

A comparative study of the feeding ecology of *Nephrops norvegicus* (L.), (Decapoda: Nephropidae) in the bathyal Mediterranean and the adjacent Atlantic*

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SUMMARY: A comparative study of the feeding ecology of *Nephrops norvegicus* was carried out on a seasonal basis simultaneously in seven locations in the Eastern and Western Mediterranean and the adjacent Atlantic: the south coast of Portugal, Faro; the Alboran Sea, Malaga; the Catalan Sea, Barcelona; the Ligurian Sea, Genoa; the Tyrrhenian Sea, Pisa; the Adriatic Sea, Ancona and the Aegean Sea, Gulf of Euboikos. The major groups observed (frequency of occurrence method) in the stomachs of *Nephrops norvegicus* were decapod crustaceans, other crustaceans (euphausiids and peracarids) and fish. The results obtained showed no significant differences between sites or seasons, and can be considered very consistent. All major taxa were present in the diet at all sites and for all seasons, a fact that can be explained by the great similarity of the bathyal fauna in all sites, which provide a major trophic resource for *N. norvegicus*. The percentage of fullness was also estimated per site and season, and we registered a clear decrease of this value during the summer period for all sites, except the Tyrrhenian Sea, where the lowest value was found in autumn. PCA - analysis did not clearly separate the regions (sites). The Shannon-Weaver (H'), index of diversity, was also determined per site and season, and we found a significant difference between the values of the Atlantic coast and the Western Mediterranean when compared with those of the Eastern Mediterranean.

Key words: Feeding, diet, *Nephrops norvegicus*.

RESUMEN: ESTUDIO COMPARATIVO DE LA ECOLOGÍA TRÓFICA DE *NEPHROPS NORVEGICUS* (DECAPODA: NEPHROPIDAE) EN EL MEDITERRÁNEO BATIAL Y EN ATLÁNTICO ADYACENTE. – Se llevó a cabo un estudio estacional comparativo de distintos aspectos de la ecología trófica de *Nephrops norvegicus*, simultáneamente en siete localidades del Mediterráneo Occidental y Oriental, así como en aguas atlánticas adyacentes: costa sur de Portugal, Faro; Mar de Alborán, Málaga; Mar Catalán, Barcelona; Mar Ligur, Genova; Mar Tirreno, Pisa; Mar Adriático, Ancona; Mar Egeo y el Golfo de Euboikos. Los grupos presa presentes con mayor frecuencia en la dieta de *Nephrops norvegicus* fueron crustáceos decápodos, otros crustáceos (eufausiáceos y peracarídos), así como peces. En los resultados obtenidos no se aprecian diferencias significativas entre localidades y estaciones anuales, lo cual puede explicarse por la elevada afinidad existente entre la fauna batial, que sirve de recurso trófico a *N. norvegicus* dentro de todas las localidades estudiadas. El porcentaje de repleción estomacal calculado para cada localidad y estación registra un claro descenso en verano para todas las localidades, excluyendo el Mar Tirreno. Para la diversidad de Shannon-Weaver (H') se obtuvieron diferencias significativas entre los valores de la costa atlántica y Mediterráneo Occidental cuando fueron comparados con los de la cubeta oriental mediterránea.

Palabras clave: Alimentación, dieta, *Nephrops norvegicus*.

*Received 9 January 1997. Accepted 20 September 1997.

INTRODUCTION

Nephrops norvegicus (L. 1758) (Decapoda: Nephropidae) is a species with a wide geographical distribution, from North-west Atlantic coasts to the East Mediterranean Sea (Zariquiey-Álvarez, 1968). Its bathymetric distribution in the Mediterranean extends from the continental shelf to bathyal grounds, reaching depths of 871 m in the western Mediterranean (Abelló *et al.*, 1988), although maximal densities are found between 245 and 485 m (Cartes *et al.*, 1994). In the Atlantic its bathymetric distribution extends from a mere 10 m to 720 m, but in the south coast of Portugal, maximal densities are found between 300 and 600 m (Figueiredo, 1988). The closely related genus *Metanephrops* (Holthuis, 1974) has a predominantly Indo-Pacific distribution, with a similar bathymetric range on the continental slope to that of *N. norvegicus* (Berry, 1969; Holthuis, 1974; Wassenberg and Hill, 1989). *N. norvegicus* is always one of the dominant species in the bathyal crustacean decapod assemblages in the western

Mediterranean (Abelló *et al.*, 1988; Cartes *et al.*, 1994), the eastern Mediterranean (Foglia and Gramitto, 1995), and the eastern Atlantic coast (Figueiredo, 1988; 1989).

Due to its great ecological and commercial importance, *Nephrops norvegicus* has been a target species for a number of biological studies (Figueiredo, 1965; Figueiredo and Nunes, 1965; Figueiredo and Thomas, 1967a,b; Sardà, 1983; 1985; 1991; Sardà, 1995), which have focused mainly on growth, reproduction and moulting, which are aspects of major importance for stock assessment and management. In contrast, there have been few studies on its diet and food consumption (Thomas and Davidson, 1962; Lagardère, 1977; Gual-Frau and Gallardo-Cabello, 1988; Sardà and Valladares, 1990; Mytilineou *et al.*, 1992), and feeding behaviour (Thomas and Davidson, 1962; Loo *et al.*, 1993). These results indicate that *N. norvegicus* is a euryphagous and non-selective species, consuming a great variety of crustaceans, fish, and molluscs, either as an active predator or scavenger. In contrast, the closely relat-

TABLE 1. – Summarised data of stomach observations per site/season. Sp: spring; Su: summer; Au: autumn; Wi: winter; P, Portugal; M, Malaga; B, Barcelona; L, Ligurian; T, Tyrrhen; A, Adriatic; G, Greece

Location	Code	Depth (m)	Total number of stomachs analized	Total number of food-items	Total number of prey-categories
Atlantic (36° 46' N-07° 50' W)	P Sp	450	23	86	27
	P Su	450	31	76	35
	P Au	450	26	136	23
	P Wi	450	41	88	21
Alboran (36° 23' N-04° 15' W)	M Su	400	12	22	16
	M Au	400	14	35	19
	M Wi	400	20	45	33
Catalan (41° 11' N-02° 15' E)	B Sp	450	14	62	28
	B Su	450	17	21	15
	B Wi	450	16	32	15
Ligurian (44° 12' N-09° 05' E)	L Sp	400	18	38	19
	L Su	400	18	36	19
Tyrrhenian (42° 14' N-10° 37' E)	T Sp	400	16	34	15
	T Su	400	18	37	16
	T Au	400	16	47	18
	T Wi	400	16	32	14
Adriatic (43° 35' N-14° 11' E)	A Sp	80-110	15	20	12
	A Su	80-110	16	34	21
	A Au	80-110	16	38	18
	A Wi	80-110	15	26	19
Euboikos Gulf. (38° 48' N-22° 59' E)	G Sp	150-200	17	56	21
	G Su	150-200	17	27	17
	G Au	150-200	20	43	23
Mean n° of prey/stomach					
West Mediterranean		2.6			
East Mediterranean		2.1			
Mean n° of different prey categories					
West Mediterranean		51.7			
East Mediterranean		34.9			

ed *Metanephrops* sp. seems to be more selective in its diet (Berry, 1969; Wassenberg and Hill, 1989). The diet of *N. norvegicus* is influenced by its body size (Mytilineou *et al.*, 1992), which is a general characteristic of several other decapod crustaceans (Cartes and Sardà, 1989; Freire and González-Gurriarán, 1995; Freire, 1996).

The above studies, refer to populations of Norway lobster from the Bay of Biscay (East Atlantic), Catalan Sea (Northwest Mediterranean) and the Aegean Sea (Northeast Mediterranean). To date, studies of the diet of *Nephrops norvegicus* have been carried out only in specific geographic areas. The main objective of the present study, beyond the description of the diet of *N. norvegicus*, is to compare the diet in different seasons in seven locations in the Mediterranean and the adjacent Atlantic.

MATERIAL AND METHODS

During 1994-1995, seasonal samples (Spring, Summer, Autumn and Winter) were collected simultaneously, in 7 different sampling sites: the south coast of Atlantic Portugal, Algarve, Faro (P), the Alboran Sea, Malaga (M), the Catalan Sea, Barcelona (B), the Ligurian Sea, Genova (L), Tyrrhenian Sea, Pisa (T), and Adriatic Sea, Ancona (A) in the Italian Peninsula, and the Aegean Sea, Euboikos Gulf, Greece (G) (Table 1). Fixation and preservation of samples with a standard methodology for all areas was carried out. Due to technical problems it was not possible to obtain samples for all seasons in all the areas.

Approximately seventy individuals of *Nephrops norvegicus* were collected in each sample for the present study. From these a subsample of 1/3 was taken for stomach content analysis (Table 1). A total of 1294 individuals were dissected for the estimation of stomach fullness, while a total of 432 stomach contents were studied for the analysis of diet composition. To avoid potential bias of the effect of body size upon diet (Mytilineou *et al.*, 1992) we selected as target individuals those with carapace lengths between 30 and 40 mm, for each site and for each season. For each individual, sex and carapace length were registered with a minimum precision of 1 mm (measurements rounded to the millimeter below). The Norway lobsters were fixed in 10% formalin or preserved in 70% alcohol after collection.

Fullness was determined visually using a scale of 11 points between empty stomach (0=0%; 1=1%-10%) and full stomach (10=91%-100%). For the diet analyses we observed approximately 20 stomachs independently of sex, since there are no major differences in feeding between males and females (Mytilineou *et al.*, 1992; own unp. data). To correct for the possible underestimation of soft prey items (Sardà and Valladares, 1990) we chose for the analysis of feeding only stomachs have contents of equal to or greater than 20% of gut volume. Stomach contents were identified to the lowest possible taxonomical level. For the comparative study of the diet between site and season, we considered the frequency of occurrence (%F), and number of food-items (N), according to traditional methods in dietary studies (Hyslop, 1980).

For the statistical treatment of data we used a multivariate analysis, since it helps to: i) enhance the data structure; and ii) synthesize the data, thereby permitting a better understanding and a better representation of results (Gauch, 1982). We used a PCA - Principal Component Analysis (Pielou, 1984). The program used was NTSYS 1.8 (Rohlf, 1993).

The PCA was carried out on the matrix of %F (frequency of occurrence per site and season). The Shannon-Weaver (Poole, 1974) diversity index (H') was calculated from numbers (N). For both calculations we used 17 prey-groups, per site and season, excluding non-identified material, and foraminifera, since their presence in the stomach contents was considered to be the result of accidental or passive ingestion with sand when preying or scavenging on larger prey.

RESULTS

The mean fullness was calculated separately for females and males (Table 2). Percentage of empty stomachs (0% to 10%) was also determined per site/season for females and males (Table 3).

A total of 1071 food-items belonging to 119 prey-categories (Table 4) were identified. Stomach contents were composed mainly of small pieces of crustacean carapace, bivalve and gastropod shells, fish vertebrae and otoliths, and other hard and soft parts of prey. From the analysis of the diet we identified 19 prey-groups, including non-identified material. We have considered as non-identified material several amorphous soft portions that we could not assign with certainty to any taxon (in

TABLE 2. – Percentage of fullness per site/season in females (F) and males (M). (-)Seasons where samples were not collected.

Sites	Sex	Spring	Summer	Autumn	Winter
Atlantic	F	43.4	40.0	66.5	46.0
	M	52.1	40.0	53.4	42.5
Alboran	F	-	25.6	47.9	67.3
	M	-	40.6	48.7	50.0
Catalan	F	80.9	19.7	-	62.7
	M	-	20.7	-	69.7
Ligurian	F	60.3	22.4	-	-
	M	55.8	19.1	-	-
Tyrrhenian	F	31.6	26.3	26.7	51.5
	M	40.9	42.3	26.1	46.3
Adriatic	F	59.8	38.8	74.5	44.4
	M	61.7	44.5	79.7	49.2
Euboikos Gulf	F	41.8	20.4	35.7	-
	M	46.0	30.0	40.0	-

TABLE 3. – Percentage of empty stomachs. (-) Seasons where samples were not collected. F: females; M: males.

Sites	Sex	Spring	Summer	Autumn	Winter
Atlantic	F	19.5	12.0	0.0	19.0
	M	16.7	16.7	15.8	22.7
Alboran	F	-	40.7	10.3	0.0
	M	-	31.4	30.8	0.0
Catalan	F	0.0	62.5	-	9.1
	M	-	48.6	-	2.9
Ligurian	F	13.9	50.0	-	-
	M	8.3	4.3	-	-
Tyrrhenian	F	42.1	38.1	33.3	20.6
	M	25.0	43.3	35.5	17.1
Adriatic	F	0.0	26.7	0.0	12.8
	M	0.0	12.5	0.0	22.2
Euboikos Gulf	F	15.2	59.3	32.1	-
	M	14.3	38.9	18.8	-

some cases it could have belonged to gelatinous plankton or molluscs, and was always in an advanced state of digestion). Percentage frequency of occurrence results were based on these 19 major groups (Table 5), including non-identified material.

In terms of percentage of occurrence (%F) decapod crustaceans were always the main prey-group followed by other crustaceans (euphausids and per-acarids) and fish (Fig. 1). Although the composition of the diet was similar in all sites studied, some minor local and seasonal variations were observed in secondary prey groups. Tunicates were very frequent in stomach contents from the Tyrrhenian Sea

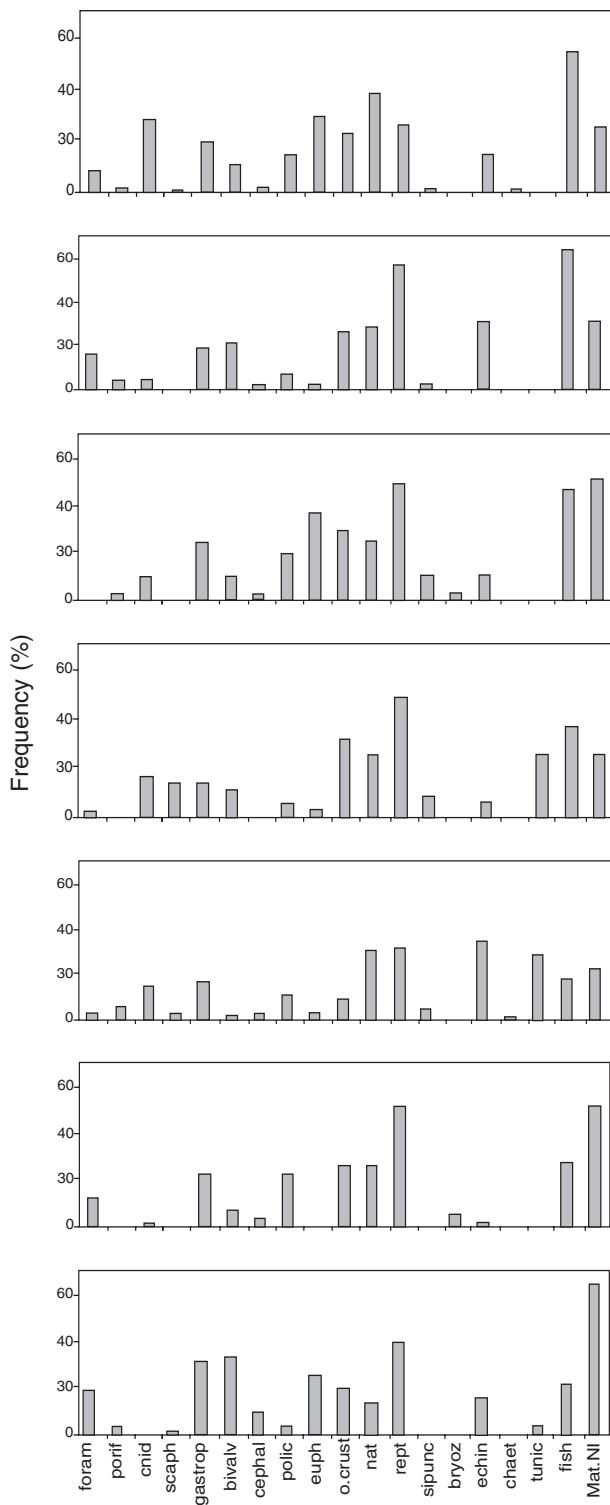


FIG. 1. – Frequency of occurrence of different prey groups in the diet of *Nephrops norvegicus* for all sites and for the entire study. Abbreviations: Foraminifera - FORAM; Porifera - PORIF; Cnidaria - CNID; Scaphopoda - SCAPH; Gastropoda - GAS-TROP; Bivalvia - BIVALV; Cephalopoda - CEPHAL; Polychaeta - POLIC; Euphausiacea - EUFH; Other Crustaceans - O-CRUST; Natantia - NAT; Reptantia - REPT; Sipunculida - SIPUNC; Bryozoa - BRYOZ; Echinodermata - ECHIN; Chaetognatha - CHAET; Tunicata - TUNIC; FISH; Non Identified Material - Mat. NI.

TABLE 4. – Prey categories found in the stomach contents

FORAMINIFERA	
<i>Bolivina</i> sp.	Isopoda
<i>Globigerina</i> sp.	Desmosomatidae
<i>Uvigerina</i> sp.	<i>Eugerda</i> sp.
<i>Quinqueloculina seminulum</i>	<i>Cirolana borealis</i>
PORIFERA	Cymothoidae
CNIDARIA	Amphipoda
Hydroidea	Gammaridea
Siphonophora	
<i>Chelophyses appendiculata</i>	<i>Leucothoe</i> sp.
<i>Stephanoscyphus</i> spp.	<i>Ampelisca</i> sp.
<i>Westwoodilla retrostris</i>	
SCAPHPOPODA	Lysianassidae
<i>Dentalium</i> sp.	<i>Orchomenella nana</i>
GASTROPODA	<i>Scopelocheirus hopei</i>
Rissoidae	Phoxocephalidae
<i>Alvania</i> sp.	<i>Harpinia</i> sp.
Turritellidae	Hyperiidea
<i>Caecum</i> sp.	<i>Vibilia armata</i>
Naticidae	<i>Phrosina</i> sp.
<i>Eulimella</i> sp.	<i>Caprella</i> sp.
<i>Chrysallida</i> sp.	<i>Phtisica marina</i>
Thecosomata	Euphausiacea
<i>Cavolinia inflexa</i>	<i>Euphausia krohnii</i>
<i>Cymbulia peroni</i>	<i>Meganyctiphanes norvegica</i>
BIVALVIA	Decapoda
Amodontida	Natantia
<i>Abra nitida</i>	<i>Aristeus antennatus</i>
<i>Abra longicallus</i>	Penaeidae
<i>Kellyella miliaris</i>	<i>Solenocera membranacea</i>
<i>Parvicardium</i> cf. <i>scabrum</i>	<i>Sergestes arcticus</i>
<i>Pavicardium</i> sp.	<i>Pasiphaea sivado</i>
Taxodontida	<i>Plesionika martia</i>
Nuculacea	<i>Processa</i> sp.
Nuculidae	Reptantia
Nucularidae	<i>Nephrops norvegicus</i>
<i>Yoldiella striolata</i>	<i>Calocaris macandrace</i>
CEPHALOPODA	<i>Callianassa</i> sp.
Teuthida	Atelecyclidae
Sepiida	<i>Ebalia</i> sp.
POLYCHAETA	<i>Monodeus couchi</i>
Aphroditidae	<i>Goneplax rhomboides</i>
<i>Phanthalis</i> sp.	
Eunicidae	BRYOZOA
<i>Lumbrineris</i> sp.	
<i>Glycera</i> sp.	SIPUNCULIDA
<i>Nephtys</i> sp.	<i>Aspidosiphon mulleri</i>
Pantopoda	ECHINODERMATA
CRUSTACEA	Echinoidea
Ostracoda	<i>Echinocardium</i> sp.
<i>Cypridina</i> sp.	Asteroidea
Copepoda	<i>Ophiuroidea</i>
Mysidacea	<i>Holothuroidea</i>
<i>Pseudomma</i> sp.	<i>Leptosynapta</i> sp.
Cumacea	<i>Stichopus regalis</i>
<i>Diastylis</i> sp.	<i>Molpadius musculus</i>
<i>Iphinoe tenella</i>	Crinoidea
Tanaidacea	<i>Antedon</i> cf. <i>bifida</i>
Apseudidae	
	CHAETOGNATA
	TUNICATA
	<i>Pyrosoma atlanticum</i>
	Chondrychthyes
	Osteychthyes
	Myctophidae
	Macrouridae

TABLE 5. – Frequency of occurrence (%) by site/season. Abbreviations as in Fig. 1.

		foram.	porif.	cnid.	scaph.	gastrop.	bivalv.	cephal.	polic.	eup.	o. crust.	nat.	reptan.	sipunc.	bryoz.	echin.	chaet.	tunic.	fish.	Mat. NI.	
Atlantic	Spring	8.0	0.0	64.0	0.0	0.0	20.0	0.0	12.0	36.0	20.0	48.0	24.0	0.0	0.0	12.0	0.0	0.0	56.0	16.0	
	Summer	16.7	0.0	23.3	3.3	13.3	6.7	3.3	13.3	30.0	20.0	43.3	33.3	0.0	0.0	20.0	3.3	0.0	46.7	33.3	
	Autumn	8.0	8.0	24.0	0.0	56.0	16.0	0.0	20.0	40.0	20.0	36.0	28.0	0.0	0.0	20.0	0.0	0.0	44.0	24.0	
	Winter	2.5	0.0	12.5	0.0	12.5	5.0	2.5	12.5	17.5	27.5	20.0	2.5	0.0	7.5	0.0	0.0	65.0	22.5		
	Annual	8.3	1.7	28.3	0.8	19.2	10.8	1.7	14.2	29.2	22.5	37.5	25.8	0.8	0.0	14.2	0.8	0.0	54.2	24.2	
Alboran	Spring																				
	Summer	18.2	0.0	0.0	0.0	9.1	27.3	9.1	9.1	0.0	18.2	18.2	36.4	0.0	0.0	27.3	0.0	0.0	63.6	45.5	
	Autumn	8.3	0.0	0.0	0.0	16.7	41.7	0.0	0.0	0.0	33.3	25.0	66.7	0.0	0.0	58.3	0.0	0.0	58.3	25.0	
	Winter	20.0	10.0	4.7	0.0	25.0	5.0	0.0	10.0	5.0	25.0	35.0	60.0	5.0	0.0	15.0	0.0	0.0	65.0	25.0	
	Annual	16.3																			
Catalan	Spring	0.0	0.0	20.0	0.0	60.0	30.0	0.0	40.0	60.0	80.0	30.0	50.0	20.0	0.0	40.0	0.0	0.0	60.0	90.0	
	Summer	0.0	6.7	6.7	0.0	6.7	6.7	0.0	20.0	13.3	13.3	46.7	0.0	6.7	0.0	0.0	0.0	0.0	53.3	26.7	
	Autumn	0.0	0.0	6.3	0.0	18.8	0.0	6.3	6.3	43.8	12.5	31.3	50.0	12.5	0.0	0.0	0.0	0.0	31.3	50.0	
	Winter	0.0	0.0	2.4	9.8	0.0	24.4	9.8	2.4	19.5	36.6	29.3	24.4	48.8	9.8	2.4	9.8	0.0	0.0	46.3	51.2
	Annual	0.0																			
Ligurian	Spring	0.0	0.0	0.0	0.0	22.2	5.6	0.0	5.6	5.6	27.8	22.2	50.0	5.6	0.0	5.6	0.0	50.0	16.7	27.8	
	Summer	5.6	0.0	33.3	27.8	5.6	16.7	0.0	5.6	0.0	33.3	27.8	44.4	11.1	0.0	5.6	0.0	0.0	55.6	22.2	
	Autumn																				
	Winter																				
	Annual	2.8	0.0	16.7	13.9	13.9	11.1	0.0	5.6	2.8	30.6	25.0	47.2	8.3	0.0	5.6	0.0	25.0	36.1	25.0	
Tyrheanian	Spring	0.0	18.8	6.3	0.0	0.0	0.0	0.0	12.5	6.3	0.0	25.0	31.3	12.5	0.0	31.3	0.0	37.5	6.3	12.5	
	Summer	0.0	0.0	16.7	0.0	5.6	0.0	0.0	11.1	5.6	5.6	50.0	33.3	5.6	0.0	22.2	5.6	38.9	11.1	16.7	
	Autumn	6.3	6.3	18.8	12.5	50.0	0.0	0.0	18.8	0.0	12.5	31.3	31.3	0.0	0.0	56.3	0.0	6.3	25.0	50.0	
	Winter	6.3	0.0	18.8	0.0	12.5	6.3	12.5	0.0	0.0	18.8	12.5	31.3	0.0	0.0	31.3	0.0	31.3	31.3	12.5	
	Annual	3.0	6.1	15.2	3.0	16.7	1.5	3.0	10.6	3.0	9.1	30.3	31.8	4.5	0.0	34.8	1.5	28.8	18.2	22.7	
Adriatic	Spring	7.7	0.0	0.0	0.0	30.8	0.0	0.0	7.7	0.0	15.4	46.2	0.0	7.7	0.0	0.0	0.0	15.4	61.5		
	Summer	28.6	0.0	0.0	28.6	7.1	0.0	42.9	0.0	42.9	28.6	50.0	0.0	7.1	0.0	0.0	0.0	28.6	71.4		
	Autumn	12.5	0.0	6.3	0.0	25.0	6.3	0.0	25.0	0.0	12.5	37.5	56.3	0.0	6.3	0.0	0.0	12.5	31.3		
	Winter	0.0	0.0	0.0	0.0	6.7	13.3	6.7	6.7	0.0	33.3	20.0	53.3	0.0	6.7	0.0	0.0	0.0	53.3	46.7	
	Annual	12.1	0.0	1.7	0.0	22.4	6.9	3.4	22.4	0.0	25.9	51.7	0.0	5.2	1.7	0.0	0.0	27.6	51.7		
Euboikos Gulf	Spring	37.5	0.0	0.0	6.3	62.5	43.8	12.5	0.0	25.0	6.3	43.8	0.0	0.0	31.3	0.0	6.3	25.0	50.0		
	Summer	23.5	5.9	0.0	0.0	41.2	5.9	5.9	11.8	23.5	58.8	0.0	0.0	0.0	0.0	0.0	0.0	11.8	47.1		
	Autumn	0.0	5.0	0.0	0.0	30.0	15.0	10.0	5.0	40.0	35.0	10.0	15.0	0.0	0.0	15.0	0.0	5.0	25.0	85.0	
	Winter																				
	Annual	18.9	3.8	0.0	1.9	30.2	32.1	9.4	3.8	24.5	18.9	13.2	37.7	0.0	0.0	15.1	0.0	3.8	20.8	62.3	

almost year-round. Cnidarians (mainly siphonophora) were also frequently found in stomach contents throughout the year, while Gastropods were more frequent in the Adriatic and in Euboikos Gulf than in other areas.

The Principal Component Analysis (PCA) results were based on the values of frequency of occurrence per site and season (Figs. 2, 3). No clear OTUs (Operational Taxonomic Units: site per season) distribution structure can be seen on axes 1, 2, which explain only 36.2 % of the total variability (Table 6). The contribution of the variables to these principal axes (Fig. 2) suggests the presence of a “horse-shoe” effect (Gauch, 1982) which can be the

consequence of the gradient of their occurrence, between the low average values on a reduced number of OTU's and high average values for a significant number of OTU's. This would explain both the slow decrease in the extracted eigenvalues and the above mentioned lack of a spatial structure among the OTU's.

Through the examination of Fig. 2, we notice one situation, Catalan in Spring (BSp), that is a clear outlier. The food contents in this sample were clearly dominated by gastropods, euphausiids, non decapod crustaceans and fish, which pull BSp to the inferior left quadrant of the graph (Fig. 3).

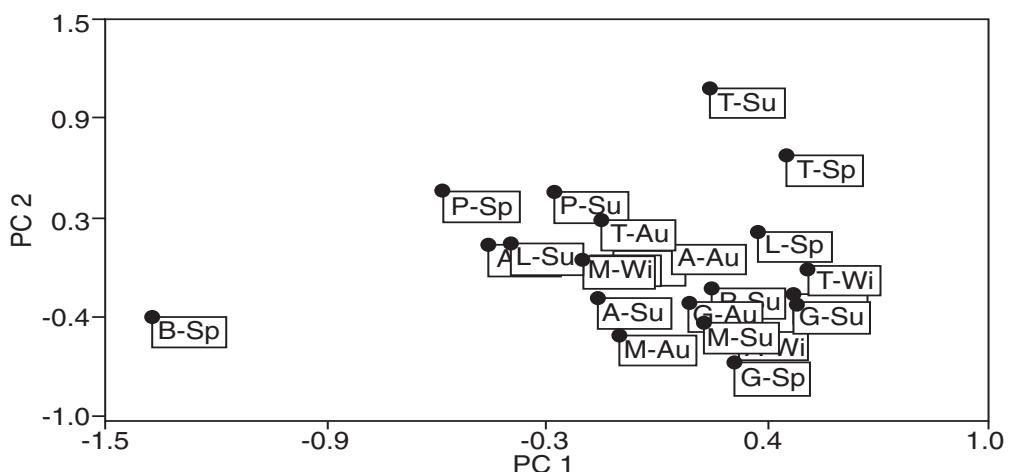


FIG. 2 – PCA on the matrix of the frequency of occurrence of different prey groups per site and season; projection of OTU's over axis 1 and 2. Labels: first letter stands for location; P- Atlantic, M- Alborán, B- Catalan, L- Ligurian, T- Tyrrhenian, A- Adriatic, G- Euboikos Gulf; the two following letters stand for season: Sp- Spring, Su- Summer, Au- Autumn, Wi- Winter.

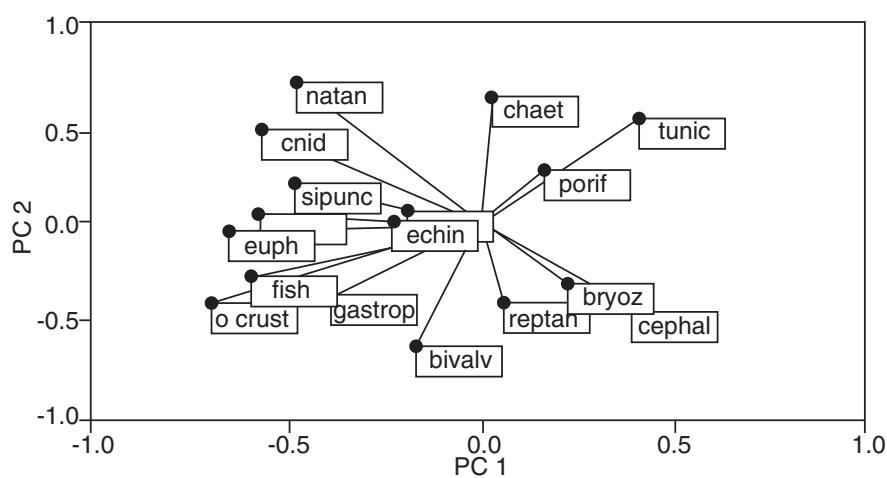


FIG. 3. – PCA on the matrix of different prey groups per site and season; projection of variables over axis 1 and 2. Labels: Porifera - PORIF; Cnidaria - CNID; Scaphopoda - SCAPH; Gastropoda - GASTROP; Bivalvia - BIVALV; Cephalopoda - CEPHAL; Polychaeta - POLIC; Euphausiacea - EUFH; Non Decapod Crustaceans - O.-CRUST; Natantia - NATAN; Reptantia - REPTAN; Sipunculida - SIPUNC; Bryozoa - BRYOZ; Echinodermata - ECHIN; Chaetognatha - CHAET; Tunicata - TUNIC; FISH .

TABLE 6. – Principal Component Analysis; Vector matrix.

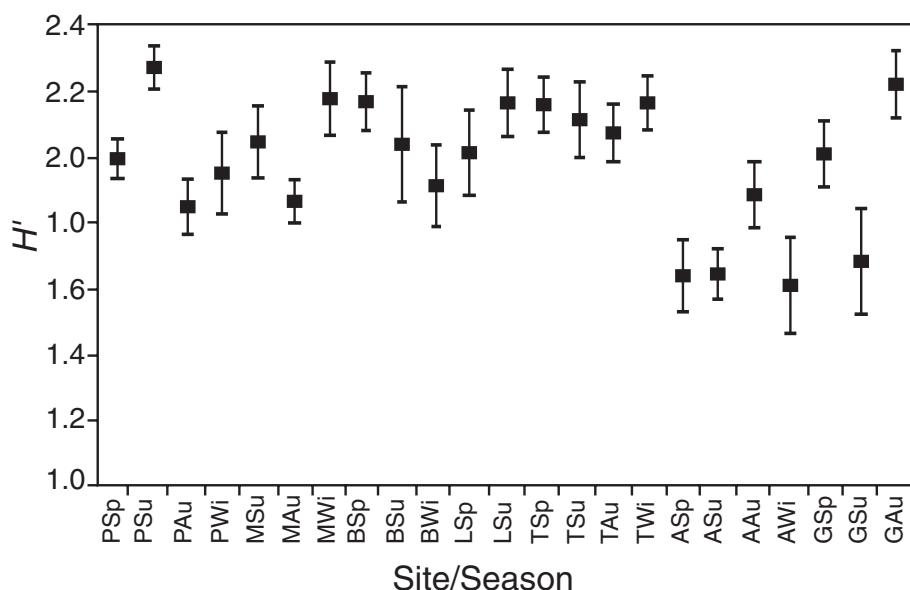
Variable	principal components		
	1st	2nd	3rd
Porifera - PORIF	0.169	0.265	0.031
Cnidaria - CNID	-0.562	0.477	0.195
Scaphopoda - SCAPH	-0.175	0.056	0.177
Gastropoda - GASTROP	-0.390	-0.351	0.178
Bivalvia - BIVALV	-0.169	-0.612	0.423
Cephalopoda - CEPHAL	0.388	-0.447	0.575
Polychaeta - POLIC	-0.572	0.045	-0.554
Euphausiacea - EUPH	-0.645	-0.038	0.301
Other crustaceans O-CRUST	-0.702	-0.404	-0.171
Natantia - NATANC	-0.475	0.712	-0.164
Reptantia - REPTAN	0.057	-0.398	-0.428
Sipunculida - SIPUNC	-0.482	0.203	0.024
Bryozoa - BRYOZ	0.232	-0.309	-0.768
Echinodermata - ECHIN	-0.225	0.009	0.581
Chaetognatha - CHAET	0.030	0.644	0.045
Tunicata - TUNIC	0.414	0.534	0.204
FISH	-0.559	-0.316	0.017
Eigenvalues	3.160	2.988	2.001
Percentage	18.590	17.580	11.770
Cumulative percentage	18.590	36.170	47.980

Based on the values of diet diversity (H'), Western Mediterranean and Atlantic sites are different from those of the Eastern Mediterranean basin (Fig. 4). The sites of Atlantic, Alborán Sea, Catalan Sea, Ligurian Sea, and Tyrrhenian Sea show very homogeneous and significantly higher ($p<0.05$; non-parametric Kruskall-Wallis test)

(Siegel and Castellan, 1988) values than those from the eastern Mediterranean (Adriatic and Euboikos Gulf). Seasonal variations can be observed among sites. In general, for the western sites, Autumn and Winter were characterised by a lower diversity, while eastern stations did not follow this pattern.

DISCUSSION

From our general results of the diet composition study, we can deduce that *Nephrops norvegicus* is a generalist species in terms of the food resources it exploits; results which are consistent with previously published work (Lagardère, 1977; Gual-Frau and Gallardo-Cabello, 1988; Mytilineou *et al.*, 1992). According to aquarium observations, their feeding behaviour is based upon active prey capture (Thomas and Davidson, 1962) as well as scavenging activity. In our observations, we found fish remains (chondrichthyes), and other large prey (crabs), as well as small prey such as amphipods or isopods, among which were several necrophagous lysianassids and cirolanids; a finding also reported by Lagardère (1977). Sand, mud or foraminiferans can be ingested in a passive way from sediment, a fact also reported by the same authors. Foraminiferans were among the smallest whole ingested particles, with a minimum size of 1 mm. In the present study we could not find any smaller particles which could be attributable to ingestion by suspension feeding (Loo *et al.*, 1993).

FIG. 4. – Diversity Index (H') per site - Atlantic (P), Alboran (M), Catalan (B), Ligurian (L), Tyrrhenian (T), Adriatic (A), Euboikos Gulf (G) - and season - Spring (Sp), Summer (Su), Autumn (Au), Winter (Wi); (e.g. PSp = Atlantic in Spring).

Metanephrops sp., which seems to occupy a similar habitat and is quite similar both in size and morphology to Norway lobster, seems to be characterized by a more selective feeding behaviour, capturing larger prey (or parts of it) such as fishes, decapods and squids (Wassenberg and Hill, 1989).

The percentage of empty stomachs in *Metanephrops* spp. is much higher than that observed in the present study, in spite of the fact that in the Summer period our values of percentage of empty stomachs reached 62.5% for females and 48.6% for males. In general the fullness percentage, which can be considered as an indicator of the feeding activity, showed a tendency to be lower in the summer period for all sites, for both sexes. This period corresponds to the peak of gonad maturity, Stage IV (Orsi Relini, 1998), where the enlargement of the gonad compresses the stomach in the females, thus preventing maximum stomach fullness. In fact the highest percentage of empty stomachs occurred in this period.

According to Mytilineou *et al.* (1992), in the North Aegean Sea percentage of empty stomachs was greater than 50% in September and December for females, a fact that was related to the period of egg bearing. This fact could not be confirmed in the present work, but we found that 59.3% of the female stomachs in the summer period, were empty, corresponding to the peak of mature females.

Our low values of percentage of fullness for males in the same period is still to be explained, since there is no biological factor, such as reproduction or molting (Gramitto, 1988) that showed any synchronicity with the summer period. The low selectivity showed by *Nephrops norvegicus* in its feeding activities, is particularly emphasized by the occurrence in the stomachs of plastic material (nylon threads, probably from fishing gears), plant remains, wood, and charcoal, etc. These may be ingested by accident while feeding on prey, in or on, the plastic material/plants/wood.

The basis of the diet of *Nephrops norvegicus* consists of decapod crustaceans, euphausiids, peracarids, and fishes, and does not differ geographically or seasonally. The preferred prey groups are those which are dominant, either in the megabenthic communities (Pérès, 1985; Figueiredo, 1989; Froglia and Gramitto, 1995) or in suprabenthic-zooplankton communities (Franqueville, 1971). There are some differences in secondary groups, especially in pelagic taxa such as Siphonophora,

Gastropoda, Thecosomata, and Tunicata Pyrosomidae. These kinds of food-resources are particularly dependent on seasonal plankton blooms that occur in the area. These findings support the results of the PCA analysis, since the benthic-bathyal fauna is quite constant through in the geographic area studied.

The higher values of diversity (H') observed in the Western Mediterranean sites can be related to: 1) deeper collecting grounds and 2) different biogeographic distributions. The higher number of prey per stomach in the Western-Mediterranean could be related to a higher density of the food resources in the particular environment. There is no data available on macrofaunal densities, that would allow comparison between the two basins, but some comparative data on meiofauna indicates clearly higher biomass values in the Western Mediterranean (Thiel, 1983).

ACKNOWLEDGEMENTS

Thanks are due to Prof. F. Andrade and Prof. M. Castro for their help in the statistical treatment of data and to Prof. K. Erzini for the English revision of the manuscript. This study was financed by the EC, DG. XIV (MED92/008).

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