dayton, 1972). *P. oceanica* forms meadows that occur as a continuum of many plants able to mitigate the wave energy, with the leaves favouring the sedimentation of suspended particulates and protecting from coastal erosion. *P. oceanica* plays a key role in the food web due to its ability to maximize the amount of biomass produced with respect to the energy flow, a strategy that allow to enhance the ecosystem's resilience (Boudouresque et al., 2006).

Examining the characteristics of the meadows and associated populations allows to assess the health status of the ecosystem, so that *P. oceanica* has been selected as a bioindicator of Mediterranean coastal waters quality due to its wide distribution and sensitivity to sources of human disturbance. *P. oceanica* is extremely sensitive to various kinds of disturbance, despite it is able to establish stable and long-lived systems under undisturbed conditions (Duarte, 1991; Di Carlo et al., 2007). Under both natural (e.g. Pleistocenic climate changes) and human impacts, the regression of the meadow occurs over both small or large scale, usually affecting the superficial zone of the prairie, more exposed to the pressure exerted by human activity and, therefore, more vulnerable (Pérès and Picard, 1975; Bourcier, 1989; Peraino and Bianchi, 1995; Marbà et al., 1996; Boudouresque et al., 2009). Among the main impacts affecting *P. oceanica* meadows it can be listed the trawling, which destroys the meadows at large scale, all sorts of pollution, including sewage, dumping and oil spills, introduced species and, finally, moorings, dredging and any infrastructure altering the physical characteristics of the environment (Meinesz et al., 1991; Guidetti and Fabiano, 2000; Badalamenti et al., 2006). This latter, in particular, may reduce the hydrodynamic regime, causing an excess of sedimentation that results in a 'choking' of *P. oceanica*. Aquaculture activities can also impact *P. oceanica* meadows (Pusceddu et al., 2007), by increasing the supply of organic material at the bottom, in the adjacent areas and in the water column, reducing water transparency and limiting the photosynthetic capacity of plants with consequent decrease in biomass and density (Pusceddu et al., 2007). A series of different methodologies, listed in Table 2.1, may thus be performed in order to assess the health status of the meadows in Mediterranean area.

Table 2.1 - The analyses on *Posidonia oceanica* most routinely employed by the Mediterranean research laboratories, separated in destructive and not destructive techniques (from Montefalcone, 2009)



Destructive techniques	Not desctructive techniques
Epiphytic assemblages of leaves and rhizomes: • Quantitative analysis of biomass (Buia et al., 2004) and coverage (Morri, 1991) • Qualitative analysis of specie composition (Balata et al., 2007)	Shoot density (number of shoots per square metre) and its classification following the absolute scales by Giraud (1977) and by Pergent et al. (1995)
Leaf biometry and related descriptors (Giraud, 1977): • Type of leaves (adult, intermediate or juvenile) • Number of leaves per shoot • Length and width of leaves • Leaf surface area per shoot and per square metre (the latter defined as the "Leaf Area Index") • Presence of dead brown tissue • Percentage of broken leaves (Coefficient A) and the cause of their damage (water movement or grazing), referring to the protocol of Boudouresque and Meinesz (1982)	Upper and lower limits of the meadow: • Bathymetric position of limits • Typology of the lower limit, according to Meinesz and Laurent (1978) and to Pergent et al. (1995) • Monitoring the position of limits over time, throughout fixed marks ("balise"), in situ photographs, aerial diachronic photographs (Pergent-Martini et al., 2005)
Indirect estimation of the past primary production of leaves and rhizomes, throughout: • Lepidochronology (Pergent, 1990) • Internodal length (Peirano, 2002) • Plastochrone interval (Cebrian et al., 1994)	Structure of the matte: • Presence of intermatte channels and of dead matte • Measuring the baring of the rhizomes as defined by Boudouresque et al. (2006) • Evaluating the homogeneity and the compactness of the matte and measuring the percentage of plagiotropic rhizomes and the thickness of the matte (Pergent-Martini et al., 2005)
	Percentage of bottom covered by living P. *oceanica* (see also Table 2)
	Relative shoot density (number of shoots per square metre multiplied for the cover of living P. *oceanica*) (Romero, 1986)
	Mobile fauna associated to the meadow and the presence of other macrophytes (Pergent-Martini et al., 2005)

Given the major role played by *P. oceanica* in Mediterranean coastal ecology, the regression of the meadows may affect many aspects of the associated community structure, which is moulded by the interactions between the plant, the epiphytes and the animals through processes of co-evolution. Environmental gradients, such as the intensity of hydrodynamics and the temperature, are the driving force that influence, directly and indirectly, the algal fraction (along the layer leaf) and animal community (Mazzella et al., 1989). Changes in environmental parameters can determine differences in the structure of the meadows and, consequently, in the structure and distribution of the community.

The assemblages associated with *P. oceanica* vary on a geographic, seasonal and bathymetric scale, but some species are constantly present throughout the Mediterranean. *P. oceanica* habitats are characterized by extremely high levels of biodiversity. A fundamental contribution to the high biodiversity of *P. oceanica* system is given by the epiphytic community (Klumpp et al., 1992; Moncreiff et al., 1992; Nelson and Waaland, 1997), characterized by a great variability over a small spatial scale (form cm to m) and by a greater uniformity over large-scale (km), thus showing a patchy distribution (Balata et al., 2007). The epiphytic flora contributes to the overall primary production system of *P. oceanica* (Cebriàn and Duarte, 2001; Romero, 2004; Boudouresque et al., 2006), furthermore representing the main source of food for most of herbivores associated with seagrass meadows (Fig. 2.2). Another fundamental component in the *P. oceanica* ecosystem is the vagile fauna (Kikuchi and Pérès, 1977), which includes all of the associated organisms free to move independently although being sedentary. The vagile fauna show a zonation along the depth gradient and in relation to seasonal variation, with a distribution that is the result of adaptation to abiotic conditions, thus reflecting the presence of environmental gradients (Mazzella et al., 1989, 1990; Gambi et al., 1992). The main taxonomic groups of vagile fauna associated with *P. oceanica* meadows are molluscs, polychaets, annelids, echinoderms and crustaceans. Among the latter amphipods predominate, representing one of the most abundant taxonomic group (Marsh, 1973; Mazzella and Russo, 1989).

2.2 Amphipods

Amphipods, with more than 8,000 described species (Bellan-Santini, 1999), are the most numerically important order inside the superorder of Peracarid Malacostraceans Crustaceans, whose phylogeny remains to a large extent an unresolved mess with the possibility that it may be a polyphyletic group (Martin and Davis, 2001). The subdivision of amphipods is constantly debating, but traditionally they are subdivided in four sub-orders: Gammaridea (maybe paraphyletic and contain the vast majority of amphipod families), Caprellidea (strictly marine, with a peculiar morphology), Hyperiidea (exclusively planctonic, characterised by important development of the eyes), and Ingolfiellidea (interstitial, with a lower species diversity) (Barnard and Karaman, 1991).

Amphipods exhibit a variety of different morphologies but all have certain basic features. The general 'type amphipod' is a small crustacean (about 10 mm), with an arched, laterally flattened body (Fig. 2.3) that can be divided in three main parts. The head is a cephalothorax resulting by the fusion of the head with the first thoracic segment. It bears a pair of sessile compound eyes, two pairs of uniramous antennae and three pairs of mouthparts (mandibles and two pairs of maxillae). The first thoracic segment bears the maxillipeds, prehensile appendages involved in food handling (Bellan-Santini, 1999).

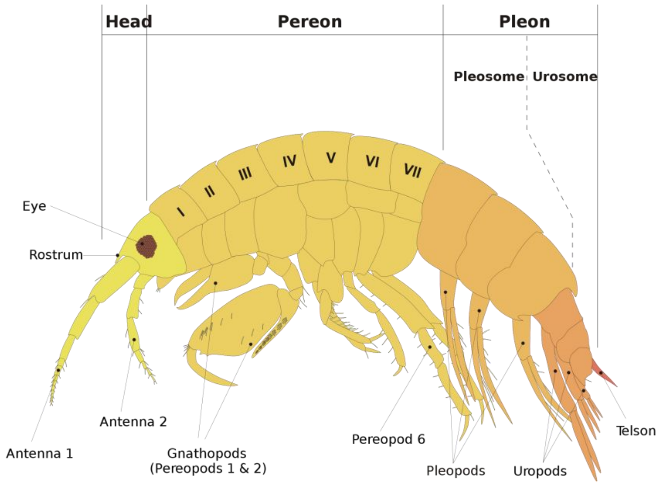


Figure 2.3 - Typical morphology of an amphipod crustacean.

The thoracic part, called pereon, includes seven segments each of them bearing a pair of pereiopods consisting of seven articles: the coxa, the basis, the ischium, the merus, the carpus, the propodus and the dactylus. The first four pairs of pereiopods are pointed towards forwards and the last four pairs backwards, a peculiar feature that gives its name to the order, ‘amphi-’ meaning ‘both’ and ‘poda’ meaning ‘foot’ or ‘leg’ (Bellan-Santini, 1999). The pereiopods of the first two segments are modified to be prehensile appendages and take the name of gnathopods (‘gnato-’ mening ‘jaw’ combined with ‘poda’), while the other five pairs are adapted for locomotion. In most cases, each of the pereiopods of the 6 last segments bear gills. They have separate sexes and some species present accentuated sexual dimorphism (Riedl, 2010). In mature females, the coxa of pereiopods can present a large ventral lamellar projections, called oostegites, that participate in the formation of the thoracic marsupium, a mid-ventral brood pouch characteristic of all peracarids. Breeding takes place with external fertilization, the female’s marsupium hosts the fertilized eggs and subsequent larval stages, then young amphipods are released in the environment under the form of juveniles that are morphologically close to adults (Barnard and Karaman, 1991), so that amphipods completely lack a dispersal larval phase (direct development). Mediterranean amphipods species show a rapid growth and a relatively short life in the range of 4-6 months up to 2 years (Bellan-Santini, 1998, 1999; Delgado et al., 2009).

Pleon is the abdominal part, composed of the last 6 segments of the body. It can be divided in two parts: the pleosome, (or epimeron), constituted of 3 segments (the epimers) each bearing a pair of pleopods used for swimming, and the urosome also contains 3 segments, each of them bearing a pair of appendages (uropodes), which are very variable in shape and sometimes involved in the mating process. The final segment is the telson, which is can be a single plate, or partially or totally divided into two lobes (Bellan-Santini, 1999).

Amphipods inhabit a variety of different environments, including rivers, ponds, lakes, interstitial or underground waters, coastal marine environments, abyssal trenches and hydrothermal vents. Some of them are terrestrial forms and others are able of various symbiotic associations with vertebrates and invertebrates. This habitat diversity is correlated with an high diversification in the feeding type with herbivores, suspension or deposit feeders, scavengers, parasites, predators, detritivores, etc... (Bellan-Santini, 1999). This important adaptive radiation led the amphipods to become one of the dominant groups of marine invertebrates in numerous ecosystems. The large number of species and their wide dissemination, as well as the variety of ecological niches occupied by different species led the amphipods to become one of the dominant groups of marine invertebrates and puts them in a position to be used in the field of ecological indicators. Amphipods are particularly sensitive to polluted sediments showing an overall decline in the abundance and diversity in species with increasing pollution (Gómez-Gesteira and Dauvin, 2000; Dauvin and Ruellet, 2007) and, therefore, used in monitoring the environmental impacts on the prairies themselves (Sánchez-Jerez and Ramos-Esplá, 1996; Sánchez-Jerez et al., 2000).

Vagile invertebrates, in particular amphipods, are often regarded as key-components of seagrass systems because of their importance in food webs. The knowledge about their trophic ecology is still poor, but amphipods are generally considered to be primary consumers and/or detritivores constituting an important link between producers and higher trophic levels. Amphipods are mainly generalist herbivores, feeding vegetal epiphytes (diatoms and macroalgae) and associated detritus on the leaves, but some are deposit/suspension feeders, omnivores, deposit feeders, carnivores and detritus feeders (Gambi et al., 1992; Lepoint et al., 2000; Vizzini et al., 2002)

Epiphyte-derived organic matter has a relevant importance in the diet of amphipods associated with *P. oceanica* meadows, which consume epiphyte growing on various parts of the seagrass, with species-specific preferences (Mazzella et al., 1992), making the organic matter constituting them available to upper trophic levels and so holding a central role in the food webs associated with *P. oceanica* meadows (Bell and Harmelin-Vivien, 1983; Pinnegar and Poulin, 2000). For these reasons, abundance of leaf epiphytes is an important factor driving the patterns of amphipod community structure (Zakhama-Sraieb et al., 2011).

In seagrass meadows, the seagrass, the epiphytes that grow on it and the grazers able to consume either the seagrass or its epiphytes are linked by a complex interplay of reciprocal interactions, termed seagrass/epiphyte/grazer system. Fluctuations in this system can influence the functioning of the whole meadow (Jernakoff et al., 1996; Valentine and Duffy, 2006) and amphipod crustaceans, because of their great abundance, could play an important role in the determination of the structure of the community (Connell, 1975).

P. oceanica meadows exhibit a higher numerical abundance and specific diversity of amphipods than unvegetated sand bottom areas, showing differences also from communities found in other common soft-bottom Mediterranean macrophytes (Scipione and Zupo, 2010). Although the amphipods fauna associated with *P. oceanica* is rich and particular, with a lot of species considered, real exclusive taxa of this biotope do not exist (Buia et al., 2000).

The meadow-associated community can be regarded as a complex assemblage of species that may be encountered also in other biotopes. The fauna of the foliar stratum is very similar to biocenoses encountered in photophilous algae on rocky shores, while the fauna of the rhizome layer matte is comparable to the fauna of precoralligene and coralligene bottoms, or marine caves. Finally, communities of the matte show similarity with those associated to sediment on detrital soft bottoms (Ruffo et al., 1989). Such distinction is, however, unclear because of the ability of this animals to perform vertical migrations creating interaction between the different compartments and causing a partial overlap of the assemblages (Borg et al., 2006).

2.3 Spatial/Temporal variation

Posidonia oceanica meadows are habitats characterized by a high spatial heterogeneity and variability even over small scales, ranging from meters to centimeters (Balestri et al., 2003; Borg et al., 2005, 2006; Montefalcone et al., 2008; Sturaro et al., 2014, 2015). Factors that could modify the morpho-functional traits of the plants include physical disturbance, topographic complexity, nutrient availability as well as differences in microhabitats. Such factors may operate over very small scales, thus altering plants distributional patterns over comparable distances (cm to dozens of m), and so causing the well documented high spatial heterogeneity of meadow features (Balestri et al., 2003; Zupo et al., 2006a, 2006b).

P. oceanica system is also characterized by a certain degree of seasonally-based variability, as observed in many other long-lived seagrasses with large-sized rhizomes (Duarte, 1991). Their ability in storing and reallocating resources allows the plants to support growth patterns that are relatively independent from fluctuating environmental conditions, but prone to be influenced by changing seasons (Marbà et al., 1996; Guidetti et al., 2002). Leaf area index and shoot weight (see Table 2.1) reach their maximum during late spring and summer, when both the foliar production of *P. oceanica* and the development of epiphytes are higher (Guidetti et al., 2002). During these periods, litter constantly accumulates, especially via erosion of the apexes of the leaves due to the heavy epiphytic load and associated grazing activities. At the beginning of the autumn the significant development of epiphytes together with the increasing hydrodynamism, both contribute to the massive fall of senescent leaves (Guidetti et al., 2002). During the late autumn and winter, most of the litter is degraded or exported, albeit not immediately renewed due to the lowered productivity of *P. oceanica* (Mateo and Romero, 1997; Gobert, 2002; Gallmetzer et al., 2005).

Seagrass meadows are spatially heterogeneous ecosystems, where a number of microhabitats coexist, creating intricate structures that favour a patchy distribution of associated invertebrates. Effective conservation and management of seagrass communities thus require a clear understanding of the processes controlling the patterns of distribution of associated organisms, with particular regard to the variation in species abundance and diversity through space and time. Temporal and spatial variation of the structure of *P. oceanica* meadows, as the leaf canopy height and shoot density (Table 2.1), are key drivers in determining spatial and temporal patterns of distribution, therefore influencing species richness and abundance of the leaf-stratum-motile macro invertebrate assemblages (Bedini et al., 2011; Michel, 2011). Canopy height and shoot density are related to both habitat complexity and availability of different microhabitats, influencing food availability for grazers, in terms of epiphyte abundance, enhancing the role of meadows as refuges from predation (Mazzella and Ott, 1984; Borg et al., 2010). Associated vagile fauna is therefore strongly influenced by the features of both the plant and of its epiphytes, showing specific adaptations to different micro-environments (Mazzella and Ott, 1984).

Among all, amphipods are one of the most important components of the *P. oceanica* vagile fauna (Ledoyer, 1962; Mazzella et al., 1989), playing a relevant role in the transfer of energy to the higher trophic levels and represent an important source of food for higher trophic levels, as decapods and fishes (Bell and Harmelin-Vivien, 1983; Chessa et al., 1983; Sparla, 1989). Depth is advocated as fundamental in the subdivision of amphipods, and studies on the bathymetric variation suggest that communities are structured in 3 assemblages. The shallow water community, located between the surface and 1-2 m depth, is very similar to the photophilous algae fauna. Such assemblage is able to withstand high hydrodynamism and is mainly represented by herbivores related to the erect algal epiphytic layer, which constitutes the primary food source for amphipods. The intermediate amphipod community ranges from 5-10 m to 20-25 m depth, and is characterized by a more diversified assemblage that is considered the most typical of *P. oceanica* meadows. It is mainly represented by herbivores-deposit feeders, due to the high deposition of particulate organic matter on leaves that may favour the presence of 'detritus cleaner' species (Nagle, 1968; Howard, 1982; Lewis and Hollingworth, 1982; Scipione, 1989). Finally, the third assemblage is found at depths higher than 25 m, and is similar to the amphipod assemblages found in bare soft bottoms, characterized by a preponderance of deposit-suspension feeders and deposit feeders-carnivores. These features are probably due to the more heterogeneous structure of the meadows and the overlapping with surrounding soft bottoms (Scipione and Fresi, 1984; Mazzella et al., 1989; Gambi et al., 1992; Michel, 2011). This bathymetric pattern of distribution is often related to the trophic structure of assemblages: higher food availability could explain a higher abundance of herbivorous organisms in shallow stands, while carnivorous organisms may colonize the deeper parts of meadows (Mazzella et al., 1992).

Studies on spatial variation of amphipod assemblages have been carried out in meadows from Spain (Sánchez-Jerez et al., 2000; Vazquez-Luis et al., 2009), continental French (Ledoyer, 1968), Corsica (Degard, 2004; Sturaro, 2007), Sardinia (Como et al., 2008; Sturaro, unpublished data), Italian Tyrrhenian coasts (Scipione and Fresi, 1984; Chimenz et al., 1989; Mazzella et al., 1989; Gambi et al., 1992; Scipione et al., 1996), Italian Adriatic coasts (Scipione and Zupo, 2010) and Tunisia (Zakhama-Sraieb et al., 2006; Zakhama-Sraieb et al., 2011). These studies have evidenced that, while common features can be highlighted, it is difficult, if not impossible, to evidence a general pattern (Michel, 2011). Most of the variability in the total abundance, specific diversity of communities and identity of dominant species could be probably explained by local differences of the meadow parameters.

Moreover, many studies suggest that spatial variation could exist at very small scale (e.g. 1-10 m) (Gambi et al., 1992; Sánchez-Jerez et al., 1999a; Degard, 2004; Zakhama-Sraieb et al., 2011), while variations at larger scales (about 100 m) rather concern amphipod specific richness and diversity (Sturaro, 2007). Motile macro-invertebrate assemblages associated with seagrasses may vary spatially in relation to responses of organisms to environmental gradients and, temporally, in relation to the life cycle of organisms and changes in the structure of seagrass beds (Heck and Orth, 1980). Temporal variation can also be considered scale dependent, particularly in the case of motile animals such as amphipods, the situation is further complicated by vertical (nychthemeral) and horizontal migration patterns.

Nychthemeral variation is an important pattern of movement, showing an increasing abundance of amphipods in the foliar stratum during the night (Ledoyer, 1969; Sánchez-Jerez et al., 1999b). Such pattern of migration is likely explained by the greater nocturnal activity of amphipods (Bellan-Santini, 1999), described as a mechanism of predation avoidance. A large number of predators of the vagile invertebrates are fish (e.g. *Labrus merula*, *Symphodus rostratus*), which mostly feed during the day and hunt their preys using visual stimuli (Bell and Harmelin-Vivien, 1983). Like other groups of vagile invertebrates, amphipod crustaceans developed mechanisms of vertical migration as a strategy to avoid this kind of predation. During the day, they preferentially stay in the lower layers of the meadow (rhizomes, matte, Ledoyer, 1969), rising to the foliar stratum (where they are more vulnerable) only during the night when the predation pressure is lower (Ledoyer, 1969). Moreover, these vertical migrations could limit the competition for food or habitat, by allowing animals to exploit available resources in all compartments (foliar stratum, rhizome layer and litter cover) (Sánchez-Jerez et al., 1999b).

Important seasonal influences on the spatial distribution of invertebrates within the meadows may also exist (Bedini et al., 2011). Amphipod abundance and diversity is generally maximal in late summer and autumn and minimal in winter and early spring (Mazzella et al., 1989; Gambi et al., 1992; Scipione et al., 1996). Specific traits of the meadow often cannot explain such variability so that the autumnal maximum can be linked to seasonal differences of other abiotic and biotic factors, like lower predation pressure and individual dynamics of vagile invertebrates (Nelson, 1979a, 1979b; Michel, 2011; Michel et al., 2014). Other sources of variability in the temporal patterns of abundance of motile fauna are related to temporal changes in epiphyte diversity and covering. Herbivores, probably, follow the seasonal changes of epiphyte biomass and the abundance of carnivorous assemblages would vary less over a one-year period (Mazzella et al., 1992). Long-term temporal variation could also occur, but the different seasonal distributions of dominant species within the same trophic group are most likely due to different life cycles, competition phenomena, or various grazing adaptations to plant epiphytes (Greze, 1968).

2.4 Metacommunity

The knowledge of distribution and abundance patterns of species is fundamental to understand the role of biodiversity in ecosystem functioning (e.g. maintaining water quality, atmospheric CO_2 levels, or primary production; Loreau, 2000; Naeem, 2001; Holyoak et al., 2005). Biodiversity is structured by processes operating at several hierarchical scales, including populations of single species, interacting populations of different species, whole communities and ecosystems. Patterns of biodiversity are innately spatial, scaling from local ecosystems to landscapes to entire biogeographic regions (e.g. Wiens, 1989; Levin, 1992; Holt, 1993; Rosenzweig, 1995; Maurer, 1999; Hubbel, 2001; Chase and Leibold, 2003). Of particular interest are cases where patterns of diversity are linked to changes in community composition along environmental gradients.

During the last years, ecologists have increasingly questioned whether the existing conceptual framework of community ecology is adequate for describing the dynamics of communities that are connected across space. The metacommunity concept has emerged as a new and exciting way to think about spatially extended communities, leading novel questions about emergent patterns of species diversity and distribution. A metacommunity can be defined as a set of local communities that are linked by dispersal (Hanski and Gilpin, 1991; Wilson, 1992), where a community may be defined as a collection of species occupying a particular locality or habitat. These definitions describe a hierarchy of scales and emphasize the ways in which processes occurring at smaller scales interact with those at larger scales (Levins and Culver, 1971; Vandermeer, 1973; Crowley, 1981; Law et al., 2000; Mouquet and Loreau, 2002).

A motivation for studying metacommunities comes from the need to conserve biodiversity in landscapes experiencing fragmentation. Habitat fragmentation creates patchy landscapes in which dispersal may be required for persistence, and is acknowledged to be an important factor driving the loss of biodiversity (Wilcove et al., 2000). Fragmentation studies typically use empirical trends to predict how communities will change during fragmentation process, investigating the ability of species traits to predict responses to fragmentation itself.

However, such studies rarely attempt to explicitly deal with community structure due to the lack of a general theory framing the measures and analyses of natural fragmented communities. In single species metapopulation models, the subdivision of the habitat resulting from fragmentation can only be detrimental because, as fragmentation proceeds, previously stable populations in large undivided habitats become increasingly small and isolated. This makes them vulnerable to local extinction through demographic stochasticity, with a reduced capacity for the patches to be recolonized (Harrison and Taylor, 1997). The absence of a theory able to provide mechanisms for responses to fragmentation potentially limits our ability to predict how communities will change under altered circumstances and our ability to effectively manage communities and metacommunities by manipulating habitat factors al landscape scales. These substantial gaps in the knowledge require a clear understanding of the role of spatial structure and dynamics in ecological communities to maintain biodiversity, to manage species and ecosystem properties and to provide adequate practices in conservation biology.

A community is often defined as an area within which all individuals are equally likely to interact, precluding any spatial heterogeneity in distribution or abundance. This simplified view assumes that mass action and mean field conditions are adequate descriptors of the dynamics, as seen in population dynamic models such as the classic Lotka-Volterra equations and their extensions (May, 1973; Pimm and Lawton, 1978; McCann et al., 1998). It is also often not clear whether the results of these investigations are applicable in all generality to more complex systems at larger spatial scales (Naem, 2001).

A metacommunity is easiest to conceptualize when all the interacting species utilize the same set of discrete habitat patches and have local populations that use resources at the same within-patch scale. However, many communities lack discrete boundaries, and many populations are regulated over multiple spatio-temporal scales. In addition, the exact spatial placement (i.e. spatially explicit) of habitats can influence metacommunity dynamics, so that species can differ in the extent to which they disperse. Inter-patch dispersal at sufficiently low rates can lead to variation in species composition from patch to patch. Although existing models of metacommunities (Hubbell, 2001; Mouquet and Loreau, 2002, 2003) give a highly simplified representation of the spatial complexity of natural assemblages, they are useful in developing theories for more complex metacommunity scenarios. Metacommunity dynamics consist of either the spatial dynamics or regional properties of communities occupying two or more interconnected patches. In contrast to metapopulation dynamics, metacommunity dynamics should involve more than two interacting species. Differently from community dynamics, the metacommunity concepts should be applied to a system in which the dynamics of individual species were altered by both species interactions (of more than two species) and dispersal. Variation in the extent to which species interact has profound consequences for metacommunity dynamics. Dispersal may influence both local and regional dynamics, with different species likely to have their own rates of movement that represent a combination of evolved abilities and responses to their environment (Holling, 1986; Clobert et al., 2001; Rodrìguez 2002).

The number of spatial scales that are required to represent the dynamics of real metacommunities is not yet clear. Many current models of metacommunity dynamics are based on a three-level hierarchy of scales. At the smallest scale, micro-sites can hold a single individual and are nested within localities (equivalent to habitat patches) that hold local communities similar to those in conventional species interaction models. In turn, local communities are connected to other communities as part of a metacommunity occupying a region. Not only the number or the extent, but also the real arrangement of patches/localities (i.e. the so called spatially explicit models) should be considered in explaining metacommunity patterns, as ignoring explicit spacing may led a too simplified view of the reality (Hanski and Gaggiotti, 2004).

Four conceptual models can be considered to describe metacommunities, and each one illuminates different aspects of spatial community dynamics. Theoretical and empirical work on metacommunity largely falls along four broad perspectives that we refer to as the patch dynamic, species sorting, mass effects and neutral perspectives. The first perspective (patch dynamic) extends metapopulation models for patch dynamics to more than two species, and it can be considered to build on the equilibrium theory of island biogeography (MacArthur and Wilson, 1967). Patch dynamic assumes the existence of multiple identical patches (e.g. islands) that undergo to both stochastic and deterministic extinctions (Harrison and Taylor, 1997). Under this view, dispersal should counteract extinctions by providing a source of colonization into empty patches. For coexistence to occur, dispersal rates must be limited so that dominant species cannot drive their competitors or prey to regional extinctions. The equilibrium theory of island biogeography also assumes a prominent role for extinction and colonization in setting levels of biodiversity on islands: species from a fixed pool of mainland species randomly colonize islands (patches), so that mainland species diversity determines the regional species diversity. However, such a perspective is not always realistic because many systems do not have a large mainland with a fixed species composition. Indeed, the equilibrium theory of island biogeography considers only the number of species in a community and does not include community (trophic) structure, species identities, or niche differentiation (Chase and Leibold, 2003).

The second approach (species sorting perspective) is based on theories of community change over environmental gradients (Whittaker, 1972), and considers the effects of local abiotic gradients on the population vital rates and species interactions (Leibold, 1998). The ensemble of local patches is heterogeneous in some local factors, and the outcome of local population dynamics (species interaction and individual species responses) depends on these spatially varying aspects of the abiotic environment. This perspective has much in common with traditional theory on niche separation and coexistence (Dobzhansky, 1951; Pianka, 1966; MacArthur and Levins, 1967). The main differences are that, under the metacommunity perspective, local and regional mechanisms of coexistence are intimately linked, and about the role of regional diversity in making local communities appear saturated. The result is that species distributions are closely linked to local conditions and are largely independent of unrelated purely spatial effects (Leibold and Norberg, 2004). Patch dynamic and species sorting perspectives assume a separation of time scale between local dynamics and colonization-extinction dynamics, but important regional dynamics may also emerge when local population dynamics are quantitatively affected by dispersal.

The mass effect perspective (Shmida and Wilson, 1985) represents a multi-species version of source-sink dynamics (Holt, 1985, 1993; Pulliam, 1988) and rescue effects (Brown and Kodric-Brown, 1977). Differences in the population density at different locations (or asymmetric dispersal) can drive both immigration and emigration between local communities. Immigration can supplement birth rates and enhance the densities of local populations beyond what might be expected in closed communities, and emigration can enhance the loss rates of local populations. Such ‘mass effect’ due to dispersal can have potentially strong influence on the relationship between local conditions and community structure (Holt, 1993). Coexistence in such a metacommunity is obtained through a regional balance of local competitive abilities and, as a consequence, species are locally different but regionally similar in their competitive abilities (Mouquet and Loreau, 2002). The way with which mass effect allows the local coexistence of species is constrained in complex ways (Amarasekare and Nisbet, 2001) as coexistence requires spatial variance in fitness, which cannot be maintained at high levels of dispersal among patch types.

All of the above approaches assume that species differ significantly from each other either in their niche relations with local factors and/or in their abilities to disperse or avoid local extinctions. In the absence of any such differences among species, the behaviour of metacommunities can be dramatically different from models with trade-off or species-specific differences (Caswell, 1978; Hubbel, 2001; Chave, 2004). Neutral models predict a gradual loss of all competing species via a potentially slow process of random walks. The resultant temporal change in species composition has termed ecological drift by Hubbel (2001). Although neutral model, alone, cannot explain how differences in local and regional diversity are maintained, the 'neutral' view can be regarded as a null hypothesis for the other three views described above (Bell, 2000), able to describe the dynamics of communities where species are close to being equivalent, or where transient dynamics are very long.

Clearly, all of four perspectives outlined above capture interesting aspects of metacommunity dynamics. However, it is unlikely that all of the species interacting in a given (meta)community will uniformly conform to any one of these perspectives and, therefore, should be viewed as a continuum where each processes will play interactive roles in structuring real metacommunities. Moreover, many other factors not included in these four perspectives are likely to influence metacommunity dynamics, such as local dynamic or the evolution of species pool (Shurin et al., 2000). Such identified paradigms should indeed be viewed as a starting point, rather than a complete framework, for metacommunity ecology.

The metacommunity concept advanced understanding of meso- and large-scale ecology, as well as the distribution of organisms along environmental gradients (Holyoak et al., 2005; Presley et al., 2010). Spatial variation in species composition can be studied by following complementary avenues based on mechanisms (Cottenie, 2005) and patterns (Leibold and Mikkelson, 2002). In the first approach (mechanistic), variation in community composition at different localities is based on the above mentioned paradigms of patch dynamics, species sorting, mass effects and neutrality (Leibold et al., 2004; Holyoak et al., 2005). A different but complementary approach in studying metacommunities is the evaluation of how species distribute along environmental gradients, emerging from the above mentioned mechanisms and manifest as particular metacommunity structures.

Several conceptual models of spatial structure have been developed to describe patterns of species distribution, each one based on the coherence of the species responses to environmental gradients and species turnover. To distinguish multiple hypothetical patterns, Leibold and Mikkelson (2002) developed a rigorous quantitative approach based on species incidence matrices, describing the presence/absence of a species in a given site. The approach of Leibold and Mikkelson (2002) is based on the assumption that most of underlying structures in metacommunities can be described by three elements, that is, coherence, range turnover and range boundary clumping. These elements, in turn, give six idealized structures (e.g. random, checkerboard, nested, evenly-spaced, Gleasonian and Clementsian) (Fig. 2.4), assuming that species distribution are molded by interactions (e.g. competition, habitat associations) or responses to abiotic factors (e.g. temperature, rainfall) that vary among sites and so constitute an environmental gradient (Leibold and Mikkelson, 2002; Presley et al., 2010).

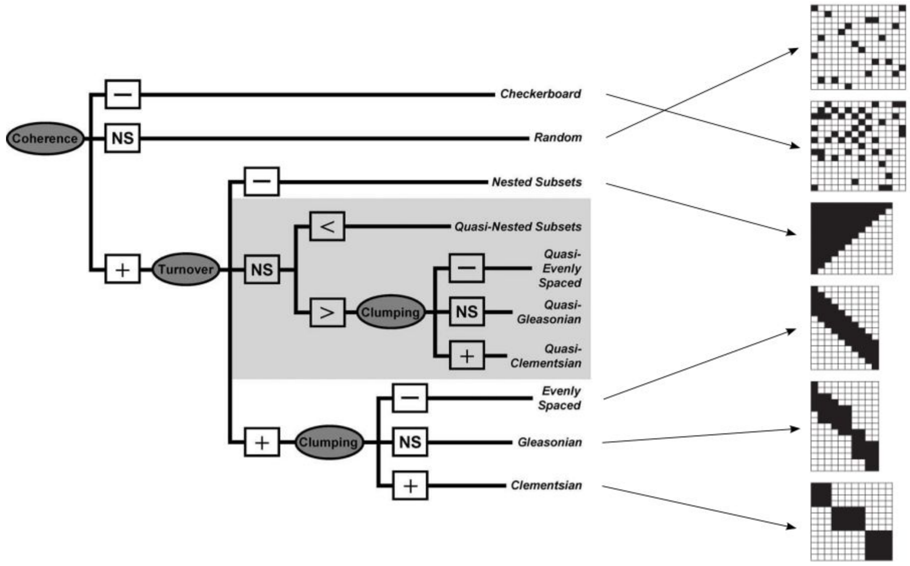


Figure 2.4 - Framework representing the hierarchical approach based on analysis of Elements of Metacommunity Structure and combinations of results that are consistent of each of six idealized structures (Leibold and Mikkelson, 2002), three patterns of species loss for nested subsets, six quasi-structures, and structures of compartments within Clementsian distributions.

The idealized patterns of species distribution are laying their foundations on early theories of species coexistence. For instance, Clementsian patterns are based on communities with distinctive species compositions sharing evolutionary history, but having interdependent ecological relationships. This results in boundary ranges that are coincident and form a sort of compositional unity along different parts of the environmental gradient (Clements, 1916). Alternatively, species may exhibit idiosyncratic responses to the environment, with coexistence resulting from chance similarities in requirements or tolerances (Gleason, 1926). Moreover, in presence of strong interspecific competition, coexistence may be controlled by tradeoffs in competitive abilities, with species distributions that are more evenly spaced along environmental gradients than expected by chance (Tilman, 1982). Strong competition may also results in checkerboard patterns, when pairs of species have mutually exclusive ranges (Diamond, 1975) and occur at random with respect to other such pairs. Finally, nested patterns arise when species-poor communities are subsets of increasingly more species-rich communities (Patterson and Atmar, 1986), where species loss is associated with variation in species-specific characteristics (e.g. dispersal ability, habitat specialization, tolerance to abiotic conditions).

This theoretical framework has found its practical application in the Elements of Metacommunity Structure (EMS), which is based on the evaluation of the above mentioned structures calculated from a presence-absence interaction matrix, with sites as rows and species occurrences at sites as columns (Dallas, 2014). In this framework, the interaction matrix is first ordered via Reciprocal Averaging (RA), a multivariate ordination method that groups interactions along the matrix diagonal resulting in species with similar ranges and sites with similar species compositions to be placed together (Gauch, 1982; Dallas, 2014). The peculiarity of RA is that sites and species are ordered following latent (environmental) gradients and the scores of the resulting ordination can be related to environmental or spatial variables (Presley and Willig, 2010). However, incidence matrix can be ordered by following any relevant ecological questions.

Coherence is thus measured as the number of embedded absences in the ordered matrix, whose statistical significance is evaluated by comparing the observed absences to the number of embedded absences observed in many randomized null matrices using a *z*-test (Dallas, 2014). Turnover is defined and measured by calculating the number of times one species replaced another between sites, after species distributions are made completely coherent and, as in the case of coherence, the statistical significance is evaluated by means of a *z*-test. Finally, the boundary clumping is measured by the Morisita's index, which measures the dispersion of species occurrences among sites (Morisita, 1971) and statistical significance is determined using a chi-squared test. The EMS framework assumes the use of null-matrices obtained via randomized procedures in order to test the degree of deviation of coherence, turnover and boundary clumping from the expectation. A huge number of different randomization algorithms exists (Gotelli and Graves, 1996), all supposed to be affected by statistical errors associated with specific constrains in replication algorithms. According to some authors, the best performing algorithm typically hold row (site) totals constant and either fill occurrences among sites probabilistically based on the marginal column totals (fixed-proportional null) or by maintaining column sums (fixed-fixed null) (Ulrich and Gotelli, 2007). However, as stated by others (Presley et al., 2009), no model is free from errors and, for the sake of clarity, null-models should be context dependent and contain a minimum of reliable biology of the system under study (Presley et al., 2009).

Interpretation of the results of EMS should, however, take with caution to avoid misunderstanding. Indeed, some studies have interpreted non-significant results to be evidence that the null hypothesis (H_0) is true, although a non-significant result does not mean that H_0 can be accepted. Simply, may be the data do not provide enough evidence to determine if H_0 is true or false (Wackerly et al., 2008; Gelman, 2013). By the way, the EMS framework still remains one of the best methods for determining metacommunity structure.

3. MATERIALS AND METHODS

3.1 Study area

Organisms were collected in *P. oceanica* meadows from three sampling localities of the central Tyrrhenian Sea: two located along the mainland coastal area of Montalto di Castro (Chiarone and Punta Morelle) and one located in the insular area of Giannutri Island (Fig. 3.1).

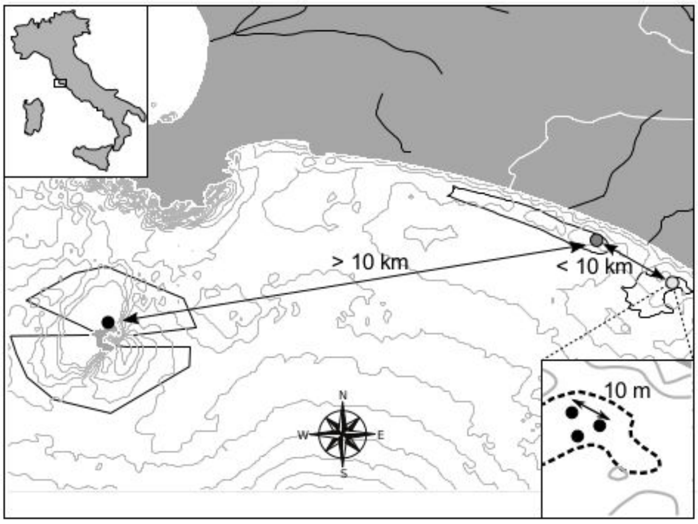


Figure 3.1 - Overview of the study area. Black, light and dark grey circles are for Giannutri Island (GIAN), Chiarone (CHIA) and Punta Morelle (MOR), respectively. Arrows show the approximate distances between sampling sites at macro (> 10 km) and meso-scale (< 10 km). Insert at the bottom left shows a sketch of the sampling strategy at micro-scale (~ 10 m).

Chiarone (CHIA) is a Special Area of Conservation (Habitats Directive 92/43/EEC, SAC IT6000001) bounded by the estuaries of Chiarone River (to the North) and Fiora River (to the South). Depths range between 5 and 30 m, with an average of 18 m and a prevalence of sandy-muddy bottoms due to the alteration of the sedimentary regime. Punta Morelle (MOR) is a Special Area of Conservation (Habitats Directive 92/43/EEC, SAC IT6000002) with an average depth of 25 m, ranging from 10-30 m. Seabed consists mainly of sandy substrate with rocky outcrops up to about 300 m from the shore, with a diversified morphology characterized by pools and jagged bathymetric. Giannutri Island (GIAN) is part of the National Park of Tuscan Archipelago. It is a limestone island characterized by a rugged and rocky coastline, where *P. oceanica* meadows are confined to the coastal areas due to the steep slope of the rocky seabed and the scarcity of shallow water bays.

Localities were further characterized on the basis of specific environmental characteristics known to be related with the boundaries of a variety of marine species, whose distribution at regional to local-scale are often limited by factors such as salinity, nutrient supply, topographic complexity and sediments (Briggs, 1995; Sbrocco and Barber, 2013). In particular, the persistence of amphipod communities is thought to be related to a series of complex mechanisms, including indirect effects of anthropogenic impacts on the meadows. The degree of water transparency, for instance, is an important parameter in regulating the importance of *P. oceanica* in the carbon budget of littoral Mediterranean ecosystems, as its depth limit is closely linked to light penetration underwater (see review in Duarte, 1991). Moreover, seagrass meadows produce excess of organic carbon over community requirements (Gattuso et al., 1998), which are believed to store an important fraction of the excess carbon they produce in the sediments (Duarte and Cebrián, 1996). Besides internal production, the deposition of organic matter can also be associated to a significant input of external nutrients, which develops communities with particularly high biomass (Duarte and Chiscano, 1999) and slow decomposition rates (Romero et al., 1992; Mateo and Romero, 1997), thus influencing the composition of invertebrate communities.

Localities were therefore characterized by means of four key environmental parameters, namely: i) salinity, ii) sea surface temperature, iii) chl-a concentration and iv) water transparency measured by the diffuse attenuation coefficient at 490nm (kd_{490}). Data about salinity and temperature were downloaded as 1 km (30 arc-second) grid from MARSPEC (www.marspec.org), a high-resolution global marine dataset that combines variables from the benthic and pelagic environments into a single database (Sbrocco and Barber, 2013). Temperature and salinity were downloaded as raw monthly climatological layers for the reference season. Chl-a concentration and kd_{490} were downloaded from AquaMODIS (http://oceancolor.gsfc.nasa.gov/cms/) as seasonal climatology (reference period 2002-2014) as 4 km resolution raster, downscaled throughout the contiguous study extent to the MARSPEC 1 km grid system using bilinear interpolation.

Spatial data are however characterized by specific properties, such as heterogeneity and autocorrelation, which can make them difficult to visualize and interpret. Heterogeneity means that processes can vary locally and are not necessarily the same at each spatial location, while spatial autocorrelation means a certain degree of relationship between variables at some location. Spatial heterogeneity and autocorrelation may sometimes invalidate two basic assumptions of many standard statistical analyses, that is, data independence and distribution. Moreover, spatial data may sometimes be highly dimensional (i.e. high number of variables measure at each observation) and thus difficult or redundant to visualize and interpret. However, a small amount of intrinsic dimensionality in the data sets may exists so that not all variables are needed to understand specific processes of interest. Therefore, one solution is to reduce the dimensionality of the data to capture the maximum information present in original data and remove spurious or redundant data, minimizing the error between the original data and the new lower dimensional representation (Fodor, 2002).

Environmental parameters were therefore subjected to a Principal Component Analysis (PCA), to identify combinations of variables that best explain the variance in the data, reducing dimensionality and defining suites of variables that may be functionally related. As PCA assumes normality in the distribution of data, it is sensitive to the relative scaling of the original variables and, when these assumptions are violated, the resulting principal components may not be independent. Therefore, variables were centered to 0 and scaled by their variance using a *z*-score transformation. Localities were finally characterized by averaging the scores of the first axis of the PCA within the arbitrary boundaries given by the extent of protected areas. Spatial statistic analyses were performed with SAGA-GIS (SAGA Development Team, 2008).

3.2 Sampling methods

Sampling was carried out by SCUBA diving at the same depth range (15-20 m), as depth gradient and correlated factors are thought to play a crucial role in defining amphipod assemblages (Scipione et al., 1983; Mazzella et al., 1989). An air-lift sampler (500 µm mesh size), originally described in Bussers et al. (1983), was used in a 40 x 40 cm quadrant subjecting each sample to suction during two minutes of constant air flow (Fig. 3.2).

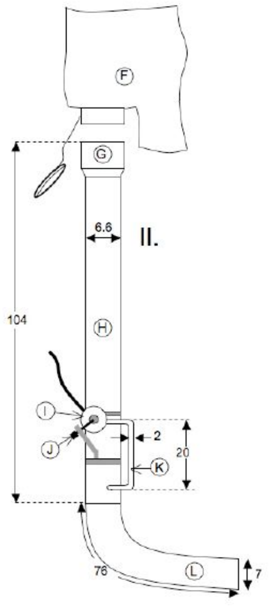


Figure 3.2 - Air-lift sampler (500µm mesh size), originally described in Bussers et al. (1983).

Samples were sieved on a 500 µm mesh and fixed in a 70% ethanol solution as soon as possible and then sorted out 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 Ruffo (1982), with taxa nomenclature following the World Register of Marine Species (WoRMS, 2015; http://www.marinespecies.org).

To investigate the spatial variation and structuring mechanisms of amphipod communities over the years, three sampling sites for each three localities (CHIA, MOR, GIAN) were considered in August 2012 and 2013 (Fig. 3.3). To evaluate instead the seasonal fluctuations, samples were collected only in the area of Giannutri Island during 2014, in the months of February, May, August and November, taking three random samples for each season in the two sites of Punta Secca and Secca di Punta Secca (Fig. 3.4).

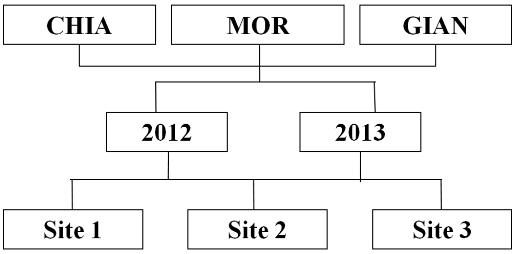


Figure 3.3 – Sampling design for the spatio-temporal analyses of amphipod assemblages from *Posidonia oceanica*.

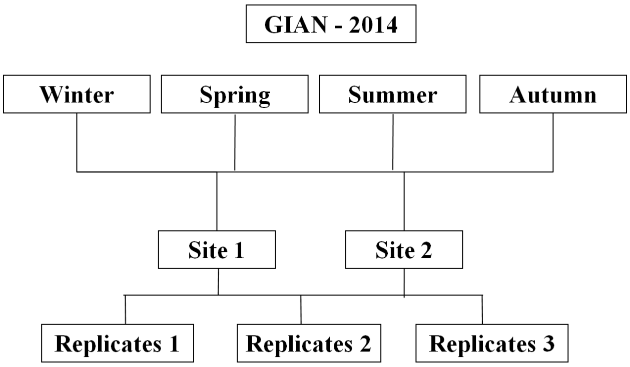


Figure 3.4 – Sampling design for the seasonal analyses of amphipod assemblages from *Posidonia oceanica* in Giannutri Island (GIAN).

To understand how the assemblages of amphipods varied in space and time, three level of spatial scales were considered to analyze the metacommunity structure: micro-, meso- and macroscale. Microscale analysis consists in describing the patterns within each locality (CHIA, GIAN, MOR). At mesoscale level, patterns of metacommunity were described considering the two coastal localities of Montalto area (CHIA *vs*. MOR) while, finally, the macroscale analysis involved also the area of Giannutri (GIAN *vs*. CHIA *vs*. MOR).

3.3 Statistical analyses

3.3.1 Spatio-temporal analysis

Data resulting from the taxonomic analysis of seasonal and annual samples were arranged as sites x species matrices, and specific community parameters, total abundance (*n*), species richness (*S*), Shannon-Wiener diversity index (*H'*) and Pielou's evenness (*J*) were measured.

A diversity *t*-test based on bootstrap randomization with 1,000 replicates was used to test for seasonal differences among sites in GIAN. Mean values (± SD) of indices were measured for each locality (CHIA, MOR, GIAN) and differences with respect to 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) were measured by means of a two-way ANOVA. Prior to analysis, homogeneity of variances was checked using Levene's test and transformations were applied when necessary.

The structure of amphipod assemblages was compared by a two-way permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001), considering the factor Time (four and two levels fixed for the seasonal and annual comparison, respectively) and Localities (three levels fixed and orthogonal) with 9,999 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 useful ordination. Analyses were based on the Bray-Curtis similarity matrices calculated from the square root transformation of abundance data to overcome the contribution of rare species. A similarity percentage analysis (SIMPER) was used to identify those species that most influence the dynamics and the structure of communities.

Statistical analyses were performed with PRIMER v6 (Clarke and Gorley, 2006) and PAST 2.17 (Bing et al., 2013).

3.3.2 Pattern analysis

3.3.2.1 Commonness and rarity in community structure

For each scale of analysis, data were arranged as incidence matrices, which describe the presence of a given species (row) in a given site (column) (Presley and Willig, 2010; Silva et al., 2013). Most of marine communities have highly asymmetric distribution, with few abundant species and many rare species that frequently carry relevant information about the structuring of communities, as they may represent a relevant percentage of the total. The percentage of rare species at different scales of investigation was therefore quantified using the inflection point criterion on the rank-abundance curve, that is, the region of the curve at which the curvature changed (Siqueira et al., 2012). A piecewise regression on the raw abundance data was used to stress the real differences between common and rare species (Magurran, 2004), and comparing the goodness of fit of the piecewise regressions with the equivalent linear regressions by ANOVA.

3.3.2.2 Elements of Metacommunity Structure

To determine the pattern of best fit for amphipods distributions at different spatial scales, was used the Elements of Metacommunity Structure (EMS) approach by investigating coherence, species turnover and boundary clumping (Leibold and Mikkelson, 2002; Presley and Willig, 2010). The first step in EMS is to create an ordination of sites and species with respect to specific gradients or by means of ordination techniques able to uncover latent environmental gradients, so that different techniques and types of data (i.e. quantitative *vs*. qualitative) lead to different results in the analysis of the observed patterns. For this reason, quantitative data should be used only if there are reliable estimates of abundances for each species for each site. Sampling in natural conditions is by definition subjected to errors, especially in marine environment where biases are often related with the strongly asymmetric trends in patterns of species abundance.

Sites by species incidence matrices were ordered via reciprocal averaging technique, also known as correspondence analysis, which re-order rows and columns using repeated averaging of species and sites scores and maximizing their correspondence (Leibold and Mikkelson, 2002; Presley and Willig, 2010). Reciprocal averaging allows to reach a compromise between minimizing the number of range interruptions and the number of gaps in the community compositions of sites (Leibold and Mikkelson, 2002; Presley et al., 2009) and to detect variation in species distributions subjected to latent processes such as environmental gradients or variation in unmeasured environmental variables (Gauch et al., 1977). The primary axis represents the best possible ordering of sites and species to maximize their correlation, although in reciprocal averaging multiple ecologically meaningful ordinations may be possible, with each ordination axis capable of representing a distinct pattern of species distributions along distinct gradients (Presley et al., 2009). In reciprocal averaging, the percent inertia (i.e. the degree of correlation between sites and species achieved by the ordination) of the primary axis could be relatively low with respect to the second axis (Gauch, 1982). Therefore, to evaluate the relative correspondence achieved by the ordinations on each axis, inertia values should be compared with those from different axes to understand whether or not more than one dimension may provide insights into EMS.

To test for a statistical significance in metacommunity patterns, a series of different, scale-dependent null-models were employed to resemble the incidences in the sites by species matrices, as different scales should constraints the distribution of species in different ways. Null-models in ecology are known to be affected by different statistical pitfalls, often related with types of models employed, spanning from extremely liberal (highly prone to type I errors, Gotelli, 2000) to extremely conservative (highly prone to type II errors, Gotelli, 2000). However, while trying to minimize the statistical errors associated with them, the appropriate choice of a null-model should be context-dependent, having in mind the biology of the system under study (Presley et al., 2009).

Amphipods are known to have low active dispersal ability due to the lack of pelagic larval forms (Thomas, 1993), also showing a wide range of responses to habitat modification (Vázquez-Luis et al., 2009), spanning from high specificity to tolerance towards alteration resulting from pollution, invasion by alien species and other disturbances (Guerra-García and Garcìa-Gòmez, 2001). Therefore, at different spatial scales, spanning from few tens of meters (micro-scale) up to tens of kilometers (macro-scale), the geographic isolation (insularization) of the meadows and the abiotic conditions should exert different roles in structuring communities. At micro-scale (average distance ca. 10 m), no apparent effect of distance and abiotic conditions should influence the pattern of species distribution (Table 3.1) and, therefore, a null-model in which the total number of occurrences (fill) are fixed and all sites and species are equiprobable (Gotelli, 2000) was used. At meso-scale (average distance <10 km), the distance between localities increases its importance in the structuring of communities, although similar abiotic conditions (Table 3.1) and, therefore, was used a null-model that only maintains species frequencies (Jonsson, 2001). Finally, as the macro-scale involves high distances between localities and different abiotic conditions, species distribution should depends on their frequencies of occurrence and abiotic tolerance (Table 3.1). Therefore, a null-model with fixed rows (diversity of sites) and column marginal frequencies as probabilities of selecting species was employed.

A final remark should be done with respect to the dimension (i.e. number of rows x columns) of the matrices, which may influence the statistical significance of the randomization procedures. To avoid specific statistical pitfalls, we used a number of randomization in the EMS algorithm proportional to the maximum number of possible substitutions in a matrix, and iterated *n* times the micro-scale analysis until a stable solution was reached. Although such a statistical artifice can somehow reduce the degree of uncertainty in the interpretation of results, these should however be taken with caution.

Table 3.1 - Hypothesized effects of space and environment on the distribution of amphipods in *Posidonia oceanica* meadows at different spatial scales.

Scale	Space	Abiotic environment	Rationale
Micro	No	No	Species have the same probability of colonization. Communities are supposed to be structured by biotic interactions
Meso	Si	No	Colonization may be influenced by the dispersal capacity of the species. Communities are supposed to be structured by biotic interactions
Macro	Si	Si	Colonization is influenced by the dispersal ability of the species and their responses to the environmental gradients. Communities are supposed to be structured by the biotic responses of species to abiotic environment

Coherence was evaluated by counting the number of embedded absences in a matrix ordered according to the primary axis. Significant negative coherence results if the number of embedded absences randomly obtained is lower than the observed number of embedded absences, and indicates that species presences follows a checkerboard pattern. A non significant coherence means that the metacommunity is randomly structured whereas a significant positive coherence suggests that species are distributed according to the same gradient (Leibold and Mikkelson, 2002; Silva et al., 2013). When positively coherent, the EMS analysis continues evaluating species turnover and boundary clumping, to compare the distribution of species among sites. Turnover was measured as the number of times one species was replaced by another species between two sites. If the turnover is significantly low, the metacommunity shows a nested distribution, conversely, if the metacommunity exhibits a non significant or a significant positive turnover, it is consistent with the remaining distribution patterns. Finally, the boundary clumping was evaluated with Morisita's index (Morisita, 1971), to distinguish among evenly spaced, Gleasonian and Clementsian distributions (Leibold and Mikkelson, 2002; Silva et al., 2013).

4. RESULTS AND DISCUSSION

4.1 Seasonal fluctuations in amphipod communities associated with *Posidonia oceanica* meadows of Giannutri Island

4.1.1 Results

Samples were collected at Giannutri Island in 2014 during four seasonal sessions, providing a total of 1,144 individuals belonging to 62 species and 24 families. The most abundant species were *Apherusa chiereghinii* (110 individuals), *Liljeborgia dellavallei* (105 individuals), *Apolochus neapolitanus* (91 individuals), *A. picadurus* (73 individuals), *Gitana sarsi* (66 individuals). Some species were present in every season at varying abundances, such as *Dexamine spinosa* (63 individuals overall), and *Synchelidium longidigitatum* (35 individuals overall). Other species were recovered in single seasons: *Caprella acanthifera* appeared only in springtime while *Maera grossimana*, *M. hamigera* and *Gammarella fucicola* were present only in autumn, this latter at appreciable abundance (42 individuals).

The comparison between the two sampling points (Punta Secca-A and Secca di Punta Secca-B) showed substantial homogeneity, since only the number of individuals (*n*) significantly varied (Table 4.1) between sites in each season (bootstrap diversity *t*-test, $p < 0.001$ in all cases). Differences were observed for other parameters without a seasonal pattern, therefore suggesting that no real differences exist: dominance (*D*) in summer (bootstrap diversity *t*-test, $p = 0.012$), Shannon diversity (*H'*) and evenness (*J*) in autumn (bootstrap diversity *t*-test, $p = 0.040$ and $p = 0.021$, respectively). The number of taxa (S) did not show any significant difference between sites in all seasons (bootstrap diversity t-test, $p > 0.05$).

Table 4.1 - Comparison of seasonal pattern of diversity between localities: S = number of species; n = total number of individuals; D = dominance; H' = Shannon's diversity index; J = Pielou's evenness index. Sp = Spring; S = Summer; A = Autumn; W = Winter. A is for Punta Secca, B is for Secca di Punta Secca

	SpGIAN-A	**SpGIAN-B**	p	**SGIAN-A**	**SGIAN-B**	p
S	21	26	0.191	25	19	0.752
n	97	118	< 0.001	180	76	< 0.001
D	0.08	0.082	0.909	0.084	0.123	0.02
H'	2.75	2834	0.538	2699	2.42	0.128
J	0.903	0.87	0.223	0.839	0.822	0.92
	AGAIN-A	**AGAIN-B**	p	**WGIAN-A**	**WGIAN-B**	p
S	24	21	0.555	18	17	0.86
n	94	103	< 0.001	103	99	< 0.001
D	0.126	0.168	0.049	0.116	0.116	0.982
H'	2576	2221	0.052	2434	2411	0.875
J	0.811	0.73	0.021	0.842	0.851	0.784

A two-way PERMANOVA was carried out to test for the factors that mainly affected the structural differences in community composition, showing the significant influence of 'seasonality' ($F = 3.019$, $p < 0.001$) and no influence of the factor 'space' ($F = 1.333$, $p > 0.06$). The nMDS ordination plots evidenced highest variability in specific seasons and less pronounced differences in others, with a partial overlap of Winter, Spring and Summer, in contrast with a clear separation of the Autumn (Fig. 4.1, Kruskal stress = 0.18).

Since the two sampling points showed to be substantially homogeneous, data were cumulated *per* season and analyzed comparing the diversity indices, in order to highlight the fluctuations of the community throughout the course of the year.

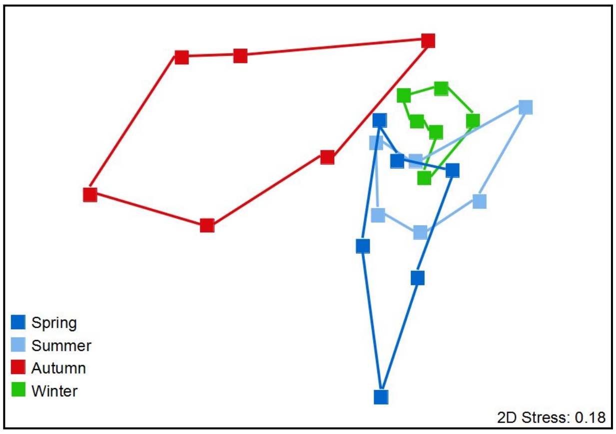


Figure 4.1 - nMDS ordination plot of the sampling sites in different seasons.

The number of recovered taxa and the Shannon diversity index increased from winter ahead during the year, reaching their maximum peak in autumn (Table 4.2).

Table 4.2 - Seasonal trend of the biodiversity components. *S* = number of species; *n* = total number of individuals; *D* = dominance; *H'* = Shannon's diversity index; *J* = Pielou's evenness index. *Sp* = Spring; *S* = Summer; *A* = Autumn; *W* = Winter.

	Sp	**S**	**A**	**W**
S	31	31	34	24
n	215	256	197	202
D	0.072	0.083	0.106	0.107
H'	2.966	2.781	2.722	2.545
J	0.864	0.81	0.772	0.801

The number of individuals increased from winter to spring, reaching a peak in the summer and then dropping to a minimum in autumn. Species evenness and dominance followed an opposite trend, as expected, while the equitability had its maximum peak in spring, corresponding to the minimum for the dominance (Table 4.2). SIMPER analysis highlighted the species that most influenced the seasonal similarity of communities (Table 4.3).

Table 4.3 - SIMPER analysis showing the seasonal similarity between sampling sites. Averaged Similarity percentage values are reported per season.

Spring	AVERAGED SIMILARITY = 46.36				
	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Apherusa chiereghinii	2.29	7.9	1.23	17.03	17.03
Gitana sarsi	1.65	6.76	2.79	14.58	31.62
Dexamine spinosa	1.52	6.05	5.33	13.05	44.67
Apolochus neapolitanus	1.44	4.07	1.33	8.79	53.46
Apolochus picadurus	1.05	3.09	0.78	6.67	60.13
Liljeborgia dellavallei	1.23	3.09	0.77	6.67	66.79
Phtisica marina	1.08	3.03	0.77	6.55	73.34
Synchelidium longidigitatum	0.87	2.19	0.78	4.72	78.06
Siphonoecetes neapolitanus	0.97	2.08	0.78	4.49	82.55
Caprella acanthtifera	0.86	2.06	0.76	4.43	86.99
Perioculodes aequimanus	0.69	1.42	0.48	3.07	90.06
Summer	AVERAGED SIMILARITY = 48.33				
	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Liljeborgia dellavallei	2.48	9.97	4.5	20.63	20.63
Gitana sarsi	2.13	8.8	3.61	18.2	38.83
Apherusa chiereghinii	1.81	6.51	4.7	13.47	52.3
Apolochus picadurus	1.95	5.74	1.28	11.87	64.17

Phtisica marina	0.97	3.16	1.3	6.54	70.71
Apolochus neapolitanus	1.14	3.07	1.28	6.34	77.05
Dexamine spinosa	1.34	2.31	0.75	4.78	81.83
Iphimedia minuta	0.86	1.9	0.76	3.94	85.77
Synchelidium longidigitatum	1.1	1.87	0.77	3.87	89.63
Orchomene humilis	1.05	1.4	0.47	2.89	92.52
Autumn	AVERAGED SIMILARITY = 33.44				
	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Gammarella fucicola	2.32	9.08	1.29	27.14	27.14
Apherusa chiereghinii	2.01	7.13	1.02	21.31	48.45
Dexamine spinosa	1.09	4.41	1.26	13.19	61.64
Apolochus neapolitanus	1.57	3.65	0.72	10.92	72.56
Liljeborgia dellavallei	1.18	3.23	0.76	9.67	82.23
Perioculodes aequimanus	0.99	2.41	0.76	7.2	89.44
Gitana sarsi	0.47	0.53	0.26	1.58	91.02
Winter	AVERAGED SIMILARITY = 57.72				
	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Liljeborgia dellavallei	2.39	11.3	2.19	19.58	19.58
Apolochus neapolitanus	2.24	10.96	3.12	18.98	38.56
Apolochus picadurus	1.97	8.07	3.48	13.99	52.55
Apherusa chiereghinii	1.52	7.15	3.54	12.39	64.94
Synchelidium longidigitatum	1.31	5.96	6.46	10.32	75.26
Dexamine spinosa	1.52	4.69	1.29	8.13	83.38
Gitana sarsi	1.36	4.5	1.26	7.8	91.18

In winter the dominant species were *Liljeborgia dellavallei*, *Apolochus neapolitanus* and *A. picadurus* contributing over 50% to the structuring of the community. In Spring, there were slightly significant differences, with *Apherusa chiereghinii*, *Gitana sarsi*, *Dexamine spinosa* and *A. neapolitanus* as dominant species. In Summer, a sort of continuity with the previous seasons emerged, and the species found were *L. dellavallei*, *G. sarsi* and *A. chiereghinii*. In autumn, a change in the dominant species occurred with *Gammarella fucicola* prevailing, followed by *A. chiereghinii* and *D. spinosa*. Pairwise comparisons between seasons (Table 4.4) showed the highest dissimilarities when comparing the autumn assemblages with respect to both summer and winter, while a similarity emerged between winter/spring/summer. This revealed the presence of two distinct patterns consisting of a set of winter-to-summer species and another one represented by autumn species. Such difference was mainly related to the appearance of *G. fucicola* as the most relevant species in differentiating the autumnal assemblage with respect to the others. The same species was never listed among those accounting for the cumulative 50% average diversity recorded between seasonal comparisons not involving the autumn (i.e., winter/spring and spring/summer).

Table 4.4 - SIMPER analysis showing the pairwise dissimilarity between seasons.

Winter/Spring	AVERAGE DISSIMILARITY 54.67					
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Liljeborgia dellavallei	2.39	1.23	3.83	1.41	7.01	7.01
Apherusa chiereghinii	1.52	2.29	3.55	1.98	6.49	13.5
Apolochus neapolitanus	2.24	1.44	3.01	1.24	5.52	19.02
Apolochus picadurus	1.97	1.05	2.99	1.64	5.46	24.48
Phtisica marina	0.64	1.08	2.37	1.14	4.33	28.81
Siphonoecetes neapolitanus	0.24	0.97	2.34	1.21	4.29	33.1
Caprella acanthifera	0	0.86	2.3	1.2	4.21	37.31
Dexamine spinosa	1.52	1.52	2.27	1.39	4.16	41.47
Gitana sarsi	1.36	1.65	2.26	1.18	4.14	45.61
Iphimedia minuta	0.17	0.86	2.09	1.02	3.82	49.43

Spring/Summer AVERAGE DISSIMILARITY 55.45

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Liljeborgia dellavallei	1.23	2.48	3.32	1.37	5.99	5.99
Apherusa chiereghinii	2.29	1.81	3.26	1.66	5.87	11.86
Apolochus picadurus	1.05	1.95	2.92	1.36	5.26	17.12
Dexamine spinosa	1.52	1.34	2.65	1.67	4.78	21.9
Orchomene humilis	0.54	1.05	2.5	1.14	4.5	26.4
Apolochus neapolitanus	1.44	1.14	2.43	1.24	4.38	30.78
Siphonoecetes neapolitanus	0.97	0	2.27	1.24	4.09	34.87
Synchelidium longidigitatum	0.87	1.1	2.17	1.25	3.91	38.79
Iphimedia minuta	0.86	0.86	2.17	1.29	3.91	42.69
Caprella acanthtifera	0.86	0	2.15	1.18	3.87	46.57
Orchomene similis	0	0.8	2.13	0.79	3.85	50.41

Summer/Autumn AVERAGE DISSIMILARITY 71.29

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Gammarella fucicola	0	2.32	6.25	1.82	8.77	8.77
Apolochus picadurus	1.95	0.37	4.72	1.75	6.63	15.4
Gitana sarsi	2.13	0.47	4.67	1.63	6.55	21.95
Apolochus neapolitanus	1.14	1.57	3.91	1.11	5.49	27.44
Liljeborgia dellavallei	2.48	1.18	3.84	1.56	5.39	32.83
Apherusa chiereghinii	1.81	2.01	3.45	1.45	4.84	37.68
Dexamine spinosa	1.34	1.09	2.81	1.47	3.95	41.62
Perioculodes aequimanus	0.29	0.99	2.57	1.18	3.6	45.22
Orchomene humilis	1.05	0.17	2.53	1.08	3.54	48.77
Synchelidium longidigitatum	1.1	0.33	2.35	1.17	3.3	52.07

Autumn/Winter AVERAGE DISSIMILARITY 67.93

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Gammarella fucicola	0	2.32	6.74	1.89	9.92	9.92
Apolochus picadurus	1.97	0.37	5.12	2.3	7.54	17.46
Apolochus neapolitanus	2.24	1.57	4.42	1.43	6.51	23.97
Liljeborgia dellavallei	2.39	1.18	4.35	1.49	6.41	30.38

Apherusa chiereghinii	1.52	2.01	3.68	1.55	5.42	35.8
Gitana sarsi	1.36	0.47	3.3	1.53	4.86	40.66
Synchelidium longidigitatum	1.31	0.33	2.82	1.45	4.15	44.81
Perioculodes aequimanus	0	0.99	2.76	1.2	4.07	48.88
Dexamine spinosa	1.52	1.09	2.74	1.34	4.03	52.91

4.1.2 Discussion

This study analyses the structure of amphipod community from Giannutri Island, together with its seasonal variation over a year, in order to understand which factors most influence the assemblages and which species are mostly involved in the dynamics of the studied community.

The results obtained from the univariate analysis of diversity showed no significant differences between the sampling sites, with both locations showing almost identical assemblages in all seasons. This finding suggests that *P. oceanica* meadows located in the gulf between Punta Secca and Secca di Punta Secca can be considered as a *continuum* and shows homogeneous environmental conditions in the different patches, which are therefore likely to be linked together. Assemblages show no variations of the diversity indices except for the number of individuals, which changes in every season, therefore suggesting no fragmentation for amphipod communities inhabiting the seagrass meadows.

Recent studies (Sturaro et al., 2014) have shown high degree of fragmentation of amphipods associated with *P. oceanica* (Bay of Revellata, Corsica, France), exhibiting a large variation in density and biomass at different spatial scales. This dissimilarity could be explained by the different sampling design of the two studies: Sturaro et al. (2014) analyzed a wider geographical scale so that their samples were separated by kilometres instead of hundreds of meters like in our study. Moreover, *P. oceanica* meadows from Giannutri Island appeared to be dense and uniform and lay in a homogeneous site with respect to physical, chemical and biological factors. On the contrary, the study carried out in the Bay of Revellata aimed at maximizing the heterogeneity among the studied sites to test for differences between areas subjected to different protection levels.

Seasonality was the most relevant factor in determining the changes in the assembly, as evidenced by PERMANOVA, showing that each season has its own unique community, characterized by a set of species only partially coincident with that of other seasons. This results in each season having its own trend, as highlighted by the nMDS graphic, albeit some overlap exists between winter, spring and summer, showing a common pattern of species in these three seasons. On the contrary, autumn assemblage does not overlap with any other season, in agreement with the results of precedent studies (Michel, 2007). This finding evidences that the community undergo a turn-over of species in autumn, which therefore represents the moment of maximum change. However our data involve observations from a single year, so that further studies extending the time-length of the record are needed to confirm such pattern.

The marked difference of autumnal assemblage is mainly due to the high number of taxa recorded (the highest among the four seasons) and to the emergence of species that do not appear in any other period. The annual cycle of *P. oceanica* may help explaining this pattern through the variation in the abundance of debris in the meadow. During spring and summer leaves production of *P. oceanica* reaches its maximum, in parallel with the development of epiphyte community, with a constant production and a consequent increase of the debris through the erosion of foliar apices due to both epiphytic load and grazing. In autumn, the senescent leaves fall massively, according to the life cycle of the plant itself coupled with the progressive increasing of hydrodynamism, thus resulting in a massive coverage of the litter. This autumn related change in the availability of organic debris could trigger the emergence of species typical of this season, like opportunist litter-feeding that find their perfect habitat at this time (Gallmetzer et al., 2005; Michel, 2007). This hypothesis is in agreement with previous studies showing that the characteristics of the flowering plants are among the factors that best explain the variability of amphipod assemblages, and that a substantial part of the variation in assemblies of the vagile fauna is attributable to the density, biomass and coverage of epiphytes (Schneider and Mann, 1991; Edgar and Robertson, 1992; Sánchez-Jerez et al., 2000; Scipione and Zupo, 2010; Zakhama-Sraieb et al., 2011). More recent studies have hypothesized that the characteristics of the prairie may explain only a small part of the variation of associated communities, so that factors such as predation pressure by fish and large invertebrates, availability of trophic resources or behavioral needs should explain the observed changes in amphipod communities (Prato and Biandolino, 2003; Sturaro et al., 2014).

Besides the abrupt change in community composition in the entering of the autumn, there is a temporal trend in the number of taxa showing a progressive increase from winter to fall, which is the moment of maximum diversity. At this time, the species evenness is at its minimum values while the number of taxa is at its maximum. The number of individuals shows a cycle with its minimum in winter too, but the peak values are recorded in summer instead of autumn.

Our results thus suggest a dynamic year-round cycle, with a maximum of individuals in the summer, probably connected to a reproductive peak, and the higher diversity in autumn. Besides the need of a validation over a multi-annual basis, our data are generally in agreement with those reported in literature and with *P. oceanica* life cycle (Gambi et al., 1992; Degard, 2004; Bedini et al., 2011). However, the few studies considering the seasonal dynamics of amphipod communities associated to *P. oceanica* explain the maximal abundance and diversity of amphipods observed in late summer and autumn as not dependent on meadow parameters, but more linked to seasonal differences in other abiotic and biotic factors like predation pressure and single taxon dynamics (Nelson, 1979a, 1979b; Michel, 2011, 2014). Our data cannot address the role of ecological species interactions influencing the seasonal fluctuations of assemblages, but the analysis of the species most involved may provide some insights on the role of single taxon dynamics. *Apherusa chiereghinii* was found to be always the most abundant, being the taxon more representative of the whole community, as also evidenced by previous studies and so to be considered as a target species for further investigations of ecological nature. Another all-year-round very abundant taxon is *Apolochus neapolitanus*, a very common species in seaweed and in *P. oceanica* meadows. *Gammarella fucicola* is the species most responsible for the change in community structure in autumn. This species is usually found on the litter, being a detritus feeder and so it has been described as having an important role in the degradation of detritus, able to regulate the flow of matter in *P. oceanica* (Michel et al., 2014). The few studies present in literature do not show comparable results in terms of single species involved in seasonal changes since there is not a common pool of species associated with *P. oceanica* meadows. On the contrary, sets of different species are evidenced across several areas of the Mediterranean, suggesting that the geography has an important role in shaping the community. In this view, *G. fucicola* as recorded in Giannutri Island may represent a predominantly detritus feeder ‘type species’ having a ‘bloom’ in the fall due to the increase in senescent leaf biomass and subsequent increase of debris. However, which species will be predominant at changing conditions depends not only by the cycle of the seagrass, but also by local factors, thus requiring deeper studies linking mechanisms and patterns of community structure.

4.2 Spatial and temporal variation of coastal mainland *vs*. insular amphipod assemblages on *Posidonia oceanica* meadows[1]

4.2.1 Results

Two-way ANOVA showed no significant differences between localities and sampling seasons in terms of species richness (Fig. 4.2 and Table 4.5), while a significant difference in terms of total abundances has been observed between localities (Fig. 4.2 and Table 4.5). Nor the diversity (*H*') neither the evenness (*J*) have shown significant differences between localities and years (Table 4.5), although GIAN exhibited substantially higher values in the second sampling season (Fig. 4.2).

The samples collected in summer 2012 provided a total of 569 individuals, belonging to 37 species, 29 genera and 20 families (Table 4.6). The most abundant species were Caprella acanthifera (99 individuals), Phtisica marina (73 individuals) and Apolochus neapolitanus (69 individuals).

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[1] A slightly modified version of this paragraph has been accepted (pending revision) on **Marine Biodiversity** ISSN: 1867-1616

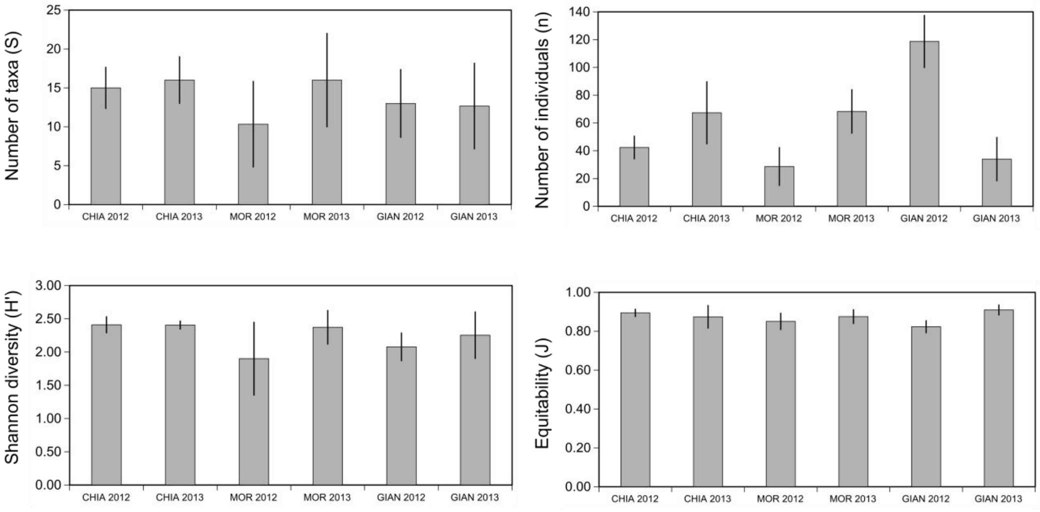

Figure 4.2 - Average values of diversity indices calculated for the different localities in the two sampling periods.

Table 4.5 - Results of the two-factor ANOVA for species richness (S), total abundance (n), Shannon-Wiener diversity (H') and Pielou's evenness (J).

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

The number of species (*S*) showed similar values across all sampling localities (Fig. 4.2), while the number of individuals (*n*) showed the highest value at GIAN, followed by CHIA and MOR (Fig. 4.2). 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 (Fig. 4.2).

Table 4.6 - Abundance of amphipod species (total number of individuals per 0.48 m^2) identified in *P. oceanica* meadows from different localities and years.

		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
Megaluropidae	*Megaluropus massiliensis* Ledoyer, 1976	0	0	0	0	0	0
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
	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
	Leptocheirus pilosus Zaddach, 1844	1	0	0	0	0	0
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

In summer 2013, the overall number of individuals was 509, belonging to 46 species, subdivided in 34 genera and 23 families (Table 4.6). *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 number 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 high evenness than 2012 (Fig. 4.2).

The nMDS ordination plots evidenced temporal heterogeneity between the assemblages in different years (Fig. 4.3).

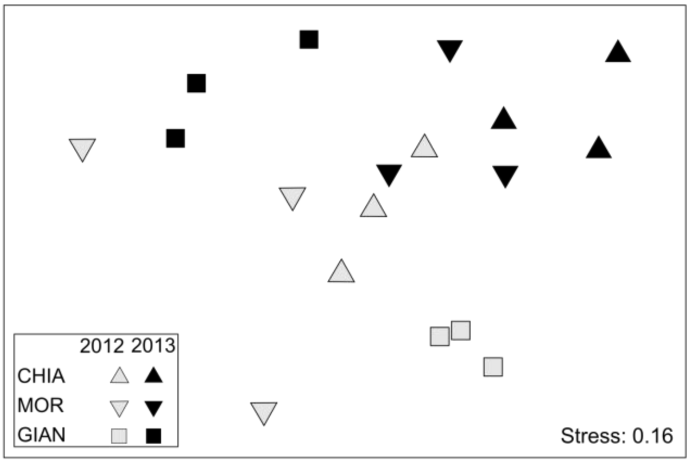

Figure 4.3 - Non metric multidimensional scaling ordination (nMDS) based on the Bray-Curtis distance measured on abundance data (3 replicates).

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 ($F = 3.499$, $p < 0.01$), as well as by 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, $p < 0.05$) or CHIA alone (2013, $p = 0.033$), whilst CHIA and MOR always showed similar assemblages ($p > 0.13$ in 2012 and 2013). SIMPER analysis showed a greater variability in between-localities dissimilarity 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 4.7), 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 in CHIA and MOR mainland sites (Table 4.7), where C. acanthifera, *M. cumbrensis* and *A. neapolitanus* accounted for most of the variation, due to their decrease in abundance or even disappearance (Fig. 4.4).

Table 4.7 - SIMPER analysis indicating dissimilarities in amphipod composition between localities and among years.

	2012			2013			2012/2013	
	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

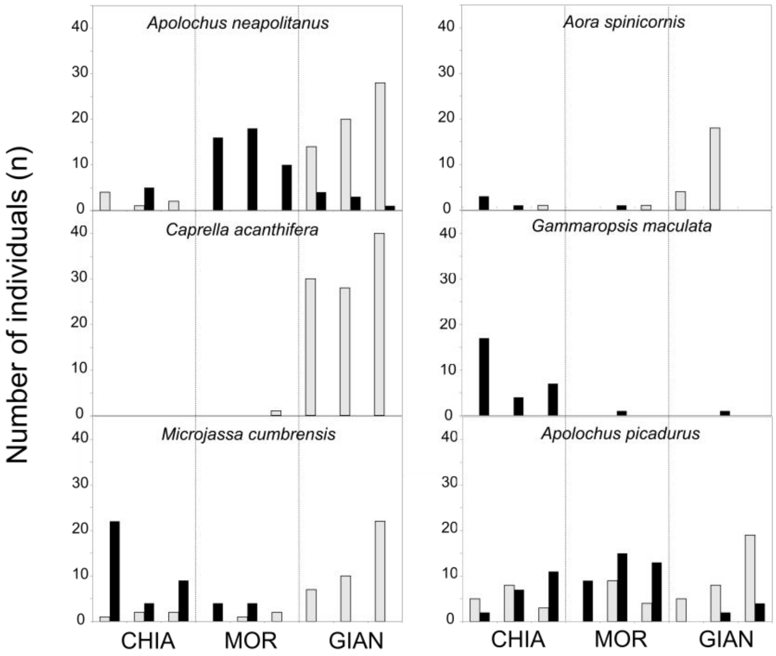

Figure 4.4 - Number of sampled individuals that mostly contributed to the dissimilarity among localities (CHIA, MOR and GIAN) and years 2012 (gray) and 2013 (black).

4.2.2 Discussion

The amphipod assemblages analyzed in three Central Tyrrhenian *P. oceanica* meadows have showed a relatively high number of species (more than 40 in both years), most of them with low frequency and abundance. Despite the relative small size of the samples, our findings are in agreement with the observations from other Mediterranean seagrass meadows studied at similar depth, type of sampling and period of the year (Scipione, 1998; Zakhama-Sraieb et al., 2011). Our results show different spatial and temporal patterns of amphipods in *P. oceanica* meadows when considering the assemblages from mainland (i.e. CHIA and MOR) *vs*. insular (i.e. GIAN) coastal meadows, the latter being characterized by a significant variability in time that contrasts with the constant composition shown by the mainland sites.

Both species diversity and evenness did not show substantial differences between localities and years, although amphipod assemblages from the insular area showed a significant temporal decrease in terms of species diversity and number of individuals. However, the degree of functional redundancy found in many marine communities (Micheli and Halpern, 2005) can make the use of such indices not suitable at all as general descriptors of community (Sánchez-Jerez and Ramos-Esplà, 1996; Sturaro et al., 2014). Indeed, most of amphipods show common responses to specific ecological functions, such as microhabitat choice, trophic preference and functional feeding mechanisms (Michel et al., 2014), so that an array of different species may occupy the same functional role.

Overall, our findings highlight the role of spatial scales in determining the patterns of amphipod distribution on seagrass meadows, which influence both the degree of connectivity and habitat similarity between localities. Geographic distance directly influences connectivity (i.e. the degree to which a "landscape" facilitates or impedes the movement of genes, individuals and species), which is considered one of the main driving forces in structuring marine communities (Kinlan and Gaines, 2003; Cowen et al., 2007). Accordingly, closely-located communities should generally be more similar than those located further apart; this so-called 'distance decay effect' (Soininen et al., 2007) can be amplified by the low dispersal ability of many amphipod species due to the absence of 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 (Sánchez-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). This geographic-related pattern is also found in the temporal responses of amphipod populations, so that closer localities show more stable assemblages with respect to the high temporal variability of insular ones.

Along the mainland study area (i.e. CHIA, MOR), seagrass meadows are equally exposed to the effects of human activities and characterized by the same amount of organic load given by the external input of two main rivers, Chiarone to the North and Fiora to the South, influencing the sedimentological regime and water turbidity (Paganelli et al., 2013). This can have indirect influence on community composition (Ben Brahim et al., 2010) by altering the structural properties of *P. oceanica* meadows (Alcoverro et al., 1997; Erftemeijer and Lewis, 2006; Castejón-Silvo et al., 2012), as well as direct effects on the abundance and distribution of specific groups of organisms associated with seagrasses (Blake and Duffy, 2010; Korpinen and Westerbom, 2010). Differences in the assemblages of amphipods in coastal mainland vs. insular localities can be affected by the different composition of substrata, albeit the persistence of species sharing common responses to similar environmental conditions, should decreases the temporal variability of local assemblages in coastal mainland meadows. Although limited in time, our findings show the variability of assemblages in insular meadows, which is probably influenced by factors related more to the natural demographic oscillation of amphipods, the irregularity of recruitment or variation in predation pressure (Nelson, 1979a, 1979b; Sturaro et al., 2015). However, to better understand the role of these complex mechanisms is of paramount importance the knowledge about the seasonal fluctuations of communities over time.

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 (GIAN) appears 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. 4.4). This between-years variation in abundance was probably related to complex mechanisms involving not only spatial patterns (e.g. distance from other source populations) but also species-specific features such as differences in recruitment, maturation and reproduction periods. Accordingly, species as *A. neapolitanus* and *C. acanthifera* in the Mediterranean exhibit large fluctuations of populations, often related to variability in food resources, natural dynamics or predation pressure (Francour, 2000; Leite, 2002).

Our results also enhance the role of co-occurring local (niche-based) and/or regional (dispersal-based) processes in the structuring of ecological communities (Leibold et al., 2004; Holyoak et al., 2005). Indeed, the relative temporal stability of assemblages in mainland coastal meadows suggests the possible role for niche-based processes (e.g. species sorting), which allow the coexistence of species sharing functional responses but able to differentiate their niche requirements (e.g. microhabitat choice; Logue et al., 2011; Michel et al., 2014). By contrast, the temporal variation of insular assemblages may be given by the species turnover related to the limited dispersal and the geographic isolation (insularization) of the meadows. 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 the characteristics explained so far and the high variability of assemblages over multiple spatial scales (Sturaro et al., 2014, 2015), amphipods on 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).

4.3 Scale matters: the geographic insurgence of metacommunity structures in amphipods of *Posidonia oceanica* meadows

4.3.1 Results

The first axis of the spatial PCA explained about 70% of total variance, mostly related to the chl-a concentration ($r = -0.701$), while the water transparency, measured as diffuse attenuation coefficient at 490nm (kd_{490}) accounted for most of the variation ($r = 0.546$) along the second axis of ordination (ca. 20%). From a geographic point of view, the highest PCA scores were found along the coastal mainland areas, while the insular area of GIAN was characterized by significant lower values (Fig. 4.5).

The piecewise regression on the rank abundance (Fig. 4.6) showed a significant breakpoint at all scales in each year ($p < 0.001$ in all cases). A higher proportion of rare species (ca. 80%) was observed at micro-scale for GIAN and MOR in both years (Fig. 4.6), while a significant temporal increase was observed in CHIA (Fig. 4.6). At meso- and macro-scale the proportion of rare species followed opposite patterns, decreasing and increasing, respectively, between the two sampling periods (Fig. 4.6).

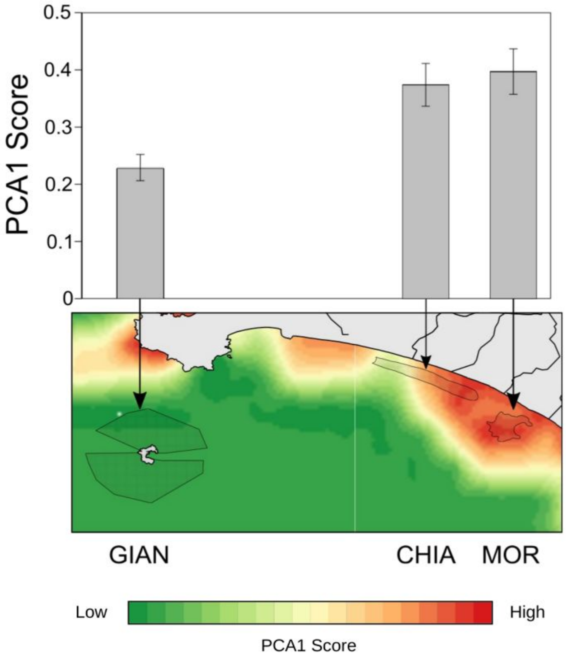

Figure 4.5 - Average values of the first axis of the spatial PCA for each sampled locality. On the bottom, the geographic representation of spatial PCA showing the distribution of PCA scores within the study area (see the Results section in the main text).

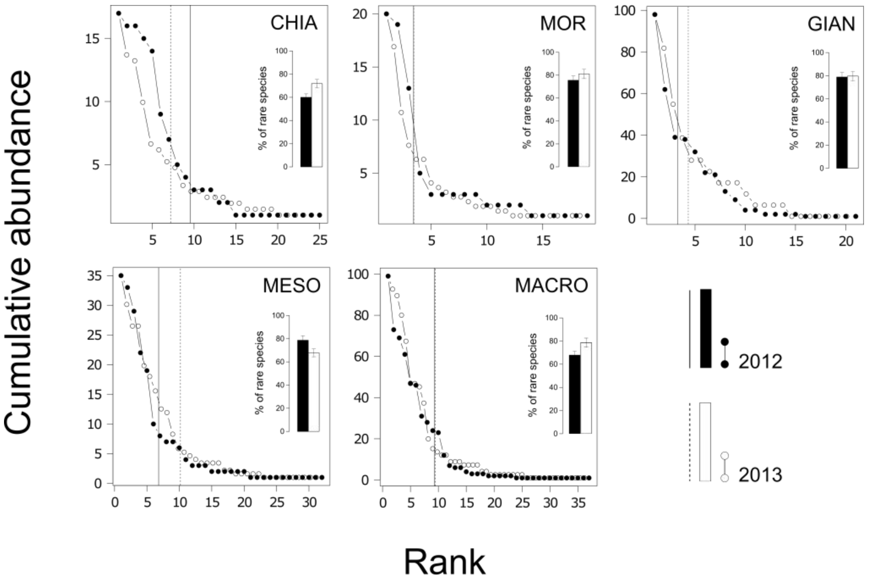

Figure 4.6 - Piecewise regression on the rank-abundance curves of amphipods at different spatial scales and years. Inset graphs show the percentage of rare species.

When considering the primary axis of variation, patterns of metacommunity structure at micro-scale were almost conservative in time, observing no species turnover in all sampled localities (Table 4.8). CHIA showed non-coherent assemblages in consecutive years, which is consistent with a random distribution of species in response to the uncovered environmental gradient (Table 4.8). MOR followed the same pattern of CHIA in 2012, albeit in 2013 exhibited a negative coherence and apparent absence of species turnover, consistent with a checkerboard pattern of assemblage that occurs when pairs of species are mutually exclusive (Diamond 1975), and if mutually exclusive responses are independent of each other along the gradient. In both sampling periods GIAN followed the same checkerboard pattern of species distribution. At meso-scale, the EMS analysis showed exactly the same pattern in years, with a not significant coherence, that is, a completely random distribution of species (Table 4.8).

Table 4.8 - Results of the EMS analysis showing the best-fit structures explaining the pattern of distribution of amphipods on seagrass meadows at different spatial scales and years. RA1 and RA2 are for the % of inertia explained by the first two axes of Reciprocal Averaging. EmAbs, Embedded Absences; Rep, Species replacements; Mor, Morisita's index.

		Coherence					Turnover			Boundary clumping		Pattern
		RA1	RA2	EmAbs	*p*	Mean (±SD)	Rep	*p*	Mean (±SD)	Mor	*p*	
Micro	CHIA	53.2	46.7	6	0.223	4.48 (±1.243)						Random
		56.7	43.3	8	0.056	4.7 (±1.703)						Random
	MOR	62.6	37.5	6	0.052	5.7 (±1.10)						Random
		60.5	39.5	11	**0.001**	5.7 (±1.636)						Checkerboard
	GIAN	73.1	26.9	8	**< 0.001**	4.4 (±0.996)						Checkerboard
		57	43	10	**< 0.001**	4.4 (±1.577)						Checkerboard
Meso		29.6	21.9	47	0.574	49.4 (±4.273)						Random
		27.4	19.9	45	0.142	54.8 (±6.666)						Random
Macro		22.3	17.1	79	**0.007**	112.8 (±12.594)	810	0.108	1633.7 (±513)	2.042	0.08	Quasi-Gleasonian
		23.2	16.1	80	**< 0.001**	150.2 (±8.35)	2211	0.397	2671.7 (±543.757)	0.124	**0.03**	Quasi-Evenly Spaced

When considering the macro-scale, patterns in species distribution changed drastically (Table 4.8). In 2012, the results were most consistent with a quasi-Gleasonian distribution (Fig. 4.7), characterized by species turnover indistinguishable from random and boundary clumping that occur idiosyncratically along the gradient (the Gleason's concept of species individualistic responses, Gleason 1926). In 2013, species distributions showed hyperdispersed boundaries (Fig. 4.7), thus indicating quasi-evenly spaced gradient whit maximal differences in tolerances among species to given gradients (Table 4.8).

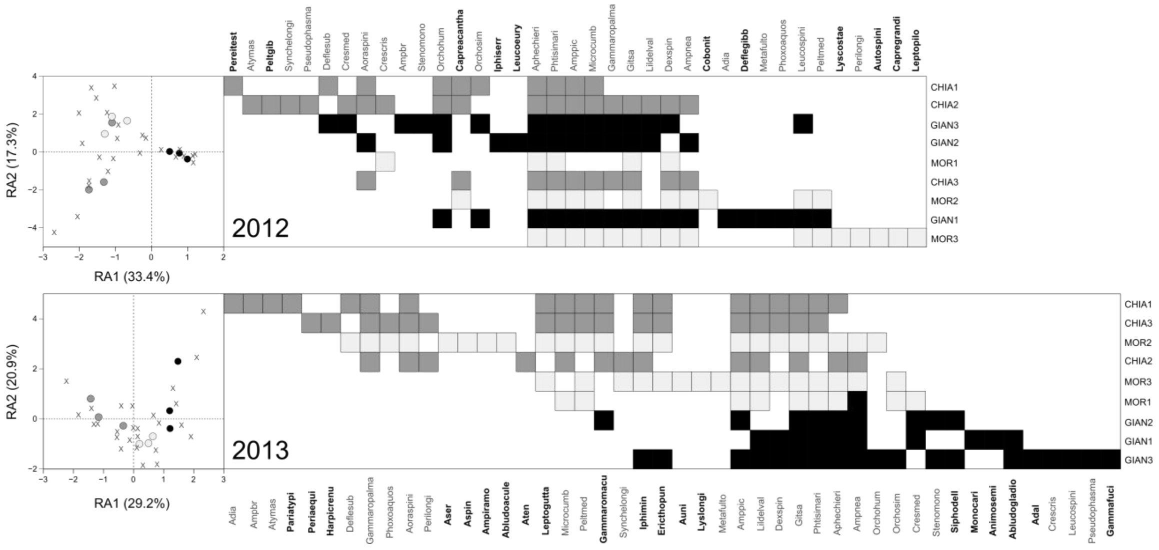

Figure 4.7 - Ordination of species (crosses) and sites/localities (circles) given by the Reciprocal Averaging (RA) and schematic representation of the metacommunity structures at macro-scale. Black, light and dark gray colors in figures are for GIAN, CHIA and MOR, respectively. Bolded acronyms are for those species found exclusively in their respective years of sampling.

The first axis of ordination (RA1) was at least five-times greater than RA2 at all scale of investigation and years (Table 4.8), indicating the presence of a single main gradient regardless the scale of observation. When ordered accordingly to the second axis of RA, the distribution of species always followed patterns characterized by the apparent absence of turnover with not significant, or at least negative coherence, meaning random to checkerboard distribution to the uncovered (albeit less informative) second gradient at all scales (Table 4.8).

4.3.2 Discussion

In this work, the elements of metacommunity structures (EMS, Leibold and Mikkelson, 2002; Presley et al., 2010) are used to uncover patterns in the distribution of amphipods on *Posidonia oceanic*a meadows at different spatial and temporal scales. Our findings show how the assemblages are scale dependent and almost conservative in time, observing the onset of species turnover for increasing geographic scales. When considering the micro scale of investigation, differences arise between insular *vs*. coastal mainland assemblages, with these latter having non-coherent responses of species to the uncovered gradients. Although most of natural assemblages are characterized by non-random structures (Gotelli and McCabe, 2002), randomness may occur when species do not respond to the same environmental gradient and, therefore, their distributions do not form a coherent structure, indicating that species occurrence with respect to the latent gradient is random (Leibold and Mikkelson, 2002). However, gradients may differ in their range of variation among spatial scales, with some variables showing large variation at small scales and others at very large scales, therefore generating contrasting results in communities dissimilarity over space (Borcard et al. 2004).

The results obtained for the insular assemblages of GIAN are consistent with a checkerboard pattern of species composition, where species occupying similar niches are expected to never occur (Gotelli, 2000) due to competitive exclusion or the influence of abiotic variables. Given the reduced scale of investigation, local abiotic conditions in GIAN are unlikely to influence the distribution of species, which is probably related to specific demographic traits such as irregularity of recruitment, variation in predation pressure and natural demographic oscillation (Nelson, 1979a, a979b; Sturaro et al., 2015).

Abiotic conditions in coastal mainland localities (CHIA and MOR) are mainly regulated by the effects of human activities, as well as by the contribution of two main rivers, Chiarone to the North and Fiora to the South, both influencing the amount of organic load, the sedimentological regime and the turbidity of coastal waters (Paganelli et al., 2013). This constant alteration of abiotic conditions over time may thus promote the persistence of pool of species that exhibit common responses to the same homogeneous environment (Meynard et al., 2011). Coexistence should therefore be driven by the ability of species to use different resources and/or microhabitats. Indeed, recent findings (Michel et al., 2014) have shown the possibility for many amphipod species to differentiate their grazing habits, with most of them having a mixed diet relying on several food items (Michel et al., 2014). This can allow a more efficient partitioning of the resources, reducing trophic niche overlap and limit the competition among species (Michel et al., 2014).

As one might expect, short distances should improve the connectivity between sites, counteracting the effects of ecological drift (i.e. neutral dynamics governed by demographic stochasticity, Bell, 2000; Hubbel, 2001) and leading the homogenization of metacommunity due to the reduction in compositional differences among patches (i.e. beta diversity). However, our results are more consistent with patterns of heterogeneity in amphipod assemblages, even at small spatial scales (Sturaro et al., 2014). Nevertheless, a certain degree of uncertainty associated with the size of incidence matrices and the choice of appropriate null models should be accounted when interpreting the results (Leibold and Mikkelson, 2002). Our findings show quite different patterns of species assemblage when considering the micro scale at MOR, characterized by a checkerboard structure in the second year of sampling. Whether or not the observed differences in MOR are the result of statistical pitfalls or real differences in community composition should however require greater sampling efforts in order to increase the number of sampling sites at micro scale, to disentangle the effects of statistical artefacts in metacommunity structure.

Although the increasing spatial scale, the geographic distance among the coastal mainland localities at meso scale (CHIA and MOR) still remains little or no influential in determining the observed pattern of species distribution, which is random for both years. A possible explanation can be given by the degree of connectivity among localities (i.e. the way with which the movement of species, individuals or genes can be facilitated among habitat patches, Urban et al., 2009), which is thought to be one of the main driving forces in structuring marine communities (Kinlan and Gaines, 2003; Cowen et al., 2007). Indeed, in the study area, both surface and bottom currents show a dynamic field characterized by prevailing North/North-West orientation with an average intensity of 30-40 cm/s during the summer. Such conditions may therefore increase the connectivity between localities, promoting the dispersal flow of species otherwise limited in their dispersal ability due to the lack of pelagic larval forms (Thomas, 1993). Under this scenario, homogeneity in abiotic conditions, coupled with the passive dispersal of most of amphipod species, may thus suggest the role of stochastic processes in regulating the structure of local (meta)communities.

At macro scale, the amphipods/seagrass metacommunity shows a moderate turnover of species, which means that the number of species replacement is not lower than expected and, therefore, a certain degree of difference in species composition between localities should exists. This is consistent with the pattern of ordination given by the RA, which shows a clear partitioning between insular *vs.* coastal mainland assemblages in 2012 and a less pronounced partitioning in 2013. The boundary clumping (i.e. the degree to which the boundaries of different species ranges clustered together, Leibold and Mikkelson, 2002) in 2012 is not significant, which leads to assume the existence of a quasi-Gleasonian metacommunity structure. Under this view, communities are considered mere collections of species, whose ranges happen to overlap in space and time (Gleason, 1926). This kind of structure assumes idiosyncratic (individualistic) responses of species to the latent gradients and, as a consequence, communities gradually change in species compositions across space (Leibold and Mikkelson, 2002; Henriques-Silva et al., 2013). Such a pattern is probably related to the spatial scale of investigation, able to reduce the connectivity between localities and increase the heterogeneity of abiotic conditions, thus promoting the emergence of a quasi-Gleasonian structure at the metacommunity level. In 2013, species do not appear to show significant clustering along the ordination axes, which is consistent with a quasi-evenly spaced gradient of amphipods assemblage on *P. oceanica* where no discrete communities appear, and species ranges are arranged more evenly than expected by random chance (Tilman, 1982). This distribution is typically generated by trade-offs associated with strong interspecific competition, with species characterized by maximal differences in environmental tolerances (Presley and Willig, 2010) and the ability to explore alternative resources (Tilman, 1982).

This between-years variation in metacommunity structure is probably due to the peculiar distribution of species, observing the appearance/disappearance of some of them between the localities from year to year. Significant abiotic changes at macro scale are unlikely to occur over short time spans, although unexpected and localized events (e.g. flash floods, storms or human activities) may change the structure of communities at micro scale, thus influencing the whole metacommunity. A further explanation can be given by species-specific features, such as differences in recruitment, maturation and reproduction periods. Indeed, some species of amphipods in the Mediterranean (e.g. *A. neapolitanus* and *C. acanthifera*) have shown to exhibit large fluctuations of populations, often related to variability in food resources, natural dynamics or predation pressure (Francour, 2000; Leite, 2002).

5. CONCLUSIONS

Posidonia oceanica is the most abundant seagrass in the Mediterranean area, where it is a ‘foundation species’, defining much of the structure of local communities by modulating and stabilizing fundamental ecosystem processes and by creating locally stable conditions for the associated species (Dayton, 1972). *P. oceanica* meadows are well known for their small-scale spatial heterogeneity (patchiness of the communities), (Balestri et al., 2003; Borg et al., 2005, 2006; Montefalcone et al., 2008) associated with little temporal variability (Duarte, 1991; Marbà et al., 1996; Guidetti et al., 2002). Spatial differences in the structure of the meadows and seagrass seasonal cycle, as leaf canopy height and shoot density, are key drivers in determining spatial and temporal patterns of the associated fauna, influencing species richness and abundance of the leaf stratum motile macroinvertebrate assemblages (Michel, 2011; Bedini et al., 2011). This latter is strongly influenced by the features of both the plant, which is a growing substrate with high seasonality and its epiphytes (Mazzella and Ott, 1984), showing specific adaptations to various microenvironments.

Crustacean amphipods constitute one of the most abundant groups of vagile fauna associated with *P. oceanica* beds because of their ability to colonize different micro habitats represented by the foliar stratum and its epiphytes, rhizome layer and matte. Moreover, they play a crucial role in recycling organic matter as important secondary producers, and serve as a food source for a large variety of marine predators. Despite their relevant importance, amphipods ecology still remains partially unknown together with the role of spatial scale and the environmental characteristic of habitats on their assemblage structure. Local differences may explain a relevant part of the variability in the total abundance, specific diversity and identity of dominant species, with many studies suggesting that spatial variation could exist even at a small scale (i.e., 1 to 10 m) (e.g. Gambi et al., 1992; Sànchez-Jerez et al., 1999a ; Degard, 2004; Zakhama-Sraieb et al., 2011). Larger scale variations (about 100 m), on the other hand, also concern specific richness and diversity of amphipods (Sturaro, 2007). Temporal variation can also be considered at several scales and important seasonal influence on the spatial distribution of invertebrates within the meadows also exists (Bedini et al., 2011).

In this work, we tried to better understand how amphipod assemblages are structured, observing the temporal variability of communities in *P. oceanica* patches, both seasonally and between years. We also wanted to verify the influence of spatial scales on the structure of amphipod communities inhabiting meadows from different localities, discussing the role of geographic distance as a proxy of species dispersal and habitat heterogeneity.

To test for seasonal cycles in amphipod assemblages and their association with seagrass life cycle, observations have been carried out at a single locality, Giannutri Island. Seasonality turned out to be a significant factor in determining changes in the assembly of communities, with each season showing its own assemblage characterized by a set of species. However, while winter, spring and summer seasons showed a pattern of common species, autumn had its own highly differentiated assemblage, characterized by the highest number of taxa and by the emergence of species not found in other seasons. These seasonal variations appear to be linked to the seasonal cycle of the plant, since the abundance and species richness is associated with the availability of food resources (i.e. ephiphytes and debris). Indeed, the emergence of *Gammarella fucicola* that characterizes (and mainly differentiates) the autumn assemblage, witnesses the dominance in the community of detritus-feeder species in this season, likely due to the increase of senescent leaf biomass and subsequent increase of the debris.

Spatial and temporal patterns have been studied by sampling in two subsequent summers in three different localities selected to represent geographically close mainland coastal areas (i.e. Foce del Chiarone, CHIA and Punta Morelle, MOR) *vs.* insular meadows (i.e. Giannutri Island, GIAN). The results showed that the assemblages from GIAN were characterized by a significant variability in time that contrasts with the constant composition shown by mainland sites. This between-years variation of insular assemblages could be related to the low turnover of species due to amphipods limited dispersal and to the geographic isolation (insularization) of the meadows, coupled with species-specific features such as differences in recruitment, maturation and reproduction periods. The relative temporal stability of assemblages in mainland coastal meadows (CHIA and MOR) suggests a possible role for local niche-based processes (e.g. species sorting), which allow the coexistence of species sharing functional responses but able to differentiate their niche requirements (e.g. microhabitat choice; Logue et al., 2011; Michel et al., 2014). Geographic distance seems to be one of the possible drivers of amphipods assemblage structure, with closer communities more similar than far away ones. However, geographic distance can be considered a proxy for specific characteristics of habitats, with closer localities environmentally similar (besides highly connected), thus suitable for a pool of species that exhibit the same functional responses to common environmental conditions (Meynard et al., 2011).

Our results suggest that the spatial scale considered likely has an indirect role in influencing the degree of species replacement across communities, as the increasing geographic distance led to the increasing probability of finding different environmental conditions. However, the 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. Thus, studies aimed at assessing at which scale dispersal-based regional processes overcome niche-based local processes is still an open question whose answer could be of help in explaining, modelling and conserving biodiversity in seagrass-systems.

Given the characteristics explained so far and the high variability of assemblages over multiple spatial scales (Sturaro et al., 2014, 2015), amphipods on 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). Therefore, a metacommunity approach in the system amphipods-*P. oceanica* may be useful to test whether taxa show similar responses to the main structuring processes affecting the entire metacommunity (Siqueira et al., 2012). To this end, our data on community structure were arranged and analysed at micro-scale (tens of metres), meso-scale (less than 10 Km) and macro-scale (tens of Km) and then analysed using the Elements of Metacommunity Structure approach (EMS, Leibold and Mikkelson, 2002; Presley et al., 2010). At micro- and meso-scale the geographic distance between sites seems to be not influential, with a random distribution of species, which is known to be related to the different species' responses to the same environmental gradients. At macro-scale, the amphipods/seagrass metacommunity shows a moderate turnover of species, which means that the number of species replacement is not lower than expected and, therefore, a certain degree of difference in species composition between localities does exist. These results highlight the existence of different, scale-dependent mechanisms of community assembly and suggest the existence of a ’minimum geographic scale’ (i.e. tens of kilometres) over which the presence of a moderate turnover appears. At such scale, environmental heterogeneity may drive community composition through both the sorting of species with particular habitat/resource requirements and through competitive interactions with possible exclusion. Species distribution is therefore related more to habitat selection and interactions than to colonization/extinction dynamics (i.e. the species-sorting perspective) (Soininen et al., 2007).

Although the limited extension of our study area does not allow an overall generalization of our findings, mechanisms of amphipods assembling on *P. oceanica* resulted to be scale dependent. The niche-based processes seem to be the main drivers in community composition, so that the increasing geographic scale should enhance the role of passive dispersal, acting at different scale and time. These observations need to be carried out over larger scales (e.g. the Mediterranean basin) to clearly highlight the geographic extent at which regional processes surpass local ones in explaining the pattern of biodiversity. This could have significant implications for the management and conservation of seagrass systems. Recent findings in conservation biology, indeed, highlighted the need to understand the patterns of biodiversity in a spatial context, focusing on the dynamic responses of habitat loss at landscape level (i.e. the secondary loss of biodiversity, Cabeza and Moilanen, 2001). Anthropogenic alterations may act at different spatial scales, ranging from local to regional and global, so that a metacommunity perspective becomes fundamental to assess the relative importance of spatial and environmental components in the variability of community assemblages (Heino, 2013). Our findings highlight the need to provide adequate degrees of protection at local scale, enhancing habitat heterogeneity within and between different spatial extents.

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