Feeding habits of pandalid shrimps in the Alboran Sea (SW Mediterranean): influence of biological and environmental factors

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ABSTRACT: The feeding habits of 4 species of *Plesionika* inhabiting the Alboran Sea (SW Mediterranean) at depths between 29 and 790 m were analyzed. Included within the trophic guild of non-migratory macroplankton feeders, *Plesionika* spp. preferably exploited mesopelagic resources (mainly euphausiids and Myctophidae). Deep-bathyal species (*P. martia*, *P. gigliolii* and *P. edwardsi*) fitted better within this guild, while the shallower living species *P. heterocarpus*, which inhabits the shelf-slope break, consumed benthic organisms (e.g. polychaetes, bivalves and tanaids). In a multi-species MDS analysis, diets of *P. martia* and *P. heterocarpus* were grouped as a function of depth. Latitude, phytoplankton pigment (PP) concentration recorded 4 wk before the sampling date (PP4) and depth were the explanatory variables of stomach fullness of *Plesionika* (all species: $R^2 = 0.674$ in a multiple linear regression model, MLR). The abundance of *P. martia* also showed a positive significant correlation (Spearman r) with PP4. Possible causes of higher shrimp aggregations in *P. martia* could be related to reproductive processes because peaks of mature females were reported at similar periods in neighboring areas. In both dominant *Plesionika* species (*P. martia* and *P. heterocarpus*), MDS dimensions for diets were also correlated with PP4, although significant correlations with other PP data taken at different periods (from simultaneous PP data to PP6, 6 wk before sampling) were also found. These trends suggest that macroplankton-feeder Pandalidae may couple some aspects of their biology with blooms of plankton and ultimately with peaks of primary production. Prey size selection occurred among *Plesionika* spp., which suggested a hunting activity. Correlations between *Plesionika* spp. size (*CL*, mm) and prey size were positive, both for fish ($R^2 = 0.437$) and for euphausiids ($R^2 = 0.440$). Otolith length (mainly of *Benthosema glaciale*) and the size of euphausiid mandibles (*Meganyctiphanes norvegica* and *Euphausia hemigibba*) increased with predator size. Further evidence of active predation by deep pandalids, for example changes in the daily feeding activity of species, were evidenced for *P. martia* with higher foregut fullness at the beginning of the daytime period (from 06:00 to 08:00 h) related to predation on euphausiids.

KEY WORDS: Pandalid shrimps · Diet · Feeding guilds · Primary production

INTRODUCTION

Decapod crustaceans are a dominant taxon at slope depths in tropical and subtropical regions, the case of the deep Mediterranean (Cartes 1993c), with an important contribution to the energy flow among the highest trophic levels. Thus, in a preliminary energy balance study performed in the Catalan Sea, food consumption deduced for decapods was similar to that cal- culated for fish (Cartes & Maynou 1998). Pandalids are one of the most characteristic and diversified families of marine shrimps. The genus *Plesionika* (Decapoda, Caridea) is widely distributed in tropical and subtropical areas (Zariquey Alvarez 1968, Crosnier & Forest 1973). *P. heterocarpus* (Costa, 1871) is abundant in the mud assemblage of the shelf-slope break and the upper slope of the Alboran Sea (SW Mediterranean), while *P. gigliolii* (Senna, 1903), *P. edwardsii* (Brandt,

1851) and *P. martia* (A. Milne Edwards, 1883) are dominant in bathyal communities of the upper and middle slope. The Alboran Sea is characterized by the dominance of pandalid shrimps, which reach the highest values of abundance along the Iberian coasts. There is a tendency to shallower distribution of *Plesionika* spp. in the Alboran Sea compared with other study areas (Carbonell & Abelló 1998). *P. heterocarpus* is distributed in the Alboran Sea from 47 to 467 m, with a bimodal distribution and the highest abundance between 100 and 150 m, and 200 and 300 m depth. *P. edwardsii* occurs from 300 to 400 m, always with very irregular and rather low densities. *P. gigliolii* is distributed from 248 to 600 m with peaks of abundance between 300 to 500 m, whereas *P. martia* was found almost exclusively on the middle slope of the Alboran Sea from 300 to 800 m (Carbonell & Abelló 1998). Similar distributions and patterns of species substitution with depth were found in neighboring areas (Cartes et al. 1993, Maynou & Cartes 2000).

The trophic habits of some pandalid shrimps were reported by Lagardère (1972, 1977), Wienberg (1980), Cartes (1993a,b, 1998) and Mura (1995). *Plesionika* species mainly exploit benthopelagic resources, preying on euphausiids and mesopelagic decapods (e.g. *Pasiphaea* spp. and Sergestidae). They can be included in a trophic guild (Cartes 1998, Cartes et al. 2002), with only some species exploiting other compartments (e.g. *P. heterocarpus*, which also consumes infauna, particularly polychaetes in the Bay of Biscay, Lagardère 1977). Scavenging on fish remains were also reported, particularly in areas where the species is not dominant (e.g. the case of *P. martia*) at the limit of its geographical distribution (Lagardère 1977). Size segregation by coexisting *Plesionika* species having the same trophic guild has also been indicated in a previous study performed in the Catalan Sea (Cartes 1994).

Although changes in temperature and phytoplankton concentration have been related to the diversity of fish communities (McClatchie et al. 1997, Jacob et al. 1998), such variables have been rarely considered at the autoecological level (Cartes et al. 2004). Most feeding/dietary studies, therefore, lack an analysis of factors influencing feeding activity (e.g. stomach fullness, daily rations) and diet, which include prey/food availability as well as spatio-temporal short-scale changes in productivity and oceanographic conditions. Beyond the description of the diets and feeding habits of the 4 pandalid species occurring in the Alboran Sea, the objective of this study was to analyze the possible influence of environmental and biological factors in the feeding and diet of *Plesionika* species. Physical (e.g. temperature and salinity), trophic (e.g. phytoplankton concentration and prey availability) and bio-

logical variables (e.g. sexual state, and density) were considered.

MATERIALS AND METHODS

During cruise MEDITS-ES02 (11 to 17 May 2002), 27 hauls were carried out between depths of 29 and 790 m along the coasts of the Alboran Sea (SW Mediterranean) from the Strait of Gibraltar (ca. 36° 00′ N, 5° 50′ W) to the Cape of Gata (36° 38′ N, 2° 05′ W), over a spatial scale of ca. 300 km. *Plesionika* shrimps were collected from trawl hauls between 69 and 715 m. Shrimps were sampled with a bottom trawl (Bertrand et al. 2000). The horizontal aperture of the gear was ca. 18 m and the vertical opening was ca. 2 m. The cod-end mesh size was 10 mm. Haul duration was 0.5 h at depths <200 m and 1 h at greater depths.

Abundance and biomass were calculated (N ind. km^{-2}) after standardizing catches to swept area (km^2). Distance and mouth trawl width were recorded using a SCANMAR system attached to the trawl for each haul.

A total of 240 specimens of *Plesionika heterocarpus*, 71 of *P. gigliolii*, 21 of *P. edwardsii* and 231 of *P. martia* were studied to establish the foregut fullness for each species (see Table 1). Individuals were measured (carapace length, *CL*, in mm with an accuracy of 0.1 mm) dorsally from the posterior edge of the eye socket to the posterior edge of the cephalothorax using a vernier caliper and weighed to the nearest 0.1 g. Information on gonadal development and ovigerous females was also collected. The wet weight of stomach contents was measured. Prey in stomach contents were ascribed in the laboratory under a stereomicroscope (10 to 40×) to the lowest possible taxonomic level.

The following indexes were calculated (see Hyslop 1980 for a review): (1) percentage of vacuity (empty stomachs / total stomachs × 100), (2) stomach fullness (stomach weight / shrimp weight × 100), (3) frequency of occurrence (%*F*) of prey, (4) percentage of numeric abundance of prey (%*N*) and (5) percentage of wet weight of prey (%*W*). The percentage of volume of stomach contents was estimated using the subjective points methods (Swynnerton & Worthington 1940) for the different prey-species or prey-groups.

Trophic diversity was calculated on the diet of each species using the Shannon-Wiener index, *H*′ (Shannon & Weaver 1949), species richness, *d* (Margalef 1958) and the evenness index, *J*′ (Pielou 1966).

General affinities between the samples (diets) were established using multivariate cluster analysis (cf. Cartes & Abelló 1992) for *Plesionika martia* and *P. heterocarpus*, after a log-transformation of matrix data, based on prey weight for each haul. Cluster analysis, using UPGMA (Pielou 1984) as the algorithm

of aggregation and 1 – *r* (the linear correlation of Pearson) as the distance, was used to classify the samples. On the basis of the similarity matrix generated, Multidimensional Scaling (MDS) techniques were applied for the ordination of samples (as a function of their prey composition) along 2-dimensional axes.

We also calculated Spearman's correlation coefficients between fullness and the projections of diet per haul along dimensions 1 and 2 of MDS. The variables were: (1) hour of sampling, depth, latitude and longitude; (2) oceanographic data (water temperature on the bottom and salinity); (3) trophic variables: phytoplankton pigment concentration recorded simultaneously to sampling date (PP_{sim}) and 1 (PP1), 2 (PP2), 3 (PP3), 4 (PP4) and 6 (PP6) weeks before the sampling date; abundance of euphausiids, natantian decapods, calanoids and suprabenthos (including mysids, isopods and amphipods) as the main available food resources; and trophic diversity (*H'*: Shannon-Wiener index); and (4) biological features of the shrimps: percentage of ovigerous shrimps, percentage of mature females, mean weight of *Plesionika* species, mean weight of prey and density of the species. All of the above variables were tested as possible explanatory variables of feeding (fullness) and dietary patterns deduced from MDS analysis.

A multiple linear regression model (MLR) relating fullness to environmental variables (hour of sampling, depth, latitude and longitude; oceanographic data; and trophic variables) was established by forward stepwise multiple regression using the complete data set (all species: 23 cases). All MLR models were generated using the software Statistica 6.0. Biological variables were not considered in this analysis due to the restricted period of our sampling.

Data of primary production at time of sampling and at different time intervals later were obtained from www.ieo.es and seawifs.gsfc.nasa.gov, which provide daily to weekly, and monthly average values for surface temperature and phytoplankton pigment concentration (PP). Maps of temperature corresponded to May 2002. Maps of PP were obtained weekly from mid March to early June to test possible relationships between feeding intensity and surface PP. Different periods, both at the time of sampling and before (2 wk, 1 mo and 2 mo) were considered. Satellite images were downloaded and the scale of PP values was superimposed on each image (Photoshop 6.0) on the position of trawls to obtain the corresponding readings of PP, always before getting the rest of the variables. The abundances of euphausiids and natantian decapod shrimps, calanoids and suprabenthos were obtained with a zooplankton net (mouth aperture 40 × 60 cm, mesh size 0.5 mm) attached to the upper part of the trawl at ca. 2 m from the bottom.

Relationships between the size of predators (*Plesionika* spp.) and their prey were also examined. Pandalid prey are usually broken in the stomach; therefore, we considered maximum otolith length for fish (myctophids, mainly *Benthosema glaciale*) and mandible height for euphausiids (chiefly *Euphausia hemigibba* and *Meganyctiphanes norvegica*). Both measurements were taken with an ocular scale on a stereomicroscope.

RESULTS

Abundance

The distributions of the abundances of *Plesionika* spp. are shown in Table 1. *P. heterocarpus* was the most abundant species in this study, both in terms of biomass and density; it reached more than 200 ind. km^{-2} in the eastern part of the area. *P. gigliolii* was more abundant than *P. martia*, whereas *P. martia* showed a higher biomass (mean value = 0.008 kg km^{-2}).

Diet composition

Plesionika heterocarpus

The diet of this species was highly diverse (Table 2): sponges, polychaetes (mainly Eunicidae), euphausiids, mysids (*Boreomysis* spp., *Leptomysis* sp. and *Siriella norvegica*), hyperiids, isopods (mainly Cirolanidae), tanaidaceans, copepods (calanoids and harpacticoids), insect remains (e.g. Diptera), gastropods (*Rissoa* sp. and *Benthonella* sp.), bivalves (Lucinidae and *Chlamys* sp.), benthic and mesopelagic fish, and benthic and planktonic foraminiferans. The frequency of prey occurrence combined with weight and number is shown in Fig. 1. Most of the diet consisted of euphausiids (*Euphausia hemigibba*) and mysids, while bivalves and fish remains were also important prey. Polychaetes, hyperiids and tanaidaceans (*Apseudes* spp.) were a secondary food source. Diversity indexes for *Plesionika heterocarpus* (Table 3) showed the highest values compared to the other 3 species, though diversity within the same species demonstrated no differences among the hauls.

A significant correlation of fullness by sample was found with latitude (Spearman r: 0.783, p < 0.012) and longitude (r: –0.683, p < 0.042), while a highly significant correlation was found with PP4 (r: 0.950, p < 10^{-5}) and trophic diversity (r: 0.750, p < 0.019). No pattern in diet composition was found with MDS analysis, but correlations with the projections of samples in dimensions 1 and 2 of MDS (n = 9) showed a significant cor-

Table 1. *Plesionika* species. Sampling data and abundance (N ha⁻¹) in the present study

Date	Location	Depth (m)	Number of individuals			
			P. heterocarpus	*P. gigliolii*	*P. martia*	*P. edwardsii*
11 May 02	36.618 N; 4.426 E	69–70	23.587			
11 May 02	36.570 N; 4.352 E	194–205	8.724			
11 May 02	36.604 N; 4.324 E	166–173				
12 May 02	36.690 N; 4.274 E	45–43				
12 May 02	36.640 N; 4.056 E	272–275	52.374	0.235		
12 May 02	36.622 N; 4.054 E	330–330	1.462	0.700		
12 May 02	36.508 N; 4.157 E	525–534			0.755	
13 May 02	36.557 N; 4.508 E	71–77	30.096			
13 May 02	36.471 N; 4.557 E	100–141				
14 May 02	36.350 N; 5.205 E	52–34				
14 May 02	36.308 N; 5.157 E	119–128	0.481			
14 May 02	36.286 N; 5.059 E	357–350	3.323			
14 May 02	36.237 N; 4.983 E	633–668			0.648	
14 May 02	36.239 N; 4.921 E	701–722			0.721	
15 May 02	36.356 N; 4.687 E	576–536			1.502	
15 May 02	36.322 N; 4.429 E	765–755			0.257	
15 May 02	36.335 N; 4.285 E	721–709			1.280	
15 May 02	36.440 N; 4.170 E	623–598			0.544	
16 May 02	36.601 N; 3.875 E	562–546			1.288	
16 May 02	36.652 N; 3.823 E	342–320		1.917		
16 May 02	36.703 N; 3.576 E	67–68				
16 May 02	36.676 N; 3.271 E	371–386		2.401		1.982
16 May 02	36.657 N; 3.209 E	638–592			0.535	
17 May 02	36.590 N; 2.817 E	178–181	102.463			
17 May 02	36.635 N; 2.789 E	59–59				
17 May 02	36.653 N; 2.659 E	47–49				
17 May 02	36.692 N; 2.556 E	137–141	1.706			

relation of dimension 1 with mean weight of prey (r: 0.750, p < 0.019); dimension 2 was correlated with PP4 (r: −0.700, p < 0.035).

Plesionika gigliolii

This species showed lower trophic diversity indexes (Table 3). It preyed on euphausiids (*Euphausia hemigibba* and *Meganyctiphanes norvegica*), mysids, hyperiids, insect remains, mesopelagic fish (*Benthosema glaciale* and *Notoscopelus elongatus*) and also consumed planktonic foraminiferans. The most important prey for this species were mesopelagic fish (>30% of the weight of diet composition), mysids (>20% in number) and euphausiids (*Meganyctiphanes norvegica*) (Fig. 1). Hyperiids were a secondary food source.

Plesionika edwardsii

This species was found to prey on euphausiids, polychaetes and mesopelagic fish (*Notoscopelus elongatus* and Stomiiformes). Sand, bivalves and gastropod remains were also found. Nylon threads were found in 50% of foreguts.

Plesionika martia

The diet of *Plesionika martia* seemed to be less diversified than that of *P. heterocarpus* (Table 3). It preyed on mesopelagic decapods (*Pasiphaea* spp., *Sergia robusta* and *Sergestes arcticus*), polychaetes (mainly *Glycera* sp.), euphausiids, hyperiids (*Phrosina semilunata*, *Phronima sedentaria* and *Vibilia armata*) and mesopelagic fish (Myctophidae and Stomiiformes, mainly *Cyclothone braueri*). In terms of weight, number and occurrence (Fig. 1), the most important prey were mesopelagic decapods, hyperiids (*Phrosina semilunata*) and mesopelagic fish (mainly *Benthosema glaciale* and Stomiiformes). Euphausiids (*Meganyctiphanes norvegica*) were dominant in a small percentage of foreguts.

MDS analysis of the diet composition for *Plesionika martia* separated groups of samples mainly as a function of latitude (Fig. 2) giving a stress of 0.166. Hauls L16, L17, L18 and L19 were grouped in the right part of Axis (dimension) 1, and hauls L13, L14, L15 and L23 on the left. The samples on the right all pertained to the same area. No other trends were observed. However, no other latitudinal groups were observed and latitude was not correlated with either of the 2 dimensions of MDS (see below).

Table 2. Composition of the diet of *Plesionika* species. 1: *P. edwardsii*; 2: *P. gigliolii*; 3: *P. heterocarpus*; 4: *P. martia*. *Taxa used for statistical analysis

Prey	Predator	Prey	Predator
PORIFERA*	1	*Apseudes spinosus**	3, 4
Pachastrellidae	3	*Apseudes* sp.	1, 3
Hyalonema thomsoni	3	Copepoda	
CNIDARIA*		Harpacticoidea	3
Hydrozoa	4	Calanoidea	3
POLYCHAETA		Unidentified*	3
Errantia		INSECTA	
Aphroditidae*	3	Diptera*	2, 3
Glycera sp.*	2, 3, 4	MOLLUSCA	
Eunicidae*	3	Bivalvia	
Eunice dubitatus	3	Lucinidae	3
Nephthys sp.	4	*Chlamys* sp.	3
Unidentified*	1, 2, 3	Unidentified Bivalvia*	3
ARTHROPODA		Gastropoda	
CRUSTACEA		*Benthonella*	3
Decapoda		*Turritella* sp.	1
Natantia*	4	*Rissoa* sp.	3
Pasiphaea sp.*	2, 4	*Margarites cinereus*	3
Sergestidae*	4	Pyramidellidae (Odostomia)	3
*Sergia robusta**	4	Unidentified Gastropoda	
*Sergestes arcticus**	4	Cephalopoda	
Acanthephyra sp	3	Teuthoidea	3
Unidentified*	3, 4	Sepiolidae*	3, 4
Brachyura	2, 3	Unidentified Cephalopoda*	1, 3
Unidentified Crustacea	1, 2, 3	ECHINODERMATA	
Euphausiacea*	1, 2, 3, 4	Echinoidea*	3, 4
*Euphasia hemihibba**	3	Ophiuroidea	
Euphasia kronii	3	Holothuroidea	
Euphasia sp.	3	*Cucumaria* sp.	2, 3
Nicthiphanes couchii	3	*Lapidoplax* sp.	3
Nematoscelis megalops	4	CHAETOGNATA*	2, 3
*Meganyctiphanes norvegica**	2, 3, 4	OSTEICHTHYES	
Mysidacea*		Mesopelagic fish*	1, 2, 3, 4
Boreomysis sp.	3	Benthic fish*	1, 3, 4
Siriella sp.*	3	*Cyclothone braueri**	4
Leptomysis sp.*	3	Myctophidae*	3, 4
Unidentified Mysidacea	3	*Benthosema glaciale**	2, 3, 4
Amphipoda*	2	*Hygophum* sp.	3, 4
Gammaridea	3	*Notoscopelus elongatus*	1, 2
Hyeridea*	1, 2, 3	*Diaphus* sp.	4
Euthemisto sp.	4	Stomiiformes*	1, 2, 4
*Phrosina semilunata**	2, 3, 4	Macrouridae	3
*Phronima sedentaria**	2, 3, 4	Belonidae	3
Vibilia armata	3, 4	Unidentified*	
Isopoda		FORAMINIFERA*	2, 3
Cirolana sp.*	3, 4	*Globigerina*	2, 3
Gnathia sp.	2, 3	*Elphidium* sp.	3
Other Flabellifera	3	*Bolivina* sp.	3
Unidentified		*Quinqueloculina* sp.	2, 3
Tanaidacea		Vegetal rests	2
Apseudidae*	2, 3	Detritus	1, 3

Table 3. Trophic diversity indexes in the diet of *Plesionika* spp.

Species	S	N	d	J′	H′
P. edwardsii	10	10	3.909	1	2.303
P. gigliolii	26	26	7.673	1	3.258
P. heterocarpus	62	62	14.78	1	4.127
P. martia	28	28	8.103	1	3.332

The diet of *Plesionika martia* was quite different among the 2 groups. In the first, hyperiids (i.e. *Phrosina semilunata*) were dominant in the diet with myctophids (i.e. *Benthosema glaciale* and *Hygophum* sp.) and *Cyclothone braueri*. In the second group, the dominant prey were euphausiids (i.e. *Meganycthiphanes norvegica*), polychaetes, decapods (i.e. *Pasiphaea* spp. and Sergestidae) and Stomiiformes.

Correlations with the projections of samples in dimensions 1 and 2 (n = 9) showed that Dimension 1 significantly correlated (non-parametric Spearman correlation) with PP1 (Spearman r: −0.800, p < 10^{-3}), PP4 (r: 0.920, p < 10^{-4}), biomass (r: −0.733, p = 0.024), abundance (r: −0.783, p = 0.012), Decapoda Natantia (r: −0.858, p < 10^{-3}), Calanoidea (r: −0.861, p < 10^{-3}), suprabenthos (r: −0.796, p = 0.010) and mean weight of prey (r: 0.783, p = 0.012). A significant correlation with the projection of samples in Dimension 2 was found with PP$_{sim}$ (r: −0.744, p < 0.021), trophic diversity (r: −0.733, p < 0.024) and the percentage of mature females (r: 0.736, p < 0.023).

Overall *Plesionika* spp. analysis

The global results of the percentage of empty stomachs ranged from 0 to 12% for *Plesionika heterocarpus*, and was 48% for *P. edwardsii*, between 17 and 33% for *P. gigliolii* and between 25 and 55% for *P. martia*. Therefore, the overall feeding intensity between species decreased with depth. The trends within species for fullness (Fig. 3) were increased fullness for *P. hetero-carpus* in an eastward direction and increased fullness for *P. martia* at its shallower depth-range distribution. Few hauls were available to obtain any pattern for *P. gigliolii*. However, 73% of *P. gigliolii* specimens with empty stomachs were females with well-developed
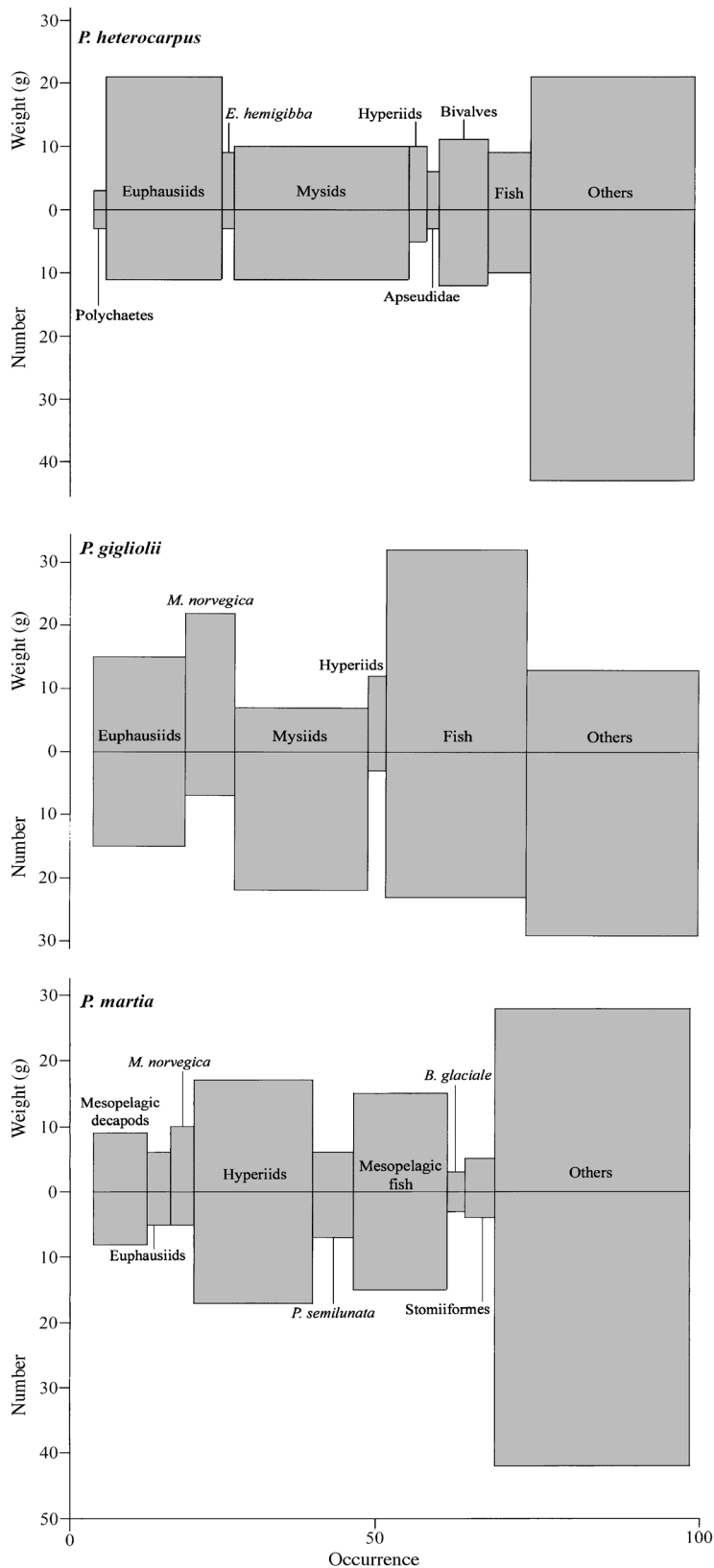
Fig. 1. Frequency of occurrence of prey combined with weight and number for (a) *Plesionika heterocarpus*, (b) *P. gigliolii* and (c) *P. martia*

green gonads (13% ovigerous). *P. martia* showed less developed gonads in comparison to *P. gigliolii* and in this species, 13% of specimens with empty stomachs were females (23% ovigerous).

A significant correlation was found between fullness by haul and depth (Spearman r: –0.569, $p < 10^{-3}$), hour (r: –0.442, p < 0.034), PP_{sim} (r: 0.462, p < 0.026), PP1 (r: 0.461, p < 0.027), PP6 (r: 0.417, p < 0.048), density of *Plesionika* spp. (r: 0.541, $p < 10^{-3}$), mean weight of *Plesionika* spp. (r: –0.477, p < 0.021) and mean weight of prey (r: –0.450, p < 0.030).

Cluster analysis (Fig. 4) of the diet composition for all the species showed the segregation of several groups of samples: the first was represented by *Plesionika martia* samples, except in haul L7. The second group was formed by 2 subgroups: one formed only by *P. heterocarpus* samples and the other by *P. gigliolii*, *P. edwardsi* and *P. martia* (Haul 7) samples. *P. heterocarpus* and *P. gigliolii* co-occurred in 2 hauls (L5 and L6) but they were separated into 2 distinct sub-groups. On the other hand, haul L22 of *P. edwardsi* and of *P. gigliolii* segregated into the same sub-group. MDS analysis segregated groups of samples mainly as a function of depth giving a stress of 0.215. All *P. martia* samples are grouped in the left part of Axis (dimension) 1 and *P. heterocarpus* samples in the lower part of the right side. *P. gigliolii* and *P. edwardsi* samples are grouped in the upper part (Fig. 4).

Correlations with the projections of samples in dimensions 1 and 2 (n = 23) showed that D1 significantly correlated (non-parametric Spearman) with depth (r: –0.803, $p < 10^{-6}$), PP_{sim} (r: –0.803, $p < 10^{-6}$), PP1 (r: –0.803, $p < 10^{-6}$), PP6 (r: –0.803, $p < 10^{-6}$), abundance (r: –0.803, $p < 10^{-6}$), Calanoidea (r: –0.803, $p < 10^{-6}$), trophic diversity (r: –0.803, $p < 10^{-6}$), density of *Plesionika* spp. (N of ind. km^{-2} of the species) (r: –0.803, $p < 10^{-6}$), mean weight of *Plesionika* spp. (r: –0.803, $p < 10^{-6}$) and mean weight of prey (r: –0.803, $p < 10^{-6}$).

A significant correlation with the projection of samples in D2 was found with PP4 (r: –0.495, p < 0.016), Decapoda Natantia (r: 0.645, $p < 10^{-4}$) and suprabenthos abundance (r: 0.724, $p < 10^{-5}$).

Two MLR fullness models were obtained for the *Plesionika* spp. diet (Table 4). In model MLR_1 (1), fullness is significantly correlated with hour, PP4, latitude and PP6. The fitted equation (Table 4) showed that this model explains 80.3% of the variability of log fullness. In model MLR_2 (2), fullness was significantly correlated with latitude, PP4 and depth, but the goodness-of-fit

decreased to $R^2 = 0.674$. The tolerance, which indicates the existing correlation between pairs of independent variables, was between 0.912 and 0.112 in MLR_1, and
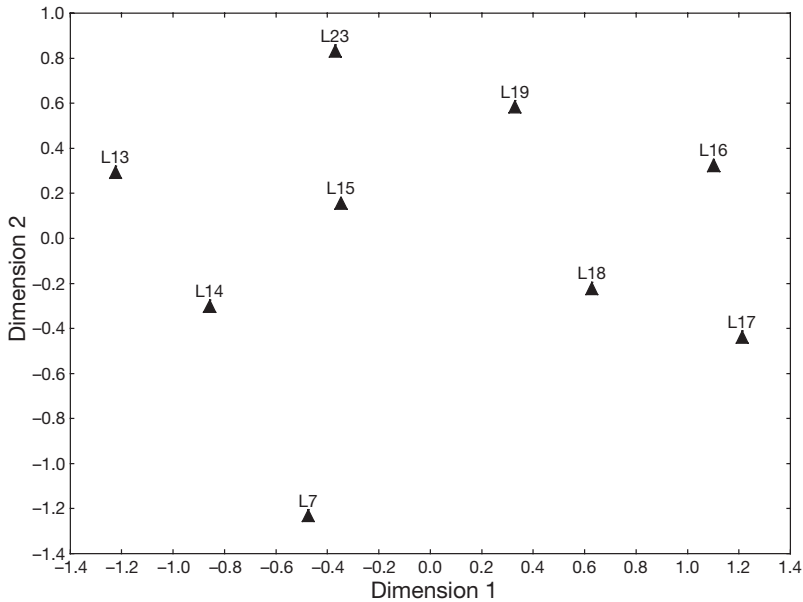

Fig. 2. Aggregation of foregut content samples for *Plesionika martia* and Multidimensional Scaling, MDS. Designations are haul numbers

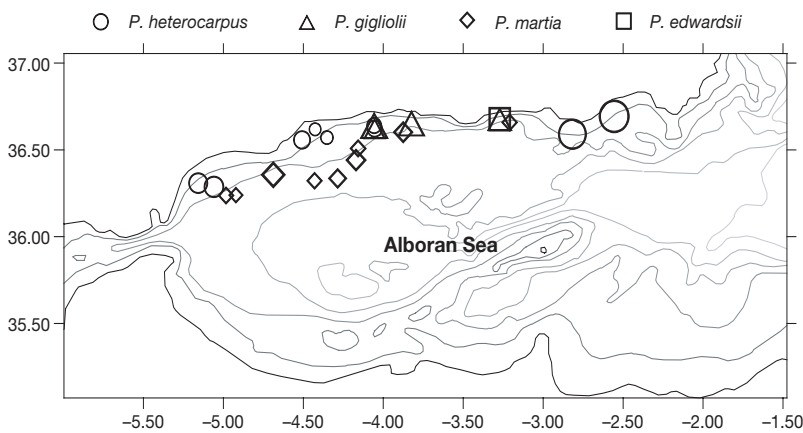Fig. 3. Fullness mapped in the study area (Alboran Sea) for the 4 species. Symbol size represents degree of fullness

between 0.889 and 0.719 in MLR_2. The relationship between fullness and the above mentioned parameters is better expressed by MLR_2 as higher values of tolerance (less redundancy, meaning low correlation between variables) were observed.

Trophic diversity in *Plesionika heterocarpus* was relatively high (Table 3); in *P. martia* and *P. gigliolii* trophic diversity was intermediate, while in *P. edwardsii* it was low due to the few hauls available.

Prey-predator size relationships

Correlations between *Plesionika* spp. size (*CL*, mm) and prey size (Fig. 5) were positive, both for fish ($R^2 = 0.437$) and for euphausiids ($R^2 = 0.440$). Fish prey was mainly comprised of *Benthosema glaciale* and secondarily of *Hygophum* spp. and *Notoscopelus elongatus*. Euphausiid species, for which mandibles were measured, included *Euphausia hemigibba* and *Meganyctiphanes norvegica*. There was a positive correlation between the hour of sampling and the occurrence of euphausiids in guts. Correlations between the hour of sampling and fullness were negative for *P. martia* (higher fullness at the beginning of the cycle: morning) and positive for *P. heterocarpus*.

DISCUSSION

Plesionika species appear to prefer similar prey in different areas along their wide geographical range. They can be considered as a trophic guild of 'macroplankton-epibenthic feeders' (Cartes 1998) or 'non migratory macroplankton feeders' (Cartes et al. 2002). This guild includes species whose diets are mainly based on pelagic resources, captured in the Benthic Boundary Layer, and located a few meters above the bottom (Wishner 1980, Hargreaves 1984, Angel 1990). Deep bathyal

Table 4. Characteristics of the multiple linear regression (MLR) models constructed to predict fullness. Hour of sampling (*H*), latitude (*Lat*), Primary production 4 wk before sampling (PP4), Primary production 6 wk before sampling (PP6) and depth (*D*) were the considered independent variables; $p \leq 0.05$ for all the independent variables. *DIM1*: dimension 1 from MDS analysis

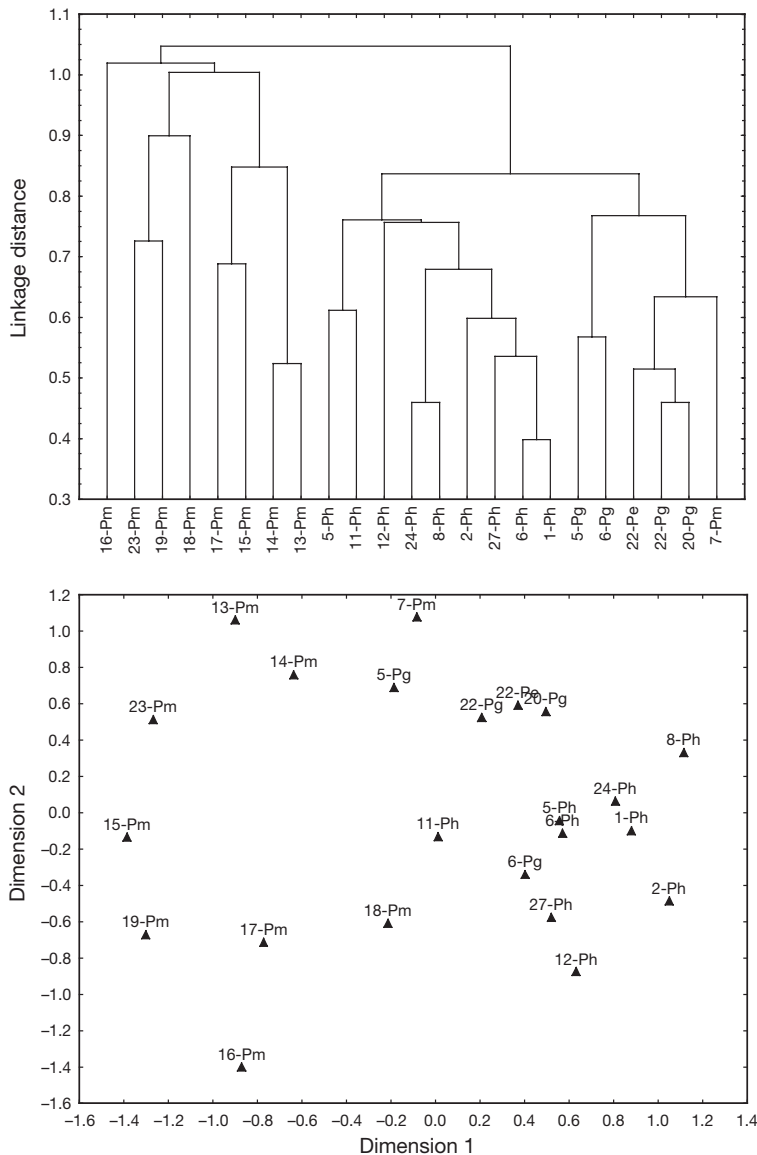| Model	n	r^2	p
(1) log fullness = −210.468 − 0.697 log *H* − 1.114 log PP4 + 133.825 log *Lat* − 3.146 log PP6	25	0.803	$<10^{-5}$
(2) log fullness = −68.359 + 44.578 log *Lat* − 1.945 log PP4 − 0.219 log*D*	25	0.674	$<10^{-4}$
log *DIM1* = −3.397 + 1.999 log*D*	25	0.608	$<10^{-4}$

Fig. 4. Aggregation of foregut content samples for all the species of *Plesionika* and MDS. Codes: 13-Pm means Haul 13, *P. martia*, etc.

species dwelling on the middle-slope assemblage (below ca. 350 m) (Abelló et al. 1988, Cartes et al. 1994) clearly fit within this guild. *P. martia*, therefore, preyed mostly on mesopelagic decapods, hyperiids and meso-pelagic fish in the Alboran Sea. On the NW African Slope and in the Catalan Sea, *P. martia* was found to prey mainly or exclusively on euphausiids (*Mega-nycthiphanes norvegica*) and mesopelagic decapods (*Pasiphaea sivado*) (Lagardère 1972, Cartes 1993a, 1993b). In the Bay of Biscay, however, this species has been suggested to be a scavenger (Lagardère 1977). *P. edwardsii* also seemed to prey mostly on meso-pelagic species (*M. norvegica*, *P. sivado* and *Boreo-mysis arctica*), as observed in the Catalan Sea (Cartes

1993a,b). In the same way, the most important prey for *P. gigliolii* were mesopelagic species (myctophid fish, mysids, euphausiids and hyper-iids), though at a qualitative level some benthic prey (polychaetes, foraminiferans, echinoderms) were also frequently ingested in the Sardinian channel (Mura 1995). Although some of these species also exhibit periods of benthic feeding activity, in which they prey on slow-moving organisms such as crustaceans and fish remains (Cartes 1998), benthic prey are always secondary in their diet.

In contrast, *Plesionika heterocarpus*, the shal-lowest species, is the only species whose diet is increasingly and even mainly based on benthic organisms, both in the Bay of Biscay, where *P. heterocarpus* mostly preys on polychaetes (Lagardère 1977) and in the South Aegean Sea where molluscs, decapods and polychaetes dom-inate its diet (Labropoulou & Kostikas 1999). Benthos is also important in the diet of *P. hetero-carpus* in the Alboran Sea, compared with its contribution to the diet of the rest of *Plesionika* species. In fact, benthos resources should have greater importance as a food-source in shelf communities, which agrees with a generally rec-ognized decrease in benthos biomass with depth (Rowe 1983). Higher diversification of benthic prey inhabiting the continental shelf, in compar-ison to pelagic prey consumed on the slope by pandalids, may also explain the higher dietary diversity in *P. heterocarpus* compared to species of the deeper, mesopelagic feeders, *P. martia* and *P. gigliolii*. From an energetic point of view, the decrease in benthic biomass with depth may tend towards a strategy of caloric maximization by benthopelagic consumers preying on highly energetic mesopelagic organisms (T. Madurell & J. E. Cartes unpubl.). This trend was suggested on mid-slope depths in the Ionian Sea, an oligo-trophic area where densities of benthos are low.

Decapod crustaceans generally occupy a lower trophic level than fish, also in the deep-sea domain (e.g. Polunin et al. 2001). Decapods, therefore, have been rather considered as scavengers or detritivorous (Gage & Tyler 1992). Some detailed studies point, how-ever, to active predation by decapods on hyperiids and Cirolanidae (e.g. by *Plesionika martia*) as shown by the occurrence of whole remains of these taxa in guts. Prey size selection constituted further evidence of hunting activity: maximum otolith length (mainly of *Benthosema glaciale*) increased with predator size and the same pattern was observed for euphausiid mandibles (*Mega-nyctiphanes norvegica* and *Euphausia hemigibba*). As shrimp size increased, there was a pronounced shift
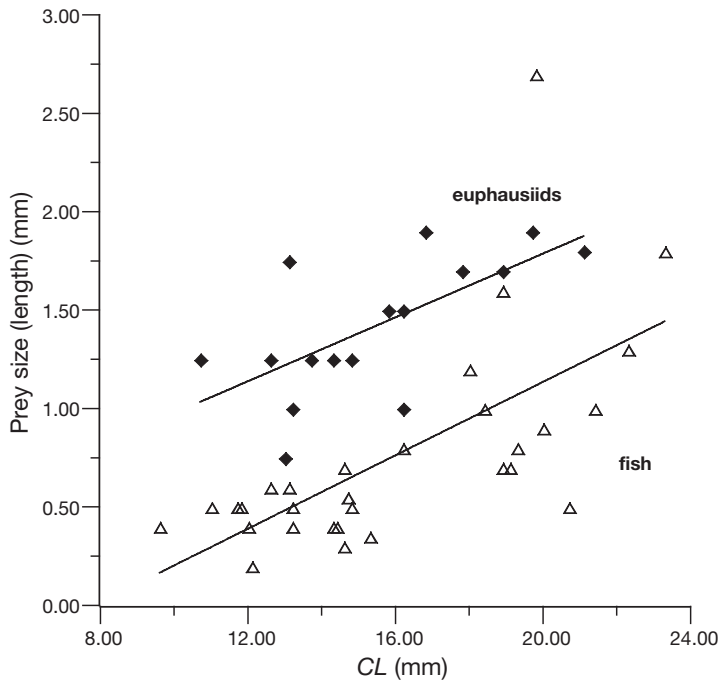
Fig. 5. Relationship between prey-size (mandible height for euphausiids and otolith length for fish, mm) and predator-size (*CL*, mm)

towards larger prey: *P. martia* mainly prey on *M. norvegica*, while the smaller *P. heterocarpus* mostly on *E. hemigibba.* Until now, this kind of prey-predator size relationships have only been evidenced for fish (Macpherson 1978), which ingest entire prey.

Fig. 6. *Plesionika martia.* Relationship between hour of sampling, fullness and euphausiid weight (in g) in the foregut content

Active predation by decapods might be related to the occurrence of significant changes in the daily feeding activity of species. Some pandalids (e.g. *Plesionika martia*) exhibit predation on *Pasiphaea* spp. restricted to the early hours of day-light (Cartes 1993c). In the Alboran Sea, foregut fullness of *P. martia* was higher at dawn (from 06:00 to 08:00 h) related to predation on mesopelagic species (euphausiids in this case) (Fig. 6). Diel vertical migrations of mesopelagic fauna (Franqueville 1971, Merrett & Roe 1974, Omori 1974, Roe 1974, 1983, Hargreaves 1984) comprising mesopelagic prey species such as *Pasiphaea* spp., *Sergestes arcticus*, fish and euphausiids (Cartes 1993a) seemed to be important in influencing feeding activity rhythms in the deep sea decapods. In contrast, the rather epibenthic feeder *P. heterocarpus* displayed an opposite pattern of feeding activity (higher fullness between 11:00 and 14:00 h).

Scavenging is concluded to be a secondary activity in the feeding habits of pandalids: insect remains (e.g. Diptera), probably transported by bottom drifts, were also found in the Alboran Sea samples in *Plesionika heterocarpus* and even in *P. gigliolii* at depths of 272 m. In all the species, osteichthyes remains consisted of large scales, which were probably ingested in the water column (Hopkins & Baird 1975, Cartes 1993a).

Feeding intensity is positively related to the degree and index of fullness and negatively related to the percentage of empty stomachs (Bowman & Bowman 1980). The low values of vacuity index indicate that feeding intensity is high for *Plesionika heterocarpus* and decreases for deeper bathyal species, particularly for the deepest-dwelling species, *P. martia*. The high proportion of empty stomachs in decapod species that inhabit deep slope zones has been previously reported (Wenner 1979, Cartes & Abelló 1992, Cartes 1993b) and seems to be a general pattern for such species as an adaptation to the deep sea environment, where trophic resources are scarce. In general, size did not affect the feeding intensity of the species examined, while the sexual state did, with higher vacuity among mature females of *P. gigliolii* with large well-developed green gonads. Among decapod crustaceans, this last aspect has only previously been documented for *Liocarcinus depurator* (Freire 1996), although it has been widely reported for fish (e.g. Velasco & Olaso 1998, Dia et al. 2000, Morte et al. 2001).

Most Pandalidae prey on pelagic macroplankton species, particularly on the slope. Therefore, some aspects of the biology of these species (e.g. recruitment, swarms to spawn) may probably be coupled with blooms of plankton and ultimately with peaks of pri-
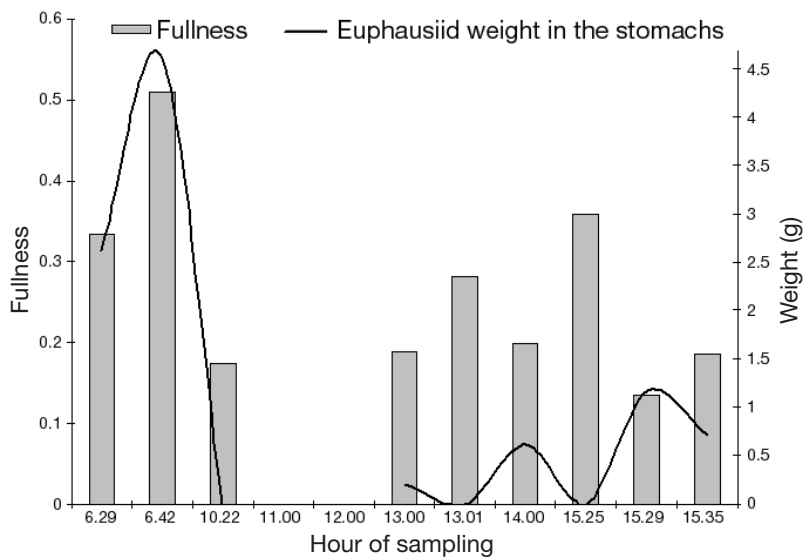
mary production. In the pelagic domain, a delay between peaks of phytoplankton blooms and krill was suggested by different authors in the North Sea (Noji 1991, Dam et al. 1993). Krill concentration may be the result of oceanographic features coupled with favorable feeding conditions. The shear zones and the sluggish currents caused by topographical features (i.e. shelf break) may provide suitable sites that retain krill swarms (Ichii et al. 1998). The response to these signals at bathyal depths probably occurs by fluxes of particulate organic matter (detritus) throughout the water column (Miquel et al. 1994) and after a transport of organic matter explained by organism migration (e.g. Ribera Maycas 1997). The Alboran Sea is probably too complicated an ecosystem in which to evidence a possible coupling between phytoplankton pigment concentration (as a measure of primary production), zooplankton and benthopelagic shrimp densities, due to the complex circulation patterns with anticyclonic gyres (Parrilla et al. 1986, Heburn & La Violette 1990) and local upwelling processes (see seawifs.gsfc.nasa. gov for maps of PP). Furthermore, *Plesionika* species abundance is expected to be more related to peaks of primary production among benthopelagic feeders (e.g. *P. martia*) than among benthic feeders (e.g. *P. heterocarpus*). In fact, abundance only followed this pattern (positive significant correlation with a delay of 1 mo, PP4) for *P. martia* (Fig. 7). Maps derived from satellites showed that PP recorded simultaneously to the sampling survey was concentrated close to the coasts (upwelling processes), while 1 mo before, maxi-
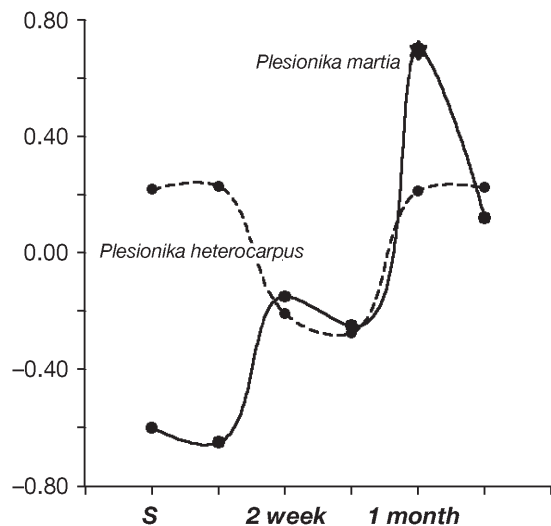
mum values were evidenced in the open sea. This seems to be related to the deeper distribution of *P. martia*.

In the deep Mediterranean, water masses usually have a constant temperature of 13.5°C at depths below 200 m (Hopkins 1985). This could explain why physical oceanographic features (e.g. temperature) correlated neither with the fullness nor with the diet of *Plesionika* spp. Stomach fullness was also correlated to PP 1 mo previously in the case of the hake *M. merluccius* along the Iberian coasts (Cartes et al. 2004). Among *Plesionika* spp., we observed a significant correlation between fullness of *P. heterocarpus* and PP4, while no significant correlation was detected for *P. martia*.

Our results indicate that stomach fullness generally increased with increasing density in *Plesionika* spp., suggesting feeding aggregations. Possible causes of these aggregations could be related, in the case of *P. martia*, to reproductive processes, rather than to feeding, because a peak of mature females was evidenced for this shrimp in May–June in the Tyrrhenian (Fanelli & Belluscio 2003) and Sardinian Seas (Campisi et al. 1998). *P. heterocarpus*, in contrast, shows a more continuous reproductive cycle (Company & Sardà 1997). In our data, *P. martia* populations were mainly composed of adult specimens (mean *CL* = 20 ± 4.9 mm) while both juveniles and adults were abundant among *P. heterocarpus* populations (mean *CL* = 12 ± 2.9 mm). Finally, further similar considerations for diet do not seem to be as easy to establish as for fullness because diet is a multidimensional variable, depending on several factors. In both dominant *Plesionika* species, however, MDS dimensions were also correlated with PP4 and further significant correlations with other PP data (from PP_{sim} to PP6) were also found.

Fig. 7. Significance (r) of the relationship between *Plesionika martia* and *P. heterocarpus* abundance and pigment phytoplankton concentration (as a measure of primary production PP) recorded in at different times before and during the sampling survey

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