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Depth and Seasonal Distribution of Some Groups of the Vagile Fauna of the *Posidonia oceanica* Leaf Stratum: Structural and Trophic Analyses

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With 9 figures

Key words: Seagrasses, *Posidonia oceanica*, vagile fauna, depth gradient, seasonality, feeding guilds.

Abstract. The taxonomical and trophic structures of the vagile fauna communities of the leaf stratum in a *Posidonia oceanica* meadow at Ischia (Gulf of Naples, Italy) were investigated at five stations along a depth gradient (1 to 25 m). Sampling was performed in July, November, February, and May. The analyzed groups – polychaetes, molluscs, tanaids, isopods, amphipods, and decapods – exhibited similar distributional trends in all seasons, with coenotic discontinuities occurring at well-defined depths. The same zonation pattern was produced by feeding-guild analysis. Eleven trophic groups were identified. The most abundant groups were: Herbivores, which were found mainly at the shallow stations; Herbivores-deposit feeders, which were widely distributed along the transect; Deposit feeders-carnivores, found mainly at the deep stations.

This study suggests that in the *Posidonia* leaf stratum, herbivores and herbivores-deposit feeders, as consumers of epiphytic micro- and macroflora and deposited particulate organic matter, play an important role in the energy transfer from producers to higher trophic levels of the system.

Problem

The vagile fauna within the *Posidonia oceanica* canopy constitutes one of the most important components of the ecosystem formed by this phanerogam (KIKUCHI & PÉRÈS, 1977). A relevant fraction of these vagile organisms, both in term of abundance and species diversity, is composed of forms linked to the leaf surface (LEDOYER, 1968). They are strongly influenced by the features of both the plant, which is a growing substrate with high seasonality (OTT, 1980), and its epiphytes (MAZZELLA & OTT, 1984), showing specific adaptations to the various microenvironments.

Only in recent years have studies focused on the structure of some components of the vagile communities in relation to the environment (SCIPIONE *et al.*, 1983; CHESSA *et al.*, 1989; MAZZELLA *et al.*, 1989), taking also into account that *Posidonia* meadows are often distributed over a wide depth range (0.5–35 m). Within this depth gradient, changes in parameters such as hydrodynamic forces, light, temperature, and sediment structure determine differences in meadow structure and, directly and indirectly, in the structure and distribution of the communities. This has also been observed at the level of individual taxocoenes such as polychaetes (GAMBI *et al.*, 1989b), molluscs (RUSSO *et al.*, 1984; 1991), isopods (LORENTI & FRESI, 1983), amphipods (SCIPIONE & FRESI, 1984), and decapods (ZUPO *et al.*, 1989).

These studies revealed the presence of a well-defined community associated with the shallowest stand of the *Posidonia* bed, and of deeper communities with site-specific depth ranges.

The trophic interactions in the *Posidonia* ecosystem are highly complex (OTT, 1981; CHESSA *et al.*, 1983) and influence community structure. Studies on the functioning of this system have mostly stressed the role of the detritus-chain in energy transfer (OTT, 1981; WITTMANN *et al.*, 1981), placing less emphasis on the grazing activity on epiphytes. This aspect, however, is of paramount importance in trophic interactions at the leaf stratum level; it has been recently addressed in individual taxocoenes by means of feeding-guild and morpho-functional analyses (RUSSO, 1989; SCIPIONE, 1989; GAMBI *et al.*, 1989b) as well as by an experimental approach (MAZZELLA & RUSSO, 1989; SCIPIONE & MAZZELLA, in press). Such investigations suggested the presence of links and interactions between plant epiphytes and animals, pointing out also interesting implications regarding co-evolution (RUSSO, 1986; MAZZELLA *et al.*, in press).

The present analysis takes into account community structure and its trophic composition. It is based on feeding guilds and considers various groups such as polychaetes, molluscs, tanaids, isopods, amphipods, and decapods, which previous studies have revealed to be relevant components – in terms of abundance and species richness – of the vagile fauna of the leaf stratum. This study aims at determining how the depth distributional pattern is maintained over time (seasons), both in taxon and trophic guild organization. This should provide basic knowledge of how biotic interactions (*e. g.*, feeding behaviour) contribute, together with abiotic factors, to determine the structure of the communities.

Material and Methods

Investigations were carried out in a *Posidonia oceanica* bed off Lacco Ameno (Island of Ischia, Gulf of Naples), which extends from 1 m to about 33 m depth (COLANTONI *et al.*, 1982; MAZZELLA *et al.*, 1989). Five stations, located along a depth transect at 1 m, 3 m, 10 m, 15 m, and 25 m, were studied. At each station, two replicate samples of vagile fauna were collected in July and November (1981) as well as in February and May (1982), for a total of 10 samples a month. Samples were collected using a hand-towed net (a rectangular frame measuring 40 × 20 cm with a net of 400 µm mesh size) by SCUBA diving according to the technique described by LEDOYER (1962) and modified and standardized by RUSSO *et al.* (1985) and RUSSO & VINCI (1991). This technique consists of a series of strokes (60) delivered in such a way as to shake the *Posidonia* leaves from the base of the shoots (RUSSO *et al.*, 1985). The method is semi-quantitative and samples can therefore be compared. However, the variety of microenvironments in the *Posidonia* canopy and the different sizes and behaviours or life habits of organisms result in different capture efficiencies for the various groups. Nevertheless, in our opinion this method is best suited to collect those vagile organisms strictly associated with the leaf stratum (LEDOYER, 1962); it also provides the best compromise between sampling effort and obtained information.

The sorting of samples in the laboratory yielded specimens belonging to the following groups: *Foraminifera*, *Polychaeta*, *Mollusca*, *Copepoda*, *Ostracoda*, *Acarina*, *Pantopoda*, *Leptostraca*, *Mysidacea*, *Cumacea*, *Tanaidacea*, *Isopoda*, *Amphipoda*, *Stomatopoda* (larvae), *Decapoda*, *Brachiopoda*, *Echinodermata*, *Chaetognatha*, and *Pisces*. Among these, polychaetes, molluscs, tanaids, isopods, amphipods, and decapods were identified to the species level and considered in the present analysis.

The feeding analysis was performed by assigning each species to a feeding guild according to literature data. Due to the different trophic behaviours often exhibited by the same species, mixed categories were created. Species with unknown trophic behaviour were assigned to the category Unknown (Un). A total of 11 feeding guilds were identified: Suspension feeders (SF), which feed on seston; Deposit feeders (DF), which feed on surface detritus; Deposit-suspension feeders (DSF), which feed both on deposited and suspended material; Deposit feeders-carnivores (DC), which feed on deposited material and fauna; Limivores (Li), which feed on buried organic material; Herbivores (He), which graze on micro- and macroalgae; Detritus feeders (DeF), which feed on *Posidonia* tissue as "detritus"; Herbivores-deposit feeders (HeDF), which feed on plant epiphytes and trapped organic material; Carnivores (Ca), which include predators or scavengers; Omnivores (Om), which may behave as carnivores, herbivores, and/or deposit-feeders; Parasites (Pa), which parasitize other animals.

Population parameters such as species richness, abundance, Qualitative Dominance (DQ % = % number of species belonging to a given taxon), Quantitative Dominance (DI % = % number of individuals belonging to a given taxon), and trophic Quantitative Dominance (% number of individuals belonging to a given feeding guild) were calculated (BOUDOURESQUE, 1971). Structural analysis of the community was performed through a Correspondence Analysis (CA) (LEGENDRE & LEGENDRE, 1984) on a reduced set of species (variables), eliminating those occurring only with one individual in all the samples (40 observations). Significance of the CA axes was calculated according to FRONTIER (1974). Differences between the two replicates of each station were compared by the Wilcoxon test (SOKAL & ROHLF, 1973). In order to evaluate intra- and intersample similarity, a mean linkage cluster analysis was performed on the centered scalar product matrix obtained by the "species vs. stations" analysis.

A functional analysis was performed using again the Correspondence Analysis on the 11 identified trophic categories (variables) and pooling the two replicates of each station (20 observations).

Results

1. Descriptive taxonomic and trophic analysis

The examined taxonomic groups were represented by 312 species and 20,591 individuals. Taxa with the highest number of species included *Mollusca* (DQ: 30.0 %), *Polychaeta* (27.2 %), and *Amphipoda* (26.6 %), while *Decapoda* (7.6 %), *Isopoda* (6.2 %), and *Tanaidacea* (2.4 %) were less represented. In terms of numbers of individuals, the best represented taxa were *Mollusca* (DI: 51.4 %), *Decapoda* (23.1 %), and *Amphipoda* (21.0 %), followed by *Polychaeta* (2.1 %), *Isopoda* (1.8 %), and *Tanaidacea* (0.6 %).

Community abundance was highest in November (7,622 individuals for 10 samples), intermediate in February (4,919), and low in July (3,772) and May (3,772). Molluscs dominated in all seasons, particularly in February (58.2 %), with the exception of May (38.1 %), when amphipods (33.9 %) were also dominant. This latter taxon was constantly abundant, particularly in July (22.7 %). Decapods were important in November (28.2 %) and February (17.6 %) (Fig. 1a).

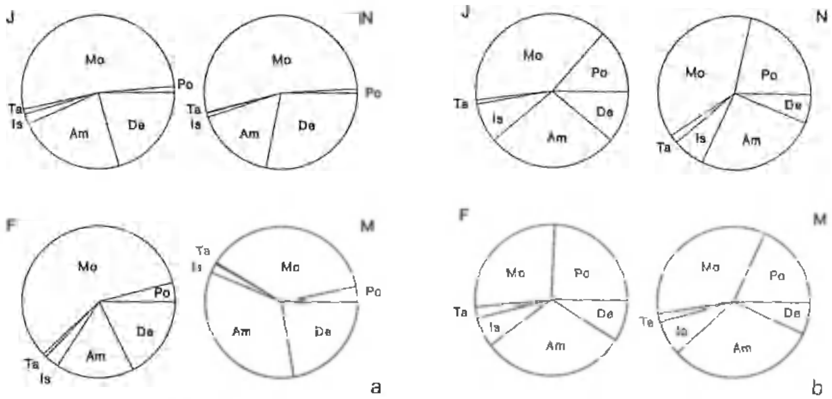

Fig. 1. Quantitative (DI %) (a) and qualitative (DQ %) (b) dominances of vagile fauna of the *Posidonia oceanica* leaf stratum in different seasons. a: July (J): 1.2 % (Po), 52.3 % (Mo), 1.0 % (Ta), 2.2 % (Is), 22.7 % (Am), 20.6 % (De). November (N): 0.8 % (Po), 53.2 % (Mo), 0.3 % (Ta), 0.8 % (Is), 16.7 % (Am), 28.2 % (De). February (F): 4.0 % (Po), 58.2 % (Mo), 0.8 % (Ta), 3.0 % (Is), 16.4 % (Am), 17.6 % (De). May (M): 3.2 % (Po), 38.1 % (Mo), 0.4 % (Ta), 2.0 % (Is), 33.9 % (Am), 22.4 % (De).
b: July (J): 13.5 % (Po), 38.7 % (Mo), 0.8 % (Ta), 8.4 % (Is), 27.7 % (Am), 10.9 % (De). November (N): 21.5 % (Po), 38.0 % (Mo), 1.8 % (Ta), 6.8 % (Is), 25.8 % (Am), 6.1 % (De). February (F): 24.4 % (Po), 27.3 % (Mo), 2.5 % (Ta), 6.3 % (Is), 30.7 % (Am), 8.8 % (De). May (M): 18.4 % (Po), 34.4 % (Mo), 1.8 % (Ta), 7.4 % (Is), 31.3 % (Am), 6.7 % (De).

The taxa with the highest number of species in all seasons were molluscs, particularly in July and November (DQ: 38.7 % and 38.0 %, respectively), followed by amphipods, particularly in February and May (30.7 % and 31.3 %, respectively), and polychaetes, mainly in February (Fig. 1 b).

The number of species along the transect increased slightly with depth, particularly in February, when the community had the lowest values at 1 m (mean of the two samples: 27) and the highest at 25 m (87). The lowest overall values were observed in July, ranging from 34.5 species at 1 m to 44.0 at 25 m. At 1 m the highest values were observed in May (64). At 3 m and 10 m in February and November, the number of species showed complementary trends (Fig. 2 a).

The number of individuals was highest at 3 m (3,462.5 total value, mean of the two replicates) in all the considered months, with an exceptionally high value in November (1,816; mean of the two replicates). In May, however, the highest values were found at 1 m (520.5), where the lowest values occurred in February (151.5) (Fig. 2 b).

The trophic analysis revealed that the dominant feeding categories of the community as a whole were Herbivores-deposit feeders (60.7 %), Deposit feeders-carnivores (16.0 %), Herbivores (10.5 %), and Carnivores (4.9 %),

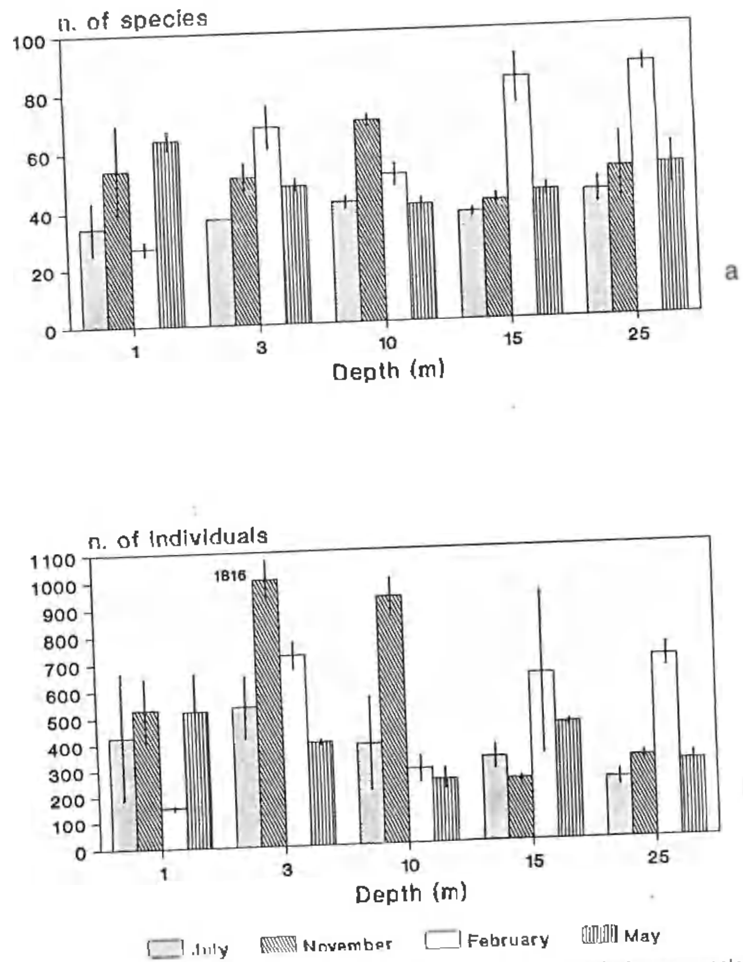

Fig. 2. Number of species (a) and number of individuals (b) of vagile fauna in the four seasons along the depth transect. The columns represent the mean values of the two replicates, the bars the single values of each replicate.

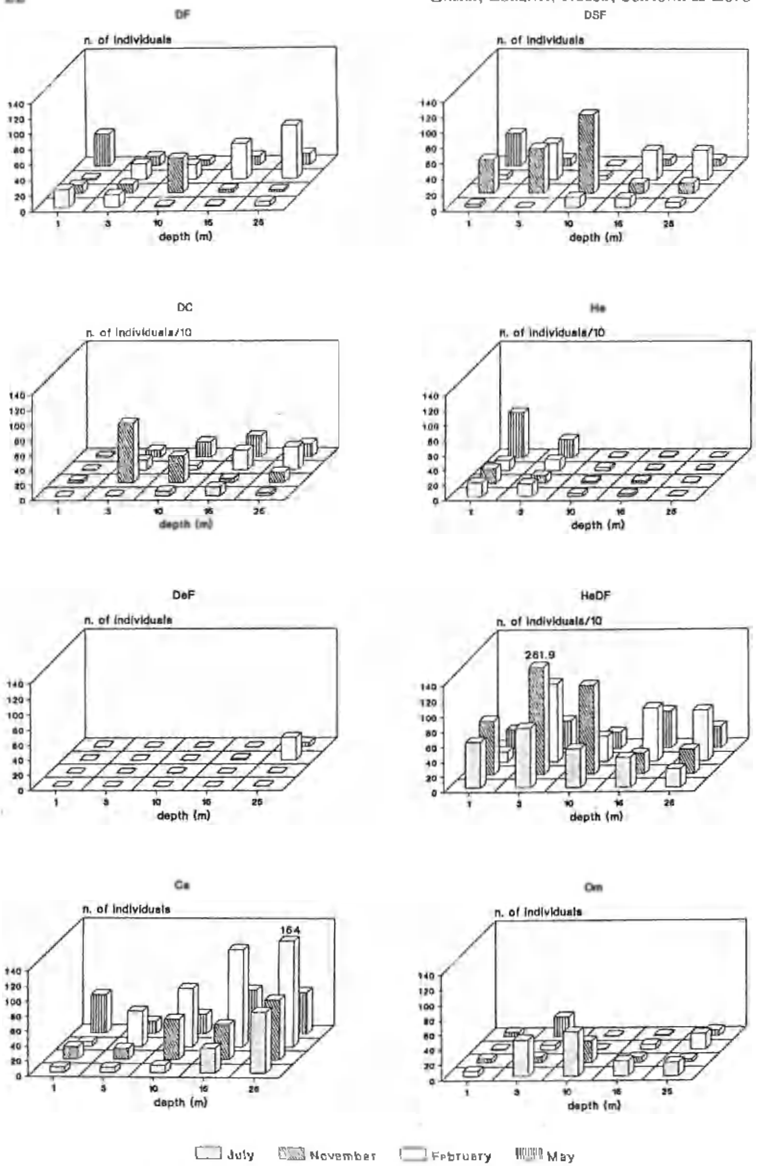

Fig. 3. Number of individuals belonging to the different feeding guilds along the depth transect and in the different seasons. The number of individuals for He, HeDF, and DC have been divided by 10 in order to maintain the same numerical scale on the Y axis.

followed by Deposit-suspension feeders (2.4 %), Deposit feeders (1.9 %), Unknown (1.5 %), Omnivores (1.4 %), Parasites (0.3 %), Detritus feeders (0.2 %), and Suspension feeders (0.2 %).

The HeDF dominated along the transect in all seasons, reaching their highest values mainly at 3 m. Herbivores were most abundant at the shallow stations in May (599 indiv. at 1 m; 244 indiv. at 3 m). Ca and DC were most common at intermediate and deep stations, the latter group attaining highest values in November at 3 m and 10 m (803 and 367 indiv., respectively). Other groups showed no particular distributional trends, exhibiting maximum number of individuals in different seasons and depths (Fig. 3).

Polychaeta

A total of 934 individuals belonging to 101 taxa were collected; 40 species were represented by only a single individual. A total of 506 individuals, belonging to 22 species of the families *Terebellidae*, *Sabellidae*, *Serpulidae*, and *Spirorbidae*, were sessile forms living permanently within tubes. Due to their life habits, these suspension-feeders are omitted from the following analysis, which therefore refers to the 79 remaining vagile or sedentary species.

Among the many species found, none was notably more abundant than or dominant over the others. The best represented family was *Syllidae*, which had the highest number of species (40) yet relatively few individuals (270). The total number of species and individuals increased from July to February, when maxima were observed, and decreased slightly in May. In each month, abundance generally increased with depth, while the number of species showed irregular trends.

With regard to spatial distribution, some species were present or slightly more abundant in the shallowest stands (1 and 3 m): *Grubeosyllis clavata* (CLAPAREDE), *G. vieitezi* SAN MARTIN, *Syllis prolifera* KROHN, *Platynereis dumerilii* (AUD. & M. EDW.), and *Polyophthalmus pictus* (DUJARDIN). Other species occurred or were more abundant in the intermediate and deep stands: *Kefersteinia cirrata* (KEFERSTEIN), *Grubeosyllis yraide* SAN MARTIN, *Eurisyllis tuberculata* EHLERS, and *Odontosyllis gibba* CLAPAREDE. The remaining taxa were present at all depths (*Sphaerosyllis hystrix* CLAPAREDE) or showed an irregular distribution pattern.

The few species present during all months were *S. hystrix*, *E. tuberculata*, *P. dumerilii*, and *Glycera tesselata* GRUBE. Seasonal differences were due to a few species being more abundant in a particular month, *e. g.* *G. clavata* and *S. prolifera* in May, *K. cirrata* and *S. hystrix* in November, or *E. tuberculata* and *P. pictus* in February. The remaining taxa showed no particular temporal pattern.

The trophic analysis yielded a total of nine feeding guilds, most coherent with the classification of FAUCHALD & JUMARS (1979). Carnivores (181 individuals in all samples), mostly *K. cirrata* and several species of the genus *Syllis* (*Syllidae*), were the most abundant guild and generally inhabited the deeper stations. Herbivores (77 individuals), mainly *P. dumerilii*, *Nereis rava* EHLERS, and *P. pictus*, were quite abundant, especially in the shallow stations and in July and

May. Deposit feeders-carnivores (53 individuals) were represented by species of the genus *Sphaerosyllis (Syllidae: Exogoninae)* and were relatively abundant along the entire transect in November and February, being negligible in the other months. Herbivores-deposit feeders (82 individuals), composed of different *Exogoninae*, were present all along the transect and were more abundant in May. The few Deposit feeders and Limivores most likely included species inhabiting the rhizomes.

Mollusca

A total of 10,330 individuals belonging to 87 species – 20 being represented by only one specimen – were identified. They were distributed in two classes as follows: *Gastropoda* (no. of indiv.: 10,292; DI: 99.7 %; no. of species: 76; DQ: 87.4 %), *Pelecypoda* (32; 0.3 %; 11; 12.6 %).

The prosobranch gastropod groups with the highest number of individuals and species were *Trochidae*, in shallow beds, *Cerithiidae*, in deep beds, and especially *Rissoidae*, at all depths (see also RUSSO *et al.*, 1983). As stressed earlier (IDATO *et al.*, 1983), the structure of the communities along the depth gradient showed a clear zonation pattern. Such structural zonation, with changes in population parameters (number of species and individuals), was also found to persist seasonally (RUSSO *et al.*, 1984; 1991).

Six feeding guilds were identified, mainly on the basis of radular structure and, therefore, of the main evolutionary trends as reflected by prosobranch systematics (RUSSO, 1986). The *Archaeogastropoda* group contains most truly grazing Herbivores inhabiting seagrass beds (*e. g.*, *Gibbula* spp., *Jujubinus* spp.); it also includes species which feed on colonial and sedentary animals (FCSA, *e. g.*, *Calliostoma* spp.) as defined by PURCHON (1977), a category distinguished from true Carnivores. This latter group also contains some mesogastropods (*Cerithiopsis* spp. and *Momophorus* spp.). Most *Mesogastropoda* in the *Posidonia* beds (mainly *Rissoidae* and *Cerithiidae*) have been grouped in the Herbivores-deposit feeders guild. The most evolved group, *Neogastropoda*, mainly specialised as active predators, has been included in the Carnivores guild.

The category Suspension feeders was composed solely of the few sestonophagous bivalves collected by the hand-towed net.

Herbivores-deposit feeders were the most abundant all along the transect and in all seasons (Fig. 4); species that contribute to the high quantitative dominance (84.9 %) of this guild were *Rissoa (Goniostoma) italiensis* VERDUIN, in the shallow bed (1–3 m), *Alvania lineata* RISSO, at intermediate depths (3–10 m), and *Rissoa violacea* DESMAREST and *Bittium latreillii* (PAYRAUDEAU) in the deep bed (15–25 m). Herbivores mainly inhabited the shallowest station (1 m) and showed a peak abundance in February, due mainly to *Gibbula ardens* (VON SALIS) (Fig. 4). Carnivores increased in dominance with depth, reaching maximum values in the deepest stations in all seasons, mainly due to *Granulina clandestina* (BROCCHI). A minor role was played by the other feeding guilds such as Parasites, FCSA, and Suspension feeders, which seemed to be more prevalent in the deep stands.

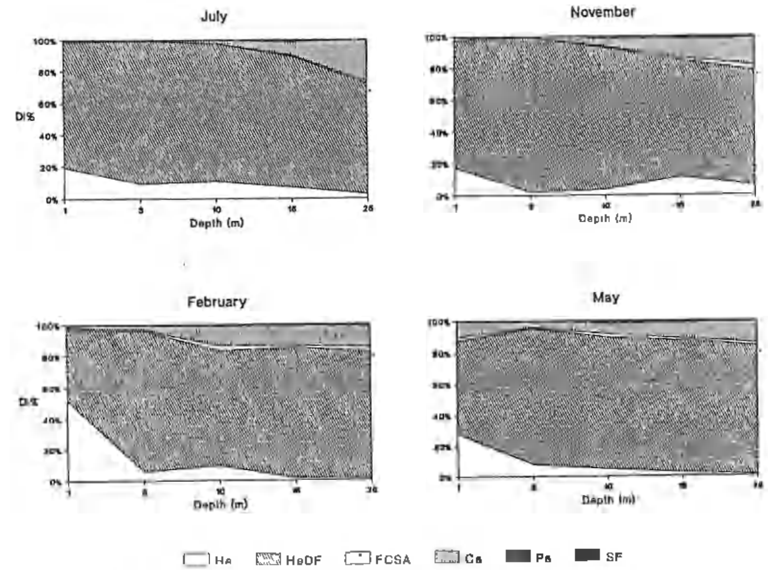

Fig. 4. *Mollusca*. Quantitative Dominance (DI %) of trophic categories along the depth transect in the four seasons.

Tanaidacea

Six species of tanaids were found, for a total of 103 individuals. Of these, 67 individuals were *Leptochelia savignyi* KROYER, which is present in all four seasons, reaching a maximum number in July (39) and showing a decreasing trend with depth. *Parapseudes latifrons* (GRUBE) and *Paratanaidae* gen. sp. were found only in February in the shallow and deep stands of the bed, respectively. The other species were present with few individuals in only one station.

The collected species were considered to be Deposit feeders; some forms *(Apseudidae)* can supplement deposit feeding behaviour with suspension feeding.

Isopoda

Isopods were present with 18 species and a total of 369 individuals. As a whole, the number of individuals reached a peak in February (148) compared with July (82), November (61), and May (77). The number of species did not vary significantly with season: July (10), November (11), February (13), May (12).

As regards depth distribution, the maximum number of individuals was found at intermediate stations (10, 15 m), except in February (25 m), while the minimum always occurred at 1 m.

Trends of the whole taxon were strongly influenced by *Cymodoce hanseni* DUMAY (179 individuals, mostly juveniles), which was by far the dominant species in November (DI: 55.7 %), February (55.0 %), and May (63.6 %); in July this role was played by *Synisoma appendiculatum* (RISSO) (40.0 %). Furthermore, *Disconectes picardi* (AMAR) reached its peak of abundance in July, whereas *Jaeropsis dollfusi* NORMAN and *Dynamene tubicauda* HOLDICH were more abundant in February. Other species (*Gnathia* cf. *vorax* LUCAS, *Astacilla mediterranea* KOEHLER) were present in all four months, although their distribution did not show any clear trend.

With regard to feeding guild distribution, Herbivores-deposit feeders were strongly dominant both in terms of species (DQ: 53.0 %) and individuals (DI: 70.0 %). Due to the numerical importance of *C. hanseni* and *S. appendiculatum* within this trophic group, temporal and spatial patterns of Herbivores-deposit feeders fundamentally reflected those shown by the two species. Parasites were represented mainly by juvenile *Gnathia*, known to feed on seagrass fishes. *J. dollfusi* was included among Carnivores, based on an observation by FRESI (1968) that this species may feed preferentially on *Hydrozoa*. Deposit-suspension feeders were represented by *A. mediterranea*.

Amphipoda

Amphipods were present with 77 species, belonging to 51 genera and 25 families, for a total of 4,217 individuals. Of these, 19 were rare (only one individual).

The number of species along the transect showed different trends in the different seasons: a slight increase with depth was recorded in July (mean of the two replicates from 9.5 to 13), while in February this increase was more pronounced. Here, minimum values occurred at 1 m (5), maximum values at 25 m (31), with a strong reduction at 10 m (11). A similar pattern of reduction was noted in May, when the highest values were present instead at 1 m (19.5). A trend opposite to that recorded in February and May was found in November, with the lowest values at 25 m (9).

The number of individuals increased with depth in February, with the highest values at 25 m (mean individuals 139) and the lowest at 1 m (11); an opposite trend was observed in the other months, particularly in May, when the greatest number was found at 1 m (343.5).

The amphipod community was mainly represented by *Apherusa chiereghinii* GIORDANI-SOIKA (total number of individuals: 903), *Amphithoe helleri* G. KARAMAN (643), *Dexamine spinosa* MONTAGU (337), *Hyale schmidti* (HELLER) (285), *Aora spinicornis* AFONSO (273), *Phtisica marina* SLABBER (222), and *Liljeborgia dellavallei* STEBBING (100); these species accounted for 65.5 % of the total. In July, the dominant species were *D. spinosa* and *P. marina*, in November and February *A. spinicornis* and *A. chiereghinii*, while in May *A. helleri* was dominant, being responsible for the highest abundance values at 1 m, as noted above.

Eight trophic categories were identified: Deposit feeders (6.1 %), Deposit-suspension feeders (10.5 %), Deposit feeders-carnivores (2.9 %), Herbivores (30.2 %), Detritus feeders (0.8 %), Herbivores-deposit feeders (35.8 %),

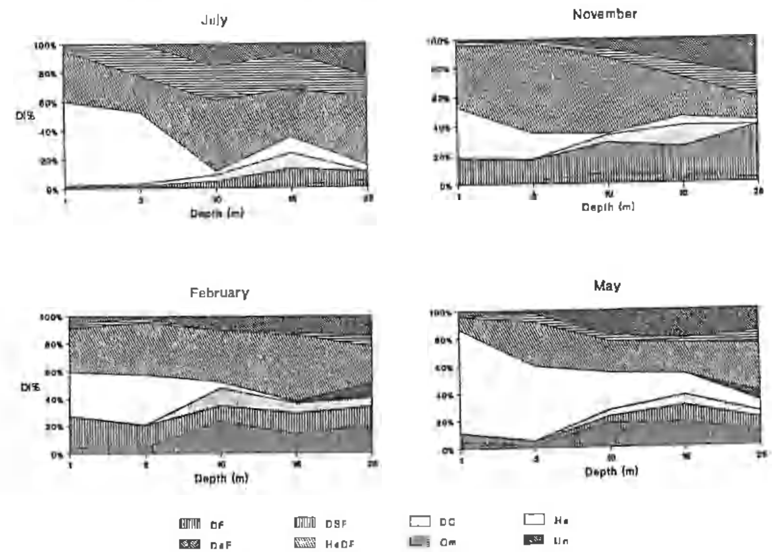

Fig. 5. *Amphipoda*. Quantitative Dominance (DI %) of trophic categories along the depth transect in the four seasons.

Omnivores (6.7 %), Unknown (7.0 %). The dominant feeding categories, He and HeDF, were mainly represented by *H. schmidti*, *Hyale camptonyx* (HELLER), *A. helleri*, *Amphithoe ramondi* AUDOUIN, *Cymadusa crassicornis* (A. COSTA), as well as by *A. chiereghinii* and *D. spinosa*, respectively.

The highest Herbivore dominances were observed at the shallow stations, mainly in July (1 m: 57.8 %; 3 m: 49.3 %) and May (1 m: 75.2 %; 3 m: 53.9 %). Herbivores-deposit feeders were present constantly all along the transect, particularly in November (50.6 %) and February (36.5 %) (Fig. 5); in these seasons, Deposit-suspension feeders were also important (17.8 % and 14.5 %, respectively). In July the Omnivores, mainly represented by the *Caprellidae* *P. marina*, were also dominant (17.7 %). In February and May, in the deeper stands, Deposit feeders such as *L. dellavallei* and Deposit feeders-carnivores such as *Lysianassidae* were also important. Detritus feeders were poorly represented by *Atylus vedlomensis* (BATE & WEST.) and *Gammarella fucicola* (LEACH) and were present only in the deepest station (25 m).

Decapoda

Sixteen species, totalling 4,632 individuals, were identified; some, such as *Pisa muscosa* (L.) and *Macropodia rostrata* (L.), belonging to the family *Majidae*, were represented only by few individuals. The strongly dominant species in all

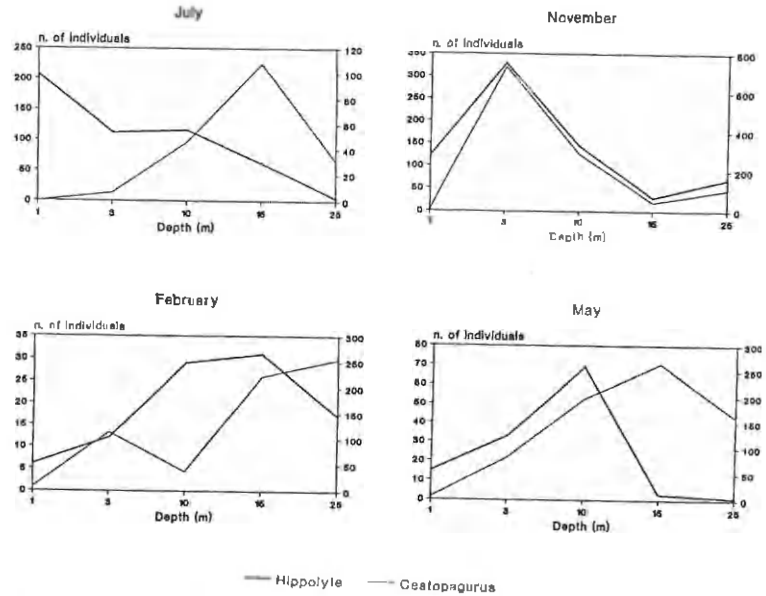

Fig. 6. *Decapoda*. Number of individuals of *Hippolyte inermis* and *Cestopagurus timidus* along the depth transect in the four seasons.

the considered months were *Hippolyte inermis* LEACH (1,419 indiv.) among the *Natantia* and *Cestopagurus timidus* (ROUX) (2,717) among the *Reptantia*. The remaining species were apparently related to particular seasons: *Galathea intermedia* LILLJEBORG more frequent in winter months; *Galathea bolivari* ZARIQUIEY ALVAREZ present only in July and February; few *Eurynome aspera* (PENNANT) in November; and *Thoralus cranchii* (LEACH) present only in November and February.

The two dominant species showed different patterns along the depth transect in the different months (Fig. 6). In July and November, *H. inermis* was more abundant at the shallower stations, in February at the intermediate stations (10–15 m). In May this species showed a strong decrease at 15 and 25 m. Compared with the distribution of *H. inermis, C. timidus* showed an opposite trend in July, a similar trend in November, while in February and May it was most abundant in the deeper stations.

Five trophic groups were identified. Due to the high abundances of *H. inermis* and *C. timidus*, their feeding behaviour strongly determined the trophic structure of the taxon. The former can be considered to be a Herbivore-deposit feeder, the latter a Deposit feeder-carnivore. In July, Deposit feeders-carnivores were more abundant at the deeper stations and Herbivores-deposit feeders at the shallow stations; in November they were equally abundant all

along the transect, with a small peak of the former at 3 m (800 indiv.). The abundance of DC increased towards the deeper stations in February and May, when the HeDF were found mainly at the shallower stations. In February and May, Carnivores were also present in greater numbers.

2. Structural analysis

a. Population structure

The Correspondence Analysis was performed on 212 species: 45 polychaetes, 67 molluscs, 7 tanaids, 13 isopods, 63 amphipods, and 17 decapods. Two axes were significant and accounted for 19.2 % and 15.0 % of total variance, respectively. Observation points of all the months considered are ordered along the first axis according to depth, with the shallow station samples at the positive pole and the deep ones at the negative pole (Fig. 7). The second axis separates the majority of the samples according to the month of collection, especially the shallow and intermediate stations (1 m, 3 m, 15 m), with February and November toward the positive pole and July and May toward the negative pole; the shallow station samples (1 m, 3 m) of May are strongly separated from the others. The two replicate-points closely adjoin each other, except in certain shallow stations (*e. g.*, 1 m in May); the distances between the replicate-points decreased with depth. The two replicates for each station were not significantly different at $P = 0.05$ (WILCOXON test). The cluster analysis also revealed that the replicates of most stations were associated at high levels of similarity; the exceptions were the stations at 1 and 10 m in July, at 25 m in November, and at 15 m in February, which were associated at an average similarity below 0.5.

The species contributing the most to axes I and II were located near the following stations:

- 1 m (May): *Grubeosyllis clavata* (II: 1.5), *Syllis prolifera* (II: 1.1), *Amphithoe helleri* (I: 21.8; II: 31.0), *Cymadusa crassicornis* (I: 1.3; II: 1.5), *Microdeutopus anomalus* (RATHKE) (I: 2.0; II: 4.1), *Elasmopus* sp. (II: 1.3), *Stenothoe monoculoides* (MONTAGU) (I: 1.1; II: 1.1), *Hyale camptonyx* (II: 1.3);
- 1 m (July): *Gibbula umbilicaris* (L.) (I: 2.4), *Hyale schmidti* (I: 3.1);
- 3 m (May–July): *Dexamine spinosa* (I: 1.1);
- 1 m (February): *Gibbula ardens* (I: 1.9; II: 1.7), *Rissoa italiensis* (I: 7.3; II: 14.8);
- 3 m (February): *Rissoa ventricosa* (DESMAREST) (II: 1.4); *Hippolyte inermis* (I: 1.5; II: 2.7);
- 3 m (November): *Alvania lineata* (II: 11.8);

intermediate and deep stations: *Cestopagurus timidus* (I: 7.0), *Pusillina dolium* (NYST) (I: 1.2), *Rissoa violacea* (I: 4.7), *Rissoella inflata* (MONTEROSATO) (I: 7.5; II: 3.3), *Coriandria cossurae* (CALCARA) (I: 2.1; II: 1.2), *Bittium latreillii* (I: 6.3; II: 5.6), *Odostomia* sp. (I: 4.2; II: 1.4), *Cymodoce hanseni* (I: 1.5), *Apherusa vexatrix* (I: 1.1).

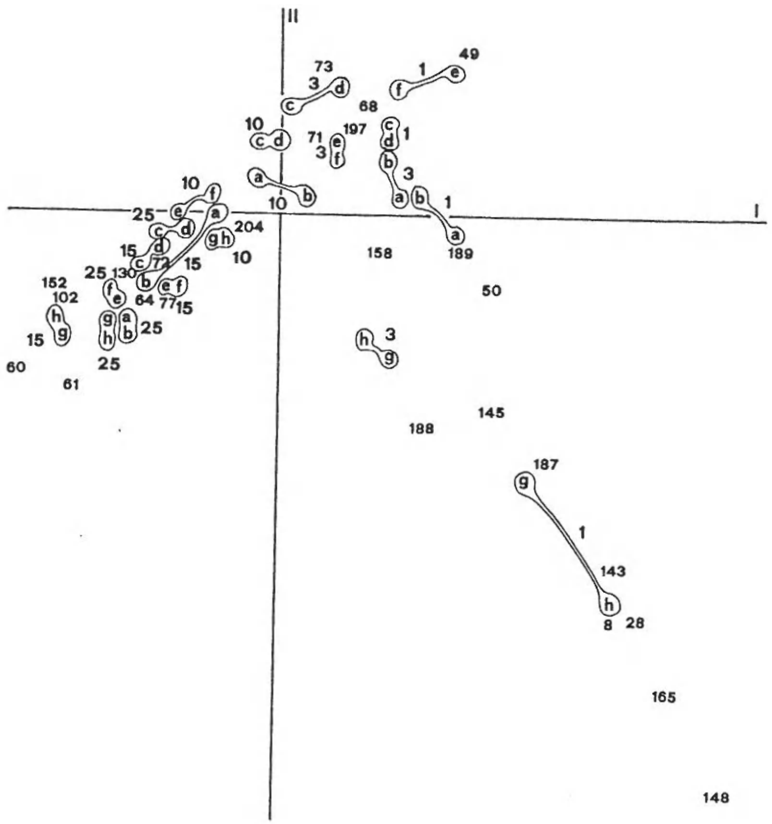

Fig. 7. Population structure of vagile fauna. Ordination model of Correspondence Analysis (CA). 212 variables (species), 40 observations (samples). Station points: 1–3–10–15–25 (depths). a–b (July), c–d (November), e–f (February), g–h (May). Species points: 8, *Grubeosyllis clavata*; 28, *Syllis prolifera*; 49, *Gibbula ardens*; 50, *Gibbula umbilicaris*; 60, *Rissoella inflata*; 61, *Coriandria cossurae*; 64, *Pusillina dolium*; 68, *Rissoa italiensis*; 71, *Rissoa ventricosa*; 72, *Rissoa violacea*; 73, *Alvania lineata*; 77, *Bittium latreillii*; 102, *Odostomia* sp.; 130, *Cymodoce hanseni*; 143, *Amphithoe helleri*; 145, *Cymadusa crassicornis*; 148, *Microdeutopus anomalus*; 152, *Apherusa vexatrix*; 158, *Dexamine spinosa*; 165, *Elasmopus* sp.; 187, *Stenothoe monoculoides*; 188, *Hyale camptonix*; 189, *Hyale schmidti*; 197, *Hippolyte inermis*; 204, *Cestopagurus timidus*.

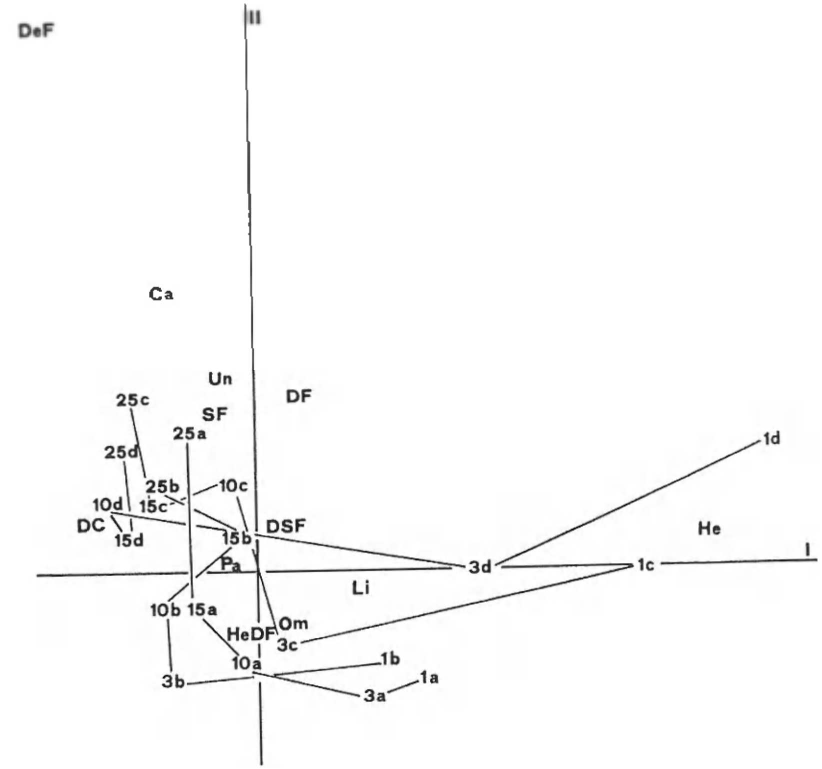

Fig. 8. Trophic structure of vagile fauna. Ordination model of Correspondence Analysis (CA). 12 variables (trophic categories). 20 observations (samples). Station points: 1–3–10–15–25 (depths), a: July, b: November, c: February, d: May. SF: Suspension feeders, DF: Deposit feeders, DSF: Deposit-suspension feeders, DC: Deposit feeders-carnivores, Li: Limivores, He: Herbivores, DeF: Detritus feeders, HeDF: Herbivores-deposit feeders, Ca: Carnivores: Om: Omnivores, Pa: Parasites, Un: Unknown.

b. Trophic structure

The ordination model – in the plane of the first two factors, which account for the following percentages of variance, FI: 57.9 % and FII: 18.9 % – shows that the station points are ordered according to depth, along a series of parabolic arches, with the shallow and the deep stations toward the positive pole of axis I and II, respectively (Fig. 8). A strong disjunction of Herbivores, located close to the 1 m stations in May and February, is evident; the other main feeding guilds are ordered according to depth: Herbivores-deposit feeders close to the intermediate stations, Deposit feeders-carnivores and Carnivores toward the deepest stations along with Suspension- and Deposit feeders; Detritus feeders are strongly polarized toward the positive pole of axis II.

Discussion

The vagile fauna of the *Posidonia oceanica* leaf stratum is clearly zoned along the transect, showing almost the same pattern in the four seasons; this confirms the results of a two-month analysis carried out in the same meadow (MAZZELLA *et al.*, 1989; MAZZELLA *et al.*, 1991).

The zonation along the depth gradient reveals the presence of a shallower community, characterized by a more pronounced seasonality, and a deeper, less variable one. A transition can be recognized between these two assemblages; it corresponds to the intermediate portion of the meadow and is characterized by special features (PIRC, 1984) such as meadow morphology and clines of physical factors (*e. g.*, thermocline, water motion). This zone is therefore a boundary between the shallow stand, where the environment is more stressful, and the more stable deep one.

In autumn and winter the communities were richer both in species and individuals, as has been observed for other phanerogams (NELSON, 1979; NELSON *et al.*, 1982) and in previous analyses (MAZZELLA *et al.*, 1989), and present a higher variability along the transect than in other seasons. This could be due to a number of seasonal factors, both abiotic, such as higher fluctuations of environmental conditions, and biotic. The latter include meadow features (reduced leaf covering and canopy height), lower predation pressure (NELSON, 1979), and individual taxon dynamics.

As for community trophic structure along the transect in the different months, a strong correlation with population structure was noted. This is evident from a comparison of the two CA ordinations (Figs. 7 and 8). Trophic structure is dominated by plant feeders (HeDF and He), which account for over 71 % of total population and show a well-defined vertical zonation. This dominance is also evident within each faunistic group, for example in the dominant taxa, molluscs and amphipods. Individual taxonomic groups showed specific trends that will be discussed separately.

Polychaetes in the *Posidonia* leaf stratum had a high species richness but low abundances. This is coherent with previous studies in Lacco Ameno (COLOGNOLA *et al.*, 1984; MAZZELLA *et al.*, 1989) and in other prairies (GAMBI *et al.*, 1989 b). Vagile polychaetes apparently do not find the leaf stratum a favorable habitat, probably due to the more stressful physical conditions, competition with other taxa, or predation pressure (CHESSA *et al.*, 1989). Polychaetes are more abundant in the rhizome layer (PRONZATO & BELLONI, 1981; SAN MARTIN & VIEITEZ, 1984; GIANGRANDE, 1985) where they generally find more favorable physical conditions (GAMBI *et al.*, 1989 a). Among the dominant family of *Syllidae*, many species are interstitial forms *(Exogoninae)*, while those syllids abundant in the shallow stand of the bed are commonly found on hard littoral bottoms covered by algae (GIANGRANDE, 1988). This is the case in *Platynereis dumerilii*, one of the most abundant species in *Posidonia* beds and frequently also recorded in environments with low competition, such as polluted hard bottoms (BELLAN, 1980). The life cycle of *P. dumerilii* has many traits of an r-strategy species (GIANGRANDE, 1989); moreover, this species is a herbivore whose role in the decay of living and dead brown algae tissue on the Atlantic coasts has been well documented (BEDFORD & MOORE, 1985). Its distribution in the shallowest Lacco Ameno stands coincides with the higher epiphytes development here (MAZZELLA *et al.*, 1989) and suggests that the species is trophically linked to the plant epiphyte and/or leaf-detritus.

Gastropods almost exclusively characterize the mollusc community on *Posidonia* leaves. Some species preferentially inhabit this environment and have evolved K-strategies of reproduction (RUSSO, 1989). The high dominance of Herbivores in February at 1 m is due to the population dynamics of the dominant species *(Gibbula ardens)* and to its trophic specialization, well-adapted to the first colonization stages of the seagrass epiphytic covering (MAZZELLA & RUSSO, 1989). In deep stands, the presence of Pa, FCSA, and SF is coherent with the decreased shoot density and light intensity occurring in seagrass stands with higher sedimentation rates. This on one hand permits better growth of encrusting animals and higher abundances of their predator molluscs (FCSA, *e. g.*, *Monophorus* spp.), and, on the other hand, important intrusions of soft bottom faunas such as bivalves (Suspension feeders) and echinoderms with their parasitic molluscs *(e. g., Vitreolina devians)*. In general, only minor variations in feeding structure seem to occur during the year. This may be explained by the high abundance of *Mesogastropoda* at all depths and in all seasons; they are mainly grouped in a single guild, HeDF, which includes several trophic specializations. Future investigations on *Mesogastropoda* biology using a variety of methodological tools should enable us to split them into new, more precisely defined guilds. At present, more accurate information on their feeding strategies is lacking, especially for most *Rissoidae* and *Cerithiidae*.

The isopod taxon shows a temporal pattern, with peak abundance in February and no obvious variation in species richness between seasons, and a spatial pattern, with low abundance at shallower depths. At least five species can be considered part of the fundamental stock of the *Posidonia* community (LEDOYER, 1966; LORENTI & FRESI, 1983). Only *Cymodoce hanseni* is strongly dominant, except in July, showing a depth-related distribution; other species show no clear trend, in part because of their low overall abundance. However, a comparison between the seasonal distribution of the two species which numerically dominate HeDF shows differences that may be due to their microhabitat range: *S. appendiculatum*, which is morphologically adapted to the leaf blade-epiphytes system, mostly occurs in May and July, when plant growth is at a peak, while *C. hanseni*, which undergoes microhabitat shifts also on a diel basis (LORENTI & SCIPIONE, 1990), shows a more even temporal distribution.

The amphipod population is one of the most important components of the *Posidonia* vagile fauna (LEDOYER, 1962; MAZZELLA *et al.*, 1989). As food for decapods and fishes, it plays a major role in the energy transfer to higher trophic levels (BELL & HARMELIN-VIVIEN, 1983; CHESSA *et al.*, 1983; SPARLA, 1989) and is clearly zoned with depth in the Lacco Ameno meadow. A shallow water amphipod community, able to withstand high water movement and mainly represented by Herbivores in May and July, is related to the erect algal epiphytic layer; this layer is more developed in these months and constitutes a primary food source for amphipods. A community mainly represented by Herbivores-deposit feeders occurs at intermediate and deep stations, where major deposition of particulate organic matter on leaves may favour the presence of "detritus cleaner" forms; these forms represent the main trophic group in the foliar stratum, as has been observed in other phanerogams (NAGLE, 1968; HOWARD, 1982; LEWIS & HOLLINGWORTH, 1982) and in a previous analysis (SCIPIONE, 1989). Deposit-suspension feeders and Deposit feeders-carnivores are better represented at the deep stations, probably because of the more heterogeneous meadow structure and an overlapping with surrounding soft bottoms. The different seasonal distributions of dominant species that are within the same trophic group – such as *Apherusa chiereghinii* and *Dexamine spinosa* – are most likely due to different life cycles, competition phenomena, or various grazing adaptations to plant epiphytes (GREZE, 1968). The detritus pathway, which constitutes an important means of energy transfer for amphipods (WITTMANN *et al.*, 1981) in *Posidonia* systems, appears to be negligible at the leaf stratum level for the presence of a separate amphipod community.

Previous studies have revealed a higher species richness in the decapod populations of *Posidonia* beds (MONCHARMONT, 1979–80; GARCIA-RASO, 1990; ZUPO, 1990). The species identified here are typical of the leaf stratum as typically sampled by the hand-towed net method. The wide distribution and high abundances of *Hippolyte inermis* and *Cestopagurus timidus* along the transect is due to their adaptability to different hydrodynamic and trophic conditions; their life cycles are also well adapted to the plant's annual cycle (PESSANI, in press; ZUPO, submitted). Less abundant species seem to be linked to a narrower depth range. For example, *Clibanarius erythropus*, as stated in a previous paper (ZUPO *et al.*, 1989), prefers shallow waters, while *Anapagurus laevis* is typical of deep waters. Herbivores-deposit feeders feed preferentially on diatoms and algal detritus, while Deposit feeders-carnivores – mainly limited to the deeper stations – feed on grazers such as copepods and small molluscs. Decapods, therefore, participate in both epiphyte and detritus food webs (ZUPO & FRESI, 1985); as a food source for large predators (*e.g.*, fishes) (BELL & HARMELIN-VIVIEN, 1983), they also represent an important path in the transfer of energy to the highest trophic levels.

As a whole, the vagile fauna distribution basically reflects the environmental gradient, although biological accommodation of single species – in terms of trophic relationships and life histories – plays a crucial role. In particular, the high dominance of Herbivores at the shallower stations in February and May is

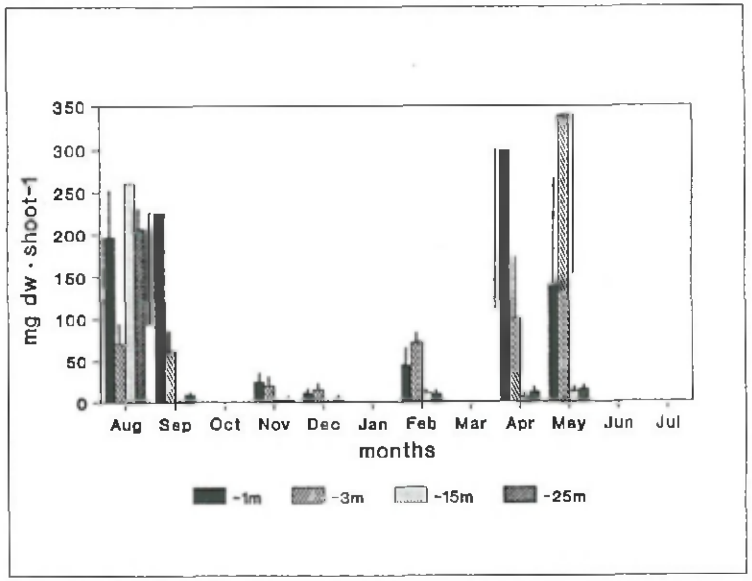

Fig. 9. Annual trends (1981–1982) of mean values of algal epiphyte biomass at different depths (from MAZZELLA & BUIA, 1989).

consistent with patterns of algal epiphyte biomass (Fig. 9; MAZZELLA & BUIA, 1989). In summer, when epiphyte biomass is more evenly distributed along the transect, herbivore presence is more uniform (see the minor polarization of July station points in the ordination model in Fig. 8). It should be noted that herbivore dominance in February and May is due to molluscs and amphipods, respectively: a key factor is the different trophic specialization of the dominant species, *i. e.*, *Gibbula ardens* and *Amphithoe helleri*, in relation to the specific epiphyte morphology present in each of the two seasons (encrusting vs. erect forms, respectively).

The explanation for the trends of the other trophic categories is less clear, apparently because of their intrinsic heterogeneity. The greater abundance of Carnivores at deep stations is due to the diversity of prey as well as to habitat stability and heterogeneity, which allows for a multiplicity of niches and interactions. Suspension feeders and Deposit feeders are linked to higher rates of deposition, which in turn are related to hydrological conditions in the water column overlying the deep portions of the stand.

Herbivore and Herbivore-deposit feeder guilds dominate the considered taxa, although different functional adaptations are conceivable in the individual taxonomic groups. This suggests that the grazing food chain is the main energy pathway at the leaf level. As epiphytes and associated detrital particles are the main food source for He and HeDF, their distribution is likely to be influenced by seasonal and depth-related growth rhythms of both the epiphytes and the seagrass (MAZZELLA & BUIA, 1989).

Some species, such as the polychaete *Platynereis dumerilii*, the molluscs *Gibbula ardens*, *Rissoa italiensis*, *Bittium latreillii*, the isopod *Cymodoce hanseni*, the amphipods *Dexamine spinosa* and *Apherusa chiereghinii*, as well as the decapods *Hippolyte inermis* and *Cestopagurus timidus*, play a key role in the community dynamics and in the food web at the leaf stratum level.

Summary

The vagile fauna of the *Posidonia oceanica* leaf stratum was studied at the level of main taxa such as polychaetes, molluscs, tanaids, isopods, amphipods, and decapods; a spatio-temporal analysis was performed on both taxonomic and trophic structures of the communities.

The investigations were carried out along a depth transect in a Lacco Ameno meadow (Island of Ischia, Italy) at five stations (1, 3, 10, 15, and 25 m) and in four seasons (July, November, February, and May). The samples were collected by SCUBA divers using a hand-towed net.

The community, mainly composed of *Mollusca* and *Amphipoda*, showed almost the same patterns along the transect in all seasons: a shallow community, characterized by higher variability, and more stable intermediate and deep communities were identified. The trophic analysis revealed the strong dominance of Herbivores-deposit feeders at all depths and in all four months; it also revealed the presence of Herbivores at the shallow stations, mainly molluscs in February and amphipods in May. Carnivores and Deposit feeders-carnivores, mainly decapods, inhabited the deep stands. On the whole, the population structure was strongly coherent with the trophic structure.

Environmental gradients, coupled with biological adaptations of the main taxa (feeding habit), determined the observed pattern.

Herbivore and Herbivore-deposit feeder abundances were consistent with the distribution and growth rhythms of the plant and epiphytes. The grazing food chain, realized mainly via epiphytes (*micro-* and *macroalgae*) and particulate organic matter, is of paramount importance in the energy transfer at the level of *Posidonia oceanica* leaf stratum.

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