Spatial and temporal variation of motile macro-invertebrate assemblages associated with *Posidonia oceanica* meadows

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The present study assesses the spatial and temporal distribution of motile invertebrates in Posidonia oceanica *meadows located off the coast of Tuscany, in the northwestern Mediterranean Sea. A hierarchical sampling design was used to evaluate changes in composition and abundance of assemblages in relation to depth and to different periods over one year. A total of 136 taxa were determined, among them 34 Mollusca, 94 Arthropoda, 5 Annelida and 1 Echinodermata. Results of both multivariate and univariate analyses showed that the macro-invertebrate assemblage structure varied along a depth gradient but this pattern was not consistent in the two study periods. Results suggest that temporal and spatial differences in the structure of* P. oceanica *meadows are key drivers in determining the structure of associated macro-invertebrate assemblages, as values of richness and abundance decreased with a decrease in leaf length and shoot density.*

INTRODUCTION

Seagrass beds represent one of the most important coastal ecosystems in terms of extent and production. Moreover, they play a fundamental ecological role as habitat-forming species, thus enhancing biodiversity. Seagrass beds allow the development of complex epiphyte assemblages and host more diverse and abundant animal communities than unvegetated areas (EDGAR, 1990; ARRIVILLAGA & BALTZ, 1999).

The influence of seagrasses on motile fauna is both structural and trophic since the habitats they form enhance habitat complexity, provide a refuge from predators, and allow different species to occupy various ecological niches in a same habitat (STONER, 1980; ORTH *et al.*, 1984). Moreover, seagrass meadows provide food via the high primary production of the plants and epiphyte algae (VAN MONTFRANS *et al.*, 1984; DUFFY *et al.*, 2003) and the development of complex detritus chains (KLUMPP & VAN DER VALK, 1984; EDGAR, 1999).

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 & ORTH, 1980). Effective conservation and management of seagrass communities requires an understanding of the processes that control patterns of distribution and abundance of organisms. Essential to such an understanding is reliable information on the variation in abundance and diversity of species through space and time.

In the Mediterranean Sea, *Posidonia oceanica* (L.) Delile is the most important seagrass for its vast extent, stability, high biodiversity and production (MAZZELLA *et al.,* 1992). The motile macro-invertebrate assemblages of the *P. oceanica* leaf stratum have been widely studied (MAZZELLA *et al.,* 1989; 1992; GAMBI *et al.*, 1992; SCIPIONE *et al.,* 1996; BEDINI *et al.*, 1997; BEDINI, 2003; BORG *et al.*, 2010). However, most investigations have focused on particular taxa or have considered only one aspect of the associated faunal distribution (SCIPIONE & FRESI, 1984; RUSSO *et al.,* 1984; 1991; 2002; GAMBI *et al.*, 1995; 1998; SCIPIONE, 1999; BEDINI & BEDINI, 2008; BORG & SCHEMBRI, 2000; BEDINI, 2006). Moreover, no information is available on this topic for the northern Mediterranean Sea.

The aim of the present study is to describe the spatial and temporal distribution of motile macro-invertebrate assemblages of *P. oceanica* in meadows distributed off the coast of Tuscany in the northwestern Mediterranean Sea. In this context, a hierarchical sampling design was used to evaluate changes in composition and abundance of assemblages in relation to depth and to different periods over one year.

MATERIAL AND METHODS

The study was carried out off the coast of Tuscany (northwestern Mediterranean Sea) in 2007 (Fig. 1). At the study sites, *Posidonia oceanica* meadows colonized a rocky bottom. Three depth ranges were considered: 8-10 m (shallow), 15-17 m (intermediate) and 23-25 m (deep). Two periods were chosen over one year: spring-summer (s-s) and autumn-winter (a-w); these correspond to periods during which *P. oceanica* meadows have different structural characteristics (MAZZELLA & OTT, 1984). Two random

Figure 1. Map of the northern coast of Tuscany. The ellipse indicates the study area.

dates were chosen in each period and three areas separated by several kms were sampled on each date and at each depth. At each site, ten replicate measures of density were made using a 40x40 cm quadrant, and ten shoots were collected to assess phonological variables. A hand-towed net (0.4 mm mesh size) was used to sample motile organisms living in the leaf stratum. Three replicate samples were collected for each depth and date. Each sample consisted of a series of 60 strokes over the seagrass leaf canopy (RUSSO *et al.,* 1985).

In the laboratory, taxa were identified and the abundance expressed as number of individuals per sample. Taxa nomenclature followed the WORLD REGISTER OF MARINE SPECIES (2011). Differences in the species composition and abundance were tested using Permutational Analysis of Variances - PERMANOVA (ANDERSON, 2001). A 4-way model was used with Depth (shallow vs. intermediate vs. deep) and Period (2 levels; spring-summer and autumn-winter) as fixed and crossed factors, Date (2 levels) as random factor nested in Period, Area (3 levels) as random factor nested in the interaction Depth x Date. The Bray-Curtis index of dissimilarity was calculated from untransformed species-abundance data. The SIMPER routine was used to establish which taxa contributed most to the dissimilarity between samples.

Differences in meadow shoot density, mean leaf length per shoot, number of taxa and total number of macro-invertebrates per sample was tested using Univariate Analyses of Variance - ANOVA (UNDERWOOD, 1997) using the same factors and levels considered in the PERMANOVA test. Homogeneity of variance was tested using Cochran's C test. The SNK test was used to identify the source of difference when ANOVA indicated a significant difference.

RESULTS

A total of 136 taxa were identified, among them 34 Mollusca, 94 Arthropoda, 5 Annelida and 1 Echinodermata (Table 1).

PERMANOVA indicated a significant interaction between Depth and Period for the species composition and abundance of macro-inverte-brate assemblages. Pair-wise tests showed that differences between depths were significant for the spring-summer period but not for the autumn-winter period; moreover, differences between periods were significant in the shallow and intermediate assemblages but not in the deep assemblages (Table 2). Differences between areas were also significant.

Table 1. List of recorded taxa. De = deep, In = intermediate, Sh = shallow, s-s = spring-summer, a-w = autumn-winter

TAXA	Sh s-s	Sh a-w	In s-s	In a-w	De s-s	De a-w
MOLLUSCA						
Alvania beani (Hanley in Thorpe, 1844)	-	-	+	-	+	-
Alvania discors (Allan, 1818)	+	+	+	+	+	+
Alvania lineata (Risso, 1826)	+	+	-	-	+	-
Barleeia unifasciata (Montagu, 1804)	+	-	+	-	+	-
Bittium reticulatum (Da Costa, 1778)	+	+	+	-	+	+
Calliostoma conulus (Linnaeus, 1758)	+	-	+	-	-	-
Calliostoma laugieri (Payraudeau,1826)	+	-	-	-	-	-
Columbella rustica (Linnaeus, 1758)	+	-	+	-	-	-
Cuthona caerulea (Montagu, 1804)	-	-	-	+	-	+
Elysia viridis (Montagu, 1804)	+	+	-	-	+	-
Eulimella acicula (Philippi, 1836)	+	-	-	-	-	-
Gibbula divaricata (Linnaeus, 1758)	+	-	-	-	-	-
Gibbula umbilicaris umbiliaris (Linnaeus, 1758)	+	-	-	-	-	-
Gibbula varia (Linnaeus, 1758)	+	-	+	-	+	-
Jujubinus exasperatus (Pennant, 1777)	+	+	+	+	+	+
Monophorus perversus (Linnaeus, 1758)	-	+	-	+	-	-
Pusillina marginata (Michaud, 1832)	+	-	-	+	+	+
Pusillina philippi (Aradas & Maggiore, 1844)	+	+	+	+	-	+
Pisania striata (Gmelin, 1791)	-	+	-	-	-	-
Rissoa auriscalpium (Linnaeus, 1758)	+	+	+	+	+	+
Rissoa guerinii (Récluz, 1843)	+	+	-	+	+	+
Rissoa labiosa (Montagu, 1803)	-	-	-	+	-	-
Rissoa membranacea (Adams J., 1800)	-	+	-	-	-	-
Rissoa monodonta (Philippi, 1846)	+	+	+	+	-	+
Rissoa variabilis (von Muehlfeldt, 1824)	+	+	+	+	-	+
Rissoa ventricosa (Desmarest, 1814)	+	+	+	+	+	+
Rissoa violacea (Desmarest, 1814)	-	+	+	+	+	+
Rissoina bruguieri (Payraudeau, 1826)	-	-	+	-	-	-
Smaragdia viridis (Linnaeus, 1758)	-	-	-	+	-	-
Tectura virginea (O.F. Muller, 1776)	-	+	-	-	-	-
Tricolia pullus pullus (Linnaeus, 1758)	+	+	+	+	+	-
Tricolia punctura (Gofas, 1993)	+	-	-	+	-	-

Table 1. cont'd

Tricolia speciosa (von Muehlfeldt, 1824)	+	-	-	-	-	-
Tricolia tenuis (Michaud, 1829)	+	-	+	-	-	-
CRUSTACEA						
Acanthonyx lunulatus (Risso, 1816)	-	-	+	-	-	-
Acartia clausi (Giesbrecht, 1889)	-	-	-	-	+	+
Alpheus dentipes (Guérin-Méneville, 1832)	+	-	-	-	-	-
Ampelisca diadema (Costa, 1853)	+	-	-	-	-	-
Ampithoe ferox (Cheuvreux, 1902)	+	-	-	-	-	-
Ampithoe helleri (Karaman, 1975)	+	-	-	-	-	-
Amphitoe ramondi (Audouin, 1826)	+	-	+	-	-	-
Aora gracilis (Bate, 1857)	-	-	+	-	-	-
Aora spinicornis (Afonso, 1976)	+	+	-	-	+	+
Apherusa alacris (Krapp-Schiekel, 1969)	-	+	-	-	-	-
Apherusa bispinosa (Bate, 1857)	+	-	-	-	-	-
Athanas nitescens (Leach, 1814)	-	+	+	-	-	-
Aurila convexa (Baird, 1850)	-	-	-	+	-	-
Calcinus tubularis (Linnaeus, 1767)	-	-	-	+	-	-
Caprella acanthifera (Leach,1814)	+	+	+	-	+	-
Caprella equilibra (Say, 1818)	+	-	-	-	-	+
Caprella rapax (Mayer, 1890)	-	-	-	-	+	-
Ceradocus orchestiipes (Costa, 1853)	+	+	+	-	-	-
Cestopagurus timidus (Roux, 1830)	-	-	-	+	-	+
Clibanarius erythropus (Latreille, 1818)	+	-	+	-	-	-
Copepoda spp.	+	+	+	+	+	+
Copilia mediterranea (Claus, 1863)	-	-	-	+	-	+
Cumacea spp.	-	-	-	+	-	-
Cypridina mediterrianea (Claus)	-	+	+	-	+	+
Dexamine spiniventris (Costa, 1853)	+	-	+	-	-	-
Dexamine spinosa (Montagu, 1813)	+	-	+	+	-	-
Diogenes pugilator (Roux, 1829)	-	-	+	-	+	-
Dynamene bidentata (Adams, 1800)	+	-	+	+	-	-
Elasmopus affinis (Della Valle, 1893)	-	+	-	-	-	-
Elasmopus rapax (Costa, 1853)	+	+	+	-	+	-
Erichthonius brasiliensis (Dana, 1853)	+	-	+	-	-	-
Eusiroides dellavallei (Chevreux, 1899)	-	+	-	-	-	-
Eurydice pulchra (Leach, 1815)	-	-	+	+	+	+
Galathea strigosa (Linnaeus, 1761)	-	-	+	-	-	-
Gammarella fucicola (Leach, 1814)	+	-	+	-	-	-
Gammarellus angulosus (Rathke, 1843)	-	-	+	-	-	-
Gammaropsis crenulata (Krapp-Schiekel & Myers 1979	+	-	+	-	-	-
Gammaropsis ulrici (Krapp-Schickel & Myers, 1979)	-	+	-	-	-	-
Gammarus aequicauda (Martlynov, 1931)	+	+	+	+	+	+
Gammarus crinicornis (Stock, 1966)	+	-	+	-	-	-
Gnathia maxillaris (Montagu, 1804)	+	+	+	+	+	+
Hippolyte inermis (Leach, 1815)	+	+	+	+	+	+

Table 1. cont'd

Hippolyte leptocerus (Heller, 1863)	-	-	-	-	-	+
Hippolyte longirostris (Czerniavsky, 1868)	+	-	-	-	-	+
Hippolyte varians (Leach, 1814)	+	+	+	-	-	-
Hyale crassipes (Heller, 1866)	+	-	-	-	-	-
Hyale schmidti (Heller, 1866)	+	-	+	+	+	+
Idotea emarginata (Fabricius, 1793)	+	-	-	-	-	-
Synischia hectica (Pallas, 1772)	+	-	+	-	+	+
Idotea pelagica (Leach, 1815)	+	-	-	+	+	-
Iphimedia serratipes (Ruffo & Schiecke, 1979)	+	-	-	-	-	-
Jassa ocia (Bate, 1862)	-	-	+	-	-	-
Leptocheirus bispinosus (Norman, 1908)	+	-	+	-	-	-
Leptochelia savignyi (Kroyer, 1842)	-	-	-	-	+	-
Leptocheirus guttatus (Grube, 1864)	+	-	-	-	-	-
Leucothoe euryonyx (Walker, 1901)	-	-	-	-	-	-
Leucothoe procera (Bate, 1857)	-	-	+	-	+	+
Leucothoe spini carpa (Abildgaard, 1789)	+	-	-	-	-	+
Liljeborgia dellavallei (Stebbing, 1906)	+	-	-	-	-	-
Lysianassa costae (Milne-Edwards, 1830)	-	+	+	-	-	-
Lysianassa longicornis (Lucas, 1849)	+	-	+	-	-	-
Lysianassa pilicornis (Heller, 1866)	+	-	-	-	-	-
Lysianella dellavallei (Stebbing, 1906)	+	-	-	-	-	-
Maera inaequipes (Costa, 1857)	+	-	+	-	+	-
Maera knudseni (Reid, 1951)	-	-	+	-	-	-
Maerella tenui mana (Bate, 1862)	+	-	+	-	-	-
Microdeutopus algicola (Della Valle, 1893)	+	-	-	-	-	-
Microdeutopus chelifer (Bate, 1862)	-	+	-	-	-	-
Microdeutopus obtusatus (Myers, 1973)	+	-	+	-	-	-
Microdeutopus versiculatus (Bate, 1856)	+	-	-	-	-	-
Mysidiacea	+	+	+	+	+	+
Nebalia bipes (Fabricius, 1780)	-	-	-	-	-	+
Orchestia montagui (Audouin, 1826)	-	-	+	-	-	-
Palaemon elegans (Rathke, 1837)	-	+	-	-	-	-
Palaemon serratus (Pennant, 1777)	+	+	+	+	-	+
Palaemon xiphias (Risso, 1816)	+	+	+	+	+	-
Parhyalella richardi (Chevreux, 1902)	+	-	-	-	-	-
Peltocoxa mediterranea (Schiecke, 1977)	-	-	-	+	-	-
Photis longicaudata (Bate & Westwood, 1862)	+	+	+	-	-	+
Photis longipes (Della Valle, 1893)	+	-	-	-	-	-
Phtisica marina (Slabber, 1749)	+	+	+	+	+	+
Podocerus variegatus (Leach, 1814)	+	-	-	-	-	-
Pseudoprotella phasma (Montagu, 1804)	+	-	-	-	-	-
Sclerochilus contortus (Norman, 1861)	-	-	-	+	-	-
Siphonoecetes dellavallei (Stebbing, 1899)	+	-	-	-	-	-
Stenothoe tergestina (Nebeski, 1881)	+	-	-	-	-	-
Synisoma capito (Rathke, 1837)	+	-	+	-	-	-

Table 1. cont' d

Synisoma lancifer (Miers, 1881)	+	-	+	-	-	-
Tmetonyx similis (Sars, 1891)	+	-	-	-	-	-
Thoralus cranchii (Leach, 1817)	-	+	-	+	-	-
Tritaeta gibbosa (Bate, 1862)	-	-	-	-	-	+
Unciolella lunata (Chevreux, 1911)	-	+	-	-	+	+
Urothoe poseidonis (Reibish, 1905)	-	-	+	-	+	-
ARACNIDA						
Thalassarachna basteri (Johnston, 1836)	-	+	-	-	-	+
Pontarachna punctulum (Philippi, 1840)	+	+	+	+	+	+
ANNELIDA						
Pirakia punctifera (Grube, 1860)	+	-	-	-	-	-
Eunice vittata (Delle Chiaje, 1828)	+	-	-	-	-	-
Nereis pelagica (Linnaeus, 1758)	-	-	+	-	-	-
Platynereis coccinea (Delle Chiaje, 1822)	+	-	-	-	-	-
Syllis gracilis (Grube, 1840)	+	-	-	-	-	-
ECHINODERMATA						
Ophioderma longicauda (Bruzelius, 1805)	-	-	-	-	-	+

The SIMPER test showed that the taxa that contributed most to differences between different depths were the Crustacean *Hippolyte inermis*, the Arachnid *Pontarachna punctulum* and the Mollusks *Rissoa variabilis* and *R. ventricosa*. These species were more abundant in shallow and intermediate assemblages than in deep assemblages (Table 3). The same species were also responsible for differences between samples collected from different periods, with a strong decrease evident from the spring-summer period to the autumn-winter period. Moreover, Copepods were more abundant in the autumn-winter period and Mysidiacea in the spring-summer period.

Values of both total number of organisms and total number of taxa per sample were higher in the spring-summer period and in the shallow
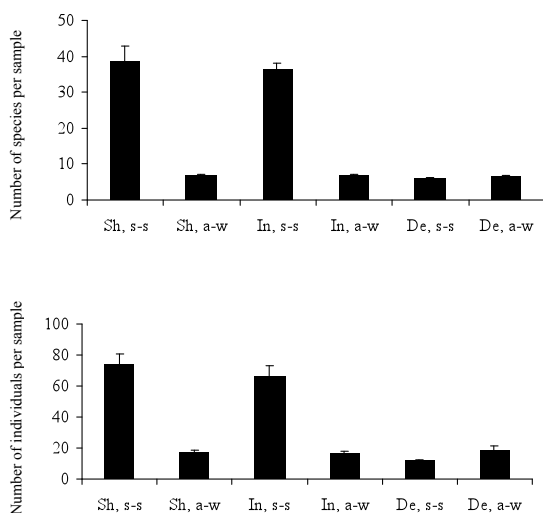

Fig. 2. Mean number of taxa and total number of individuals per sample (mean ± SE, n=6). De = deep, In = intermediate, Sh = shallow, s-s = spring-summer, a-w = autumn-winter
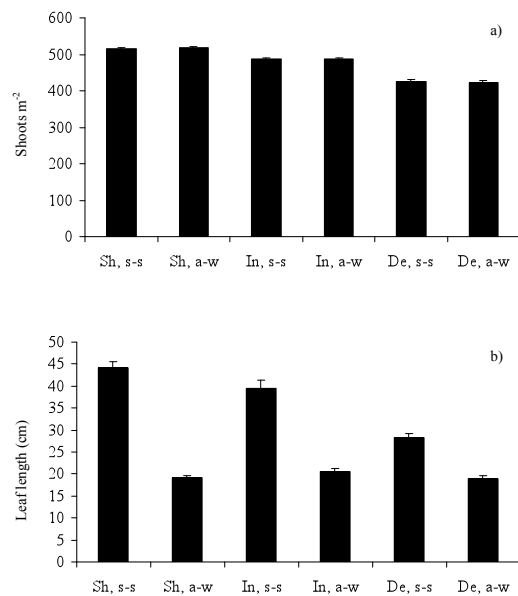

Fig. 3. Mean shoot density (mean ± SE, n=6) and leaf length per shoot (mean ± SE, n=20). De = deep, In = intermediate, Sh = shallow, s-s = spring-summer, a-w = autumn-winter

Table 2. Results of PERMANOVA on species composition and abundance of macro-invertebrate assemblages. Significant effects are in bold. De = deep, In = intermediate, Sh = shallow, s-s = spring-summer, a-w = autumn-winter

Source		df	MS	Pseudo-F	p(perm)
Depth = D		2	13945	6.383	**0.001**
Period = P		1	27638	8.990	**0.001**
Date(P) = Da(P)		2	3074.2	0.752	0.805
DxP		2	16045	7.344	**0.001**
DxDa(P)		4	2184.7	0.535	0.997
Area(DxDa(P))		24	4083.3	2.487	**0.001**
Residual		72	1641.6		
Total		107			
PAIRWISE test (DxP)	s-s: Sh, In		**0.002**	Sh: s-s, a-w	**0.001**
	Sh, De		**0.001**		
	In, De		**0.001**	In: s-s, a-w	**0.001**
	a-w: Sh, In		0.168		
	Sh, De		0.214	De: s-s, a-w	0.098
	In, De		0.518		

Table 3. Results of SIMPER showing the contribution of selected taxa to the multivariate patterns. De = deep, In = intermediate, Sh = shallow, s-s = spring-summer, a-w = autumn-winter

TAXA	Av.Abund	Av.Abund	%Contrib
	Sh	**In**	**Av.dis: 72.5**
Hippolyte inermis	15.05	8.79	19.03
Pontarachna punctulum	4.16	8.62	12.68
Rissoa variabilis	4.71	5.39	9.13
Mysidiacea	0.69	2.88	5.85
Copepoda	1.78	1.32	5.53
Rissoa ventricosa	3.38	1.07	4.57
Thoralus cranchii	0.52	0.61	2.52
Gibbula varia	1	1.06	2.1
Gnathia maxillaris	0.53	0.92	2.06
	Sh	**De**	**Av.dis: 79.8**
Hippolyte inermis	15.05	4.31	23.41
Pontarachna punctulum	4.16	2.14	9.29
Copepoda	1.78	0.72	6.32
Rissoa variabilis	4.71	0.03	5.78
Rissoa ventricosa	3.38	0.17	4.53
Mysidiacea	0.69	1.03	3.91
Bittium reticulatum	0.82	0.81	2.67
Gnathia maxillaris	0.53	0.33	1.71
	In	**De**	**Av.dis: 78.7**
Pontarachna punctulum	8.62	2.14	16.45
Hippolyte inermis	8.79	4.31	14.14

Misydiacea	2.88	1.03	7.83
Rissoa variabilis	5.39	0.03	7.21
Copepoda	1.32	0.72	5.01
Gnathia maxillaris	0.92	0.33	2.79
Bittium reticulatum	0.5	0.81	2.63
Rissoa ventricosa	1.07	0.17	2.07
Thoralus cranchii	0.61	0	1.98
	s-s	**a-w**	**Av.dis: 79.0**
Hippolyte inermis	13.8	4.96	18.98
Pontarachna punctulum	7.61	2.33	12.82
Rissoa variabilis	6.67	0.07	8.29
Mysidiacea	2.01	1.06	5.75
Copepoda	0.7	1.85	4.84
Rissoa ventricosa	2.91	0.17	3.98
Bittium reticulatum	1.12	0.3	2.43
Gnathia maxillaris	0.8	0.39	2.08
Rissoa auriscalpium	1.29	0.09	1.94

Table 4. Results of ANOVA for macro-invertebrate data. Significant differences are in bold. De = deep, In = intermediate, Sh = shallow, s-s = spring-summer, a-w = autumn-winter

NUMBER OF SPECIES

SOURCE	DF	MS	F	p
Depth = D	2	3041.7	374.58	**0**
Period = P	1	11081.8	4787.34	**0.0002**
Date(P) = Da(P)	2	2.3	0.01	0.991
DxP	2	2999.5	369.38	**0**
DxDa(P)	4	8.1	0.03	0.997
Area(DxDa(P))	24	257.3	122.98	**0**
Residual	72	2.1		
Total	107			
Cochran's C:		C = 0.137 (ns)		
snk test (DxP)		Sh: s-s > a-w	s-s: Sh > In > De	
		In: s-s > a-w	a-w: Sh = In = De	
		De: s-s = a-w		

NUMBER OF ORGANISMS

Depth = D	2	9824.2	98.43	**0.0004**
Period = P	1	29700.7	51.08	**0.019**
Date(P) = Da(P)	2	581.4	0.52	0.602
DxP	2	11109.3	111.31	**0.0003**
DxDa(P)	4	99.8	0.09	0.985
Area(DxDa(P))	24	1122.4	22.39	**0**
Residual	72	50.1		
Total	107			
Cochran's C:		C = 0.129 (ns)		
SNK test (DxP)		Sh: s-s > a-w	s-s: Sh > In > De	
		In: s-s > a-w	a-w: Sh = In = De	
		De: s-s = a-w		

Table 5. Results of ANOVA for shoot density and leaf length data. Significant effects are in bold. De = deep, In = intermediate, Sh = shallow, s-s = spring-summer, a-w = autumn-winter

| SOURCE | DF | LEAF LENGTH | | | | SHOOT DENSITY | | |
		MS	F	p		MS	F	p
Depth = D	2	14.85	2.47	0.2001		271027.34	337.20	**0.000**
Period = P	1	230.72	18.72	**0.0495**		2.29	0.00	0.965
Date(P) = Da(P)	2	12.32	17.43	**0.0000**		972.35	0.11	0.897
DxP	2	12.02	2	0.2498		153.28	0.19	0.833
DxDa(P)	4	6.01	8.5	0.2498		803.76	0.09	0.984
Area(DxDa(P))	24	0.70	1.9	**0.0075**		8983.41	15.16	**0.000**
Residual	324	0.37				592.47		
Total	359							
Cochran's C:		C = 0.082 (ns)				C = 0.133 (ns)		
		SNK test (P):	s-s > a-w			SNK test (D):	Sh >In >De	

assemblages (Fig. 2). ANOVA detected a significant interaction between Depth and Period for the two variables. Differences among areas were also significant. SNK tests showed that shallow and intermediate assemblages differed from deep assemblages in the spring-summer period but not in the autumn-winter period, while differences between periods were significant for shallow and intermediate assemblages but not for the deep one (Table 4).

Shoot density ranged between 517.1 ± 3.81 (mean ± SE, n=60) shoots m^{-2} in shallow meadows, and 421.9 ± 5.3 in deep meadows (Fig. 3a). Mean leaf length per shoot was highest in shallow meadows in the spring-summer period (44.2 ± 1.5) and lowest in deep meadows in the autumn-winter period (18.9 ± 1.7) (Fig. 3b). ANOVA showed that shoot density was significantly higher in shallow meadows compared to intermediate meadows, and also in the latter compared to the deep ones. Moreover, leaf length per shoot was higher in the spring-summer period compared to the autumn-winter period (Table 5).

DISCUSSION

Results of the present study show that the structure of motile macro-invertebrate assemblages associated with the *Posidonia oceanica*

leaf stratum changed along a depth gradient but this pattern was not consistent in different periods over one year. Thus, an important seasonal influence on the spatial distribution of invertebrates within the meadows is evident.

The composition of assemblages found in the present study agrees with those described for *P. oceanica* meadows in the central Mediterranean Sea (SCIPIONE *et al.,* 1996; MAZZELLA *et al.,* 1989; 1992; GAMBI *et al.,* 1992). The present results also confirmed that Mollusca and Crustacea are the groups more abundant in motile macro-invertebrate assemblages associated with Mediterranean seagrasses (RUSSO *et al.,* 1984; 1991; SCIPIONE & FRESI, 1984; BORG & SCHEMBRI, 2000).

Our results and those from previous investigations (RUSSO *et al.,* 1984; GAMBI *et al.,* 1992; BORG & SCHEMBRI, 2000), indicate a gradient related to depth for the motile fauna of *P. oceanica*. This pattern may be 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). Temporal variation in the structure of assemblages was also evident in the present investigation; this is in agreement with patterns described from other regions (RUSSO *et al.,* 1991; GAMBI *et al.,* 1992).

An interesting finding of the present study is the interaction between temporal and spatial patterns of variation and the relation between these patterns and changes in meadow structure.

The correlation between meadow structure and faunal assemblages is a debated issue (ATTRILL et al., 2000; BOSTROM et al., 2006; BORG et al., 2006, 2010). A positive correlation between seagrass biomass and abundance of benthic invertebrates has been described (HECK & ORTH, 1980; MATTILA et al., 1999). Habitat complexity of seagrass meadows and small-scale structural changes in both canopy height and epiphyte load appear to influence densities of decapod crustaceans (STONER, 1980; STONER & LEWIS, 1985; BELL & WESTOBY, 1986; JACKSON et al., 2006). However, some investigations did not find a significant correlation between epifaunal abundance and seagrass biomass (PIHL BADEN & PIHL, 1984; BORG et al., 2006).

A relationship between high habitat complexity and the abundance of associated species is suggested by results of the present study. As would be typically expected for *P. oceanica* meadows, shoot density decreased with depth and the leaf canopy was higher in the spring-summer period. Both spatial and temporal patterns of invertebrate distribution appeared to be influenced by the life cycle of *P. oceanica*, as values of species richness and abundance decreased with a decrease in leaf canopy height and shoot density. There are several mechanisms that may relate the structure of meadows to attributes of the faunal assemblages (PARKER et al., 2001). Canopy height and shoot density may influence seagrass meadow habitat complexity and availability of different microhabitats. Moreover, both these structural characteristics may be important in determining the role of meadows as refuges from predation. Finally, periods of high leaf canopy correspond to periods with the highest values of epiphyte abundance (MAZZELLA & OTT, 1984), determining a higher food availability for grazers (BORG et al., 2010). Temporal changes in epiphyte assemblages could explain temporal patterns of abundance of motile fauna observed in shallower stands in the present study. Herbivores, mostly abundant

in shallower meadows (MAZZELLA et al., 1992), probably follow seasonal changes of epiphyte biomass. On the contrary, the abundance of carnivorous assemblages associated with the deeper parts of the meadows would vary less over a one-year period (MAZZELLA et al., 1992).

The relationship between temporal and spatial patterns highlighted in the present study is not completely in agreement with patterns described in previous investigations carried out in the central Mediterranean Sea. RUSSO et al. (1984) observed that mollusk assemblages exhibited a clear vertical zonation that remained evident independently of seasons. MAZZELLA et al. (1989) observed a decrease in the abundance of the faunal assemblages of leaf stratum from shallow to deep meadows in November but not in May, when motile fauna had a lower abundance. The life cycle of organisms and a higher predation pressure have been considered the causes of a lower abundance of fauna associated with *P. oceanica* meadows in the spring period (MAZZELLA et al., 1992). Both biotic interactions and characteristics of meadows could be responsible for the different patterns observed in the different studies. In fact, predator pressure may influence the effects of meadow structure on the associated biota. Thus, a different abundance of fish, related to different levels of human pressure and protection, may determine changes in temporal patterns of motile invertebrates associated with seagrasses. Moreover, the richness and abundance of motile fauna could be influenced by the type of meadow (BORG et al. 2010) and characteristics of substrate and adjacent habitats (BOLOGNA & HECH, 2002; TUYA et al., 2010). The rocky bottom characterizing the studied sites could have an important role in determining spatial patterns of the biota's distribution, modifying the species composition of assemblages as per mechanisms already described for epiphytes (VAN ELVEN et al., 2004).

The patterns shown in the present investigation and previous studies by other authors suggest that temporal and spatial differences in the structure of *P. oceanica* meadows are key drivers in determining the species richness and abundance of leaf stratum motile macro-

invertebrate assemblages, even if the observed effects are influenced by several biotic and environmental factors.

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Prostorne i vremenske varijacije pokretnih makro-beskralješnjaka u livadama *Posidonia oceanica*

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SAŽETAK

Ova studija procjenjuje prostorne i vremenske raspodjele pokretnih makro-beskralješnjaka u livadama *Posidonia oceanica* u blizini obale pokrajine Toskana, u sjeverozapadnom Mediteranu. Hijerarhijska uzorkovanja korištena su za procjenu promjena sastava i obilja u odnosu na dubinu i na različita razdoblja dulja od jedne godine. Ukupno 136 svojti je utvrđeno, među njima 34 Mollusca, 94 Arthropoda, 5 Annelida i 1 Echinodermata. Rezultati multivarijantne i Uni-varijabla analize pokazali su da je struktura makro-beskralješnjaka kolebala po dubini gradijenta, ali ovaj uzorak nije bio dosljedan u dva razdoblja istaživanja. Rezultati ukazuju na to da su vremenske i prostorne razlike u naselju livada *P. oceanica* ključni pokretači u određivanju strukture povezane sa sastavom makro-beskralješnjaka, kao što su vrijednosti bogatstva i obilja smanjene sa smanjenjem dužine lista i gustoće izdanaka.

Ključne riječi: dubina, makro-beskralješnjaci, Sredozemno more, *Posidonia oceanica*, sezonski učinci