DIETS OF TWO DEEP-SEA DECAPODS: *NEMATOCARCINUS EXILIS* (CARIDEA: NEMATOCARCINIDAE) AND *MUNIDA TENUIMANA* (ANOMURA: GALATHEIDAE) ON THE WESTERN MEDITERRANEAN SLOPE

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ABSTRACT

The composition of the diet of the deep-water decapods *Nematocarcinus exilis* and *Munida tenuimana* were established in samples obtained between 552-2266 m on the Catalan Sea slope. Both species fed on fish remains and on slow-moving benthic resources (*Benthonella tenella*, ostracods, pteropod remains, *Stephanoscyphus* spp.). However, pelagic resources (siphonophores, euphausiids, hyperiid amphipods represented a high proportion of *M. tenuimana*'s diet, but only down to 1200 m. In contrast, siphonophores were the only relatively abundant prey of pelagic origin in the diet of *N. exilis*. Seasonal changes in the diet, mainly related to the consumption of pelagic prey, were almost exclusively restricted to depths down to 1200 m. Below 1200 m both species exhibited a higher consumption of teleost fish remains, detritus of pelagic decapods, pteropods, and foraminiferans. This increase in detritivorous habits with depth seems to be an adaptation to environments with lower trophic resources.

INTRODUCTION

Nematocarcinus exilis (Bate, 1888) (Caridea: Nematocarcinidae) and *Munida tenuimana* G. O. Sars, 1872 (Anomura: Galatheidae) are two of the most abundant slope-dwelling species in the Catalan Sea. Both species are typical of the bathyal mud assemblages in the Western Mediterranean (Pérès 1985), where the physical conditions of the deep-water mass remain fairly constant at depths below 200 m (cf Hopkins 1985). The caridean shrimp *N. exilis* has been described as a characteristic species on the lower slope subzone (Pérès 1985). Its depth distribution in the Catalan Sea ranges from 1243 to 2011 m (Abelló & Valladares 1988). *N. exilis* has also been recorded at depths between 1352 and 2265 m, with densities increasing with depth and the highest densities recorded between 1700 and 2200 m (Cartes 1991). Similar species of the genus inhabit bathyal and abyssal environments in the Atlantic Ocean (Crosnier & Forest 1973, Lagardère 1977, Wenner & Boesch 1979, Markle et al. 1988), where they are one of the most characteristic faunistic groups.

Galatheid crabs constitute a homogeneous group whose member species are widely distributed on bathyal bottoms in deep oceanic regions (Lagardère 1977, Haedrich et al. 1980, Wenner 1982, Gore 1983, Saint Laurent 1985, Markle et al. 1988). *Munida tenuimana* is one of the most characteristic species of decapod crustaceans on the middle and lower slope in the Western Mediterranean. This species is distributed at depths ranging from 300 to 1900 m (Abelló et al., 1988, Cartes 1993a), being abundant between 552 and 1883 m, but disappearing entirely below 1900 m (Cartes 1991). The geographical distribution of *M. tenuimana* encompasses the Northeast Atlantic and Mediterranean (Zariquiey Alvarez 1968, Rice & de Saint Laurent 1986, Hartnoll et al. 1992).

The diet of *M. tenuimana* has been studied in the Bay of Biscay (Lagardère 1977). The majority of stomach contents formed a seemingly amorphous mass which on closer examination was found to consist of microplancton (peridinians, tintinnids, radiolarians, coccolithophores, etc.). Various polychaetes (aphroditids, nephthyds), crustaceans (*Boreomysis* sp., copepods) and fish remains complete the diet of *M. tenuimana*. There are no previously published data on the feeding habits of *N. exilis*. Because both decapods are characteristic deep-sea species, the study of their diets and trophic habits is of great interest and contributes to the overall knowledge of deep-sea environments.

MATERIALS AND METHODS

The methodology and criteria followed in this study have been widely described in earlier papers (cf. Cartes & Sardà 1989, Cartes & Abelló 1992, Cartes 1993b, c). All specimens were collected using an OTSB-14 bottom trawl in the Catalan Sea area during 1988-1989 (Table 1). A total of 288 specimens of *N. exilis* and 1058 specimens of *M. tenuimana* were dissected to establish stomach fullness (f). The percentages of empty ($f < 20\%$) and very full stomachs ($f \geq 75\%$) were recorded. The stomachs with the highest fullness values were selected to establish the diet, in order to minimize digestion effects. Prey were identified to species or to the lowest possible taxonomic level. Accordingly, a total of 353 specimens of *M. tenuimana* and 169 specimens of *N. exilis* were examined to determine the composition of the diet of each species (Table 1). The size range sampled was 11-18 mm carapace length (CL) for *N. exilis* and 12-25 mm CL for *M. tenuimana*.

The diet results have been expressed as the percentage frequency of occurrence (%F) and percentage abundance (%N) (cf. Hyslop 1980, Cartes & Sardà 1989). Foraminiferans and the microplanktonic organisms contributing to an amor-

Table 1. Catch data for *Nematocarcinus exilis* and *Munida tenuimana* from the Western Mediterranean.

Station	Date	Location	Depth (m)	Number of specimens	
				M. tenuimana	*N. exilis*
P 12	24/10/88	41 03 N - 2 04 E	669- 626	14	–
P 25	13/07/89	41 03 N - 2 03 E	650- 700	18	–
P 28	14/07/89	41 03 N - 2 03 E	710- 730	11	–
P 29	14/07/89	41 02 N - 2 03 E	610- 640	22	–
P 33	20/10/89	41 04 N - 2 04 E	552- 644	40	–
P 34	21/10/89	41 04 N - 2 04 E	614- 643	20	–
B3/3	25/06/88	40 27 N - 2 00 E	1823-1773	4	–
B3/5	26/06/88	40 37 N - 3 38 E	2266-2239	–	13
B3/6	27/06/88	40 29 N - 2 42 E	1857-1819	3	12
B3/7	27/06/88	40 06 N - 2 51 E	1621-1539	3	–
B3/8	28/06/88	40 18 N - 2 60 E	1737-1720	2	11
B3/16	04/07/88	40 49 N - 1 51 E	1249-1193	21	–
B3/19	05/07/88	40 26 N - 2 10 E	1827-1883	33	–
B3/22	06/07/88	40 09 N - 2 14 E	1631-1578	5	5
B3/25	07/07/88	39 55 N - 2 09 E	1224-1184	28	–
B3/28	11/07/88	40 26 N - 2 38 E	1927-1820	3	10
B4/3	27/07/88	41 08 N - 3 32 E	2188-2156	–	20
B4/4	28/07/88	40 57 N - 3 01 E	2071-1880	–	11
B4/8	29/07/88	41 06 N - 2 59 E	1916-1762	–	23
B4/9	30/07/88	40 49 N - 2 32 E	1816-1796	–	14
B5/2	25/10/88	40 20 N - 1 42 E	1609-1562	–	3
B5/3	25/10/88	40 28 N - 1 58 E	1779-1744	17	–
B5/4	26/10/88	39 54 N - 2 22 E	1100-1054	20	–
B5/7	27/10/88	40 19 N - 1 53 E	1754-1698	8	11
B5/8	27/10/88	40 31 N - 1 48 E	1680-1575	–	13
B5/13	28/10/88	40 59 N - 1 58 E	961-1087	13	–
B5/16	29/10/88	41 04 N - 2 20 E	1120-1008	16	–
B5/19	30/19/88	41 04 N - 2 53 E	1795-1740	6	23
SP-2	16/10/89	40 50 N - 1 34 E	862- 989	20	–
SP-3	17/10/89	40 26 N - 1 59 E	1772-1808	26	–

phous mass of stomach contents (Lagardère 1977) were not quantified. The volume of the different prey groups was estimated based on the subjective points method (Swynnerton & Worthington 1940).

For both species, samples were aggregated using multivariate cluster analysis (Linear correlation-UPGMA) (cf. Cartes & Abelló 1992) to detect affinity groups with similar dietary composition. Then, for purposes of comparison, samples were aggregated by depth and seasonal groups partially based on the cluster analysis results. The depth groups established conformed to slope zonation reported in previous papers (Cartes & Sardà 1993): upper middle slope (550-800 m); lower middle slope (900-1200 m), and lower slope (below 1300 m).

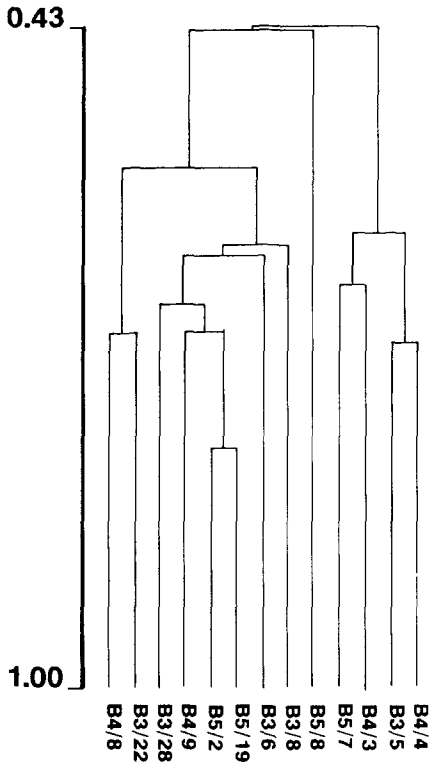Lastly, trophic diversity was calculated using the Shannon-Wiener index

Fig. 1. Aggregation of *Nematocarcinus exilis* samples (linear correlation – UPGMA). Only sample codes are indicated. Additional sample data are explained in Table 1.

(Shannon & Weaver 1963), and dietary overlap between the different depth and seasonal groups was calculated using the percentage of similarity (Schoener 1970).

RESULTS

Nematocarcinus exilis

The results of cluster analysis pointed to a high affinity between all the samples (diets), suggested by the relatively high minimum linear correlation (0.43) value. Samples collected at depths below 2000 m were aggregated in the cluster analysis (Fig. 1), though they were not completely separate from the other, shallower samples. No seasonal differences were distinctly observable in the diet in the 1500-1900 m depth interval. Nevertheless, the samples were all classified into three different depth and seasonal sample groups.

   The composition of the diet was very similar in all the groups established. Fish remains were always the dominant resource, both in terms of occurrence and abundance (Table 2). Fish remains mainly consisted of isolated ossicles, vertebrae, or scales. In contrast, whole remains, containing otholits, mandibles or

Table 2. Diet composition of *Nematocarcinus exilis*. %F: percentage frequency of occurrence; %N: percentage abundance.

	1500-1900 m				2000-2300 m	
	Jul 75		Oct 50		Jul 44	
	%F	%N	%F	%N	%F	%N
HYDROZOA	48.0	22.5	28.0	13.2	31.8	12.1
Ch. appendiculata	30.6	12.1	8.0	2.0	4.5	1.3
Stephanoscyphus spp.	25.3	10.4	20.0	11.2	29.5	10.8
POLYCHAETA	8.0	3.5	6.0	2.1	29.5	8.2
Aphroditidae	1.3	0.6	2.0	0.7	–	–
Glycera sp.	–	–	–	–	15.9	4.4
Nepthys sp.	1.3	0.6	–	–	–	–
Nereidae	4.0	1.7	2.0	0.7	–	–
Sternaspidae	1.3	0.6	2.0	0.7	4.5	1.3
Unidentified	; –	–	–	–	4.5	2.5
CRUSTACEA						
Decapoda Natantia						
Benthopelagic species	34.7	14.2	76.0	27.0	52.3	17.1
Pasiphaea multidentata	17.3	7.1	18.0	5.9	34.1	8.2
Acanthephyra pelagica	17.3	7.1	64.0	21.1	27.3	8.9
Nektobenthic species						
Pontophilus norvegicus	1.3	0.6	–	–	–	–
Unidentified	5.3	2.2	6.0	2.6	13.6	3.8
Macrura (*Stereomastis sculpta*)	–	–	–	–	4.5	1.3
Unidentified	6.7	2.8	–	–	2.3	0.6
Mysidacea (*Boreomysis arctica*)	2.7	1.1	–	–	–	–
Hyperiidea	5.3	2.3	2.0	0.7	2.3	0.6
Phrosina semilunata	1.3	0.6	–	–	2.3	0.6
Other Hyperiidea	4.0	1.7	2.0	0.7	–	–
Isopoda	–	–	–	–	4.5	1.2
Ilyarachna sp.	–	–	–	–	2.3	0.6
Other Paraselloidea	–	–	–	–	2.3	0.6
Cumacea	4.0	1.7	6.0	2.6	18.2	5.1
Cyclaspis longicaudata	2.7	1.1	4.0	1.3	6.8	3.2
Bathycuma brevirostris	–	–	2.0	1.3	–	–
Platysympus typicus	1.3	0.6	–	–	–	–
Unidentified	–	–	–	–	6.8	1.9
Ostracoda Platycopa	1.3	0.6	2.0	0.7	25.0	10.1
Copepoda Calanoidea	–	–	–	–	2.3	0.7
Unidentified	5.3	2.2	2.0	0.7	6.8	1.9
MOLLUSCA						
Bivalvia	–	–	–	–	2.3	0.6
Gastropoda	25.3	10.4	48.0	15.8	43.2	10.2
Pteropoda	8.0	3.3	12.0	3.3	18.2	5.1
Benthonella tenella	17.3	7.1	36.0	10.5	25.0	5.1
Other gastropoda	–	–	6.0	2.0	–	–
Prosobranchia (egg capsules)	1.3	0.6	2.0	0.7	–	–
Cephalopoda	1.3	0.6	4.0	0.7	–	–
Unidentified	–	–	–	–	4.5	1.9
CHAETOGNATHA	1.3	0.6	–	–	2.3	1.3
OSTEICHTHYES	85.3	34.1	96.0	28.3	68.2	20.3
Macrouridae	2.7	1.1	–	–	–	–
Other osteichthyes	82.7	33.0	96.0	28.3	68.2	20.3
Chondricthyes	–	–	–	–	2.3	1.3
OTHER	1.3	0.6	4.0	2.0	4.5	1.9
UNIDENTIFIED (Fecal pellets)	–	–	14.0	4.6	4.5	1.3
FORAMINIFERA (Benthic species)	32.0		38.0		47.7	
Micromollusc remains	2.7		–		6.8	

Nematocarcinus exilis
LOWER SLOPE (1500 - 1900 m)
(S)

Ac   St   SIPH
Pm   FOR
7 8 7.1 6 4
          14 OTHERS
    55.9
OST

LOWER SLOPE (1500 - 1900 m)
(A)

Ac   St FOR
15.6 5 4.6 OTHERS
Pm   11.9
9
5.3
Bent
    48.7
OST

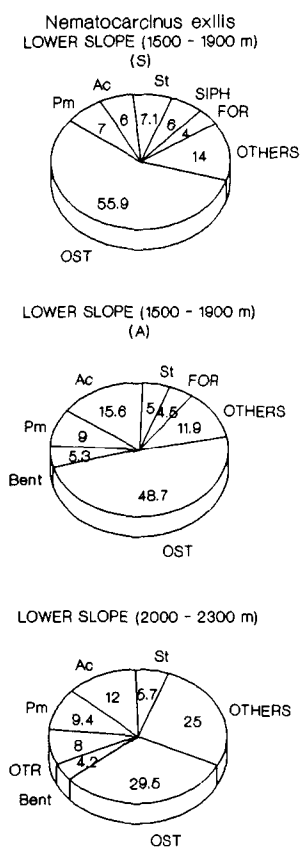LOWER SLOPE (2000 - 2300 m)

Ac   St
Pm   12 6.7
9.4   25   OTHERS
8
OTR 4.2
Bent 29.5
OST

Fig. 2. Proportion (by volume) of the main prey groups in the diet of *Nematocarcinus exilis* by depth and seasonal intervals. SIPH: siphonophores; St: *Stephanoscyphus* spp.; Pm: *Pasiphaea multidentata;* Ac: *Acanthephyra pelagica;* OTR: benthic ostracods; Bent: *Benthonella tenella;* FOR: foraminiferans; OST: fish remains. A: autumn samples; S: summer samples.

eye lenses were very scarce, confirming *N. exilis* to be a scavenger species. In terms of abundance secondary prey items recorded included siphonophores (*Chelophyes appendiculata*), hydrozoan polyps (*Stephanoscyphus* spp.), remains of large bathypelagic decapods (*Pasiphaea multidentata, Acanthephyra pelagica*), gastropods (*Benthonella tenella*), and foraminiferans. Certain peracarid crustaceans (mysids and cumaceans) and polychaetes were less important dietary constituents.

Depth-related changes in the diet were minor. The only aspect of note was the low incidence of siphonophores below 2000 m. Benthic calcified ostracods were, in contrast, more abundant below 2000 m. Seasonal changes in the diet were also relatively insignificant in *N. exilis*. The high proportion of siphonophores in summer samples was the most important feature observed. In terms of the volume of dietary constituents the results (Fig. 2) indicated a smaller proportion of fish remains and a relatively large percentage volume of ostracods below 2000 m. Similarly, siphonophores were only abundant in summer between 1500-1900 m.

Feeding activity and trophic diversity. Stomach fullness values were relatively high in

Table 3. Stomach fullness (f) values for *Nematocarcinus exilis* and *Munida tenuimana* by depth and seasonal intervals.

| | SLOPE REGIONS | | | | | |
| | | | | | LOWER | |
	UPPER MIDDLE		LOWER MIDDLE		1400-1900 m	2000-2300 m
Munida tenuimana	Mar-Jul	Oct	Jul	Oct	Jul-Oct	
number of specimens	65	103	226	257	465	
f < 20%	41.5	46.0	74.3	83.3	77.4	
f ≥ 75%	23.1	20.4	8.0	4.3	3.7	
Nematocarcinus exilis					Jun-Jul	Oct	Jun-Jul
number of specimen					103	44	141
f < 20%					36.9	20.5	35.5
f ≥ 75%					28.2	20.5	17.7

N. exilis. Only 33.7% of the 288 foreguts examined were empty (f < 20%), whereas 21.9% were very full (f ≥ 75%). Below 2000 m empty stomachs were observed to increase slightly (no significant difference; p < 0.05), and the percentage of very full stomachs decreased accordingly (Table 3).

Broadly speaking, trophic diversity (H') in *N. exilis* was relatively low, in that nearly one-third of the diet was based on a single prey item (fish remains) (Table 2). The highest H' value (3.971) was recorded on the deepest part of the slope considered, i.e. for samples collected from 2000 to 2300 m. Lastly, dietary overlap was high between all the groups established, particularly between the two seasonal groups on the upper portion of the lower slope (73.376). The values between the different depth groups were lower (63.179-64.680).

Munida tenuimana

The cluster analysis results (Fig. 3) displayed a first dichotomy that separated a group that included all the samples collected on the upper middle slope (552-669 m) in autumn. Sample B3-1000 was not associated with any group, probably because of the small number of specimens analyzed.

Three separate aggregations were detected in a second group of samples. First, the rest of the samples taken on the upper middle slope were separated from the deeper samples collected at depths below 1000 m. Of these deeper samples, two further subgroups were distinguishable and were usually separated by the 1100-1200 m isobaths. The samples taken on the lower middle slope in autumn formed a homogeneous aggregation, whereas the other samples collected in this same depth interval in summer were associated with the deepest samples from the lower slope. Thus, partly based on the results obtained by cluster analysis, the stomach contents of *M. tenuimana* were distributed amongst the following five

different groupings in which the influence of depth and seasonality appeared to be similar:

1. On the upper middle slope (610-730 m) in summer, the diet of *M. tenuimana* was based on fish remains and the endobenthic macruran *Calocaris macandreae* (Table 4). The origin of fish remains must be considered similar to that indicated for *N. exilis*. Less important contributions were made by bivalves and pteropod shells, siphonophores (*Chelophyes appendiculata*), and the mysid *Boreomysis arctica*. The total absence of euphausiids from the diet in these samples is noteworthy. In terms of volume (Fig. 1) fish remains and *C. macandreae* remained the preferred prey items, with mysids, polychaetes, and siphonophores still important as secondary prey items.

2. In this same zone in autumn, the dominant resource was the euphausiid *Meganyctiphanes norvegica* (Table 4). Pteropod and fish remains, mysids (*B. arctica*), *C. macandreae*, and unidentified crustaceans accounted for about 60% of the diet. At this season the diet also included a wide variety of prey items that were pelagic in origin (*Vibilia armata, Phrosina semilunata, Pasiphaea multidentata, Ch. appendiculata*, etc.). In terms of volume (Fig. 4), euphausiids were clearly predominant. *C. macandreae*, hyperiid amphipods, fish and *M. tenuimana* remains, and remains of microplanktonic organisms were also important.

3. On the lower middle slope (992-1224 m) in summer, pelagic prey items such as *Ch. appendiculata, V. armata*, and *Acanthephyra pelagica* predominated in the diet (Table 4), also remaining the basis of the diet in terms of volume (Fig. 4).

4. In the same region of the lower middle slope (862-1101 m) in autumn, excepting the fish remains, which were the most exploited resource at this level, all other important resources in the diet of *M. tenuimana* were also planktonic in origin (Table 4), *A. pelagica*, euphausiids, and *P. multidentata*. Siphonophores were entirely absent from the diet. In terms of percentage volume, fish remains, *A. pelagica*, and euphausiids were also the dominant resources (Fig. 4).

5. On the lower slope (1754-1927 m) the samples collected in summer and autumn were not separated into seasonal groups on account of their high level of similarity. The diet was based on fish remains, pteropod shells, and gastropods (*B. tenella*). Planktonic resources were quite scarce at this level. Euphausiids were completely absent, and only hyperiids were relatively abundant in the diet (Table 4). In terms of volume (Fig. 4) fish remains, *P. multidentata*, and *A. pelagica* were the most prevalent resources, with hyperiids, polychaetes, and siphonophores as secondary food items.

Feeding activity and trophic diversity. Munida tenuimana exhibited an extremely high proportion of empty foreguts (71.7%), and a correspondingly low percentage of very full stomachs (7.6%). In general, stomach fullness tended to decrease progressively with depth (significant differences; p < 0.01) (Table 3).

Dietary diversity was relatively high in *M. tenuimana* (Table 5) in all the differ-
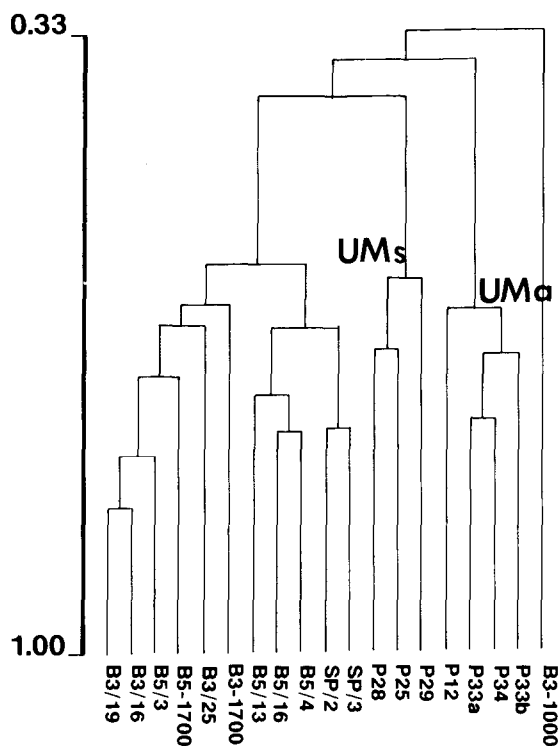
Fig. 3. Aggregation of *Munida tenuimana* samples (linear correlation – UPGMA). Only sample codes are indicated. Additional sample data are explained in Table 1.

ent depth and seasonal groups. Dietary overlap between groups yielded high values, hence it was possible to compare the three sample groups below 1000 m (Table 6). Conversely, the affinity between the two seasonal groups on the upper middle slope was lower, probably because of stronger seasonal influences on the diet at that level.

Finally, interspecific dietary overlap between both species was also high (62.340) on those areas of the slope where they coexist.

DISCUSSION

The diet of *Nematocarcinus exilis* underwent only minor changes with depth and season, probably because of the high environmental stability on the lower slope. The influence of seasonality on the diet in *Munida tenuimana* was important only down to 1200 m, mainly related to the consumption of pelagic prey, and was likewise low on the lower slope. Seasonal variations in the diets of deep-sea species is a common phenomenon on the upper and middle slope regions, as in the case of pandalid shrimps (Lagardère 1977, Cartes 1993c).

Resources of pelagic origin were important in the diets of both species, especially in *M. tenuimana*. These resources must be obtained both by active predation

Table 4. Diet composition of *Munida tenuimana*. %F: percentage frequency of occurrence; %N: percentage abundance.

| | Upper middle slope | | | | Lower middle slope | | | | Lower slope | |
| | Jul 51 | | Oct 74 | | Jul 49 | | Oct 69 | | Jul-Oct. 110 | |
	%F	%N	%F	%N	%F	%N	%F	%N	%F	%N
HYDROZOA	11.8	4.8	17.6	2.3	49.0	18.6	–	–	9.9	4.4
Ch. appendiculata	11.8	4.8	17.6	2.3	49.0	18.6	–	–	9.0	4.0
Stephanoscyphus spp.	–	–	–	–	2.0	0.8	–	–	0.9	0.4
POLYCHAETA	15.7	8.8	5.4	3.1	10.2	3.9	5.6	3.0	14.4	4.4
Aphroditidae	5.9	2.4	4.1	2.3	–	–	–	–	3.6	1.2
Glycera sp.	2.0	0.8	1.4	0.8	2.0	0.8	–	–	1.8	0.8
Hyalinoecia sp.	–	–	–	–	–	–	1.4	1.0	–	–
Eunicida unid.	2.0	0.8	–	–	–	–	–	–	–	–
Nepthys sp.	2.0	0.8	–	–	–	–	–	–	–	–
Nereidae	2.0	0.8	–	–	–	–	1.4	–	–	–
Sternaspidae	–	–	–	–	6.1	2.3	1.4	1.0	5.4	2.4
Unidentified	9.8	4.0	–	–	2.0	0.8	1.4	1.0	4.5	2.0
NEMATODA	3.9	1.6	1.4	0.8	–	–	–	–	–	–
CRUSTACEA										
Decapoda natantia										
Benthopelagic species	7.8	3.2	2.7	1.5	22.4	7.8	24.6	17.2	32.4	13.3
Pasiphaea multidentata	7.8	3.2	2.7	1.5	6.1	0.8	7.2	5.1	18.0	8.1
Acanthephyra sp.	–	–	–	–	14.3	5.4	17.4	12.1	14.4	5.2
Sergestidae	–	–	–	–	4.1	1.6	–	–	–	–
Nektobenthic species	5.9	2.4	2.7	1.5	–	–	–	–	–	–
Aristeus antennatus	3.9	1.6	–	–	–	–	–	–	–	–
Plesionika sp.	2.0	0.8	2.7	1.5	–	–	–	–	–	–
Pontophilus norvegicus	–	–	–	–	–	–	–	–	0.9	0.8
Unidentified	3.9	1.6	4.1	2.3	14.3	5.4	14.5	10.1	15.3	6.9
Macrura										
Calocaris macandreae	35.3	16.0	10.8	6.1	–	–	2.8	2.0	–	–
Anomura	3.9	1.6	6.8	3.8	4.1	1.6	4.2	3.0	1.8	0.8
Pagurus alatus	2.0	0.8	–	–	–	–	–	–	–	–
Munida tenuimana	2.0	0.8	6.8	3.8	4.1	1.6	4.2	3.0	1.8	0.8
Post-larvae	2.0	0.8	–	–	–	–	–	–	–	–
Unidentified	9.8	2.4	1.4	0.8	8.2	3.1	2.8	2.0	7.2	3.6
Euphausiacea	–	–	28.4	–	–	–	13.0	9.1	–	–
Mysidacea	13.7	5.6	10.8	6.1	–	–	–	–	1.8	0.8
Boreomysis arctica	11.8	4.0	–	–	–	–	–	–	0.9	0.4
Eucopia sp.	2.0	0.8	–	–	–	–	–	–	0.9	0.4
Unidentified	2.0	0.8	10.8	6.1	–	–	–	–	–	–
Amphipoda										
Gammaridea	–	–	–	–	–	–	2.8	2.0	2.7	1.2
Rhachotropis sp.	–	–	–	–	–	–	1.4	1.0	0.9	0.4
Unidentified	–	–	–	–	–	–	1.4	1.0	1.8	0.8
Hyperiidae	2.0	0.8	9.5	5.4	42.9	21.7	2.8	2.0	4.5	2.4
Phrosina semilunata	2.0	0.8	2.7	1.5	4.1	2.3	–	–	1.8	0.8
Vibilia armata	–	–	1.4	0.8	28.6	14.0	–	–	0.9	0.4
Phronima sedentaria	–	–	5.4	3.1	10.2	5.4	2.8	2.0	2.7	1.2

Table 4 cont.

|	UPPER MIDDLE SLOPE				LOWER MIDDLE SLOPE				LOWER SLOPE	
	Jul 51		Oct 74		Jul 49		Oct 69		Jul-Oct. 110	
	%F	%N	%F	%N	%F	%N	%F	%N	%F	%N
Isopoda	5.9	2.4	1.4	0.8	–	–	–	–	2.7	1.2
Cirolana borealis	2.0	0.8	1.4	0.8	–	–	–	–	–	–
Munnopsursus atlanticus	3.9	1.6	–	–	–	–	–	–	0.9	0.4
Ilyarachna sp.	–	–	–	–	–	–	–	–	0.9	0.4
Other Paraselloidea	–	–	–	–	–	–	–	–	0.9	0.4
Tanaidacea Apseudomorpha	–	–	–	–	–	–	1.4	1.0	0.9	0.4
Cumacea	2.0	0.8	–	–	2.0	0.8	1.4	1.0	3.6	2.4
Epileucon longirostris	2.0	0.8	–	–	–	–	1.4	1.0	–	–
Cyclaspis longicaudata	–	–	–	–	–	–	–	–	1.8	1.2
Bathycuma brevirostris	–	–	–	–	2.0	0.8	–	–	–	–
Platysympus typicus	–	–	–	–	–	–	–	–	1.8	0.8
Unidentified	–	–	–	–	–	–	–	–	0.9	0.4
Ostracoda Myodocopa	–	–	1.4	0.8	–	–	–	–	–	–
Copepoda Calanoidea	–	–	–	–	–	–	2.8	2.0	–	–
Unidentified	5.9	2.4	10.8	6.1	10.2	3.9	1.4	1.0	7.2	3.6
MOLLUSCA										
Bivalvia	13.7	7.2	1.4	5.3	–	–	–	–	2.7	0.8
Other Taxodonta	–	–	–	–	–	–	–	–	0.9	0.4
Abra longicallus	3.9	1.6	–	–	–	–	–	–	–	–
Other bivalvia	9.8	5.6	1.4	5.3	–	–	–	–	1.8	0.4
Gastropoda	21.6	4.8	35.1	16.1	30.6	14.0	18.8	15.1	46.8	25.8
Pteropoda	9.8	4.8	21.6	12.2	22.4	8.5	14.5	10.1	36.0	16.9
Alvania sp.	2.0	0.8	–	–	–	–	–	–	–	–
Benthonella tenella	9.8	3.2	13.5	3.1	12.2	4.7	4.2	3.0	18.0	8.1
Other gastropoda	–	–	1.4	0.8	2.0	0.8	2.8	2.0	0.9	0.8
Cephalopoda	–	–	–	–	–	–	1.4	1.0	0.9	0.8
Unidentified	2.0	0.8	–	–	2.0	0.8	–	–	3.6	1.6
ECHINODERMATA	–	–	5.4	3.1	2.0	0.8	–	–	1.8	0.8
Echinoidea	–	–	5.4	3.1	–	–	–	–	–	–
Ophiuroidea	–	–	–	–	2.0	0.8	–	–	0.9	0.4
Myriotrochinae	–	–	–	–	–	–	–	–	0.9	0.4
OSTEICHTHYES	58.8	26.4	12.2	6.9	44.9	17.1	33.3	23.2	45.0	19.8
Cyclothone sp.	3.9	1.6	–	–	–	–	–	–	–	–
Myctophidae	–	–	–	–	–	–	–	–	0.9	0.4
Other osteichthyes	58.8	24.8	12.2	6.9	44.9	17.1	33.3	23.2	44.1	19.4
OTHER	–	–	9.5	5.3	–	–	1.4	1.0	3.6	1.2
Egg capsules (Gastropods)	–	–	1.4	0.8	–	–	–	–	–	–
UNIDENTIFIED	2.0	0.8	10.8	6.1	–	–	2.8	3.0	2.7	1.6
FORAMINIFERA	13.7		10.8		26.5		18.8		43.2	
Micromollusc remains	5.9		9.5		4.1		7.2		11.7	
Microplanktonic remains	17.6		–		5.1		–		–	
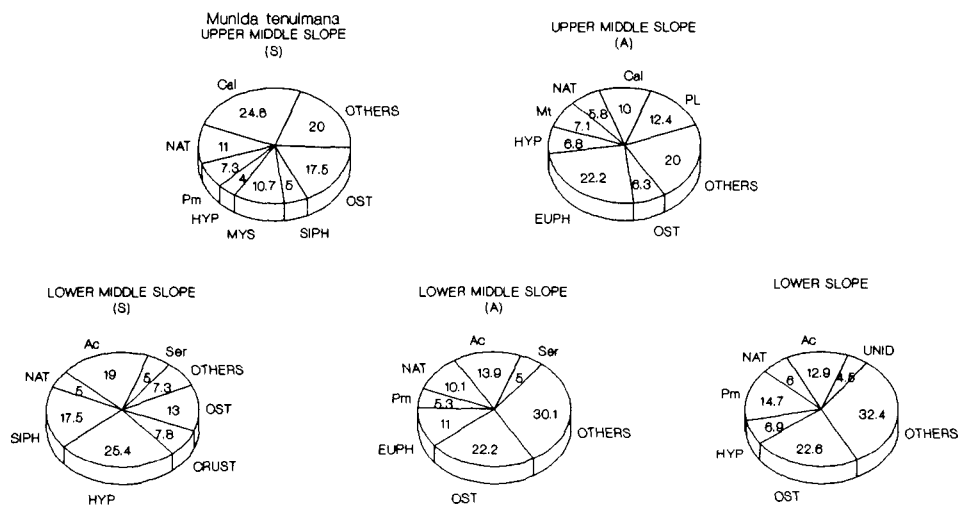
Fig. 4. Proportion (by volume) of the main prey groups in the diet of *Nematocarcinus exilis* by depth and seasonal intervals. Ser: *Sergestes arcticus;* NAT: natantian decapods; Cal: *Calocaris macandreae;* Mt: *Munida tenuimana;* EUPH: euphausiids; MYS: mysids; HYP: hyperiid amphipods; CRUS: unidentified crustaceans; PL: planktonic remains; UNID: unidentified. For explanations of all other abbreviations see Fig. 2.

and consumption of sedimented material. Euphausiids were highly abundant in the diet of *M. tenuimana* on the middle slope in autumn, whereas siphonophores and hyperiids were more abundant in summer. The share in the diet was basically in consonance with the seasonal abundance of each group in the plankton in the Western Mediterranean (Franqueville 1971). The contribution of euphausiids in the diet decreased progressively with depth, according to a suggested reduction of mid-water biomass in the Western Mediterranean (Bernard 1958). On the lower slope euphausiids were entirely absent from the diets of both species, an aspect already reported for polychelid lobsters in the same area (Cartes & Abelló 1992). Siphonophores and hyperiids were important in the diet of *M. tenuimana* only below 1000 m and in the diet of *N. exilis* to around 2000 m, a tendency also observed in the decapods *Aristeus antennatus* and *Stereomastis sculpta* in the Catalan Sea (Cartes 1991, Cartes & Abelló 1992). Depth boundaries for siphonophores based on the results of the stomach content analysis were probably related to their abundance close to the sea-bed, about which no direct data are available for this area. However, by way of indirect evidence, the teleost fish *Alepocephalus rostratus,* whose diet is based on coelenterates (Mauchline & Gordon 1983, Gordon & Mauchline 1990), is abundant in the studied area down to 2000 m (Stefanescu 1991). In the Northeast Atlantic, where alepocephalids are abundant down to 1750 m (Gordon & Mauchline 1990), peaks of abundance for medusae and siphonophores were recorded close to the sea-bed (10-50 m off the bottom) down to 1700 m (Hargreaves et al. 1984).

Table 5. Trophic diversity (H') values for *Nematocarcinus exilis* and *Munida tenuimana* by depth and seasonal intervals.

					SLOPE REGIONS	
						LOWER
	UPPER MIDDLE		LOWER MIDDLE		1400-1900 m	2000-2300 m
Munida tenuimana	Mar-Jul	Oct	Jul	Oct	Jul-Oct	
Diversity (H')	4.090	3.966	3.687	3.822	4.118	
Nematocarcinus exilis					Jan-Jul	Oct	Jun-Jul
Diversity (H')					3.463	3.166	3.971

Bathypelagic decapods such as *Pasiphaea multidentata* and *Acanthephyra pelagica* were other important pelagic resources in the diets of *N. exilis* and *M. tenuimana*. Large mandibles of decapod prey-species occurring in the stomach contents of both species were sometimes nearly as large as the predators' own stomachs, which must be indicative of detritivorous feeding behaviour by *M. tenuimana* and *N. exilis* on sedimented planktonic material (cf Bathmann 1988, Angel 1990). Similar detritivorus behaviour may account for the ocurrence of microplanktonic organisms (Lagardère 1977) in the stomach contents of *M. tenuimana*. Although such behaviour may have been the source of all the planktonic prey items ingested, the outer appearance of hyperiids, siphonophores and euphausiids in the foreguts of *M. tenuimana* and *N. exilis,* which consisted of whole remains, pointed to active predation on such prey. Prey size selection constituted further evidence of hunting activity. Accordingly, smaller hyperiid prey species (*Vibilia armata*) predominated, and small prey items (siphonophores, hyperiids, etc.) were generally more prevalent than large pelagic decapods. Although ingestion of pelagic, sedimented detritus and predation on pelagic organisms occurring close to the bottom are the most common accepted arguments to justify the presence of pelagic organisms in the guts of bottom-living species (cf Lagardère 1977, Sedberry & Musick 1978, Tyler 1988, Angel 1990), another possible explanation for the described predatory activity in *M. tenuimana* and *N. exilis* may reside in movements carried out to feed in the BBL, which has been defined as a layer of benthopelagic organisms dwelling close to the sea bed (Wishner 1980, Hargreaves 1984, Hargreaves et al. 1984, Angel 1990). Although mid-water excursions by *M. tenuimana* seem unlikely from the morphology of this species,

Table 6. Dietary overlap between the different groups established in the diet of *Munida tenuimana*.

	UPPER MIDDLE SLOPE (Oct)	LOWER MIDDLE SLOPE (Jul)	LOWER MIDDLE SLOPE (Oct)	LOWER SLOPE (Jul-Oct)
UMs (Jul)	43.841	41.655	45.123	51.432
UMs (Oct)	–	42.388	45.497	41.563
LMs (Jul)	–	–	49.400	61.896
LMs (Oct)	–	–	–	61.742

adult pelagic stages have, been reported in the life cycle of a neighbouring species *Munida gregaria* (Williams 1980, Zeldis 1985).

The rare occurrence of whole fish remains in the foreguts (cf Cartes 1993c) indicated that both *M. tenuimana* and particularly *N. exilis* are scavengers which search actively for this type of resources (Lagardère 1977). The decrease of fish remains in the diet of *N. exilis* below 2000 m is probably related to a concomitant decrease in fish biomass with increasing depth (Stefanescu 1991). Both species also feed on slow-moving benthic resources (gastropods, ostracods, pteropod remains, or hydrozoan polyps) encountered in the surface layer of the bottom sediment. In contrast, the share of both mobile suprabenthic (peracarid crustaceans) and endobenthic prey (glycerid polychaetes) in the diet was quite low (Cartes & Abelló 1992). No group of benthic resources attained the same level of prevalence recorded for pelagic prey items in the diet of *M. tenuimana*. This suggests that pelagic resources were exploited more intensively over short time periods when they were abundant in the plankton. Changes in trophic diversity observed on the middle slope might be linked to these fluctuations in resource availability. Specialization on euphausiids in the upper middle slope or hyperiids and siphonophores on the lower slope would bring with it a drop in H' values.

On the lower slope both species exhibited a high consumption of teleost fish remains, detritus of pelagic organisms, pteropods, and foraminiferans. This increase in detritivorous and opportunistic habits with depth seems to be a general adaptation to environments with lower trophic resource levels (Carey 1972, Dayton & Hessler 1972, Sokolova 1972) and has also been reported in abyssal decapods (Wenner 1979, Gore 1984, 1985). This trend was more evident in *N. exilis*, which may be regarded as a microphagous species with a very low energy expenditure for feeding activity.

Munida tenuimana populations were relatively abundant at nearly constant densities all along the slope but fell off drastically below 1900 m. In the deep Mediterranean, where temperature and salinity are constant (Hopkins 1985), trophic factors (Haedrich et al. 1980) are likely to have a greater influence on species distributions. Certain preferential prey items in the diet of *M. tenuimana* on the middle slope (e.g. *C. macandreae*, euphausiids) were not available on the slope below 1200 m (Lagardère 1977, Cartes 1991). In addition, dietary overlap between *M. tenuimana* and *N. exilis* was high on that part of the slope where both species coexist. Thus, *N. exilis* followed a trophic strategy quite similar to that of *M. tenuimana* on the lower slope, augmenting its detritivorous habits still further with depth. Therefore, possible competition for food resources may also have contributed to the bathymetric segregation between both species (Rex 1973).

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