SEASONAL VARIATIONS OF AMPHIPOD ASSEMBLAGES IN A *POSIDONIA OCEANICA* (LINNAEUS) DELILE, 1813 MEADOW FROM THE CENTRAL TYRRHENIAN SEA (ITALY)

BY

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ABSTRACT

Temporal variability in species composition and abundance may enhance coexistence in ecological communities, especially when subjected to strong seasonal patterns. Species distribution through time may be related to many factors, such as changes in the structure and functioning of preferred habitats, variations in ecological interactions or asynchronous patterns in species life cycles. Here, data from a one-year survey of amphipod assemblages from a nearly undisturbed *Posidonia oceanica* meadow are used to investigate the seasonal patterns in species abundance and identity. Our results highlight the presence of a core group of species inhabiting the meadow throughout the year, although an in depth analysis reveals three differentiated seasonal assemblages corresponding to autumn, winter, and a warm season clustering of both spring and summer. The observed patterns suggest the interplay between different mechanisms drives the coexistence of amphipods over the whole year, including niche partitioning, predation pressure, and variations in life history traits.

Key words. — *Posidonia oceanica*, amphipods, seasons, niche, ecological interactions, Tuscan Archipelago

RIASSUNTO

Variazioni temporali nella composizione e abbondanza delle specie sono alla base della coesistenza interspecifica nelle comunità ecologiche, specialmente quando si registra una forte stagionalità. La distribuzione temporale delle specie può essere correlata a molti fattori, quali i cambiamenti nella struttura e nel funzionamento degli habitat preferiti, le variazioni nelle interazioni ecologiche oppure l'asincronia dei cicli vitali delle specie. In questo lavoro, sono state studiate per un

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anno le comunità di anfipodi di una prateria di *Posidonia oceanica* scarsamente interessata da disturbo antropico, al fine di indagare i modelli stagionali di abbondanza e distribuzione delle specie. I risultati evidenziano la presenza di un gruppo di specie che abita la prateria durante tutto l'anno, anche se un'analisi più approfondita evidenzia profondi differenziamenti della struttura di comunità corrispondenti all'autunno, all'inverno e ad una stagione calda costituita da primavera ed estate. I pattern osservati, se confrontati con le pregresse conoscenze della variazione stagionale dei posidonieti e dell'ecologia degli Anfipodi, suggeriscono che sia l'interazione tra più meccanismi a promuovere la coesistenza tra le varie specie durante l'anno quali ad esempio la suddivisione della nicchia, la pressione di predazione e le variazioni nelle caratteristiche dei cicli vitali.

Parole chiave. — *Posidonia oceanica*, Anfipodi, Stagioni, Nicchia, Interazioni ecologiche, Arcipelago Toscano

INTRODUCTION

Environmental temporal variations are thought to play a relevant role in both defining species abundance within communities and promoting species coexistence, with direct and indirect mechanisms involved in controlling the diversity and composition of ecological communities across time (Shimadzu et al., 2013). Niche differentiation, along with the spatial and temporal partitioning of resources (see McMeans et al., 2015 and references herein), allows for species-specific responses to both types of environmental variations and limiting factors are listed among the most relevant of these mechanisms (Chesson, 2000; Ruokolainen & Hanski, 2016).

Seasonal fluctuations are evident, and marked temporal variations are known to influence species abundance, although the consequences of this variation for species coexistence are still under investigation. These studies are especially needed in the marine environment, where the seasonal patterns may differ from those recorded on land (Shimadzu et al., 2013). The seasonal changes of marine habitats may influence key life-history features of different species, such as developmental and growth rates, species migration, spawning or nesting time, and even offspring sensitivity to acidification (e.g., Urra et al., 2013; Murray et al., 2014).

In the Mediterranean Sea, seagrass meadows are one of the most complex and important ecosystems, and are subjected to strong seasonal fluctuations in plants' biological features, such as biomass and productivity (Guidetti et al., 2002). *Posidonia oceanica* (Linnaeus) Delile, 1813, is the dominant seagrass and is one of the most important primary producers in coastal waters by playing a fundamental ecological role as a habitat-forming species (Kendrick et al., 2005). The three-dimensional structure of the meadows, consisting of a thick foliar canopy and of an articulate layer of roots and rhizomes, helps develop complex epiphyte assemblages and offers a variety of suitable microhabitats hosting hundreds of

animals and plant species, as well as fungi and micro-organisms (Buia et al., 2000; Borg et al., 2006; Bedini et al., 2011; Mascart et al., 2015).

Among invertebrates, amphipods are one of the most abundant and diverse groups of the vagile fauna associated with *P. oceanica* (cf. Mazella et al., 1989; Gambi et al., 1992; Sturaro et al., 2015). These small peracaridean crustaceans without pelagic larval stages, are known to maintain a close relationship with the substrate and are sensitive to environmental changes, so their community composition is widely used as an environmental indicator (de-la-Ossa-Carretero et al., 2012; Marusso et al., 2013). Within *P. oceanica*, amphipods play an important role by transferring energy from lower to higher trophic levels (Michel et al., 2015; Zaabar et al., 2015). Furthermore, *P. oceanica* is more than a trophic resource for amphipods, which may actively choose seagrass as a substratum to find protection from predation or to complete their life cycle (Sanchez-Jerez, 1999; Sturaro et al., 2016).

Given the complexity of understanding temporal patterns and relationships between *P. oceanica* and amphipods, as well as the need to improve community-based analyses, a yearly survey of amphipod assemblage structure from a *P. oceanica* meadow located in Giannutri Island (central Tyrrhenian Sea) was carried out. The aim of this study is to investigate temporal changes in the structure of amphipod assemblages across the seasons.

MATERIALS AND METHODS

Study area

Investigations were carried out in a *Posidonia oceanica* meadow from Giannutri Island (central Tyrrhenian Sea, Italy). This small limestone island, characterized by a rugged and rocky coastline, is part of the National Park of Tuscan Archipelago and a Special Area of Conservation (Habitats Directive 92/43/EEC, SACIT51A0024). The seagrass meadows around the island cover about 32 ha and are characterized by a coastal extension with a sharp lower limit due to the slope of the rocky seabed and the low amount of shallow bays (Borriello et al., 2010).

Samples were taken from two sites, Punta Secca (A) and Secca di Punta Secca (B) (fig. 1), within Zone 2 of the protected area, which is nearly undisturbed since human activities need to be authorized by the Park authority.

Sampling

Samples were collected by SCUBA diving at a constant depth between 15-20 m within 40×40 cm quadrats (0.16 m^2) using an air-lift sampler (500-μm mesh
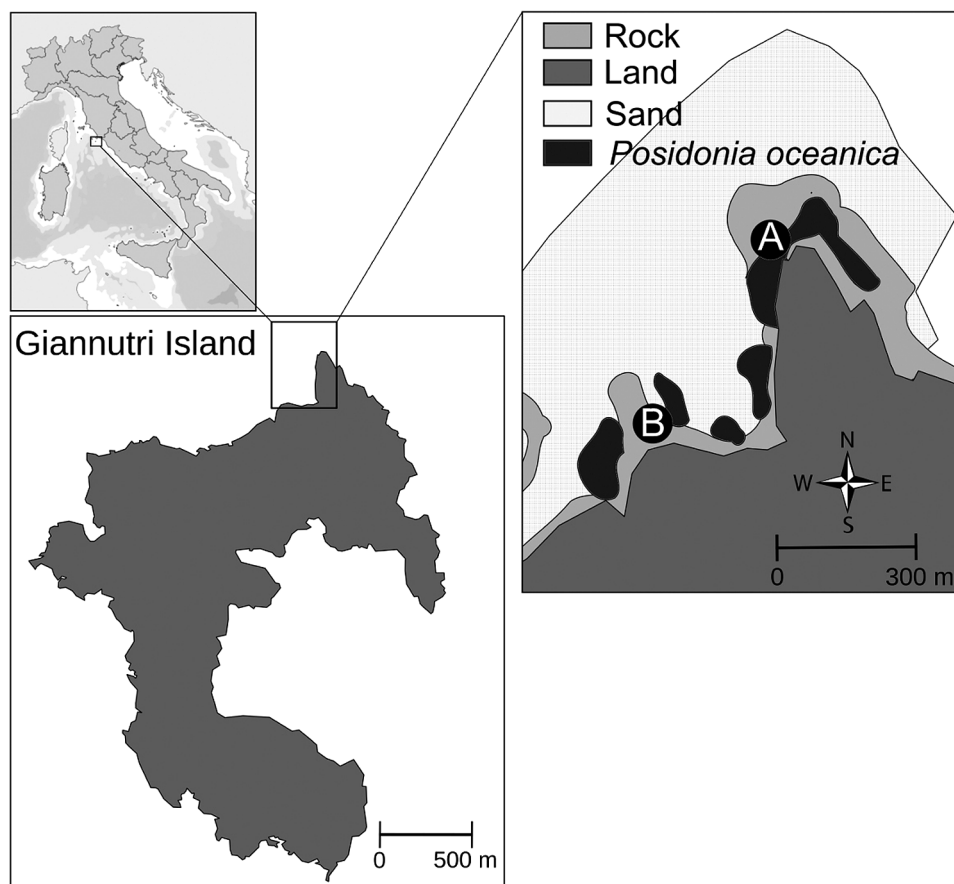
Fig. 1. Geographic location of the study area and sampling sites (A and B) in Giannutri Island (Italy).

size), as described in Michel et al. (2010). The suction time was the same for each sample collected (3 min). At each site, three replicates at intervals of 10 m range were taken in February, May, August and November 2014, for a total of six samples per season. Samples were preserved in 70% ethanol until sorted out in the lab using a stereomicroscope. Identification to the species level was based on the handbooks by Ruffo (1982, 1989, 1993, 1998), the nomenclature was updated according to the World Register of Marine Species (WoRMS, last accessed January 2017).

Statistical analyses

The structure of amphipod assemblages between seasons and sites was compared by a two-way permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001), with Season (Se, four levels) and Site (Si, two levels) as fixed factors and Replicate (Re, three levels) as a random factor nested in Site with 9999

permutations. A non-metric multidimensional scaling analysis (nMDS), based on abundance data, was performed to visualize multivariate patterns. The goodness of fit statistics in the nMDS ordination diagram was assessed using the Kruskal stress value (Kruskal & Wish, 1978), and considering 0.12 as the threshold value for a reliable ordination (Clarke, 1993). PERMANOVA and nMDS analyses were based on the Bray-Curtis similarity matrices calculated from the double square root transformation of abundance data, to maintain the contribution of rarest species without over-weighting. This bulk of analyses allowed for defining three temporally homogeneous clusters of seasons, which were then used to perform any further analysis.

A similarity percentage analysis (SIMPER, Clarke & Warwick, 2001) was performed to identify the species that mostly contributed to dissimilarity among temporal clusters. The temporal distribution of these species was highlighted by means of a ternary plot, which graphically depicts the proportion of species abundance in the identified clusters and has the advantage of plotting three-variable data in a two-dimensional plot.

The overall number of species (S), the Shannon-Wiener diversity index (H'), and the dominance based on the Simpson diversity index (D) were calculated from mean seasonal values, and potential differences were estimated by a bootstrap t-test (Magurran, 2004). Statistical analyses were performed using PAST 3.12 (Hammer et al., 2001) and PRIMER v6 (Clarke & Gorley, 2006).

<center>RESULTS</center>

A total of 873 individuals were sampled, and 718 were identified to the species level, belonging to 62 species and 27 families (table I). Overall, the most abundant species was *Apherusa chiereghinii* Giordani-Soika, 1949, with 110 individuals, followed by *Liljeborgia dellavallei* Stebbing, 1906 (105 specimens) and *Apolochus neapolitanus* (Della Valle, 1893) (91 specimens).

The two-way PERMANOVA showed no significant influence of the factor Si ($F = 1.641$; $p = 0.078$) on the structure of amphipod assemblages. This showed spatial homogeneity among study sites, so all samples (Punta Secca and Secca di Punta Secca) can be considered as part of a unique locality. The two-way PERMANOVA also highlighted a significant influence of factor Se ($F = 2.965$; $p<0.001$). Yet no differences in amphipod assemblages between spring and summer were identified (pairwise comparison, $F = 1.013$; $p = 0.104$), which can therefore be considered as a single temporal group. Winter and autumn assemblages differed among themselves ($p<0.05$) and from the above mentioned spring-summer season ($p<0.05$ in all cases). These differences were highlighted

TABLE I

List of identified families and species with the total number of individuals collected in each season

Suborder	Family	Species	Winter	Spring	Summer	Autumn
Gammaridea	Ampeliscidae	*Ampelisca rubella* A. Costa, 1864		1		
		Ampelisca tenuicornis Liljeborg, 1855		2		
	Amphilochidae	*Apolochus neapolitanus* (Della Valle, 1893)	32	17	12	27
		Apolochus picadurus (J. L. Barnard, 1962)	27	10	31	5
		Gitana sarsi Boeck, 1871	15	18	29	4
	Atylidae	*Atylus vedlomensis* (Bate & Westwood, 1862)		1		
		Nototropis guttatus A.Costa, 1853			3	2
	Cressidae	*Cressa cristata* Myers, 1969		1	2	1
		Cressa mediterranea Ruffo, 1979	4	1	20	
	Cyproideidae	*Peltocoxa gibbosa* (Schiecke, 1977)			1	
		Peltocoxa mediterranea Schiecke, 1977		2	3	
	Dexaminidae	*Dexamine spiniventris* (A. Costa, 1853)		3	2	
		Dexamine spinosa (Montagu, 1813)	20	15	19	9
		Guernea (*Guernea*) *coalita* (Norman, 1868)			1	
	Iphimediidae	*Iphimedia minuta* G. O. Sars, 1883	1	9	7	1
		Iphimedia vicina Ruffo & Schiecke, 1979		1		
	Leucothoidae	*Leucothoe euryonyx* Walker, 1901	4			1
		Leucothoe serraticarpa Della Valle, 1893	1			
		Leucothoe spinicarpa (Abildgaard, 1789)	2	3	1	
	Liljeborgiidae	*Idunella nana* (Schiecke, 1973)				1
		Liljeborgia dellavallei Stebbing, 1906	38	14	39	14

T ABLE I
(Continued)

Suborder	Family	Species	Winter	Spring	Summer	Autumn
	Lysianassidae	*Lysianassa costae* Milne Edwards, 1830	1	5	1	4
		Orchomene grimaldii Chevreux, 1890	1			2
		Orchomene humilis (A. Costa, 1853)	3	6	14	1
		Orchomene massiliensis Ledoyer, 1977		3		
		Orchomene similis Chevreux, 1912			10	
		Socarnes filicornis (Heller, 1866)				7
		Tryphosa nana (Krøyer, 1846)		9	1	1
		Tryphosella minima (Chevreux, 1911)	1			
	Oedicerotidae	*Deflexilodes subnudus* (Norman, 1889)	7	2	1	
		Perioculodes aequimanus (Kossman, 1880)		6	3	10
		Pontocrates arenarius (Bate, 1858)			2	
		Synchelidium longidigitatum Ruffo, 1947	12	7	14	2
	Opisidae	*Normanion chevreuxi* Diviacco & Vader, 1988	4			
	Phoxocephalidae	*Harpinia antennaria* Meinert, 1890				1
		Harpinia crenulata (Boeck, 1871)				1
		Harpinia zavodniki G. Karaman, 1987				1
		Metaphoxus simplex (Bate, 1857)				2
	Stenothoidae	*Stenothoe dollfusi* Chevreux, 1887		1	1	
	Uristidae	*Ichnopus taurus* A. Costa, 1853	1			
		Tmetonyx nardonis (Heller, 1866)			1	

TABLE I
(Continued)

| Suborder	Family	Species	Winter	Spring	Summer	Autumn
Senticaudata	Aoridae	*Aora gracilis* (Bate, 1857)				1
		Aora spinicornis Afonso, 1976				1
		Microdeutopus armatus Chevreux, 1886	3			
	Calliopiidae	*Apherusa chiereghinii* Giordani-Soika, 1950	15	39	23	33
	Caprellidae	*Caprella acanthifera* Leach, 1814		7		
		Phtisica marina Slabber, 1769	5	11	7	1
	Cheirocratidae	*Cheirocratus sundevallii* (Rathke, 1843)				1
	Corophiidae	*Leptocheirus guttatus* (Grube, 1864)		2		
		Leptocheirus pilosus Zaddach, 1844			1	
	Ischyroceridae	*Ericthonius punctatus* (Bate, 1857)		2	1	1
		Siphonoecetes (*Centraloecetes*) *dellavallei* Stebbing, 1899		6	3	
		Siphonoecetes (*Centraloecetes*) *neapolitanus* Schiecke, 1979	2	9		3
		Microjassa cumbrensis (Stebbing & Robertson, 1891)	2		1	
	Kuriidae	*Micropythia carinata* (Bate, 1862)			2	1
	Maeridae	*Maera grossimana* (Montagu, 1808)				3
		Hamimaera hamigera (Haswell, 1879)				8
	Nuuanuidae	*Gammarella fucicola* (Leach, 1814)		1		41
	Phliantidae	*Pereionotus testudo* (Montagu, 1808)		1	1	1
	Photidae	*Gammaropsis dentata* Chevreux, 1900	1			
		Gammaropsis maculata (Johnston, 1828)	1			5
	Pontogeneiidae	*Eusiroides dellavallei* Chevreux, 1899				1
Total			203	215	257	198
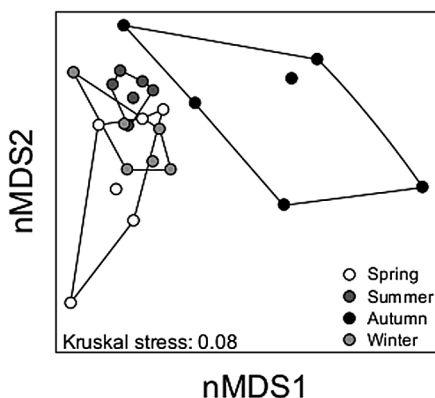
Fig. 2. Non-metric multidimensional scaling (nMDS) ordination based on the Bray-Curtis distance measured on amphipod abundance data.

by the pattern of ordination in the nMDS plot, which showed a clear-cut separation of the autumn from all other seasons (fig. 2).

Autumn samples laid separately from all the others and exhibited a higher dispersion, while the winter samples were closer to the spring-summer ones. This pattern was confirmed by the SIMPER analysis that showed a relatively low dissimilarity in the assemblage of amphipods between winter and spring-summer (average dissimilarity = 49.25) with 14 species responsible for about 50% of the differentiation (table II). Higher differences were found comparing autumn versus both spring-summer and winter (average dissimilarity 67.79 and 65.29, respectively), thus confirming the high peculiarity of the assemblage in this season.

The temporal distribution of the species responsible for most of the differentiation between the three time periods showed two dominant species, *Gammarella fucicola* (Leach, 1814) and *Socarnes filicornis* (Heller, 1866), strictly related to autumn samples, while *Leucothoe euryonyx* (Walker, 1901) and *Deflexilodes subnudus* (Norman, 1889) were fairly related to winter samples (fig. 3). *Cressa mediterranea* Ruffo, 1979, *Orchomene humilis* (A. Costa, 1853), *Iphimedia minuta* G. O. Sars, 1883, *Gitana sarsi* Boeck, 1871 and *Phtisica marina* Slabber, 1769 were instead associated with spring-summer time. It is worth noting that the most abundant species recorded: *A. chiereghinii*, *L. dellavallei* and *A. neapolitanus* were not strictly associated with any season.

Assemblage parameters, calculated from mean seasonal values, showed significant variations among all temporal clusters (fig. 4), with significant differences in terms of the Shannon diversity index and number of species (t-test, $p < 0.05$ in all cases). Higher values of dominance were found in autumn compared with spring-summer and winter assemblages (t-test, $p < 0.05$ in both cases), which did not show any significant difference among each other (t-test, $p = 0.71$).

TABLE II

Results of the SIMPER analysis (Clarke & Warwick, 2001) showing dissimilarities ($\bar{\delta}$) between the three seasonal groups (W, Winter; Sp-S, Spring-Summer; A, Autumn)

$\bar{\delta}$	Species	Average abundance				$\bar{\delta}_i$	$\bar{\delta}_i$/SD
		W	Sp-S	A	W		
49.25	*Deflexilodes subnudus*	0.74	0.25			4.43	1.20
	Iphimedia minuta	0.17	0.70			4.40	1.14
	Phtisica marina	0.56	0.87			4.30	1.10
	Apolochus neapolitanus	1.48	1.01			4.11	1.03
	Dexamine spinosa	1.10	1.07			4.04	1.08
	Orchomene humilis	0.22	0.57			3.92	0.90
	Apolochus picadurus	1.37	1.05			3.87	1.19
	Cressa mediterranea	0.39	0.36			3.73	0.87
	Synchelidium longidigitatum	1.13	0.79			3.70	1.03
	Leucothoe euryonyx	0.53	0.00			3.51	0.95
	Liljeborgia dellavallei	1.52	1.23			3.47	0.92
	Gitana sarsi	1.05	1.36			3.31	0.90
	Siphonoecetes neapolitanus	0.20	0.40			3.09	0.79
	Apherusa chiereghinii	1.22	1.35			2.90	1.17
67.71	*Gammarella fucicola*		0.08	1.38		6.72	1.90
	Gitana sarsi		1.36	0.40		5.11	1.55
	Apolochus picadurus		1.05	0.25		5.06	1.46
	Phtisica marina		0.87	0.17		4.08	1.38
	Apolochus neapolitanus		1.01	1.00		3.95	1.20
	Liljeborgia dellavallei		1.23	0.87		3.65	1.18
	Perioculodes aequimanus		0.40	0.80		3.58	1.21
	Synchelidium longidigitatum		0.79	0.33		3.39	1.21
	Iphimedia minuta		0.70	0.17		3.26	1.14
	Apherusa chiereghinii		1.35	1.27		3.16	1.02
	Socarnes filicornis		0.00	0.58		3.05	0.91
	Orchomene humilis		0.57	0.17		2.84	0.92
	Dexamine spinosa		1.07	0.95		2.68	0.96
65.29	*Gammarella fucicola*			1.38	0.00	7.82	2.04
	Apolochus picadurus			0.25	1.37	7.00	2.48
	Gitana sarsi			0.40	1.05	4.76	1.44
	Synchelidium longidigitatum			0.33	1.13	4.57	1.52
	Perioculodes aequimanus			0.80	0.00	4.39	1.33
	Apolochus neapolitanus			1.00	1.48	4.34	1.14
	Liljeborgia dellavallei			0.87	1.52	4.31	1.22
	Deflexilodes subnudus			0.01	0.74	4.24	1.35
	Socarnes filicornis			0.58	0.00	3.45	0.91
	Phtisica marina			0.17	0.56	3.36	0.99
	Apherusa chiereghinii			1.27	1.22	3.27	1.26

Species are ordered by decreasing contribution (P50% cumulative contribution). The table includes the average abundances, the contribution from the ith species to the average dissimilarity, expressed as a percentage ($\bar{\delta}_i$) and a ratio ($\bar{\delta}_i$/SD; where SD is the standard deviation) indicating discriminating species.
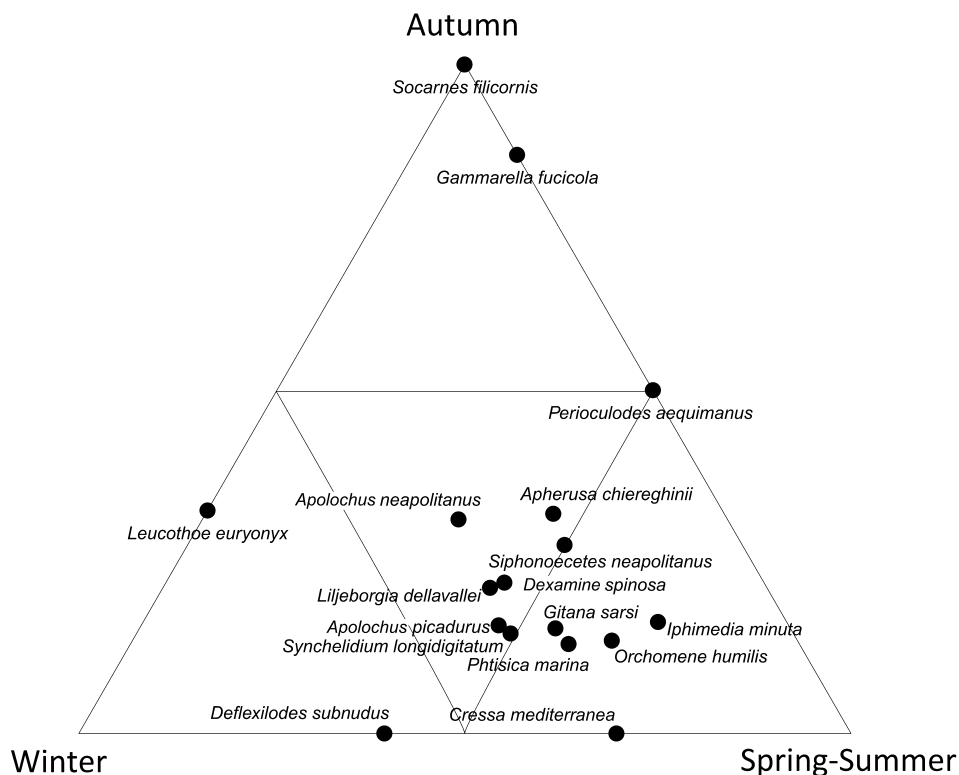
Fig. 3. Ternary plot showing the distribution of the main species as identified by the SIMPER analysis within the three seasonal groups.

DISCUSSION

The results showed the presence of a pool of species (*Apherusa chiereghinii*, *Apolochus neapolitanus*, *Liljeborgia dellavallei*, *Dexamine spinosa* (Montagu, 1813) and *Apolochus picadurus* (J. L. Barnard, 1962)) found throughout the whole year in the studied *Posidonia oceanica* meadow, which is in agreement with other observations from the Mediterranean Sea (Zakhama-Sraieb et al., 2006, 2011; Scipione & Zupo, 2010; Bellisario et al., 2016). However, a more in depth analysis based on year-round data showed a strong seasonal variation in the species composition of amphipod assemblages, along with their abundance and diversity. This pattern identified three main seasonal groups, represented by autumn, winter, and the warm season (e.g., spring and summer).

During the warm season amphipod assemblages were characterized by a high number of individuals partitioned in a relatively high number of species, thus causing a significant contraction in terms of species dominance. During autumn, the structure of amphipod assemblages changed and became dominated by two
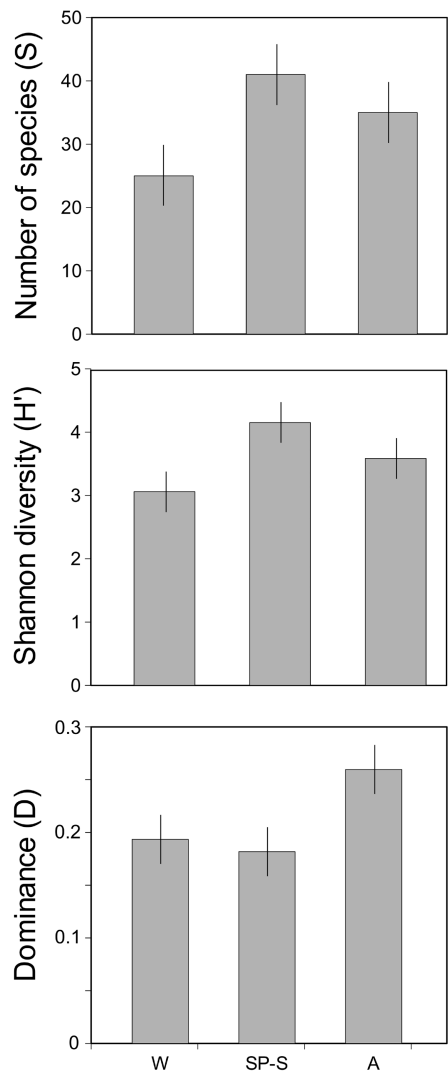
Fig. 4. Species number (S), Shannon diversity index (H'), and dominance (D) measured in the identified seasonal groups (W, Winter; Sp-S, Spring-Summer; A, Autumn). The Standard Error of the bootstrap t-test is reported.

species, *Socarnes filicornis* and *Gammarella fucicola*. Winter showed the lowest values in terms of species diversity and abundance, and two weakly associated species, *Leucothoe euryonyx* and *Deflexilodes subnudus*.

Similar seasonal patterns were already observed in Peracarids associated with other seagrasses like *Zostera* (*Zostera*) *marina* Linnaeus, 1753 and explained by the plant seasonality in growth and production rates (Ott, 1980; Karaçuha et al., 2009; Esquete et al., 2011; Zaabar et al., 2015). The link between seasonal

fluctuations and species coexistence has recently been shown in a long term study on an estuarine fish community, while studies on crustaceans are still lacking (Shimadzu et al., 2013). The data presented here refers to a single year and do not concern seagrass meadow features, which prevents a direct comparison with changes in amphipod assemblages. However, some general considerations can be drawn from the seasonal patterns of *P. oceanica* life cycle, suggesting that amphipod assemblages and species coexistence may be promoted by different mechanisms, mostly related to direct and indirect effects of the changing host plant structure. A possible explanation for the high number of species observed during the warm season may involve a more efficient partitioning of the abundant food resources available at that time, implying a reduction in trophic niche overlap. Indeed, recent studies highlighted the existence of interspecific differences in the feeding habits of most amphipods, especially within the preferred grazing compartment of each species (e.g. *A. chiereghinii*, *Aora spinicornis* Afonso, 1976 or *G. aequicauda*) (Michel et al., 2015).

During the warm season, seagrasses reach their highest productivity and show a peak in epiphyte assemblages, as well as in their spatial coverage (Ott, 1980; Bedini et al., 2011), allowing for selective foraging by amphipods, which are known to exhibit strong species-specific dietary preferences (Michel et al., 2015). This feeding behaviour may have a direct effect on amphipod coexistence through niche subdivision, but also an indirect one through a facilitation process on the epiphytic community with grazing activity increasing the diversity of epiphytes, thus promoting the coexistence of even more amphipods (Duffy et al., 2001, 2003; Jaschinski et al., 2008).

However, the spatial partitioning of food resources is not the only mechanism able to explain the high diversity of amphipods in our samples, since a certain degree of temporal partitioning should be considered. Many amphipod species show a diel vertical migration behaviour, so they use the lower layers of the meadows during the day and migrate to the higher foliar stratum during the night for grazing activity (Sanchez Jerez et al., 1999; Michel et al., 2015). Moreover, the habitat complexity during the warm period would allow a reduction in the predation pressure by high-order predators, which has been pointed out as related to seasonal changes in the number and diversity of amphipod species (Nelson, 1979). As suggested by Sturaro et al. (2016), this can be relevant for amphipods which have been demonstrated to show species-specific responses to predation, which are probably related to their life history strategies and ecological behaviour.

During the autumn the structure of amphipod assemblages changed and became dominated by two species, *S. filicornis* and *G. fucicola*, which are mainly detritivorous with a degree of a mixed diet (Guerra-Garcia et al., 2014). The relatively high species diversity and the dominance of few species, however, suggest that

other mechanisms, unrelated to trophic habits, may act to determine the observed patterns of amphipod assemblages in autumn. For example, increasing predation pressure may selectively involve more vulnerable species whose life traits and/or ecological behaviours cannot counteract the progressive decrease of habitat complexity due to the decay of leaf tips (Ott, 1980; Gallmetzer et al., 2005). Accordingly, species, such as *G. fucicola*, have an advantage by being able to both feed on epiphytes from the whole plant, including leaves, litter, and rhizomes, and accomplish its whole biological cycle within the seagrass litter, which provides an effective refuge against predation (Lepoint, 2006; Michel et al., 2015).

Along the seasonal succession, the productivity of seagrass is least in winter, when young leaves start developing, which is associated with the lowest production of epiphytic biomass (Ott, 1980). The high hydrodynamic regime typical of this season and the sparse canopy provided by the short leaves both strongly affects the removal of leaf litter and the settlement of individuals (Hovel et al., 2002; Mascart et al., 2015), likely explaining the lower diversity of winter amphipod assemblages.

Although limited in space and time, our results reinforce the view that the relationship between *P. oceanica* and the associated amphipods should be highly complex (Sturaro et al., 2015), implying multiple scales and interactive factors which can mould local assemblages through the year. These regulating factors include, but are not limited to, the interplay between spatial and temporal niche partitioning driven by the seasonal changes in the structure and functioning of the seagrass. Other mechanisms may equally contribute to assemblage composition through seasons, such as predation pressure or life history strategies, although their effects at the assemblage level are still unclear (Sturaro et al., 2014). Further studies expanding the spatial and temporal investigation of the seasonal patterns in assemblage composition, possibly coupled with seasonal seagrass feature variation, may shed light into the mechanisms behind the temporal variation of amphipod assemblages in *P. oceanica*.

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