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Metabolic rates and energy content of deep-sea benthic decapod crustaceans in the western Mediterranean Sea

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Abstract

A total of 23 species of deep-sea benthic decapod crustaceans were collected in the Catalan Sea (western Mediterranean) at different depths (200–1250 m) but at the same environmental temperature (13°C) in winter 1992 and winter 1993. Studies on oxygen consumption and energy content were carried out on crustaceans exhibiting two life strategies: nektobenthic species (benthic species with a slight locomotory ability) and benthic-endobenthic species (strictly benthic species). The two deep-sea life styles were associated with two different patterns of metabolic rate and energy content. On the whole, metabolic rates, energy contents, and organic matter contents were higher for the nektobenthic life strategy than for the benthic-endobenthic life strategy. When results were related to depth of maximum abundance of the species considered, it appeared that the nektobenthic species in the upper slope community (200–450 m depth) had a significantly lower energy content (as kJ g^{-1} of ash-free dry mass) than the nektobenthic species in the middle slope community (550–1250 m depth), but no significant trend was found when the energy content was expressed as a function of wet mass. The benthic-endobenthic species exhibited a significant decrease in metabolic rates, an increase in energy content (when expressed as a function of ash-free dry mass), no significant trend in energy content (as a function of wet mass) and a significant increase in water content with increasing depth over the two depth strata considered (200–450 and 550–1250 m). It was concluded that the lower metabolic rates of deeper-living benthic-endobenthic species, when compared to the shallower-living species, were the result of general locomotory reduction. It is likely that the shallower-living species rely more heavily on visual predation than the deeper-living species (light-limited environment), and this fact is discussed as an explanation of the general metabolic reduction for the benthic-endobenthic Mediterranean species along the

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depth gradient considered in the present study (200–1250 m). © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The continental slope in the Catalan Sea in the western Mediterranean at depths between 200 and 1250 m shows high densities of decapod crustaceans, which play an important ecological role (Maurin, 1962). Diversity is high: penaeids, carideans, and a variety of anomuran and brachyuran crabs are well represented. Two depth-related decapod crustacean communities have been well identified: upper slope communities (200–450 m) and middle slope communities (500–1250 m) (Abelló *et al.*, 1988; Cartes and Sardà, 1992; Cartes *et al.*, 1994). Interestingly, the abundance and biomass of decapods as a group are higher in the oligotrophic Catalan Sea than in the eutrophic regions of the North Atlantic, where other deep-sea benthic invertebrates predominate (Cartes and Sardà, 1992).

The Mediterranean Sea has some unusual physical characteristics. In the study area (41°N, 02° E; Fig. 1), the surface layer consists of Atlantic water down to 200 m and undergoes marked annual hydrological and thermal fluctuations. The temperature of the intermediate water mass located between 200 and 600 m is 13°C, with yearly fluctuations of less than 0.5°C (Reyss, 1971; Hopkins, 1985). Salinity ranges from 38.5 to 38.6. Temperature and salinity are even more stable (12.8°C; 38.4) at depths below 600 m, in the Mediterranean deep water mass (Reyss, 1971). Oxygen concentrations are high throughout the water column at 4.7–5.5 ml O₂ l⁻¹. The minimum values recorded between 200 and 1000 m were 4.7–4.9 ml O₂ l⁻¹ (Hopkins, 1985). The temperature of the water column between surface and sea bed in winter is a constant 13°C (Hopkins, 1985).

Oxygen consumption rates and the chemical composition of pelagic crustaceans and fishes have been studied at temperate and subtropical latitudes, where there are temperature gradients from the surface to the bottom (Childress and Nygaard, 1973, 1974; Childress, 1975; Torres *et al.*, 1979; Donnelly and Torres, 1988; Childress *et al.*, 1990b; Cowles *et al.*, 1991). These authors reported decreasing oxygen consumption in midwater species with depth. The musculature of fishes decreases with depth, and the protein content of crustaceans is lower in deep-sea species. These characteristic physiological and biochemical changes in deep-sea species have been attributed to depth, aside from the possible influence of temperature or larger size (Childress, 1971; Torres *et al.*, 1979). Decreases in metabolic rates in midwater fishes and crustaceans have likewise not been attributed to hydrostatic pressure (Teal and Carey, 1967; Teal, 1971; Meek and Childress, 1973).

Studies carried out in Antarctica have also demonstrated lower respiration rates, structural chemical composition, and enzymatic activity in mesopelagic fish and

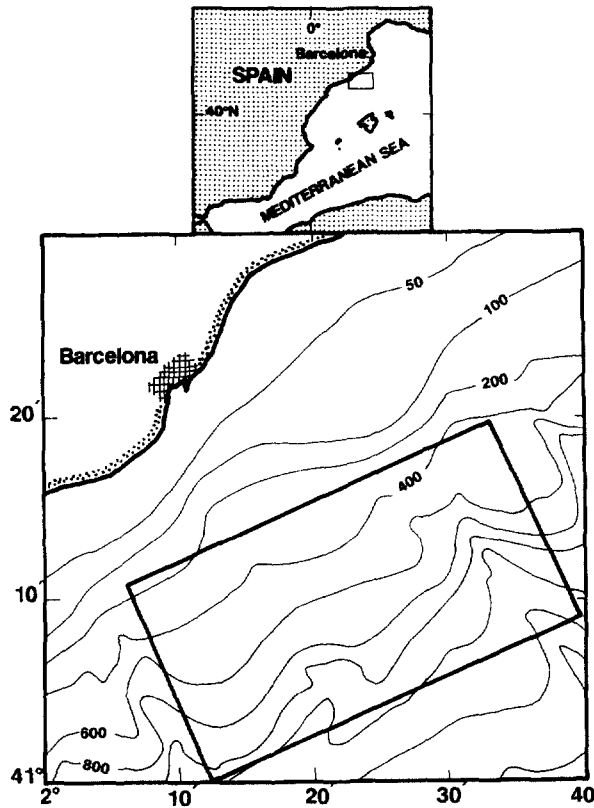


Fig. 1. Study area (rectangle) located at 41°N , 02°E in the Catalan Sea between the Balearic Islands and the Iberian Peninsula.

crustaceans than in their epipelagic counterparts (Ikeda, 1988; Torres and Somero, 1988). The problem of temperature gradients, which exist in temperate zones, is not a factor in that region, which is thermally unstratified (-0.5 – 2°C between 0 and 1000 m).

In contrast to the extensive literature dealing with deep-sea midwater species, fewer studies have considered metabolism in benthic deep-sea organisms in relation to depth (Smith, 1978; Childress *et al.*, 1990a). Childress *et al.* (1990) found lower oxygen consumption rates in deep-sea benthic species than in shallow species but attributed the decrease primarily to lower temperature.

Energy contents in living organisms have been presented and discussed by several workers (Slobodkin and Richman, 1961; Prus, 1970; Cumins and Wuycheck, 1971; Wacasey and Atkinson, 1987; Dauvin and Joncourt, 1989). More detailed studies on specific taxonomic groups have found inter and intraspecific variations in energy content values according to season, habitat, and life strategy (Griffiths, 1977; Norrbin and Båmstedt, 1984). It must be recalled that an animal's total energy content depends

upon the amount of carbohydrate, protein, and lipid present and that those levels are an expression of an animal's adaptive characteristics; organisms tend towards an optimum biochemical composition depending upon their adaptation strategy.

The object of the present paper is to characterize two deep-sea benthic decapod life strategies (nektobenthic and benthic-endobenthic strategies) on the basis of oxygen consumption and energy content. Variations in these parameters were studied in species from two communities at different depths (upper slope, 200–450 m depth, and middle slope, 550–1250 m depth), in a thermally unstratified area (13°C), and the results are discussed and compared with the findings of other researchers in areas with strong thermal gradients.

2. Materials and methods

2.1. Specimens

Specimens were collected at depths between 200 and 1250 m in the western Mediterranean (Catalan Sea) using a deep-sea benthic otter trawl, OT-MS (Sardà *et al.*, in press), during winter 92 and winter 93.

The species included in this study accounted for over 95% of the total decapod crustacean abundance and biomass on the upper and middle slopes in the area (Abelló *et al.*, 1988; Cartes and Sardà, 1992). Table 1 presents the depth ranges and the depths of maximum abundance for the species examined in this study. The depth distributions have been studied extensively by several authors (Abelló *et al.*, 1988; Cartes and Sardà, 1992; Cartes *et al.*, 1994). *Liocarcinus depurator* and *Goneplax rhomboides* are most abundant on the shelf but also make up a considerable share of catches taken on the slope (Abelló *et al.*, 1988). The species were classified as nektobenthic or benthic-endobenthic, according to their habit (Crosnier and Forest, 1973; Cartes and Sardà, 1992). Berried females and non-adult sizes were excluded from this study.

2.2. Metabolic measurements

All individuals used in the metabolic rate assessments were captured in winter, when the temperature is 13°C throughout the entire water column, to avoid the possibility of thermal shock. Towing time was $\frac{1}{2}$ h so that the individuals collected would be alive and in good condition. Undamaged specimens were immediately stored in chambered 30 l coolers at 13°C and were transported to the laboratory, where they were held individually in separate containers in a cold room at that same temperature. All experiments were carried out between 12 and 36 h after capture using filtered sea water in the dark at a constant temperature of 13°C ($\pm 0.1^\circ\text{C}$) and a pressure of 1 atmosphere. A control respiration chamber without any specimen was used to determine oxygen consumption by microbial activity and thus to obtain the baseline value for each run. The baseline value was subtracted from the total consumption rate measurements made for the specimen-containing respiration chamber.

Oxygen partial pressure was monitored using a Clark-type polarographic oxygen electrode in a Type 1125 pulsed dissolved oxygen system by Endeco/YSI Inc, Marion, Massachusetts (1992). The stir bars revolved at the minimum speed setting to ensure uniform water circulation throughout the container and thus a homogeneous distribution of dissolved oxygen. The time required to consume all the oxygen in the different-sized chambers ranged from 10 to 24 h, depending upon the size of the animal and its level of activity during the run.

In order to compare the metabolic rates between species, the specific average respiration rate was calculated as the mean of the individual rates recorded over the range of partial oxygen pressures between 80 and 30 mm Hg. This range of oxygen pressures was adequate for normal activity by all specimens assessed and was taken as representative of the metabolic rate for the species concerned. Childress (1975) and Donnelly and Torres (1988) employed a similar system of comparison over ranges of 70 to 30 mm Hg and 80 to 30 mm Hg, respectively.

For the purpose of representing the metabolic rates of live animals, the oxygen consumption data have been expressed in relation to wet mass (WM) (Childress and Somero, 1979). The data have been plotted against the depth of maximum abundance for the species considered. We assume that this depth provides the optimum physico-chemical conditions for the metabolic requirements of the respective species. To avoid the size effect on metabolic rates, the mass specific metabolic data have been corrected to 10 g wet mass. A scaling coefficient of -0.20 was assumed (Childress *et al.*, 1990a).

2.3. Energy content, water % WM, and organic % DM

The fresh mass of each individual was recorded. Specimens were subsequently dried at 100°C for 24–48 h, depending upon the species, until a constant mass was obtained. The difference between wet mass (WM) and dry mass (DM) was taken to be the water content. Finally, the whole dried animals were ground in a mortar and pestle, and the homogenized samples were stored in a desiccator until the analyses for ash and energy content were performed.

The minimum portion of the homogenized dry samples required for analysis was pelletized, and energetic determinations were made using a Gallemkamp CBB 330 ballistic bomb calorimeter. The general calorimetric procedure set out in the ASTM standards for bomb calorimetry (1971) were employed. Three replicates were performed for each analysis, and the mean of the three replicates was calculated and used whenever the three values differed by less than 3%. Energy values have been expressed as kilojoules per gram wet mass (kJ g^{-1} WM), kJ per g dry mass (kJ g^{-1} DM), and $\text{kJ per g ash-free dry mass}$ (kJ g^{-1} AFDM).

The remainder of each homogenized dry sample was converted to ash in a muffle furnace at 500°C for 5–10 h, depending upon the species. Samples were heated in the furnace for the shortest time necessary to minimize breakdown of the ash (Paine, 1966, 1971). All samples were incinerated in duplicate and the mean of the two values taken. The difference between dry mass and ash mass was taken to be the organic content.

Table 1
Depth range and depth of maximum abundance for decapod crustacean in the Western Mediterranean collected in the present study

Species	Codes species	Depth range (m)	Maximum abundance (m)	Life strategies
Suborder Dendrobranchiata				
Infraorder Penaeidea				
Family Aristeidae				
<i>Aristeus antennatus</i>	Aa	176–2261	650	^a N
Family Penaeidae				
<i>Parapenaeus longirostris</i>	Pl	70–586	300	N
Family Solenoceridae				
<i>Solenocera membranacea</i>	Sm	3–871	350	N–B
Suborder Pleocyemata				
Infraorder Caridea				
Family Oplophoridae				
<i>Acanthephyra eximia</i>	Ae	549–2261	2100	N
Family Hippolitidae				
<i>Ligur ensiferus</i>	Le	439–871	600	N
Family Processidae				
<i>Processa canaliculata</i>	Pc	70–871	350	N–B
Family Pandalidae				
<i>Plesionika acanthonotus</i>	Pa	165–1749	650	N
<i>Plesionika edwardsi</i>	Pe	256–512	350	N
<i>Plesionika gigliolii</i>	Pg	101–748	350	N
<i>Plesionika heterocarpus</i>	Ph	82–699	250	N
<i>Plesionika martia</i>	Pm	165–871	600	N
Family Crangonidae				
<i>Pontophilus norvegicus</i>	Pno	366–2261	1250	B

Infraorder Astacidea						
Family Nephropidae						B-E
<i>Nephrops norvegicus</i>	(Linnaeus, 1758)	Nn	66–871	450		
Infraorder Palinura						
Family Polychelidae						B
<i>Polycheles typhlops</i>	Heller, 1862	Pt	267–1949	750		
Family Palinuridae						B
<i>Palinurus mauritanicus</i>	Gruvel, 1911	Pma	66–748	450		
Infraorder Anomura						
Family Galatheididae						B
<i>Munida intermedia</i>	A.M. Edwards & Bouvier, 1899	Mi	35–871	450		
<i>Munida tenuimana</i>	G.O. Sars, 1872	Mt	348–1949	650		
Infraorder Brachyura						
Family Homolidae						B
<i>Homola barbata</i>	(Fabricius, 1793)	Hb	128–637	300		
Family Geryonidae						B
<i>Geryon longipes</i>	A.M. Edwards, 1881	Gl	439–1949	650		
Family Portunidae						B
<i>Liocarcinus depurator</i>	(Linnaeus, 1758)	Ld	3–871	75		
<i>Macropipus tuberculatus</i>	(Roux, 1830)	Mtu	48–1149	300		
Family Goneplacidae						E
<i>Goneplax rhomboides</i>	(Linnaeus, 1758)	Gr	3–748	75		
Family Xanthidae						B-E
<i>Monodaeus couchi</i>	(Couch, 1851)	Mc	137–1149	630		

^a N: nekto-benthic; B: benthic; E: endobenthic.

Table 2

Metabolic rates and weight for nektobenthic and benthic-endobenthic decapod crustaceans measured from 80 to 30 mm Hg oxygen partial pressure

Species	Wet mass (g)		n	MO ₂ (μl O ₂ mg ⁻¹ WM h ⁻¹)		
	Range	Mean		Mean	± SD	Corrected
Nektobenthic						
<i>A. antennatus</i>	15.60–44.26	24.34	5	0.117	± 0.018	0.140
<i>P. canaliculata</i>	1.92	1.92	1	0.095		0.069
<i>P. edwardsi</i>	7.03–15.49	11.13	4	0.099	± 0.009	0.102
<i>P. hetercarpus</i>	3.01–4.71	3.96	4	0.092	± 0.008	0.076
<i>S. membranacea</i>	2.73–4.71	3.40	5	0.061	± 0.005	0.049
Total mean				0.093	± 0.018	0.087
Benthic and endobenthic						
<i>G. longipes</i>	45.90–99.30	70.68	6	0.019	± 0.002	0.028
<i>G. rhomboides</i>	4.02–6.36	5.51	3	0.028	± 0.003	0.025
<i>L. depurator</i>	6.84	6.84	1	0.066		0.061
<i>M. couchi</i>	2.36–11.26	7.43	4	0.015	± 0.002	0.014
<i>M. intermedia</i>	8.75	8.75	1	0.028		0.027
<i>M. tenuimana</i>	4.62	4.62	1	0.027		0.023
<i>M. tuberculatus</i>	6.63–12.39	9.40	3	0.049	± 0.007	0.048
<i>N. norvegicus</i>	2.67–6.73	4.47	3	0.047	± 0.005	0.040
<i>P. mauritanicus</i>	18.89–19.59	19.24	2	0.035	± 0.005	0.040
<i>P. typhlops</i>	6.90–22.80	9.41	5	0.020	± 0.003	0.020
Total mean				0.033	± 0.015	0.033

Note: MO₂: mean oxygen consumption rates. Rightmost column: Metabolic rates corrected to 10 g wet mass. ± SD: standard deviation.

3. Results

3.1. Oxygen consumption rates

Table 2 gives the variation in oxygen consumption rates, from 0.0611 to 0.1168 ml O₂ mg⁻¹ WM h⁻¹ for the nektobenthic species and from 0.0151 to 0.0660 ml O₂ mg⁻¹ WM h⁻¹ for the benthic-endobenthic species. The metabolic rates for the nektobenthic species were significantly higher than those for the benthic-endobenthic species (*t*-test, *p* < 0.0001). *Liocarcinus depurator*, an active, shallow-water crab, was the sole exception, with an oxygen consumption rate higher than that for the penaeoidean *Solenocera membranacea*, a nektobenthic species with benthic feeding behaviour (Lagardère, 1977; Frogliola and Gramitto, 1987; Cartes, 1995).

Fig. 2 plots the oxygen consumption rate values vs the depth of maximum abundance for five nektobenthic species and ten benthic-endobenthic species. A significant decline in metabolic rates with depth of maximum abundance of benthic-endobenthic species was found ($a = 0.054$, $b = -0.4 \times 10^{-4}$, $r = 0.706$, $p = 0.0226$) (Fig. 2A). *Monodaeus couchi*, *Munida tenuimana*, *Geryon longipes* and *Polycheles typhlops*, all

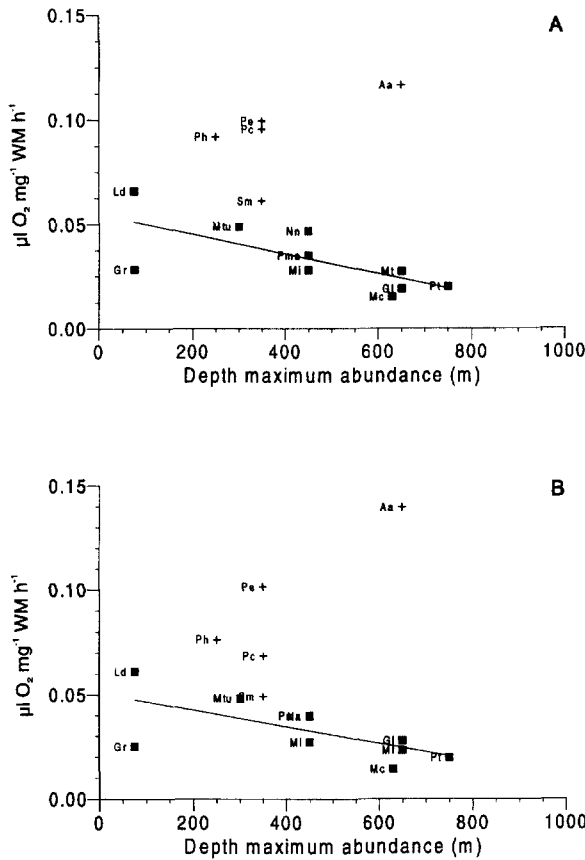


Fig. 2. Oxygen consumption rates (Fig. 2A) and oxygen consumption rates corrected to 10 g wet mass (Fig. 2B) as a function of depth of maximum abundance. No significant relationship was found between oxygen consumption rates and depth in nektobenthic species. Regression-line statistics, coefficient of correlation, and P values for regression exponents for benthic-endobenthic species are, (A): $Y = 0.05 - 0.40 \times 10^{-4} X$, $r = 0.71$, $p = 0.0226$; and (B): $Y = 0.05 - 0.40 \times 10^{-4} X$, $r = 0.66$, $p = 0.0387$. Species codes as in Table 1; +: nektobenthic species; ■: benthic-endobenthic species.

benthic-endobenthic species on the middle slope (550–1250 m), had lower oxygen consumption rates than *Macropipus tuberculatus*, *Nephrops norvegicus*, *Palinurus mauritanicus*, *Munida intermedia* and *Liocarcinus depurator*, on the upper slope (200–450 m). *Aristeus antennatus*, a nektobenthic species on the middle slope, had a higher oxygen consumption rate than the other nektobenthic species (Table 2, Fig. 2), but no significant trend was found between metabolic rates and depth of maximum abundance for the nektobenthic species. Mass normalized metabolic rates at 10 g wet mass did not have a significant effect on the results. The regression between metabolic rates corrected to 10 g on depth of maximum abundance of the benthic-endobenthic species is: $a = 0.051$, $b = -0.39 \times 10^{-4}$, $r = 0.658$, $p = 0.0387$ (Table 2, Fig. 2B).

Table 3
Water content, energy content and organic matter content for 11 nekto-benthic and 11 benthic-endobenthic decapod crustaceans from the western Mediterranean Sea

Species	Wet mass range (g)	Water content (% WM)	Energy content (kJ J ⁻¹ WM)	Energy content (kJ J ⁻¹ WM)	Energy content (kJ J ⁻¹ AFDM)	Organic content (% DM)
Nekto-benthic						
<i>A. antennatus</i>	8.18–42.31	73.69 ± 2.12 (45)	5.396 ± 0.76 (14)	21.115 ± 1.77 (14)	26.259 ± 1.28 (14)	79.75 ± 3.11 (20)
<i>A. eximia</i>	5.39–8.61	79.36 ± 2.04 (3)	3.767 ± 0.62 (2)	19.315 ± 1.23 (2)	24.517 ± 0.48 (2)	78.75 ± 2.47 (2)
<i>L. ensiferus</i>	2.97–3.96	78.38 ± 2.55 (3)	3.814 ± 0.72 (2)	19.075 ± 2.24 (2)	24.493 ± 1.06 (2)	79.49 ± 4.13 (3)
<i>P. acantonotus</i>	3.10–5.52	75.32 ± 1.70 (3)	5.071	19.024	25.206	75.48 ± 3.34 (3)
<i>P. canaliculata</i>	1.74–2.58	78.18 ± 2.09 (4)	4.027 ± 0.61 (4)	18.416 ± 1.16 (4)	23.494 ± 1.34 (4)	78.40 ± 2.24 (4)
<i>P. edwardsi</i>	4.83–15.19	74.41 ± 2.13 (22)	5.156 ± 0.56 (18)	20.252 ± 0.90 (18)	25.070 ± 1.03 (18)	80.95 ± 1.55 (20)
<i>P. gti glioli</i>	1.38–3.35	76.97 ± 2.46 (16)	4.178 ± 0.61 (10)	18.478 ± 1.42 (10)	23.796 ± 1.89 (10)	77.71 ± 2.05 (10)
<i>P. heterocarpus</i>	2.69–5.81	76.93 ± 2.44 (16)	4.033 ± 0.74 (11)	17.842 ± 1.17 (11)	23.632 ± 1.42 (11)	75.51 ± 2.31 (11)
<i>P. longirostris</i>	9.46–13.10	73.22 ± 3.53 (2)	4.347	18.707	23.425	80.15 ± 0.29 (2)
<i>P. martia</i>	2.28–9.66	75.36 ± 1.81 (10)	5.282 ± 0.64 (8)	21.430 ± 0.98 (8)	25.699 ± 0.69 (8)	83.50 ± 2.17 (9)
<i>S. membranacea</i>	1.95–6.23	78.82 ± 0.93 (11)	3.383 ± 0.26 (10)	15.893 ± 0.78 (10)	22.246 ± 0.85 (10)	71.27 ± 1.60 (11)
Total mean		76.42 ± 2.04 (11)	4.405 ± 0.70 (11)	19.050 ± 1.54 (11)	24.349 ± 1.36 (11)	78.27 ± 3.11 (11)
Benthic and endobenthic						
<i>G. longipes</i>	15.33–161.70	73.53 ± 1.54 (3)	3.144 ± 0.28 (3)	11.869 ± 0.28 (3)	22.067 ± 0.25 (3)	53.80 ± 1.49 (3)
<i>G. rhomboides</i>	0.75–4.22	63.23 ± 4.99 (2)	2.717	6.507	18.075	35.99
<i>H. barbata</i>	8.70	73.29	2.650	9.921	20.268	48.95
<i>L. depurator</i>	21.00	68.29	3.400	10.720	21.283	50.37
<i>M. couchi</i>	1.90–10.51	63.06 ± 2.77 (4)	2.226 ± 0.09 (2)	5.800 ± 0.41 (2)	20.983 ± 2.50 (2)	27.96 ± 3.72 (2)
<i>M. intermedia</i>	1.41–12.67	71.44 ± 3.49 (11)	3.170 ± 0.50 (8)	11.189 ± 2.17 (8)	19.492 ± 2.43 (8)	57.11 ± 4.46 (8)
<i>M. tenuimana</i>	1.18–7.07	71.72 ± 3.72 (18)	2.996 ± 0.46 (11)	11.147 ± 0.85 (11)	20.885 ± 1.50 (11)	53.49 ± 4.66 (11)
<i>M. tuberculatus</i>	3.25–13.39	72.64 ± 1.93 (5)	2.673 ± 0.05 (2)	10.555 ± 0.80 (2)	19.413 ± 0.09 (2)	54.39 ± 3.10 (2)
<i>N. norvegicus</i>	19.39–78.44	74.47 ± 0.96 (4)	3.343 ± 0.13 (2)	13.267 ± 0.29 (2)	21.037 ± 0.23 (2)	58.64 ± 6.26 (3)
<i>P. norvegicus</i>	0.60	80.30	3.164	16.065	22.878	70.22
<i>P. typhlops</i>	2.92–26.67	82.41 ± 2.34 (11)	2.887 ± 0.51 (8)	16.468 ± 0.86 (8)	23.126 ± 1.64 (8)	71.38 ± 3.86 (8)
Total mean		72.22 ± 6.19 (11)	2.943 ± 0.35 (11)	11.228 ± 3.31 (11)	20.864 ± 1.52 (11)	52.93 ± 12.16 (11)

Note: Number of individuals, in parentheses. ± SD: standard deviation; WM: wet mass; DM: dry mass; AFDM: ash-free dry mass.

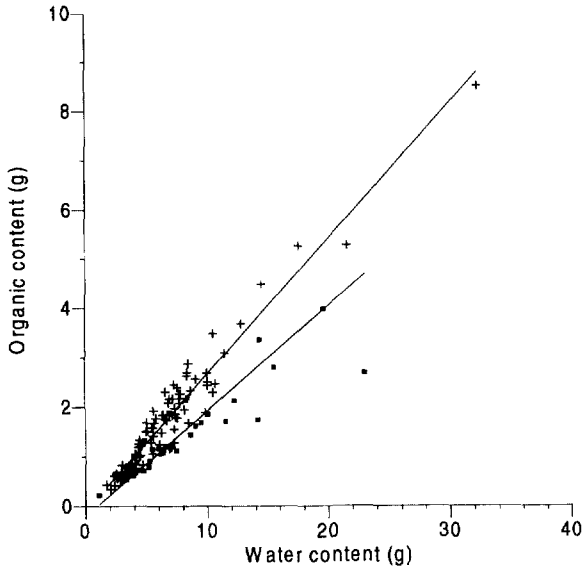


Fig. 3. Individual organic content (g) vs individual water content (g) for the decapod crustaceans considered. Regression-line statistics, coefficient of correlation, and P values for regression exponents are, nektobenthic species (+): $Y = 0.27X - 0.09$, $r = 0.97$, $n = 91$, $p = 0.0001$; benthic-endobenthic species (■): $Y = 0.21X - 0.20$, $r = 0.99$, $n = 38$, $p = 0.0001$. The difference between the slopes is significant ($p = 0.0000$, t -test).

3.2. Energy content, organic content and water content

Table 3 shows that water content was highest in *Polycheles typhlops* (82.41% WM) and lowest in *Monodaeus couchi* (63.06% WM). The highest energy values were recorded for *Aristeus antennatus* ($5.396 \text{ kJ g}^{-1} \text{ WM}$) and the lowest for *Monodaeus couchi* ($2.226 \text{ kJ g}^{-1} \text{ WM}$). Organic % DM was highest in *Plesionika martia* (83.50% DM) and lowest in *Monodaeus couchi* (27.96% DM).

The mean values for water content, $\text{kJ g}^{-1} \text{ WM}$, $\text{kJ g}^{-1} \text{ DM}$, $\text{kJ g}^{-1} \text{ AFDM}$ and organic content were significantly higher for the nektobenthic species than the benthic-endobenthic species (t -test, $p < 0.05$ in all cases), and the range of variability in the results was likewise narrower for the nektobenthic species (Table 3). This lower variability may be attributable to the fact that all the nektobenthic species belonged to just two infraorders, Penaeoidea and Caridea. In contrast, the benthic-endobenthic species belonged to six different infraorders much further apart evolutionarily.

Fig. 3 shows the regressions lines between the organic content and water content, expressed as grams of organic matter and grams of water per individual. The slopes of the regressions for nektobenthic and benthic-endobenthic species were significantly different (t -test, $p < 0.0000$), showing a higher water content, per unit of organic

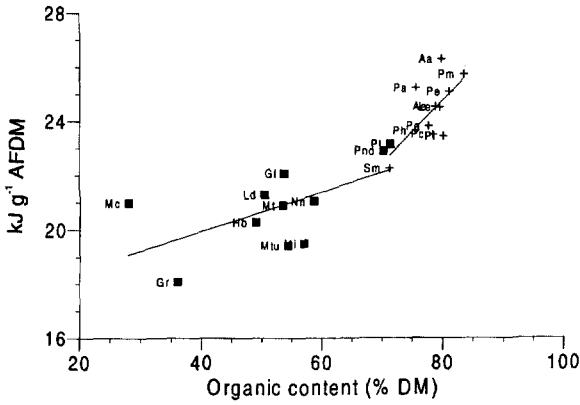


Fig. 4. Energy content (kJ g^{-1} AFDM) vs organic content (% DM) in the two life strategies considered (species codes as in Table 1). Regression-line statistics, coefficient of correlation, and P values for regression exponents are, nektobenthic species (+): $Y = 0.23X + 6.14$, $r = 0.65$, $n = 11$, $p = 0.0298$; benthic-endobenthic species (■): $Y = 0.07X + 17.1$, $r = 0.60$, $n = 11$, $p = 0.0498$.

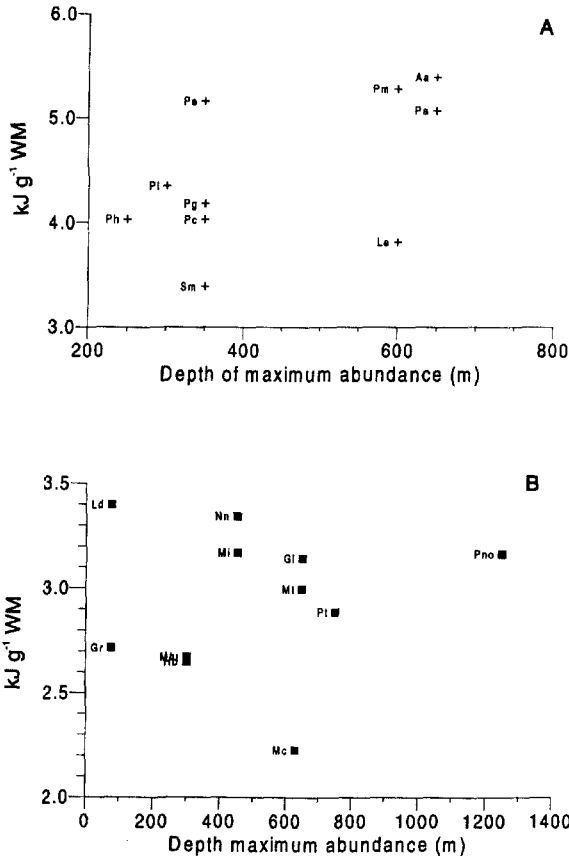


Fig. 5. Energy content (as a function of wet mass) vs depth of maximum abundance. Species codes as in Table 1; +: nektobenthic species (Fig. 5A); ■: benthic-endobenthic species (Fig. 5B).

content, in the benthic-endobenthic species. The relationship between the organic content (% DM) and its energy content (kJ g^{-1} AFDM) (Fig. 4) shows a higher increase in energy content with increasing mass in nektobenthic species. An increase in organic content from 30 to 70% DM was associated with an increase of only 5 kJ g^{-1} AFDM in benthic-endobenthic species. In nektobenthic species, the same increase in energy content (5 kJ g^{-1} AFDM) was accomplished only by an increase from 70 to 85% in organic content.

The mean specific values for energy content (kJ g^{-1} WM) vs depth of maximum occurrence are presented for the two life strategies and the two depth communities considered in this study in Fig. 5. The nektobenthic species exhibited a slight increase

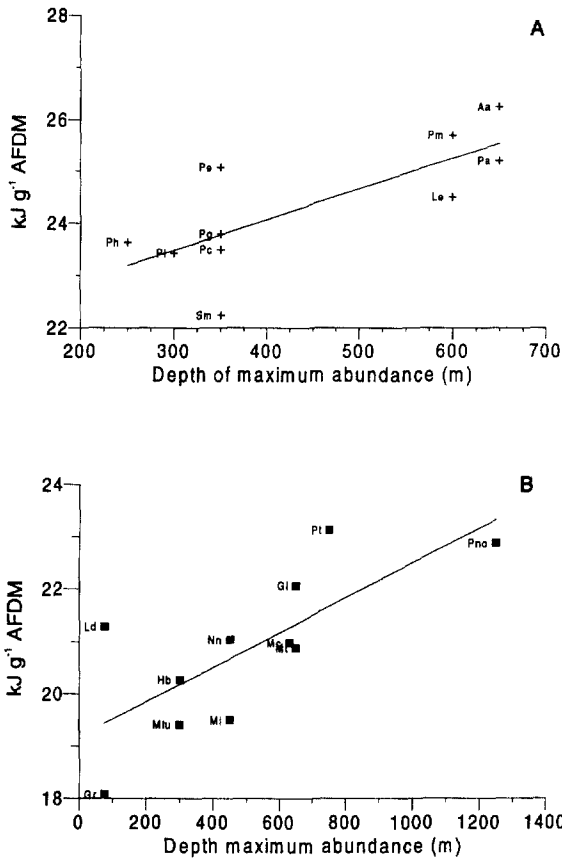


Fig. 6. Energy content (as a function of ash-free dry mass) vs depth of maximum abundance. Regression-line statistics, coefficient of correlation, and *P* values for regression exponents are, nektobenthic species (Fig. 6A): $Y = 0.006X + 21.70$, $r = 0.76$, $p = 0.0105$; benthic-endobenthic species (Fig. 6B): $Y = 0.003X + 19.20$, $r = 0.74$, $p = 0.0099$. Species codes as in Table 1; +: nektobenthic species; ■: benthic-endobenthic species.

in energy content (as a function of wet mass) with increasing depth of maximum abundance, but the regression was not significantly different from 0 ($r = 0.546$; $p = 0.1031$) (Fig. 5A). Any general trend was found between energy content (as WM) and depth of maximum abundance for the benthic-endobenthic species (Fig. 5B). When the results were expressed in terms of ash-free dry mass, a significant relationship between energy content and depth of maximum abundance was found in both nektobenthic (Fig. 6A, $r = 0.762$, $p = 0.0105$) and benthic-endobenthic (Fig. 6B, $r = 0.736$, $p = 0.0033$) species. Only the benthic-endobenthic species exhibited a significant increase in water content with depth of maximum abundance (Fig. 7).

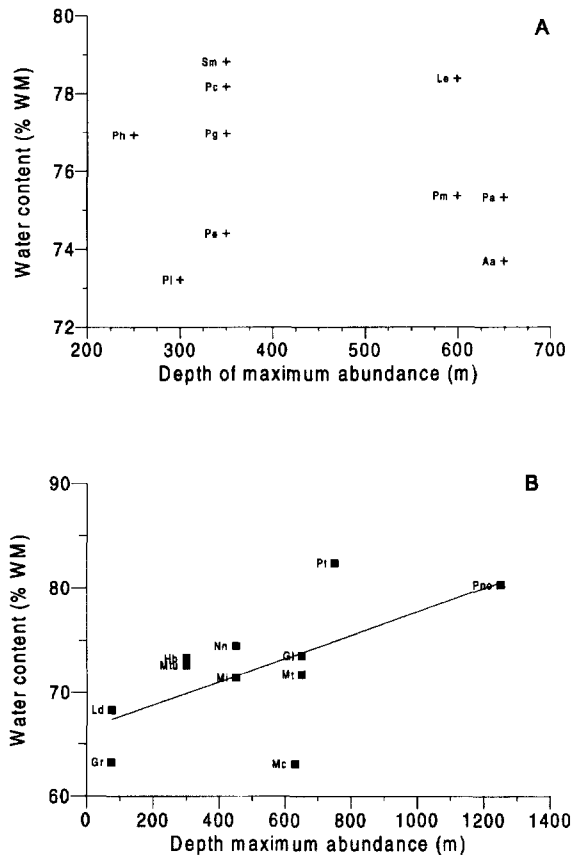


Fig. 7. Water content vs depth of maximum abundance. No significant relationship was found between water content and depth of maximum abundance in nektobenthic species (Fig. 7A). Regression-line statistics, coefficient of correlation, and P values for regression exponents for benthic-endobenthic species (Fig. 7B) are, $Y = 0.01X + 66.5$, $r = 0.63$, $p = 0.0383$. Species codes as in Table 1; +: nektobenthic species; ■: benthic-endobenthic species.

4. Discussion

The mean energy content of the deep-sea nektobenthic and benthic-endobenthic decapod crustaceans in the Western Mediterranean, 24.349 and 20.864 kJ g⁻¹ AFDM respectively, falls within the range of values reported by other investigators. Wakasey and Atkinson (1987) recorded a mean of 23.368 kJ g⁻¹ AFDM in shallow-water benthic decapods in the Canadian Arctic; Thayer *et al.* (1973) found a mean of 22.560 kJ g⁻¹ AFDM in estuarine decapods in the North Atlantic; and Dauvin and Joncourt (1989) reported a mean of 20.533 kJ g⁻¹ AFDM in shallow-water benthic decapods in the western English Channel. No values for deep-sea benthic decapod crustaceans were found in the literature for comparison with the results of the present study. The interspecific differences in energy content, depending on different life strategies, have also been noted by other workers. Griffiths (1977) and Norrbin and Båmstedt (1984) reported differences between shallow-water planktonic and benthic species, with higher values in the former. The present results have shown differences between two groups of benthic species. The nektobenthic subgroup, generally represented by penaeideans and carideans, had higher energy contents and oxygen consumption rates than the benthic-endobenthic subgroup, represented by strictly benthic decapod crustaceans.

The mean energy values found in the present study were 4.405 kJ g⁻¹ WM for nektobenthic species and 2.944 kJ g⁻¹ WM for benthic-endobenthic species. Using data on deep-sea midwater decapods from the same depth range off Southern California (Childress and Nygaard, 1974) we have calculated a mean value of 4.878 kJ g⁻¹ WM. Several authors have suggested that there is an evolutionary trend towards higher energy levels in species that inhabit regions with fluctuating food availability as compared to species that inhabit regions of greater environmental predictability (Slobodkin and Richman, 1961; Childress *et al.*, 1990b). The lower values recorded for the benthic-endobenthic species are consistent with that hypothesis, in that the sea floor habitat is more stable than the nektobenthic and midwater habitats.

Childress and Nygaard (1973, 1974) [for deep-sea midwater crustaceans and fishes] and Raymont *et al.* (1969) [for marine zooplankton] related energy content to the presence of lipids and found high lipid contents and low carbohydrate contents in those midwater species. At present, available data on deep-sea benthic decapod crustaceans are insufficient for direct quantitative comparison of the biochemical composition of animals dwelling in the midwater and benthic habitats. However, Fig. 4 shows that the increase in energy content as the organic content increased was not as pronounced in the benthic-endobenthic species as in the nektobenthic species, possibly because of a higher percentage of lipid content in the nektobenthic species. Such a higher lipid content would furnish nektobenthic and midwater species with a means for storing larger amounts of energy with a smaller increase in mass. The high water content in proportion to the low organic content found in the benthic-endobenthic species as compared to the nektobenthic species (Fig. 3) indicated that mass is not a delimiting factor in benthic-endobenthic species. The results for oxygen consumption also revealed differences between the two groups. The mean oxygen consumption

rates found in this study were $0.033 \text{ ml O}_2 \text{ mg}^{-1} \text{ WM h}^{-1}$ in the benthic-endobenthic species and $0.093 \text{ ml O}_2 \text{ mg}^{-1} \text{ WM h}^{-1}$ in the nektobenthic species. The mean value for deep-sea midwater decapod crustaceans calculated using data published by Childress (1975), Donnelly and Torres (1988), and Cowles *et al.* (1991) for a temperature ranging between 5 and 14°C was $0.115 \text{ ml O}_2 \text{ mg}^{-1} \text{ WM h}^{-1}$, higher than the value recorded here for benthic species in the western Mediterranean.

The present results suggest separate overall energy patterns for each of the three life strategies and the adaptability of those species in their habitats. *Benthic-endobenthic*: strictly benthic species that are poor swimmers and are relatively large and heavy, chiefly anomuran and brachyuran crabs. They have high water contents, low organic matter contents, and also have low oxygen consumption rates and energy contents (the composition of these species is most likely low in lipids). *Nektobenthic*: an intermediate group consisting of benthic species that are nonetheless quite good swimmers. The species in this group have intermediate energy values, water contents, and oxygen consumption rates. *Midwater*: species with more pronounced migratory behaviour in which mass is an important factor in their adaptation to the habitat. They should have higher lipid contents, lower water contents, lower carbohydrate contents, higher energy contents, and higher oxygen consumption rates as compared to the two preceding groups.

Childress and Nygaard (1974) reported a tendency for energy values (expressed both as function of wet mass and ash-free dry mass) to increase in midwater crustaceans with increasing depth from 0 to 650 m, and several other authors have described an increasing in lipid content for deep-water species when compared with shallow-water species (Lee *et al.*, 1971; Herring, 1973). The results for the nektobenthic species indicate that members of the middle slope community (550–1250 m) had a slightly higher (but not statistically significant) energy values (in terms of wet mass) than members of the upper slope community (200–450 m), and any significant tendency between energy contents and depth of maximum abundance was found for the benthic-endobenthic species (Fig. 5). The high water content per unit of organic content (Fig. 3) and the increasing water content as depth of maximum abundance (Fig. 7B) found in the benthic-endobenthic species may explain why no relationship was found between energy content (as wet mass) and depth of maximum abundance.

Trophic strategy may play a role in the observed trends in energy content and metabolism in the nektobenthic species. Cartes (1991, 1993) described how the most abundant nektobenthic species in the middle slope community, *Plesionika acanthonotus* and *Plesionika martia*, prey upon the mesopelagic species *Pasiphaea sivado* and *Pasiphaea multidentata*. The dependence of these nektobenthic species on a food resource (mesopelagic species) that fluctuated in its availability could be the reason for the high energy content of the nektobenthic species on the middle slope. Accumulation of energy reserves in species dependent upon unstable food resources has been reported by several authors (Slobodkin and Richman, 1961; Lee *et al.*, 1971; Griffiths, 1977). There were no significant variations in energy values (in terms of the whole animal, i.e., as a function of WM) in the strictly benthic species (benthic-endobenthic) with depth. Cartes (1991) reported that these species fed more directly on benthic

macrofauna and that detritus was abundant in their stomach contents. This last-mentioned feature, together with their highly stable food sources, a characteristic of the benthic environment, would tend to favour lower variability with depth in the benthic-endobenthic species than in the nektobenthic species.

Oxygen consumption increased slightly with depth in the nektobenthic species. However, oxygen consumption values were available only for a single species (*Aristeus antennatus*) on the middle slope, hence it is not possible to consider any general pattern for the nektobenthic habit in the 200–1250 m depth range. There was a significant drop in oxygen consumption with depth in the benthic-endobenthic species (Fig. 2). The decrease in metabolic rate with depth would thus be a result of a generalized structural reduction, with an increase in water content (Fig. 7B), and would not be accompanied by a marked decrease in energy content. Considering that oxygen consumption is closely related to energetic procurement (Schmit-Nielsen, 1990), the results would be consistent with the different trophic strategy of species dwelling in the benthic-endobenthic habit. Overall, benthic-endobenthic species feed more directly on detritus and benthic macrofauna, but Abelló (1986) and Cartes (1991) observed that species on the upper slope were more active feeders, preying on mobile prey items and presenting higher stomach fullness indices than species inhabiting the middle slope and lower slope.

Childress and Mickel (1985) and Childress *et al.* (1990a) concluded that midwater species underwent a reduction in metabolic rate with depth greater than that caused solely by lower temperatures, and that the observed reduction was related to a reduction in mobility. They suggested that deep-sea species have a less active predator–prey relationship because of the lower light levels: the visual interaction hypothesis. On the other hand, they concluded that strictly benthic species did not undergo a reduction in metabolic rate with depth. Such species have adapted to deeper habitats, which offer more opportunities for shelter, concealment, and feeding strategies, and thus the visual interaction hypothesis would not be applicable to a strictly benthic habit.

Summing up the findings of this study, the benthic-endobenthic decapod crustacean species in the western Mediterranean also showed a decrease in metabolic rate that was not attributable to size or temperature. Benthic-endobenthic species exhibited a significant decrease in oxygen consumption and an increase in water content with depth of maximum abundance over the depth range studied (200–1250 m). Based on these results, the visual interaction hypothesis (Childress and Mickel, 1985; Childress *et al.*, 1990) may also be applicable to species that have adopted the benthic-endobenthic life strategy in the Mediterranean Sea. The relationship between life strategy, metabolism, and energy content in the isothermal deep-sea environment in the western Mediterranean would appear to be part of the adaptation to the nektobenthic and benthic habits.

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