Temporal changes in the diet of deep-water Penaeoidean shrimp (*Parapenaeus longirostris* and *Aristeus antennatus*) off Algeria (southwestern Mediterranean)

AHMED NOUAR [1], HANANE KENNOUCHE [1], NAWEL AINOUCHE [1]
and JOAN E. CARTES [2]

[1] Laboratoire Halieutique, FSB-USTHB, N°32 El-Alia Bab Ezzouar 16111, Alger, Algeria. E-mail: nouarahmed@live.fr
[2] Institut de Ciències del Mar, CSIC, Psg. Marítim de la Barceloneta, 37-49, 08003, Barcelona, Spain.

SUMMARY: With the aim of analyzing the trophic dynamics of deep-sea shrimp over the central Algerian slope, stomach contents of 219 individuals of *Parapenaeus longirostris* and 263 *Aristeus antennatus* were collected at night at depths between 200 and 400 m on a seasonal scale in 2007. Fullness (*f*), which is a measure of feeding intensity, showed significant seasonal changes in *Aristeus antennatus*, and the highest *f* was found in pre-reproductive periods (3.3% in January; 3.0% in April) before the beginning of gonad maturation (April-September in the area). This trend was coupled with the period of high surface productivity off the central Algerian coast (November-April). In that pre-reproductive period *A. antennatus* consumed more crustaceans (e.g. large decapods such as *Processa* sp.) with a high energetic value. These kinds of seasonal oscillations in *f* were not found in *P. longirostris*, probably because it was distributed shallower than *A. antennatus* and does not have a single marked peak in its reproductive cycle. The dietary composition of *P. longirostris* and *A. antennatus* was clearly segregated in the MDS analysis, which suggests there is good resource partitioning between the two species. Foraminiferans, bivalves and polychaetes were the most frequent prey in the diet of both *P. longirostris* and *A. antennatus*. Small micro and mesoplankton prey (radiolarians, tintinnids, copepods and pteropods) were more important in the diet of *P. longirostris*, while *A. antennatus* fed more on benthos. Planktonic prey found in the diet of the two shrimp were more frequent in January-February and April-May, e.g. in periods of higher water homogeneity coupled with periods of higher surface production. The large contribution of zooplankton to the diet of the deep-water shrimp over Algerian slopes is probably due to the importance of eddies in the area, which may enhance water column production locally. The high surface temperature (lowest T in January of 15.2°C) may accelerate the degradation of the organic matter that reaches Algerian slope bottoms, thus reducing the biomass of macrobenthos. We hypothesized that this low availability of benthic food resources may favour night time migratory movements by benthopelagic shrimp off the Algerian coast in search of more productive, shallow bottoms.

Keywords: *Parapenaeus longirostris*, *Aristeus antennatus*, trophic relationships, southwestern Mediterranean, Algerian waters.

RESUMEN: VARIABILIDAD TEMPORAL DE LA DIETA DE LOS PENEOIDEOS *PARAPENAEUS LONGIROSTRIS* Y *ARISTEUS ANTENNATUS* EN ARGELIA (MEDITERRÁNEO SUROCCIDENTAL). – Con el objetivo de analizar la dinámica trófica de dos especies de gambas de profundidad en el talud continental de la zona central de Argelia se recolectaron 219 individuos de *Parapenaeus longirostris* y 263 de *Aristeus antennatus* durante pescas nocturnas entre 200 y 400 m de profundidad, a escala estacional durante 2007. La saciedad estomacal (*f*), como indicador de intensidad de alimentación, mostró variaciones estacionales significativas en *Aristeus antennatus*, con *f* más elevada en el período pre-reproductivo (3.3% en enero; 3.0% en abril), antes del inicio de la madurez gonadal (abril-septiembre en el área). Esta tendencia estuvo relacionada con el periodo de elevada productividad superficial en aguas de la costa central de Argelia (noviembre-abril). En el período pre-reproductivo, *A. antennatus* consumió más crustáceos (p. ej. grandes decápodos como *Processa* sp.) con elevado contenido energético. Por el contrario, no se detectaron tales variaciones estacionales en *f* en *P. longirostris*, probablemente porque se distribuye a menor profundidad que *A. antennatus* y no tiene un único pico de reproducción. Las composiciones de las dietas de *P. longirostris* y *A. antennatus* estuvieron claramente segregadas (en el análisis MDS), sugiriendo que existe un alto nivel de repartición

de los recursos entre ambas especies. Foraminíferos, bivalvos y poliquetos fueron las presas más frecuentes tanto en la dieta de *P. longirostris* como en la dieta de *A. antennatus*. Las pequeñas presas micro- y mesoplanctónicas (radiolarios, tintínidos, copépodos y pterópodos) fueron más importantes en la dieta de *P. longirostris*, mientras que *A. antennatus* se alimentó preferentemente de fauna bentónica. Se encontraron presas planctónicas en la dieta de ambas especies con mayor frecuencia en enero-febrero y abril-mayo, es decir en periodos de elevada homogeneidad de las masas de agua, correspondiente a periodos de mayor producción superficial. La importante contribución del zooplancton en la dieta de las gambas de profundidad en el talud de Argelia se debe probablemente a la importancia de los remolinos en el área, que influyen localmente en la mayor productividad biológica de la columna de agua. La elevada temperatura superficial (temperatura mínima de enero: 15.2°C) puede acelerar la degradación de la materia orgánica que alcanza los fondos del talud argelino, incidiendo en una reducción de la biomasa del macrobentos. Proponemos la hipótesis de que la baja disponibilidad de recursos tróficos bentónicos puede favorecer los movimientos migratorios nocturnos por parte de las gambas bentopelágicas de las costas argelinas hacia fondos someros más productivos.

Palabras clave: *Parapenaeus longirostris*, *Aristeus antennatus*, relaciones tróficas, Mediterráneo sur-occidental, aguas argelinas.

INTRODUCTION

Trophic relationships and the study of deep-sea trophic webs have been the focus of a number of studies in the deep Mediterranean and neighbouring areas, with special emphasis on the trophic role of decapod crustaceans (Lagardère, 1972; Cartes, 1994, 1995; Labropoulou and Kostikas, 1999; Kapiris *et al.*, 2000; Cartes *et al.*, 2008). Decapods are a dominant taxon among deep-sea megafauna in the deep Mediterranean (Cartes, 1993). The most commercially interesting decapod species are: *Aristeus antennatus* (Risso, 1816), *Aristaeomorpha foliacea* (Risso, 1827), and *Parapenaeus longirostris* (Lucas, 1846). Trophic factors such as prey availability and interspecific competition are especially important in a physically stable environment such as the deep Mediterranean (Cartes and Carrassón, 2004), and influence both the depth distribution and the local abundance of species. Over slope depths we found changes at a medium spatial scale in the structure and dynamics of deep sea trophic webs (e.g. along the Iberian coast: Cartes *et al.*, 2002). However, information is often limited to local areas (e.g. the Balearic Basin: Cartes, 1994; Cartes *et al.*, 2008; the Ligurian Sea: Relini-Orsi and Wutz, 1977; the Ionian Sea: Labropoulou and Kostikas, 1999). In contrast, ecological information from wide areas of the Mediterranean, such as the continental slope of North African countries (e.g. off the Algerian coast; Mouffok *et al.*, 2008) is still very scattered and fragmentary.

Algerian coasts are characterized by particular oceanographic dynamics dominated by the presence of strong mesoscale eddies (Ruiz *et al.*, 2002). The anticyclonic Algerian eddies are generated by the instability of the Algerian Current (Taupier-Letage *et al.*, 2003) that originates from Atlantic waters entering the Straits of Gibraltar. These structures can provoke high biological variability in terms of primary production and upwelling zones; for example, a production maximum (Chl *a*) is detected inshore or offshore on the shelf-slope break depending on the period of the year (Taupier-Letage *et al.*, 2003). The Algerian slope is influenced by the occurrence of Winter and Levantine Intermediate Waters (WIW, LIW) flowing eastwards along the Algerian continental slope (Benzohra and Millot, 1995). The influence of these oceanographic processes on zooplankton assemblages, secondary production and the preferred fish and decapod prey on the slope is unknown. Studies of zooplankton are restricted to descriptions of copepod assemblages (Khelifi-Touhami *et al.*, 2007), some isolated data on euphausiids that suggest high abundance of juveniles of *Nematoscelis megalops* and *Euphausia krohni* over slope depths (Casanova, 1974), and information on changes in plankton distribution along oceanographic fronts (Almeria-Oran front: Andersen *et al.*, 2004).

Off the Algerian coast, *Parapenaeus longirostris* and *Aristeus antennatus* are respectively the two dominant species in the upper (233-410 m) and middle (518-638 m) slope megafaunal assemblages (Mouffok *et al.*, 2008). *Parapenaeus longirostris* is distributed and fished over the upper part of the Algerian slope (200-400 m), reaching its highest densities over muddy-sandy bottoms with *Funiculina quadrangularis* beds (Nouar and Maurin, 2001). *Aristeus antennatus* occupies depths of 260 to 820 m during the day according to Mouffok *et al.* (2008) and of 80 to 650 m at night (Yahiaoui, 1994). This species has a wide bathymetric distribution, with depth segregation related to size and sex. It lives over muddy bottoms and seems associated with the gorgonian *Isidella elongata*. Algerian trawlers work on fishing grounds between 200 and 400 m depth throughout the year and fish these depths during the night. This is the uppermost depth range in the distribution of *A. antenatus* in the Mediterranean. The population of *A. antennatus* off Algeria is not subject to the high fishing pressure (Mouffok *et al.*, 2008) experienced by the species in other Mediterranean regions (e.g. in the Balearic Basin: Maynou, 2008).

There are a number of studies on the trophic habits of *Parapenaeus longirostris* and *Aristeus antennatus*; however, these have been carried out in different areas other than the Algerian coast in the deep Mediterranean (Catalan canyons: Cartes, 1994; 1995; Maynou and Cartes, 1997; around the Balearic Islands: Cartes *et al.,* 2008; in the eastern Basin: Labropoulou and Kostikas, 1999; Kapiris *et al.*, 2000). The aim of this study is to describe the trophic requirements and temporal changes in the diet of both species on the Algerian slope and compare these findings with similar studies from other areas of the deep Mediterranean.
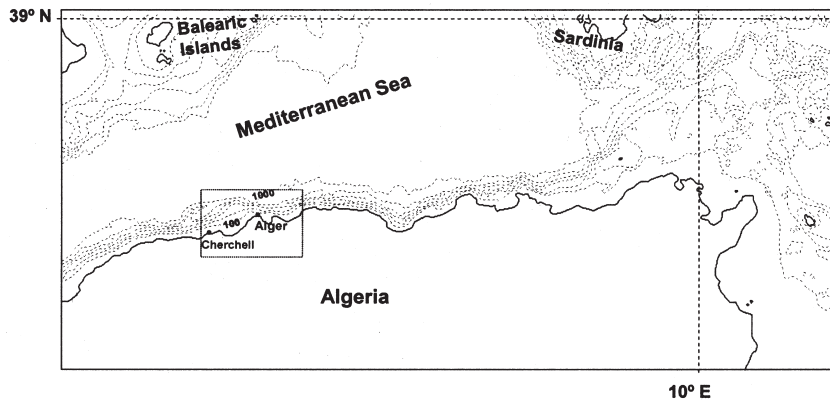
Fig. 1. – Map of the study area off the Algerian coast, indicating the area sampled between Cherchell and Alger.

MATERIALS AND METHODS

Specimens of the two shrimp *Parapenaeus longirostris* and *Aristeus antennatus* were collected in a total of 8 hauls (4 for *P. longirostris* and 4 for *A. antennatus*) performed by trawlers in 2007. These commercial vessels have an average length of 25 m and an average power of 400 HP, and operate off the Algerian coast in the region between Algiers and Cherchell harbours (36°50'N, 3°02'E; 36°37'N, 2°11'E). Hauls were performed at night over muddy bottoms at depths ranging between 200 and 400 m (Nouar, 2001). The shelf-slope break and upper slope in the study area were the steepest (Fig. 1). Muddy sediments dominated at 200 to 400 m with a low terrigenous component due to the low river discharges in the area (Nouar and Maurin, 2001).

Environmental variables were not available for the study area; however, the phytoplankton pigment concentration (*ppc*, mg Chl *a* m^{-3}) and surface temperature (*T*, °C) were obtained from satellite imagery data at http://reason.gsfc.nasa.gov/Giovanni. The phytoplankton pigment concentration was used as an indicator of the surface productivity in the area. Monthly average readings of *ppc* and *T* were obtained in two positions (36.50°N; 2.00°E; 36.40°N; 2.00°E) within the study area off the Algerian coast from November 2006 to December 2007. These locations are ca. 16 and 30 km from Cherchell harbour respectively, roughly coinciding with the depths exploited by trawlers.

Individuals were measured (CL, cephalotorax length, in mm), weighed (g) and the sex was determined. A total of 219 stomach contents of *P. longirostris* and 263 of *A. antennatus* was examined in order to determine their diet composition (Tables 1 and 2). In *A. antennatus* we studied the diet of males, and for females we distinguished between small females (CL<30 mm, including all immature females) and large females (CL≥30 mm). Taking into account the size at sexual maturity of the *P. longirostris* females, diet was studied for small (immature) (CL<22 mm) and large (CL>22 mm) males and females depending on the length-frequency distribution in the samples.

The total stomach weight (g) (including stomach wall) was also obtained, and weighed to the nearest 0.01 g. The stomachs were conserved in 10% formalin after dissection. Prey were identified to the lowest possible taxonomic level under a stereomicroscope at ×10-×40, as it was often difficult to identify prey due to its small size and advanced state of crushing.

The feeding intensity of *Parapenaeus longirostris* and *Aristeus antennatus* was estimated for each period using two indices (both expressed as percentages), the stomach fullness index (*f*) defined as the ratio between the total stomach weight and the individual weight, and the coefficient of vacuity *V* (Rosecchi and Nouaze, 1985), defined as the ratio between the number of empty stomachs and the total number of stomachs examined in a sample.

The diet was analyzed based on the percentage of frequency of occurrence of prey in guts (*%F*). *%F* is given by the following definition (Hyslop, 1980): *%F* = (number of stomachs containing a given prey item / total number of non-empty stomachs examined) x 100

%F is the simplest non-proportional method for analyzing diet, and the most useful when it is difficult

TABLE 1. – Distribution by season and sex of the individuals of *Parapenaeus longirostris*.

Season (Month)	N. of females	N. of males	Total
Winter (January)	32	54	86
Spring (May)	8	24	32
Summer (September)	30	21	51
Autumn (November)	42	8	50
Total	112	107	219

TABLE 2. – Distribution by season and sex of the individuals of *Aristeus antennatus*.

Season (Month)	N. of females	N. of males	Total
Winter (January)	64	8	72
Spring (April)	48	12	60
Summer (July)	43	17	60
Autumn (October)	51	20	71
Total	206	57	263

to count the number of prey ingested, which happens in most decapods that manipulate and crush prey before ingestion. Some prey groups reported in Tables 3 and 4 were later grouped based on their affinity. Scales and fish bones were grouped in the "fish remains" group. The invertebrate larvae include several larvae of crustacean decapods, echinoderms (ophiurids, echinids), worms and molluscs. Variations in diet as a function of the sex and size of individuals, and also according to the season, were studied considering only the main prey (preferential prey with a %F>50% and secondary prey with 10%<%F< 50%), and excluding accidental prey.

Data analysis

Data on diet (per haul: all stomachs from a single trawl combined) were analyzed by Multi-Dimensional Scaling (MDS) techniques. MDS was performed based on the resemblance matrix obtained with raw matrix data. Columns in the data matrix represented diet composition (%F) by haul, size class and/or sex. The number of specimens analyzed for diet per haul was often ca. 20 for both species. As %F was not a proportional measure of the diet, the similarity index used in the MDS ordination was restricted to the use of the non-parametric Spearman-rank correlation coefficient. The UPGMA (Unweighted-Paired Group Method Average) was used as the aggregation algorithm. An MDS was applied to the combined dietary results of *Parapenaeus longirostris* and *Aristeus antennatus* to analyze possible resource partitioning between the two species, and the separate results to analyze seasonal and size/sex variations in the diet of each shrimp species. ANOSIM tests were applied to identify significant differences among "dietary groups" (in this case comparing the periods of more homogeneous waters – winter/spring – with the seasons of water stratification – summer/autumn) after assuming %F proportions of each prey-item in the diet. All the analyses were performed using PRIMER 6 and PERMANOVA+ (Anderson *et al.*, 2008) software.

RESULTS

Changes in feeding intensity

Parapenaeus longirostris showed the highest stomach vacuity (V) in May 2007, which decreased in September and November. *f* changed little in this species (non-significant one-way ANOVA: $F_{(3, 218)}=2.2$; $p=0.08$; non-significant post-hoc comparisons), and was highest in February for females (Fig. 2) and in December for males. *Aristeus antennatus* showed the lowest V in April and the highest in July 2007. Consistently, the highest values of *f* were found in January and April, significantly decreasing in July and October (Fig. 2). *f* results were similar for both females and males. The one-way ANOVA for females showed sig-
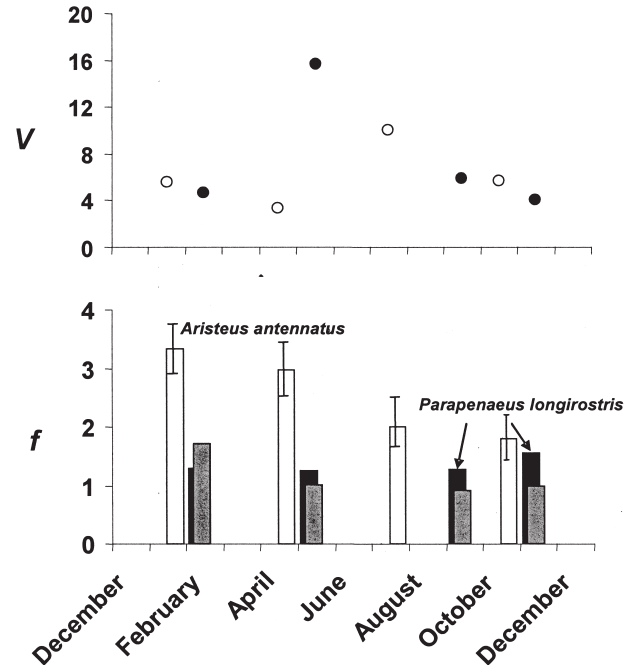

Fig. 2. – Vacuity (V) and fullness (f) indices as a function of season for *Parapenaeus longirostris* (dark symbols) and *Aristeus antennatus* (empty symbols) off the Algerian coast. For *P. longirostris* f was presented for males (black bars) and females (grey bars) separately. Confidence intervals at 95% of *A. antennatus* f included.

nificant trends in *f* ($F_{(3, 202)}=31.2$; $p<0.001$). There were significant Tukey's post-hoc comparisons between January and the rest of the seasons (p<0.001), and between April and October (p<0.01). The one-way ANOVA for males also showed significant trends in *f* ($F_{(3, 53)}=7.2$; $p<0.001$). There were significant Tukey's post-hoc comparisons between January and July-October (p<0.01) and between April and October (p<0.05).

Diet results

The diet of *Parapenaeus longirostris* was very diversified as it was based on more than 20 identified faunistic taxa (Table 3). The most frequently ingested prey taxa were foraminiferans (%F on average reaching 78% in all guts analyzed), polychaetes (51.7%), radiolarians (35.0%), algae debris (ramified brown macroalgae), fish remains and amphipods (all of these taxa represented ca. 25% of the average %F). Copepods and tintinnids can reach the status of preferential prey (with %F>50) in certain periods, e.g. copepods in winter or summer.

The diet of *Aristeus antennatus* showed 27 identified faunistic prey taxa (Table 4). The most frequently ingested prey taxa were foraminiferans (average %F reaching 88.3%), bivalves (58.9%), and unidentified worms, probably a mixture of polychaetes and other worms (41.8%). Unidentified crustaceans were also relatively important (average %F=39.7%), and

TABLE 3. – List of prey taxa and %F (frequency of occurrence) by season and sex for *Parapenaeus longirostris* off the Algerian coast.

Prey taxa	February				May			September			November		
n	Small♀	Large♀	Small♂	Large♂	Large♀	Small♂	Large♂	Small♀	Large♀	Small♂	Small♀	Large♀	Small♂
Foraminifera	81.3	91.7	95.8	50.0	100.0	88.9	80.0	100.0	88.9	75.0	60.0	72.2	71.4
Radiolaria	75.0	66.7	68.8	83.3	50.0	0.0	30.0	64.3	44.4	56.3	20.0	50.0	14.3
Tintinnida	37.5	8.3	25.0	66.7	62.5	77.8	60.0	7.1	0.0	0.0	0.0	13.9	0.0
Ctenophora	18.8	8.3	18.8	16.7	25.0	0.0	20.0	14.3	22.2	0.0	0.0	0.0	0.0
Polychaeta (*Glycera* sp.)	18.8	58.3	47.9	33.3	75.0	44.4	60.0	85.7	55.6	68.8	20.0	11.1	14.3
Nematoda	12.5	33.3	18.8	0.0	37.5	22.2	20.0	50.0	27.8	18.8	0.0	5.6	0.0
Crustacea													
Decapoda	6.3	16.7	6.3	0.0	0.0	11.1	20.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphipoda	12.5	25.0	22.9	0.0	50.0	0.0	10.0	35.7	72.2	37.5	60.0	77.8	71.4
Isopoda	0.0	8.3	6.3	0.0	12.5	11.1	0.0	0.0	0.0	6.3	0.0	0.0	0.0
Cumacea	18.8	33.3	31.3	16.7	12.5	11.1	20.0	7.1	11.1	12.5	0.0	0.0	0.0
Ostracoda	25.0	33.3	14.6	16.7	12.5	11.1	10.0	7.1	16.7	6.3	0.0	5.6	0.0
Copepoda	18.8	50.0	47.9	50.0	37.5	22.2	20.0	50.0	55.6	37.5	0.0	5.6	0.0
Cladocera	0.0	16.7	10.4	16.7	12.5	22.2	0.0	0.0	11.1	6.3	0.0	2.8	0.0
Mollusca													
Bivalvia (Nuculariidae)	43.8	33.3	31.3	16.7	0.0	11.1	0.0	92.9	94.4	62.5	40.0	30.6	42.9
Gastropoda	12.5	33.3	10.4	0.0	0.0	11.1	0.0	14.3	11.1	0.0	0.0	2.8	0.0
Pteropoda	12.5	16.7	31.3	50.0	37.5	44.4	40.0	14.3	11.1	0.0	0.0	5.6	0.0
Chaetognatha	0.0	0.0	10.4	16.7	25.0	22.2	20.0	64.3	33.3	37.5	0.0	2.8	0.0
Fish remains	18.8	50.0	43.8	33.3	25.0	66.7	50.0	85.7	22.2	6.3	0.0	52.8	71.4
Invertebrate larvae	12.5	25.0	18.8	16.7	12.5	11.1	20.0	28.6	5.6	6.3	0.0	2.8	14.3
Algae debris	50.0	25.0	31.3	50.0	12.5	33.3	10.0	42.9	27.8	6.3	20.0	0.0	28.6

TABLE 4. – List of prey taxa and %F (frequency of occurrence) by season and sex for *Aristeus antennatus* off the Algerian coast.

Prey	January			April			July			October		
	♂	♀small	♀adult	♂	♀small	♀adult	♂	♀small	♀adult	♂	♀small	♀adult
Foraminifera	62.5	92.3	82.3	100	97	100	70.6	85	95	90	85.3	100
Radiolaria	0	0	0	8.3	20.5	16.6	5.9	20	17.4	0	5.9	0
Tintinnida	12.5	3.8	0	0	5.8	0	0	0	0	0	0	0
Polychaeta	50	53.8	47.1	25	29.4	33.3	29.4	30	56.5	30	41.2	76.9
Nereis sp.	0	3.8	5.9	0	14.7	25	0	0	4.3	5	0	0
Nematoda	12.5	23.1	26.5	8.3	23.5	8.3	0	15	4.3	5	29.4	0
Crustacea												
Decapoda (*Processa* sp.)	0	19.2	20.6	0	2.9	0	5.9	0	0	0	2.9	0
Amphipoda (Oedicerotidae)	0	3.8	0	0	0	0	5.9	5	13	0	5.9	0
Cumacea	0	7.7	5.9	0	0	0	0	0	0	0	0	0
Ostracoda	25	15.4	8.8	16.6	5.8	8.3	5.8	5	4.3	5	5.9	7.7
Copepoda	12.5	15.4	14.7	8.3	2.9	0	0	0	13	5	2.9	0
Cladocera	0	23.1	14.7	16.6	11.7	0	17.6	5	13	0	2.9	0
Unidentified Crustacea	50	57.7	47	33.3	52.9	41.6	41.2	20	42.8	20	47.2	23.1
Mollusca												
Bivalvia (*Abra longicallus*)	50	88.5	64.7	66.6	82.3	83.3	47.1	40	34.8	40	55.9	53.8
Gastropoda (*Benthonella tenella*)	25	30.7	38.2	8.3	8.8	16.6	17.6	15	17.4	30	5.9	7.7
Pteropoda	0	0	0	0	0	0	0	10	4.3	0	8.8	7.7
Cephalopoda	25	3.8	0	0	0	0	5.8	0	4.3	5	0	0
Unidentified Mollusca	0	3.8	0	8.3	2.9	0	0	0	0	0	0	0
Echinodermata												
Crinoidea	0	0	5.9	0	0	0	0	0	0	0	0	0
Echinoidea (*Brissopsys liryfera*)	12.5	15.4	11.8	0	23.5	8.3	5.9	5	17.4	5	38.5	2.9
Ophiuridea (Amphipholidae)	12.5	11.5	2.9	0	0	0	0	0	0	0	0	0
Holothuroidea	0	7.7	8.8	0	0	0	0	0	0	0	0	0
Sipunculoidea	0	23.1	17.6	8.3	11.7	0	0	0	0	5	2.9	7.7
Chaetognatha	0	7.7	2.9	0	0	0	0	0	0	0	0	0
Fish remains (scales)	37.5	34.6	20.6	16.6	23.5	66.6	11.8	25	0	10	0	23.1
Unidentified worms	12.5	26.9	38.2	41.6	52.9	91.6	52.9	55	73.9	95	91.2	84.6
Fish eggs	0	3.8	14.7	0	0	0	0	5	4.3	0	0	15.4
Invertebrate larvae	12.5	0	8.8	0	0	0	0	5	0	5	0	0
Algae debris	50	88.5	73.5	13.8	61.7	91.6	17.6	25	4.3	15	17.6	0
Posidonia debris	25	7.7	8.8	8.3	2.9	0	5.9	30	4.3	15	20.6	7.7

cladocerans, copepods and ostracods were dominant among the identified taxa. As more secondary food items, brown macroalgae and *Posidonia* remains were also relatively frequent (ca. 20% of average %F).

Seasonal changes in the %F of the main prey taxa are shown in Figure 3 for *Parapenaeus longirostris* and

in Figure 4 for *Aristeus antennatus*. In *P. longirostris* foraminiferans reached a maximum %F in May and September, most prey-taxa reached their highest %F in these periods, for example polychaetes, tintinnids and fish remains (in May). Exceptions were macroalgae remains, radiolarians and copepods, which reached peaks
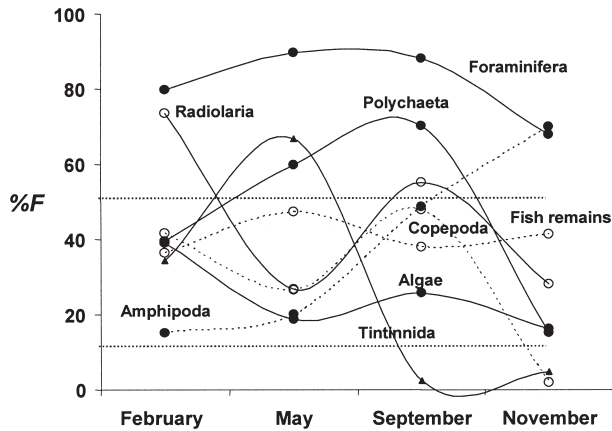
FIG. 3. – Seasonal changes in the *%F* of the main prey of *Parapenaeus longirostris*. Lines (............) indicate the *%F* at 50% and 10%, which correspond to preferential and secondary prey taxa respectively.
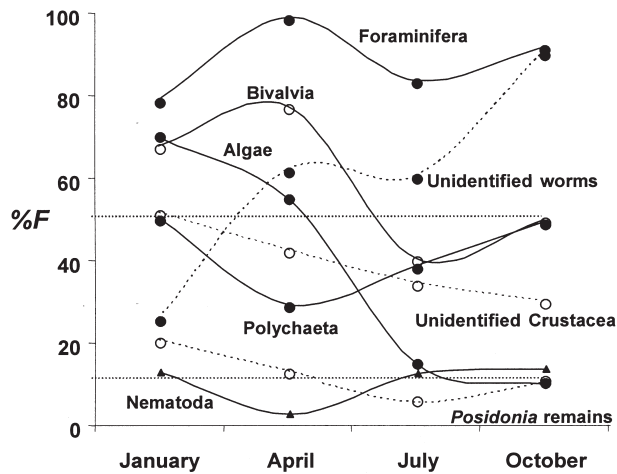

FIG. 4. – Seasonal changes in the *%F* of the main prey of *Aristeus antennatus*. Lines (............) indicate the *%F* at 50% and 10%, which correspond to preferential and secondary prey taxa respectively.

of occurrence in guts in February, and amphipods with the highest *%F* in November. In *A. antennatus* most prey taxa reached a maximum *%F* in January and/or April, e.g. foraminiferans, bivalves, algae, crustaceans, *Posidonia* remains, polychaetes (also peaking in October), and nematodes (also peaking in July-October). Exceptions were worms, which had their highest *%F* in October.

Foraminiferans, bivalves and polychates were the most frequent prey in the diets of both *P. longirostris* and *A. antennatus*. In general, secondary prey of planktonic origin (radiolarians, copepods, pteropods) were more important in the diet of *P. longirostris*.

Multivariate analyses

Interspecies analysis

The dietary composition of *Parapenaeus longirostris* and *Aristeus antennatus* was clearly segregated in
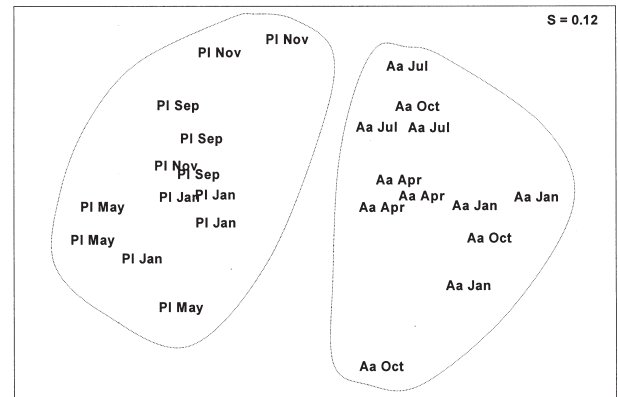

FIG. 5. – Seasonal comparison by MDS analysis of the dietary composition of *Parapenaeus longirostris* (Pl) and *Aristeus antennatus* (Aa) off the Algerian coast. S = MDS stress.

the MDS analysis (Fig. 5) with stress of 0.12. Groups corresponding to the two species had a significantly different dietary composition (ANOSIM test; R=0.87; p=0.001). This suggests good resource partitioning between the two species.

Intraspecies analysis

Prey items of *Parapenaeus longirostris* were segregated as a function of season in the MDS analysis (Fig. 6; stress 0.12), although the ordination was not as clear as for *A. antennatus* (see discussion below). The global ANOSIM test (R=0.65; p=0.001) was significant. Groups corresponding to winter (January 2007) were grouped in the central-low part, the spring (May) group on the left, and the summer-autumn (September-November) samples on the right in the plot (Fig. 6). The post-hoc ANOSIM test showed that diet samples under homogeneous water conditions (January-May) were significantly different from those under stratified water conditions (September-November) (R=0.54; p=0.01). Sex and size were not, in general, important factors
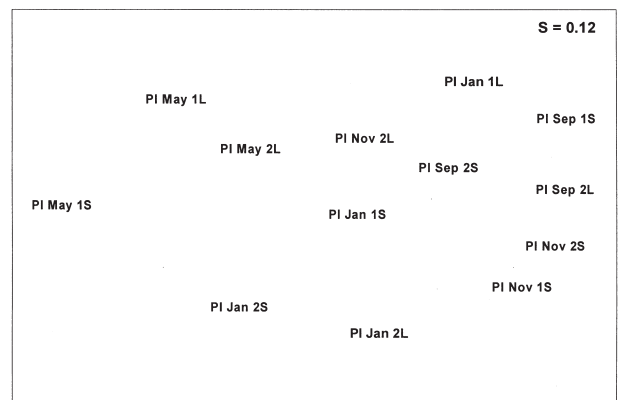

FIG. 6. – MDS on the dietary composition of *Parapenaeus longirostris* (Pl) off the Algerian coast. The month is indicated behind the species code. Sex/size codes: 1S: small males; 1L: large males; 2S: small females; 2L: large females. S = MDS stress.
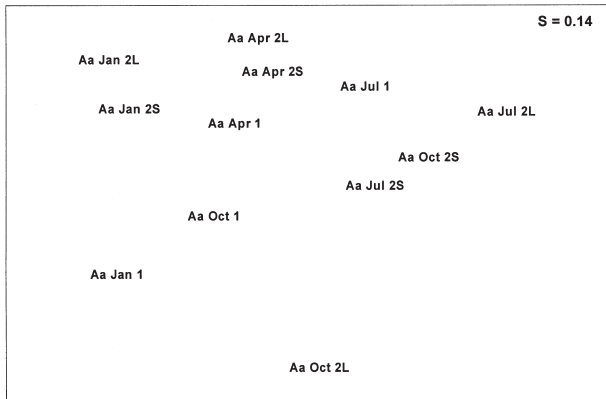
FIG. 7. – MDS on the dietary composition of *Aristeus antennatus* (Aa) off the Algerian coast. The month is indicated behind the species code. Sex/size codes: 1: males; 2S: small females; 2L: large females. S = MDS stress.

for determining dietary differences in *P. longirostris* in terms of %F. However, in January the diet of males was quite different from the diet of females, and they appear clearly separated in Figure 6. Foraminiferans, polychaetes and a number of planktonic prey groups (radiolarians, tintinnids, copepods and pteropods) were dominant in January-May, while other benthic taxa (e.g. bivalves and amphipods) were most frequently consumed under stratified conditions, with a parallel decrease in zooplankton taxa.

Diet components of *Aristeus antennatus* were segregated as a function of season in the MDS analysis (Fig. 7), with MDS also showing low stress (0.14). The global ANOSIM test (R=0.33; p=0.02) was significant. Groups corresponding to winter (January 2007) were grouped on the left, while the rest of the seasonal samples (April, July and October) progressively appeared from left to right and form top to down on the plot. The post-hoc ANOSIM test was significant (R=0.327; p=0.01) comparing homogenized water conditions (January-April) and samples under stratified water conditions (July-October). Sex and size were not important factors (in terms of %F) for determining dietary differences in *A. antennatus*. Foraminiferans and bivalves were the most frequently consumed prey and the secondary prey, nematodes and ostracods, were more important in January-April, while polychaetes and gastropods were slightly more frequently consumed in July-October.

In general, benthic prey were more important in the diet of the deepest species, *A. antennatus* while zooplankton prey-items dominated more in the diet of *P. longirostris*.

DISCUSSION

The feeding intensity (fullness, *f*) of *Aristeus antennatus* showed significant seasonal changes off central Algeria, with the highest *f* found in pre-reproductive periods (3.3% in January; 3.0% in April), before the beginning of gonad maturation (April-September peak-

ing in August: Yahiaoui, 1994) in the area. This trend was similar to that described by Cartes *et al.* (2008) off the Balearic Islands and over the Catalan canyons. Kapiris *et al.* (2000) found that in the Ionian Sea and it was coupled with the period of high surface productivity off the central Algerian coast (November-April). In this pre-reproductive period *A. antennatus* seems to consume more crustaceans (e.g. large decapods such as *Processa* sp.) with a high energetic value, as it has also been reported off the Balearic Islands (Cartes *et al.*, 2008). This type of seasonal oscillations in *f* was not determined as clearly in *Parapenaeus longirostris*, probably because this species, which is distributed in shallower depths than *A. antennatus*, does not have a single reproductive peak, as found in the deeper species. Maturing females of *P. longirostris* can be found all year round off the Balearic Islands, with peaks in November and June-August (Guijarro *et al.*, 2009). This same relationship between the amplitude of the reproductive period and shifts in *f* was found when two species of *Plesionika* spp. (*P. heterocarpus* and *P. martia*) were compared, which inhabit respectively the shelf-slope break and the mid-slope (Fanelli and Cartes, 2008). The average stomach fullness of *A. antennatus* was higher off the central Algerian coast (ca. 1.6-0.9% of body weight, once the weight of the stomach cover was removed) than around the Balearic Islands (*f* between 0.4 and 0.9%), and below that reported for the Catalan canyons (ca. 2.2-2%). These changes in biological conditions have been related to local productivity (Cartes *et al.*, 2008; Guijarro *et al.*, 2009); therefore, Algerian waters would seem to have trophic or ecological conditions for *Aristeus antennatus* that are intermediate between those found in the Catalan canyons and those on the Balearic slope. However, the daily cycle of *A. antennatus* may also have some influence on *f* in the Algerian region, where the species was caught at night, while the Balearic Basin samples were obtained during the day. It has been suggested that *A. antennatus* feeds mainly during the night (Laubier, 1986; Maynou and Cartes, 1997).

As %F is not a proportional measure of diet (Hyslop, 1980), we cannot define with precision what are the main prey types that sustain the energetic requirements of Algerian deep water shrimp. In contrast to gravimetric methods (e.g. the weight of prey), %F tends to overestimate the contribution of small prey in the diet, such as foraminiferans, that make a low energetic contribution to the diet of shrimp (and in general to megafauna). However, the use of %F allowed us to analyze the spatial and temporal changes in prey consumption, and also indirectly the changes in the ecosystem dynamics. Small micro and mesoplankton prey (e.g. radiolarians, tintinnids, cladocerans, copepods) found in the diet of *Parapenaeus longirostris* and *Aristeus antennatus* are in general coupled with periods of high surface production (January-February and April-May: Fig. 8) off the Algerian coast. Benthic meiofauna (foraminiferans and nematodes) were also
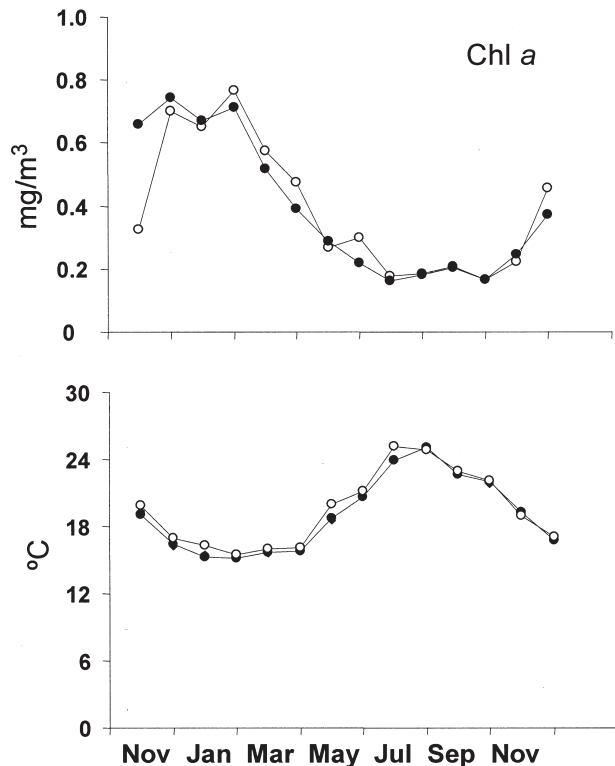
FIG. 8. – Monthly values of Chl *a* and surface temperature (T) off central Algerian coast. Monthly average readings were obtained in two positions (● 36.50°N 2.00°E; ○ 36.40°N 2.00°E) within the study area off the Algerian coast from November 2006 to December 2007.

more frequently consumed in April-May and July after the periods of the highest surface production. Meiofauna can quickly consume inputs of fresh organic matter that arrive to the sea bottom, as in the case of foraminiferans (Nomaki *et al.*, 2005). Hence, it is possible that formaniferans were ingested live, and thus contributed from an energetic point of view to the diets of Algerian deep water shrimp.

Off the central Algerian coast *Parapenaeus longirostris* and *Aristeus antennatus* were captured at night over the same bathymetric range (200-400 m). The two species were segregated in terms of the resources exploited: *P. longirostris* preyed more frequently on zooplankton while *A. antennatus* consumed more benthos. *A. antennatus* showed the highest densities in the deep Mediterranean often at depths below 500 m (Cartes, 1993; Cartes *et al.*, 2008; Mouffok *et al.*, 2008), although it is caught by trawling at only 100 to 150 m off the Calabrian coast at night (Matarrese *et al.*, 1995). Nocturnal catches of upward migrations over similar shallow (100 to 400 m) depths have not been clearly documented in other areas. Off the Catalan coast, it has been suggested that *A. antennatus* migrates upwards and inshore at night (Cartes *et al.*, 1993). These migrations would take place preferentially through canyon valleys in order for shrimp to feed (Cartes et *al.*, 1993). The role of canyons in enhancing secondary production is well known, especially at canyon heads

(Vetter and Dayton, 1998), and off Catalonia *A. antennatus* showed higher stomach fullness within canyons (Cartes, 1994). Hence, upward nocturnal movements by *A. antennatus* would be carried out to feed in more productive depths. Off the Balearic Islands, these migrations could be performed to catch mesopelagic prey, as they coincide with the upward-inshore migrations of mesopelagic fauna at night, as evidenced in Reid *et al.* (1991).

The relatively high %*F* for some small micro and mesoplankton prey (e.g. radiolarians, tintinnids, cladocerans, copepods) in the diet of deep water shrimp, especially of *Parapenaeus longirostris*, suggests that the vertical flux in bathyal trophic webs off central Algeria are very important. The % *F* for these prey taxa are clearly higher than observed in the Balearic Basin for the same species (Cartes, 1995). These same prey types (e.g. copepods, ostracods) were also more frequently consumed by *Aristeus antennatus* over the Algerian slope than off the Catalan canyons (Cartes, 1994) or around the Balearic Islands (Cartes *et al.*, 2008). Off NE Morocco, *A. antennatus* also consumed meso-macroplankton (e.g. euphausiids: Lagardère, 1972), and consumed less benthic prey than off the Catalan canyons. The large contribution of small zooplankton in the diets of deep water shrimp over Algerian slopes is probably due to the importance of eddies in the area (Ruiz *et al.*, 2002; Salas *et al.*, 2002), which may enhance primary production locally (Taupier-Letage *et al.*, 2003). However, the production response associated with Algerian eddies varies according to their trajectory, offshore and inshore location and season (Millot, 1985). Although these patterns are not yet clear, it seems that in spring Algerian eddies generate higher chlorophyll concentrations within the first 150 m of the water column off the coastal zone, while in summer the situation is highly oligotrophic (Taupier-Letage *et al.*, 2003). There is little information on the zooplankton abundance off the Algerian coast, but it has been found that shelf copepods (Khelifi-Touhami *et al.*, 2007) and slope dwelling euphausiids (Casanova, 1974) can reach high densities. The benthos, in contrast, does not seem as important in either the diet of *P. longirostris* or *A. antennatus*, probably because of the its low abundance in the area (Massutí, pers. comm).

In this area, the benthic biomass only seems relatively high in areas under the influence of river flows (Dagorne, 1973; Fig. 9). Polychaetes for example were less frequent in the diet of *P. longirostris* off Algeria than in its diet in the Balearic Basin (Cartes, 1995). Polychaetes do not seem dominant, which is in agreement with the information available for benthos off the Algerian coast (Fig. 9), where bryozoans, foraminiferans and molluscs are dominant on the shelf-slope break, over ca. 270 m (Dagorne, 1973; Fig. 9). That the benthos only makes a low contribution to the diet of shrimp due to the low benthic biomass in the environment, could in turn be related to the
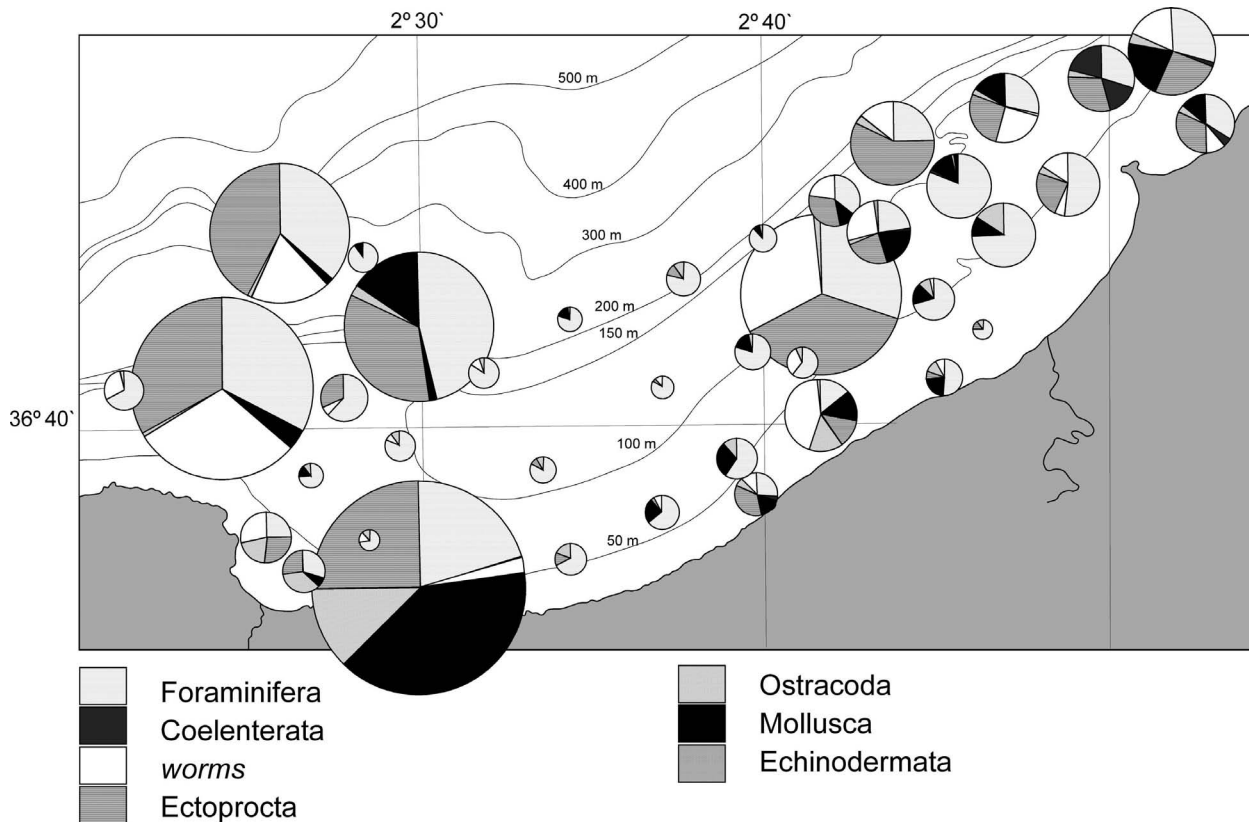
FIG. 9. – Distribution of benthos (collected with a Rossfelder grab) off the central Algerian coast between depths of 20 and 270 m, with the relative composition (abundance: number of specimens) of broad taxa indicated in the legend. Pie sizes are proportional to benthos abundance. From Dagorne, 1973.

relatively high surface T found even during winter in the area. The lowest T found at the surface in January (15.2°C) was relatively high, because T close to the bottom is ca. 12.8-14°C (Yahiaoui, 1994). This high surface T may enhance OM degradation in periods of high surface production in the area (November-April: Fig. 8), which may decrease the quality of food for benthos derived from vertical flux. An indication of low benthic biomass in the area – in comparison for example with levels found in the Catalan canyons (Cartes *et al.*, 2009) – is the practical absence of characteristic infaunal species, as is the case of *Calocaris macandreae* and *Molpadia musculus* (Massutí, pers. comm).

In conclusion, we hypothesize that the relatively high surface T may accelerate the degradation of organic matter over Algerian slopes. This would reduce the macrobenthic biomass, which must be relatively high at the uppermost part of the slope, with a biomass peak located shallower than in more eutrophic areas, like the Catalan canyons. This also occurs in the South Aegean Sea (Tselepides and Eleftheriou, 1992), where a sharp decrease in benthic biomass already occurs below 400 m. This low food availability may favour night time migratory movements by benthopelagic shrimp off the Algerian coast in order to find more productive shallow bottoms.

ACKNOWLEDGEMENTS

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