

Patterns of resource use in deep-water decapods

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ABSTRACT: The distribution patterns and feeding habits of 4 deep-water decapod species were investigated from samples collected in experimental trawl surveys carried out along the continental slope of Crete (Eastern Mediterranean) in 1994 to 1995, at depths between 100 and 1000 m. Despite their distribution overlap, the differences in the distribution patterns of the species along the depth gradient were clear, with *Plesionika ensis* and *Polycheles typhlops* occurring at greater depths than *Parapenaeus longirostris* and *Plesionika heterocarpus*. Stomach content analysis revealed that all species were active predators of benthic invertebrates, while scavenging activity became more important at depths below 500 m. The species exhibited highly diverse diets, but dietary diversity was higher for those inhabiting shallower depths. Ontogenetic dietary shifts were pronounced, although dietary patterns were also significantly affected by season and depth. Interspecific dietary overlap was less than intraspecific overlap between size classes and between months. Feeding intensity was associated with the distribution patterns of the species and decreased with depth, thus it was significantly lower for the species at the deepest depths, *P. typhlops* and *P. ensis*. Dietary patterns of the species examined were quite similar and differences noted were more consistent with depth-related changes in available food resources than with changes in the position of the species in the food web. Since dietary overlap among the species when they co-occur was high, it is possible that competitive trophic interactions accounted for the low overlap in the bathymetrical distribution of the species examined. Such interactions may be of fundamental importance on the deep-sea bottoms in the Eastern Mediterranean since environmental parameters such as temperature and salinity are rather constant.

KEY WORDS: Deep-water decapods · Distribution · Diet · Prey selection · Ontogeny · Diet breadth · Resource partitioning

INTRODUCTION

Deep-water habitats are characterized by environmental stability and by relative scarcity of available food resources (Sanders 1968, Dayton & Hessler 1972, Tyler 1988), but are poorly known. Marine invertebrate communities in deep-sea environments normally exhibit low levels of competition, even though food is not overly abundant (Grassle & Sanders 1973, Macpherson 1981, Blaber & Bulman 1987, Cartes & Sardà 1989). It has been argued that community structure in such habitats tends to be organized in such a way as to minimize interspecific competition or intraspecific competition between size classes, in order to optimize energy utilization through balanced partitioning of

available resources (Haedrich 1996, Koslow 1996). However, biological factors such as resource availability, predator-prey relationships and interspecific competition may also play a fundamental role in the local zonation pattern.

The Mediterranean, and particularly the eastern basin, is one of the most oligotrophic areas of the world's oceans. The high prevailing temperatures (13 to 14°C) as well as the scarcity of food supply below 200 m depth (Pérès 1982) are considered to be the main factors controlling community structure, since benthic organisms have to endure not only food limitation but also high temperature, inducing a higher metabolic rate and therefore higher demands for energy resources. In this context, information on the trophic interactions among species inhabiting these depths is an important element in understanding the function of the deep-water ecosystem in the Eastern Mediterranean.

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Pressure on inshore fish stocks has led to the exploitation of demersal resources in the European deep waters (400 to 1500 m) (Connolly & Kelly 1996). The ecosystem in which deep-water species live is different from that of the continental shelf, and many of these species are relatively long-lived, slow to mature and have low fecundities (Haedrich 1996). These characteristics make them especially susceptible to over-exploitation. With little known about the biology and ecology of these species, there is a shortage of adequate data to provide a rational basis for any management decisions. This information is essential to assess the impact of fishing operations on the deep-sea ecosystem.

A large number of decapod species within the bathyal families Polychelidae and Pandalidae are distributed mainly in tropical and subtropical areas (Zariquiey Alvarez 1968). *Plesionika heterocarpus*, *Plesionika ensis* and *Polycheles typhlops* are 3 of the most characteristic and abundant decapod species in bathyal mud assemblages in the deep slope of Iraklion Bay, Greece (Smith et al. 1997). The deep-water rose shrimp *Parapenaeus longirostris* is one of the most important commercial species in the Mediterranean Sea and in the western and eastern Atlantic Ocean, inhabiting muddy or muddy-sandy bottoms, at depths of 150 to 700 m (Ardizzone et al. 1990, Cartes 1995). This species dominates by both biomass and number the decapod crustacean communities from the Cretan continental slope between 200 and 400 m, comprising 24 to 45% of the total decapod catches (Labropoulou unpubl.).

The diets in natural conditions for various shallow-water decapod species have been established (e.g. Lagardère 1977, Pihl & Rosenberg 1984, Choy 1986, Wear & Haddon 1987, Freire & González-Gurriarán 1995, Freire 1996); however, the available information on the feeding habits of deep-sea decapod species, particularly in the Mediterranean, is limited. The most extensive ecological studies on the diet and feeding habits of deep-water decapods have been conducted in the Catalan Sea (Cartes & Sardà 1989, Cartes & Abelló 1992, Cartes 1993a,b,c,d, 1994, 1998) and the results suggest that scavenging activity as well as active predation play an important role in feeding.

The objective of the present study is to investigate the diet and the feeding habits of 4 deep-water decapod species occurring on the continental slope of Crete and to assess the effects of depth, season and size on the diet, prey choice and patterns of dietary overlap among these species. Consideration has also been given to the degree of dietary similarity as a possible factor determining the patterns of depth distribution of these species which are characteristic and adapted to the deep-sea environment of the Cretan slope.

MATERIAL AND METHODS

Study area and sampling procedure. Specimens were collected from experimental bottom trawl surveys at Iraklion Bay on the northern coast of Crete (South Aegean Sea, Eastern Mediterranean, Greece) between 35° 20' and 35° 28' N, and 25° 02' and 25° 20' E. The samples were taken in September 1994 and February, May and September 1995 from standard depth stations at 100, 200, 500, 700 and 1000 m, using bottom trawl (foot-rope length: 36.5 m, headline height: 1.7 m, stretched mesh size: 22 mm). At least 3 hauls at each station were carried out for each sampling survey, approximately in parallel with the 100 or 200 m isobaths, during daytime. The duration of each haul ranged from 50 to 90 min at a towing speed of 2 to 3 knots depending on the depth and the nature of the bottom. Gear selectivity was assumed to be constant because the same vessel (RV 'Philia') and fishing gear were used in the surveys. The catch from each haul was identified to species, enumerated and weighed. The samples were fixed on board, immediately after capture, in 10% buffered formalin. The substrate of the study area consisted of a dominant (85 to 98%) silt-clay fraction, while temperature in and above the sediment was remarkably constant (14.0 to 14.8°C) at all depths (Tselepidis & Eleftheriou 1992).

Laboratory methods. Stomach contents of the decapods were examined for up to a total of 20 to 30 specimens species⁻¹ for each haul and station. When catches were higher, specimens were separated into size intervals, then proportionally subsampled until a total of 30 ind. species⁻¹ were selected for stomach analysis. Carapace length (CL), from the orbital edge to the median posterior margin of the cephalothorax, was measured for each specimen using a vernier caliper, to the nearest 0.1 mm and weighed to the nearest 0.01 g. Thereafter, the stomachs were removed and the contents wet weighed. Stomach contents were identified to species or to the lowest possible taxonomic level and counted under a binocular microscope.

Data analysis. Species abundance was calculated for each haul after standardization of the results to a 1 h tow, making it possible to compare decapod abundances between sampling stations. Since the distribution of the abundance was very skewed, the data of each haul were log-transformed to compare, by means of 1-way ANOVAs, the mean values between different depths and months (Zar 1984).

The contribution of prey items in the diet of each decapod species was estimated using both the numerical abundance (*N*) and the frequency of occurrence (*F*) of prey items in the stomachs (Berg 1979, Hyslop 1980, Bowen 1983). To evaluate size-related variations in food habits, specimens of each decapod species were separated into 5 mm size classes, where possible.

Dietary breadth was calculated according to the Shannon-Wiener index, H' (Hurlbert 1978, Krebs 1989):

$$H' = \sum_{i=1}^n p_i \ln p_i$$

where p_i = proportion of a specific prey category for the n categories of prey listed. H' increases with the number of prey categories.

Dietary overlap was calculated using the simplified Morisita's index (Krebs 1989, Hall et al. 1990):

$$C_{ik} = \frac{2\sum_j p_{ij} p_{kj}}{\sum_j p_{ij}^2 + \sum_j p_{kj}^2}$$

where C_{ik} = simplified Morisita's index for predators i and k ; p_{ij} and p_{kj} = proportions of predator i and k with prey j in their stomachs. Dietary overlap increases as C_{ik} increases from 0 to 1. Overlap is generally considered to be biologically significant when the value exceeds 0.60 (Keast 1978a, Macpherson 1981, Wallace 1981, Langton 1982). Dietary breadth and overlap was estimated using the numerical abundance of prey items found in the stomachs. Bias-corrected bootstrap 95% confidence intervals, based on 1000 simulations, were used to estimate the reliability of these indices (Efron & Tibshirani 1986, Hall et al. 1990). Cluster analysis (group average) employing the Bray-Curtis similarity index (Field et al. 1982) was performed on

the standardized abundance values of prey species to describe ontogenetic, seasonal and interspecific variations in food habits, using the PRIMER algorithms (Plymouth Marine Laboratory). In order to normalize the data and avoid skew a square root transformation was applied to the abundance data prior to cluster analysis (Field et al. 1982). Multidimensional scaling (MDS) ordination analysis was also performed with the same configuration as in cluster analysis with respect to similarity index and transformation.

Statistical differences in dietary composition and stomach fullness by size, month and depth were tested by χ^2 , while 1-way ANOVAs were used to compare the mean dietary breadth among the different species, size classes, months and depths and the *a posteriori* Tukey's test was employed to locate the source of any difference (Zar 1984). All statistical inferences were based on the 0.05 significance level.

RESULTS

Bathymetric distribution and size composition

The separation in the depth ranges occupied by the 4 species in Iraklion Bay was quite clear (Fig. 1). *Polychaetes typhlops* was distributed deeper than the other

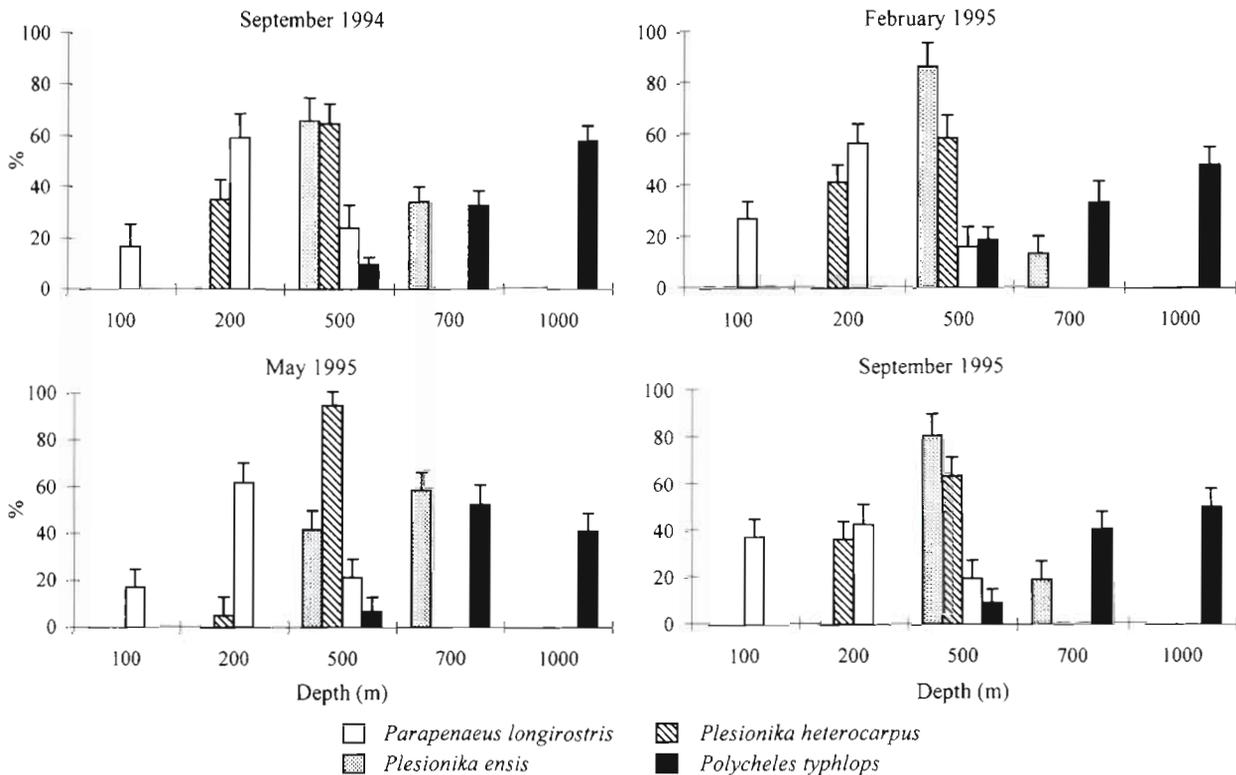


Fig. 1. Seasonal distribution (% abundance) by depth for the 4 decapod species from the Cretan slope

species, between 500 and 1000 m, whereas *Parapeneus longirostris* was found exclusively at depths down to 500 m. *Plesionika* species inhabited depths between 200 and 700 m, with *P. ensis* occurring deeper than *P. heterocarpus*. However, the distribution ranges of these species do overlap and all of them co-occurred at 500 m depth. Abundance showed significant variation with depth for all species (ANOVA tests, $p < 0.05$), while no significant effect of month on the distribution patterns of the species examined was found (ANOVA tests, $p > 0.05$). The maximum abundance for *P. longirostris* was reached at 200 m (116 ± 9.61 ind. h^{-1}), whereas for *P. heterocarpus* (176 ± 7.97 ind. h^{-1}) and *P.*

ensis (95 ± 9.31 ind. h^{-1}) the maximum abundance was found at 500 and 700 m depth, respectively. *P. typhlops* was most abundant at 1000 m, where 38 ± 7.97 ind. h^{-1} were caught.

Size distribution for each species did not differ significantly among the depth ranges or during the 4 sampling surveys ($p > 0.05$, non-parametric Kolmogorov-Smirnov tests). Sizes (CL, mean \pm SD) ranged from 5 to 39 mm (17.7 ± 6.36 , $n = 893$) for *Parapeneus longirostris*, 6.5 to 30 mm (12.6 ± 3.83 , $n = 804$) for *Plesionika heterocarpus*, 11 to 23.7 mm (18.4 ± 3.31 , $n = 469$) for *Plesionika ensis* and from 10.2 to 35.9 mm (20.1 ± 5.25 , $n = 311$) for *Polycheles typhlops*, while there was a sig-

Table 1. Percentage contribution by occurrence (*F*) and by numerical abundance (*N*) of the major prey taxa and species in the diet for the 4 decapod species from the Cretan slope. Prey occurring in $>1\%$ of the total are given (+: $<1\%$, -: absent)

Prey category	<i>Parapeneus longirostris</i>		<i>Plesionika heterocarpus</i>		<i>Plesionika ensis</i>		<i>Polycheles typhlops</i>	
	<i>F</i>	<i>N</i>	<i>F</i>	<i>N</i>	<i>F</i>	<i>N</i>	<i>F</i>	<i>N</i>
Nematoda	1.09	+	2.19	+	-	-	-	-
Polychaeta								
<i>Aphrodita</i> sp.	5.92	2.10	42.53	5.31	-	-	-	-
<i>Glycera</i> sp.	3.92	5.30	23.65	4.97	-	-	20.52	2.51
Unidentified	2.75	1.37	17.25	3.98	-	-	17.22	2.11
Crustacea								
Decapoda								
<i>Monodaeus</i> sp.	-	-	-	-	9.16	4.72	8.95	4.43
Parthenopidae	1.76	+	17.25	3.78	4.51	+	3.56	2.78
Unidentified Brachyura	3.54	1.48	17.25	2.65	9.16	5.89	3.56	5.52
<i>Pasiphaea</i> sp.	-	-	-	-	-	-	12.65	5.62
Unidentified Natantia	7.65	1.82	9.56	8.67	18.76	10.69	6.72	4.43
Thalassinidae	4.23	+	9.56	4.24	4.51	3.91	6.72	3.86
<i>Calocaris macandreae</i>	-	-	6.72	2.93	9.16	5.11	31.35	5.03
<i>Munida</i> sp.	-	-	-	-	-	-	12.65	3.14
Amphipoda	7.65	1.69	3.25	2.70	12.65	5.03	3.56	+
Isopoda								
Gnathiidae	1.09	+	3.45	2.91	2.71	+	3.56	3.14
<i>Natatolana borealis</i>	-	-	6.72	3.11	4.51	5.90	6.72	3.49
Tanaidacea	-	-	2.19	+	2.71	+	3.56	+
Ostracoda								
Myodocopa	4.23	5.86	3.25	6.52	33.78	13.17	-	-
Podocopa	3.54	7.35	9.56	8.48	42.19	4.01	6.72	4.73
Mysidacea	-	-	-	-	-	-	3.56	5.52
Copepoda Harpacticoida	28.78	12.34	2.19	1.31	-	-	6.72	3.91
Mollusca								
Bivalvia	1.76	2.97	2.19	2.99	-	-	-	-
Gastropoda	7.65	9.56	6.72	11.34	2.71	+	6.72	3.12
Pteropoda	1.09	1.16	2.19	3.76	-	-	+	+
Cephalopoda	1.09	1.03	2.19	+	4.51	4.43	-	-
Echinodermata								
Holothuriodea	1.09	+	2.19	+	2.71	+	3.56	1.32
Ophiuroidea	4.23	3.92	-	-	-	-	3.56	2.75
Ascidiacea	1.76	+	-	-	-	-	-	-
Hydrozoa	1.76	+	2.19	+	-	-	3.56	+
Foraminifera	46.45	30.73	6.72	2.73	66.87	16.89	25.75	20.06
Osteichthyes	3.54	1.71	9.56	7.19	42.19	14.56	3.56	3.46
Other	7.65	2.52	9.56	5.32	2.71	+	3.56	6.78
Mud	72.51		42.53		18.93		50.04	
No. of stomachs examined	342		130		94		227	
No. of empty stomachs	49		45		11		178	
Mean stomach content weight (g)	0.03		0.04		0.02		0.01	
Mean no. of prey items per stomach	4.94		1.91		2.85		2.71	

nificant difference in the size-frequency distribution between the species ($F_{3, 789} = 32.3$, $p < 0.001$).

Feeding intensity

The overall percentage of empty stomachs was very high in *Polycheles typhlops* (78.4%), lower in *Plesionika ensis* (34.6%) and very low for *Parapenaeus longirostris* (14.3%) and *Plesionika heterocarpus* (11.7%). In terms of the different depth ranges considered, feeding intensity significantly decreased with depth only for *P. longirostris* ($\chi^2 = 12.82$, $p < 0.01$), whereas for the other species no significant effect of depth on the proportion of empty stomachs was found (χ^2 tests, $p > 0.05$). The proportion of empty stomachs varied significantly among the size classes only for *P. typhlops*, with a maximum of 89% for the smallest specimens (CL < 15 mm). Although empty stomachs were found throughout the year, feeding intensity did not differ significantly over the sampling period for any of the species examined (χ^2 tests, $p > 0.05$).

Composition of diet

The composition of the diet by species in terms of frequency of occurrence and numerical abundance indicated that all of them were carnivorous, feeding mainly on benthic and hyperbenthic invertebrates (Table 1). Decapods clearly dominated the diets of *Plesionika heterocarpus*, *Plesionika ensis* and *Polycheles typhlops*, while foraminiferans were the dominant prey of *Parapenaeus longirostris*. The most common decapod in the diet of the species, with the exception of *P. longirostris*, was the macruran *Calocaris macandreae*. Molluscs made an important contribution to the diet of *P. longirostris* and *P. heterocarpus*, while ostracods and foraminiferans constituted an important component in the diets of *P. ensis* and *P. typhlops* respectively. Fish remains were also found in the diets of all species ranging from 1.7% in *P. longirostris* to 14.6% in *P. ensis*. Dietary breadth, as measured by the Shannon-Wiener index, indicated that all 4 species exhibited a relatively high trophic diversity (Fig. 2). The diets of *P. longirostris* and *P. heterocarpus* were significantly wider than those of the other species ($F_{3, 506} = 13.56$, $p < 0.001$), whereas *P. ensis* presented the narrowest dietary breadth.

Food in relation to depth

The occurrence of prey items in the diet of each species varied significantly with depth (χ^2 tests, $p < 0.05$)

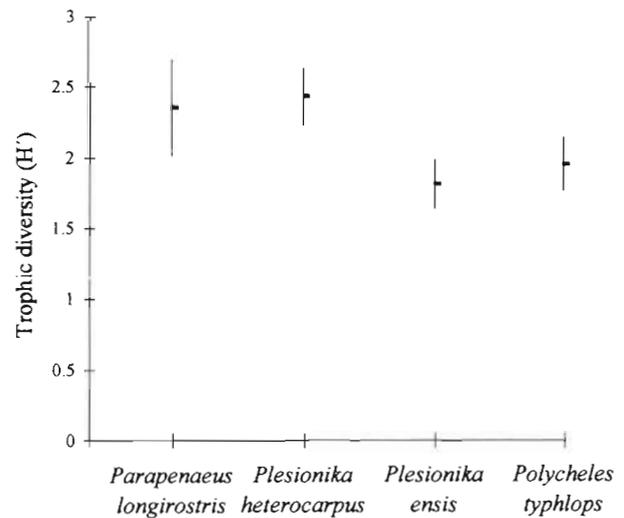


Fig. 2. Dietary breadth (Shannon-Wiener diversity index, H') for the 4 decapod species from the Cretan slope

only for the ingestion of copepods for *Parapenaeus longirostris* and foraminiferans, ostracods and cephalopods for *Plesionika ensis* and *Polycheles typhlops* together with fish and polychaetes for *P. typhlops*.

The diet of each species at the different depths indicated that they consisted of the same prey items but in a different order of importance (Fig. 3). The contribution of foraminiferans in the diet of *Parapenaeus longirostris* decreased with depth. Molluscs and small crustaceans were more abundant at intermediate depth (200 m), while ostracods were the most exploited prey at 500 m. The relative importance of ostracods, fish remains and polychaetes in the diet of *Plesionika heterocarpus* increased with depth, but that of molluscs and decapods decreased. Similarly, the contribution of fish remains in the *Plesionika ensis* diet considerably increased with depth. For *Polycheles typhlops* there was a shift towards small crustaceans, fish remains, molluscs and polychaetes with increasing depth. However, no significant effect of depth on the dietary breadth of each species was found (ANOVA tests, $p > 0.05$) (Table 2).

Dietary overlap between the decapod species at 500 m, where they co-occur, as measured by Morisita's index were in general >0.60 , indicating that they exploited quite similar prey groups (Table 3), but dietary breadth at this depth significantly differed among the species examined ($F_{3, 506} = 11.47$, $p < 0.001$).

Food in relation to size

The occurrence of prey items in the diet varied significantly among the size classes of each species exam-

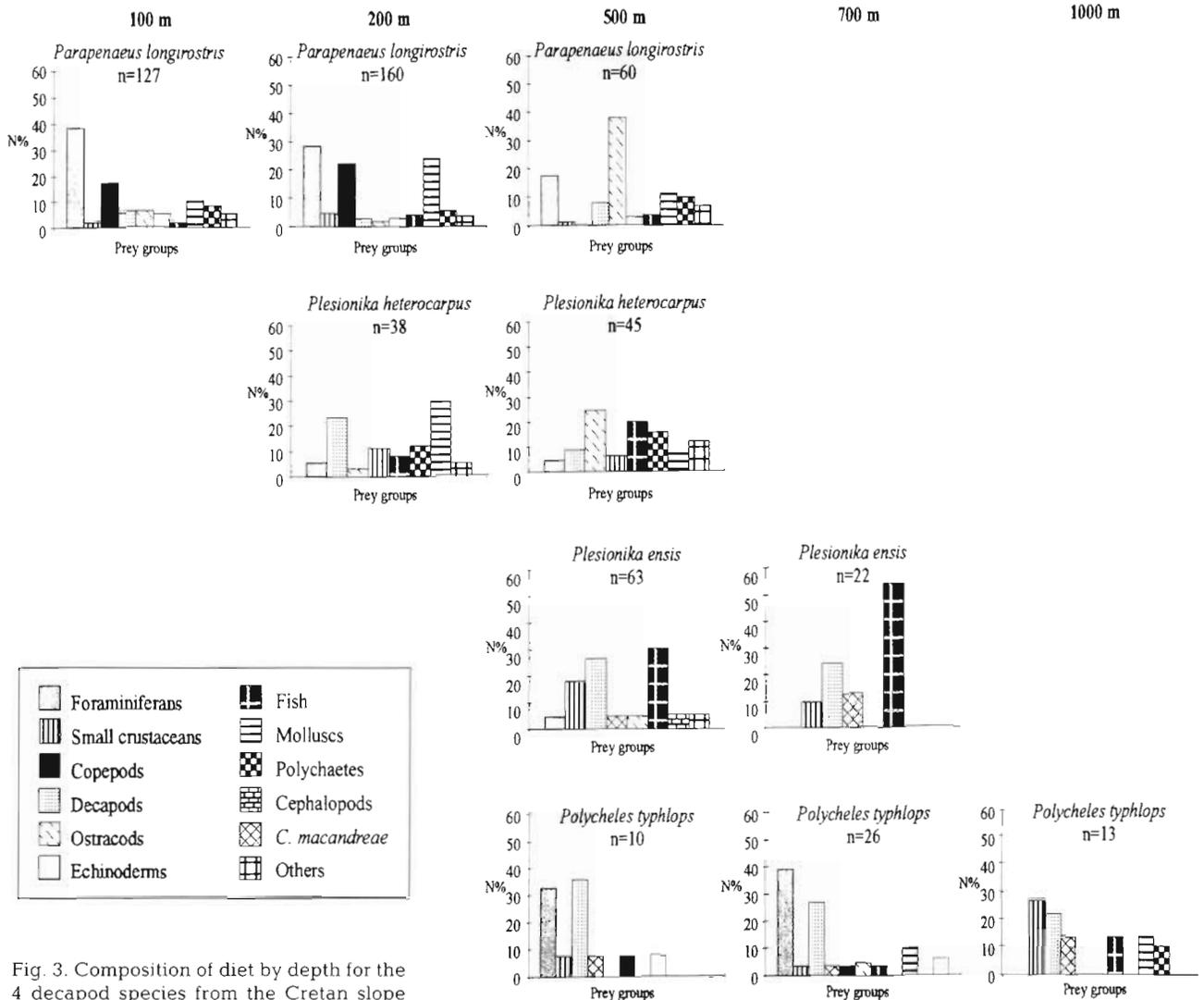


Fig. 3. Composition of diet by depth for the 4 decapod species from the Cretan slope

ined (χ^2 tests, $p < 0.05$). The numerical abundance of prey items found in decapod diets was calculated for each size class to determine dietary changes with size and to classify the ontogenetic trophic units for each of the decapod species. Cluster analysis run on trophic data for each of the species using the numerical abundance of prey species revealed the existence of size-specific feeding classes according to similar dietary habits within a given species.

All species were characterized by similar feeding patterns, namely different feeding habits between small and large individuals, but differed in their size boundaries (Fig. 4). However, 4 major groups were discriminated, each one consisting entirely of the specimens of each species examined. At the prey taxa level polychaetes, gastropods and natantian decapods contributed 56.3% to the similarity of Group 1,

ostracods (Myodocopa), foraminiferans and fish contributed 62.6% to the similarity of Group 2, foraminiferans, copepods and polychaetes contributed most (61.7%) to the similarities within Group 3, while brachyuran decapods, *Calocaris macandreae* and foraminiferans comprised more than 70% of the similarity in Group 4. The examination of the prey taxa dominated in each group implies that prey differences between the groups are quantitative rather than qualitative. Mean intraspecific dietary overlap was greater than mean interspecific overlap, which did not exceed 43%. Hence, this analysis indicated that interspecific differences in diet were greater than differences between size classes of the same species. No significant effect of size on the dietary breadth were found for any of the species examined (ANOVA tests, $p > 0.05$) (Table 2).

Table 2. Dietary breadth (Shannon-Wiener diversity index, H') by depth, size and season for the 4 decapod species from the Cretan slope. Ranges in parentheses: 95% bootstrap confidence intervals

	<i>Parapenaeus longirostris</i>	<i>Plesionika heterocarpus</i>	<i>Plesionika ensis</i>	<i>Polycheles typhlops</i>
Depth (m)				
100	2.37 (2.04–3.10)	–	–	–
200	2.29 (1.89–3.09)	–	–	–
500	2.43 (1.95–3.31)	2.19 (1.71–2.97)	1.96 (1.18–2.34)	1.89 (1.16–2.22)
700	–	2.68 (2.23–3.43)	1.81 (1.27–1.95)	1.89 (1.56–1.92)
1000	–	–	–	1.95 (1.51–1.99)
Size class (mm)				
<10	1.81 (1.23–2.79)	2.19 (1.80–2.88)	–	–
10–14	2.36 (2.03–3.09)	2.51 (1.99–3.33)	1.61 (0.83–1.99)	1.69 (1.19–1.79)
15–19	2.74 (2.43–3.45)	2.57 (1.93–3.51)	1.96 (1.39–2.13)	1.99 (1.56–2.02)
20–24	2.57 (2.17–3.37)	–	1.84 (1.27–2.01)	1.92 (1.55–1.98)
25–29	2.53 (2.17–3.29)	–	–	2.05 (1.23–2.47)
>29	2.09 (1.58–3.00)	–	–	–
Season				
Sep 1994	2.68 (2.34–3.42)	2.39 (1.89–3.19)	1.92 (1.41–2.03)	1.95 (1.42–2.08)
Feb 1995	2.11 (1.91–2.71)	2.36 (1.94–3.08)	1.89 (1.43–1.96)	2.01 (1.52–2.10)
May 1995	2.19 (2.01–2.77)	2.49 (1.92–3.36)	1.76 (1.32–1.81)	2.09 (1.63–2.15)
Sep 1995	2.22 (2.03–2.81)	2.37 (1.97–3.07)	1.63 (1.30–1.76)	1.64 (1.27–1.71)

Seasonal variation in dietary composition

Analysis of the seasonal occurrence of prey groups in the diet of each decapod indicated significant differences in the frequency that occurred in their stomach contents (χ^2 tests, $p < 0.05$). By considering the abundance of all prey species in decapod diets on a seasonal basis, cluster analysis revealed 4 groups, each one corresponding to the seasonal samples of each decapod species (Fig. 5). Prey taxa contributing most to the similarity of each group were foraminiferans, copepods and polychaetes for Group 1, polychaetes, gastropods and natantian decapods for Group 2, ostracods, foraminiferans and fish for Group 3, and brachyuran decapods, *Calocaris macandreae* and foraminiferans for Group 4. Mean intraspecific dietary overlap was greater than mean interspecific overlap, which did not exceed 38%. Consequently, this analysis indicated that, despite the seasonal variation in prey consumption exhibited by each decapod species,

interspecific variation was more pronounced, suggesting that the choice of prey types by each species was relatively consistent over the year. Dietary breadth showed no significant overall effect of season (ANOVA tests, $p > 0.05$) (Table 2). Although seasonal influences were also examined as a function of decapod size, no significant differences were found in size composition of the specimens for any of the species examined throughout the study (ANOVA tests, $p > 0.05$).

DISCUSSION

The results of the present study indicate that species differences in habitat use account mostly for the differences observed in the dietary patterns of the 4 deep-water decapods on the Cretan slope. At high levels of spatial overlap there is no evidence of trophic partitioning, at least along the prey type resource axis. Thus, the observed differences in preference and utilization of prey are primarily related to species distribution patterns. The patterns of resource use exhibited by each species were fairly consistent during the species' life span and did not change significantly during ontogeny. Since dietary overlap among the species when they co-occur is high, it appears that competitive trophic interactions account for the low overlap in the bathymetrical distribution of the species examined.

Changes in decapod species composition along the slope in Iraklion Bay were reflected by changes in both abundance and occurrence, even though the species

Table 3. Dietary overlap (simplified Morisita's index) for the 4 decapod species at 500 m depth, where they co-occur. Ranges in parentheses: 95% bootstrap confidence intervals

	<i>Parapenaeus longirostris</i>	<i>Plesionika heterocarpus</i>	<i>Plesionika ensis</i>
<i>Plesionika heterocarpus</i>	0.82 (0.70–0.91)		
<i>Plesionika ensis</i>	0.83 (0.76–0.88)	0.76 (0.57–0.89)	
<i>Polycheles typhlops</i>	0.69 (0.52–0.82)	0.62 (0.51–0.77)	0.78 (0.59–0.82)

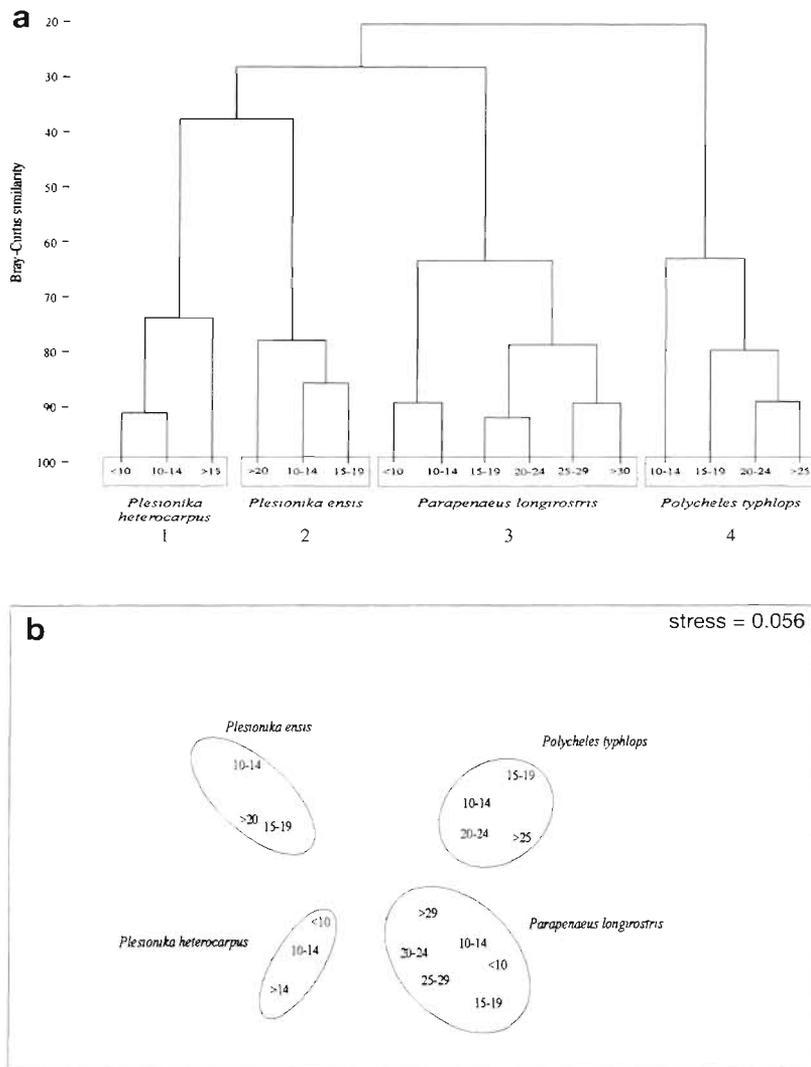


Fig. 4. (a) Classification and (b) ordination of dietary samples for the 4 decapod species from the Cretan slope

examined were found to occur over relatively broad depth ranges in the study area. Not only did the abundance of the species examined vary significantly with depth, but, when the depth ranges of species' occurrence overlapped, they appeared to have different depths where they reached their maximum abundance. Hecker (1990) suggested that the changes in species composition between different megafaunal assemblages are due to the substitution of the dominant species, throughout the depth gradient. A somewhat similar distribution pattern, with decapod species showing overlapping depth range but with different depths of maximum density, has also been demonstrated for deep-water species in the northwestern Atlantic (Wenner & Boesch 1979) and in the Western Mediterranean (Abelló & Cartes 1992). Although it

could be argued that the sampling methodology used in the present study was different in respect to sampling gear and that no quantitative comparisons could be made, the distribution patterns of the species were generally in agreement with those reported from the Western Mediterranean regarding the depth ranges at which species occur (Abelló et al. 1988, Cartes & Sardà 1993, Cartes et al. 1994).

The most important quantitative boundary was located at around 500 m, which separated the species of the upper slope from those of the bathyal region. At this depth a remarkable decline with respect to species richness, abundance and biomass of benthic macrofauna, as well as to environmental factors such as total organic carbon and chlorophyll *a*, has been reported (Tselepidis & Eleftheriou 1992). Nevertheless, certain factors of the benthic environment in the study area were remarkably stable with depth. Sediment structure consisted of a dominant silt-clay fraction throughout, temperature in and above the sediment was fairly constant and redox-potential was very high, indicating the existence of a well-oxygenated surface layer poor in organic loading (Tselepidis & Eleftheriou 1992). These observations together with the strong relationship between chlorophyll *a* and macrobenthic community structure and the dominant feeding types (Karakassis & Eleftheriou 1997) led to the conclusion that food availability is the principal regulating factor on the Iraklion slope.

The composition of food suggests that the deep-water decapods on the Cretan continental slope prey upon benthic organisms that can be divided into 3 main categories (Cartes & Sardà 1989): (1) organisms that live completely or partially buried, digging out small galleries in the substrate, such as *Calocaris macandreae*, polychaetes and bivalves; (2) organisms living on or partially beneath the surface of the substratum, such as amphipods, isopods, gastropods and echinoderms; and (3) bathypelagic organisms that may be found close to the bottom during the day as a result of vertical migrations (i.e. natantian decapods). Most of these prey groups are sessile or possess little mobility, while planktonic prey were completely absent from

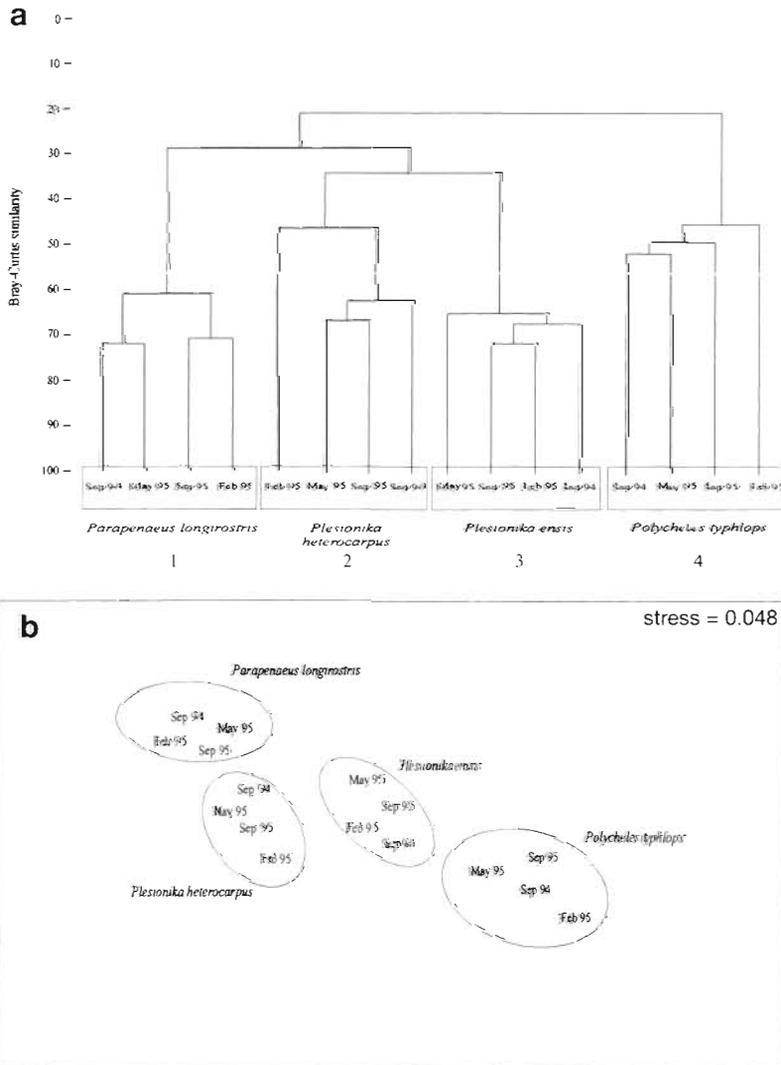


Fig. 5. (a) Classification and (b) ordination of monthly dietary samples for the 4 decapod species from the Cretan slope

Sea were active predators on macroplankton, with benthic resources being of secondary importance. Furthermore, it appears that the contribution of macroplanktonic and mesopelagic organisms in the diet of deep-water decapods from the Western Mediterranean, although secondary (Cartes & Maynou 1998), is much more pronounced than in these species. The great significance of mesopelagic food resources to deep-water fish communities has been emphasized by many researchers (Gartner et al. 1997 and references therein) and has been interpreted both as evidence of the occurrence of mesopelagic prey near the bottom (Sedberry & Musick 1978, Marshall 1979) and of off-bottom migrations by some demersal species into the mesopelagic realm to feed (Haedrich 1974, Haedrich & Henderson 1974, Blaber & Bulman 1987). The absence of pelagic or mesopelagic species from the diet of the decapods examined in the present study could be due to the fact that these organisms predominate in the diet of the demersal fish assemblages inhabiting the continental slope of Crete (Labropoulou unpubl.). Although it could be argued that no information is available from the present study on the dietary composition over a 24 h cycle, it is possible that the observed dietary patterns are determined to a certain extent by competitive interactions between decapod species and demersal fish in sharing the available food resources.

the diet of the species examined. Thus, it appears that the species studied are primarily active predators of benthic macroinvertebrates. Sediment was a common constituent of stomach contents in the species examined. The regular presence of sediment can be due either to the ingestion of sediment along with infauna or to predation on prey that, themselves, contain sediment at the time of ingestion (e.g. deposit feeders). Since deposit feeders were the dominant feeding type of macrobenthic organisms, accounting for 55 to 60% at all depth zones (Karakassis & Eleftheriou 1997), it could be argued that the sediment found in the stomachs is more likely to be related to the ingestion of deposit feeders.

Unlike the results of the present study, Cartes (1993a) found that *Plesionika* species from the Catalan

The occurrence of fish and cephalopods remains can be attributed to scavenging activity that plays an important role in the feeding of *Plesionika ensis* and *Polychelus typhlops*. Furthermore, the contribution of fish and cephalopods in the diet of both species increased with depth, indicating that scavenging became more important at depths below 500 m. On the contrary, scavenging behaviour made only a small contribution to the diet of *Parapenaeus longirostris* and *Plesionika heterocarpus*, which were found exclusively at depths down to 500 m. Cartes & Abelló (1992) reported that the contribution of scavenging activity to the diet of *P. typhlops* at depths between 550 and 750 m in the Balearic Basin was nearly 40%, but considerably decreased from 1000 to 1900 m. Whether this trend was evident for *P. typhlops* from

the Cretan slope could not be detected in the present study, since no data were available from depths below 1000 m.

Comparisons of the dietary composition between the different length classes revealed that all 4 species undergo changes in their feeding habits with ontogeny. However, almost the same prey taxa occurred in the stomachs of all size classes for each species, but there are differences in the relative proportions of each taxon. Clearly, trophic ontogeny in the species examined proceeds as a continuum of dietary changes rather than by distinct segregation of food resources between size classes. It appears that these decapods do not develop a diet directed at more specific sectors of the available food resources as they grow larger. Thus, these changes may reflect a combination of changes in prey availability and prey size in relation to predator, rather than an alteration in their benthic feeding habits.

Dietary diversity, as measured by the Shannon-Wiener index, indicated that species exhibited relatively diversified diets, but the diets of the species inhabiting shallower depths were wider than those of *Plesionika ensis* and *Polycheles typhlops*. These interspecific differences appear to reflect marked variations in food abundance or availability of the different prey at different depths. Dietary breadth did not vary between the size classes, months or depths for each species, and values were in all cases rather similar. Hence, since the bathyal bottoms of the Cretan slope exhibit a low degree of diversity (Tselepides & Eleftheriou 1992), all species examined could be considered as generalized feeders. However, since the decapod species at 500 m depth, where they co-occur, have access to the same available prey, their differences in diet must reflect differences in some other factors such as feeding behaviour and/or their adaptation to different habitats. *Parapenaeus longirostris* and *Plesionika heterocarpus* were found to be more abundant at shallower depths, where the diversity of benthic species is higher, while the distribution of *P. heterocarpus* and *P. typhlops* over deeper waters coincided with the remarkable decline in benthic species richness and diversity in the bathyal zone (Tselepides & Eleftheriou 1992). Perhaps this is the major reason for the observed dietary patterns over the depth range where these 4 species coexist. On the other hand the narrower feeding niche of *P. heterocarpus* and *P. typhlops* allows these species to inhabit deeper substrates, where food availability and species diversity are relatively low, whilst the wider feeding niche of *P. longirostris* and *P. heterocarpus* could constrain their distribution to shallower, more productive waters. Habitat-related factors causing shifts in feeding modes may be dictated to some extent by intrinsic species-typical characteristics

which delimit a fundamental search strategy for prey. Nevertheless, the observed species differences in preference and utilization of prey are possibly due to their depth-related ecological separation.

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 throughout the sampling period indicate that feeding intensity is high for both *Parapenaeus longirostris* and *Plesionika heterocarpus*. On the contrary, the low stomach-fullness values recorded for *Polycheles typhlops* and *Plesionika ensis* suggest that feeding intensity for these 2 species is very low. It is clear that, in general, season and size did not affect the feeding intensity of the species examined, while depth had a significant interspecific effect on food intake, which decreased with increasing depth. The high proportion of empty stomachs in decapod species that inhabit deep slopes has been reported previously by Wenner (1979), Cartes & Abellò (1992) and Cartes (1993b), and seems to be a general pattern for these species as an adaptation to the deep-sea environment, where trophic resources are scarce. Regarding the influence of depth on the feeding intensity of decapods, the available information from the literature is not conclusive. Childress et al. (1990) suggested that decline in metabolic rates of deep living crustaceans as a function of depth is due primarily to variation in temperature. However, for those benthic decapods which are particularly visually oriented and/or partially pelagic some significant depth-related decline in metabolism beyond that due to the decline in temperature was found. The influence of temperature on the patterns of food intake discussed here must be negligible, given the fact that species live over very narrow temperature ranges. Besides, our results seem to contradict the findings of Childress et al. (1990) that the decline in metabolic rate with depth is related to higher locomotor capacities of those decapod species that are visually oriented and active swimmers, because, for *P. typhlops*, a benthic, reptant and slow-moving decapod, feeding intensity was found to be the lowest. On the other hand our results are in agreement with those of Maynou & Cartes (1998), who found that food consumption varied by an order of magnitude from the slow-moving, crab-like species to the actively swimming mesopelagic shrimps. However, it should be noted that feeding intensity is only indicative of the metabolic activities of the species, therefore detailed studies on daily rations, evacuation rates and energy requirements are important to quantify the food consumed under natural conditions.

Optimal foraging theory predicts a specialization in diet as the absolute abundance of preferred prey types increases (Pyke 1984, Hart 1986). According to Keast

(1978b), dietary overlap is dependent upon available resources. However, dietary overlap is not always an indicator of competitive interactions between species. Colwell & Futuyma (1971) concluded that demonstrable overlap in resource use by 2 species in nature can be evidence either for or against the existence of competition. Partitioning among species has been argued to reduce interspecific competition. To establish competition as a critical factor for resource partitioning it must be shown that the food resources are in short supply (Pianka 1981). Although it is well documented that food availability is the limiting factor in the Cretan slope (Tselepidis & Eleftheriou 1992, Karakassis & Eleftheriou 1997), information on the carrying capacity of the deep-water environment for the sustainable levels of abundance, biomass and diversity is still required to prove that competition is a regulating factor in an environment depauperate in energy resources.

In summary, the trophic habits of the 4 deep-water decapods on the Cretan slope indicated that they were active predators of benthic organisms, while scavenging activity became more important at depths below 500 m. Dietary patterns of the species examined were quite similar and differences noted were more consistent with depth-related changes in available food resources than with changes in the position of the species in the food web. Competitive trophic interactions possibly account for the low overlap in the bathymetrical distribution of the species examined. Such interactions may be of fundamental importance on the deep-sea bottoms in the Eastern Mediterranean since environmental parameters such as temperature and salinity are rather constant.

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