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Growth parameters of deep-water decapod crustaceans in the Northwestern Mediterranean Sea: a comparative approach

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Abstract Relative and absolute growth were studied in 17 species of deep-water decapod crustaceans, spanning nine families of six different infra-orders, in the Northwestern Mediterranean Sea. The overall maximum abundance of these species lay between 200 m and 750 m (i.e. upper- and mid-slope species). Relative and absolute growth rates were compared by contrasting the slopes of the size–weight relationships for the different species and calculating the von Bertalanffy growth-equation parameters asymptotic length (L_{∞}) and growth rate (k). The size–weight relationships differed significantly as function of the species' life habits. The results revealed a significant decrease in weight relative to size in mesopelagic species (which carry out diel vertical migrations), an almost isometric relationship between size and weight in the less mobile nektobenthic species, and a significant increase in weight relative to size in strictly benthic species. The mean allometric coefficient for each group increased significantly from mesopelagic to benthic species. However, no general trend was observed in the growth-performance index, Φ (an index used to compare absolute growth rates between species, as a function of habit and depth of maximum abundance for all species combined), suggesting that the deep-water decapod crustaceans studied have similar absolute growth rates. Nevertheless, comparison of growth-parameter and growth-performance index values within families did reveal differences. Mesopelagic species of the families Sergestoidae and Pasiphaeidae showed slightly increased growth rates with increasing depth of distribution. Nektobenthic species of the genus *Plesionika* followed a trend opposite to that shown by me-

sopelagic species, with a higher growth rate for the shallowest-dwelling species (*P. heterocarpus*) than the deepest-dwelling species (*P. acanthonotus*). Taking growth as one of the major components of an organism's energy budget, the growth rates for the decapod crustacean species in this study were significantly lower than those reported in the literature for shallow-water penaeid crustacean species (which are distributed in higher-temperature habitats than deep-water Mediterranean crustaceans) and higher than those reported for mesopelagic myctophid fish species. Hence, the well-defined growth trends shown by deep-water decapod crustacean species in the Northwestern Mediterranean Sea, compared to the less well-defined trends in the other taxa, is discussed in the framework of the overall dynamics of their ecosystem.

Introduction

Moult cycles, synchronisation between moulting and reproduction, berrying in some species, and size-related growth rates are the main intrinsic factors introducing uncertainty into estimates of growth parameters in crustaceans (Drach 1939; Passano 1960; Aiken 1980; Hartnoll 1983; Caddy 1987). External parameters such as temperature, hours of daylight, and food availability may also stimulate or inhibit growth processes (Venner 1985). All these aspects have received considerable attention in species held in captivity and in coastal-water peneids held in pounds. While certain studies have dealt specifically with the influence of various processes relating to the effect of metabolism, muscle growth and hormonal stimulation on growth in crustaceans, and the effect of regeneration on moulting in carideans and peneids (Descouturelle 1976; Richard 1978; Emmerson 1980) and in spiny and clawed lobsters (Aiken 1980; Morgan 1980; Conan 1985), no general studies have used standardised methodology that would make them comparable between species. Nevertheless, individual growth studies using cultured specimens and free-living

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animals have made a substantial contribution to the present state of knowledge of specific growth processes in shallow-water crustaceans (Cobb and Phillips 1980; Bliss 1983) and in midwater species (Childress et al. 1980; Childress and Price 1983).

Modal progressions in the time-series of the size-frequency distributions compiled from random samples of commercial catches or experimental catches made by research vessels have proved to be one of the most useful methods of estimating growth parameters for crustaceans in the field (Sparre et al. 1989). This type of research is carried out regularly in the case of coastal peneids (Garcia and Le Reste 1987), but for species dwelling at greater depths, it is carried out only for species of considerable commercial interest, such as the nekto-benthic shrimp *Pandalus borealis* or the benthic Norway lobster *Nephrops norvegicus* (Anonymous 1997a, b). Growth of deep-water crustaceans is generally considered to be slower, chiefly because of the lower temperature and low productivity of deeper waters, although the literature is sparse (Mauchline 1972; Gage and Tyler 1991). *N. norvegicus* (Sardà 1985; Mytilineou et al. 1998) and *Aristeus antennatus* (Relini Orsi and Relini 1985; Sardà and Demestre 1987; Demestre 1990), at depths > 400 m, and *Liocarcinus depurator* (Abelló 1986) and *Solenocera membranacea* (Demestre and Abelló 1993), at depths < 400 m, are some of the most important commercial species in the Western Mediterranean Sea on which growth studies have been published.

As growth and reproduction are two of the major processes that require the greatest energy inputs in the life cycle of decapod crustaceans, the object of the present paper was to estimate the relative and absolute growth parameters for 17 decapod crustacean species in the Western Mediterranean Sea. With a view to use in general studies on ecology, standardised methodology was employed in preparing the estimates to ensure that the results would be comparable. The results are discussed in terms of the main environmental parameters, e.g. depth and temperature and in terms of life habits. The Mediterranean Sea affords optimal conditions for comparative studies of the growth rates of deep-water species, because at depths > 200 m temperature is constant at $13\text{ }^{\circ}\text{C} \pm 0.5\text{ }^{\circ}\text{C}$ (Hopkins 1985), thereby avoiding one of the major factors introducing variability in growth rates.

Materials and methods

The 17 decapod crustacean species compared in the present study are members of the crustacean fauna of the slope community in the Western Mediterranean (Fig. 1) and belong to nine families of six different infra-orders (Table 1). Together, the species studied account for > 90% of decapod crustacean biomass on the slope in the Northwestern Mediterranean Sea (Abelló et al. 1988; Cartes and Sardà 1992; Cartes et al. 1994a).

Once a month from November 1992 to October 1993, trawl catches were made off Barcelona at depths between 250 and 800 m

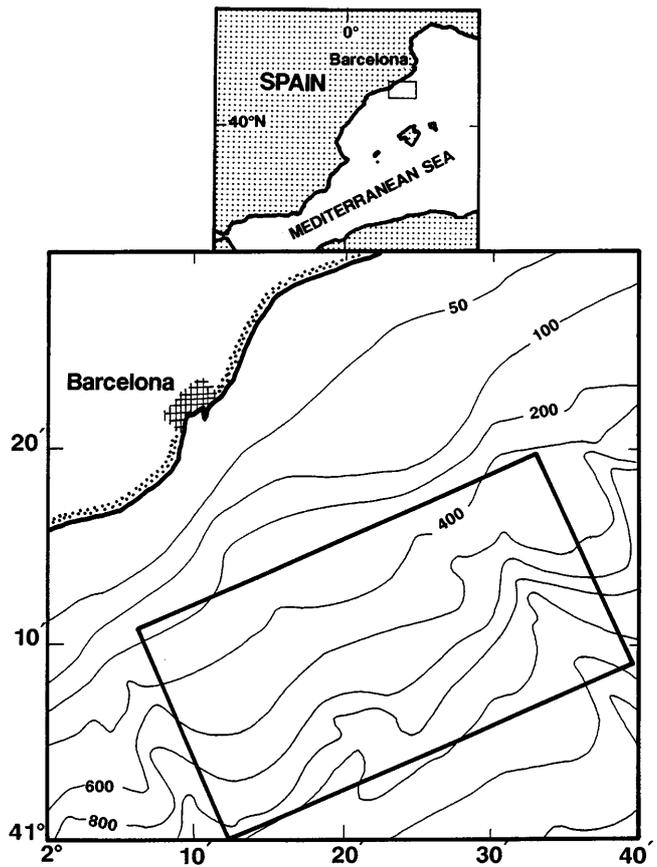


Fig. 1 Study area (rectangle) in Catalan Sea, Northwestern Mediterranean (41°N ; 02°E). Depth contours (m) are shown

with commercial fishing vessels (Fig. 1, Table 2). Six additional seasonal sampling cruises were carried out from spring 1991 to summer 1992 by the R.V. "García del Cid" to increase the depth range sampled (down to 1300 m). To avoid sampling bias, a similar type of gear was used for all trawls: commercial otter trawl, Maireta-system otter trawl (OTMS; Sardà et al. 1998), and semi-balloon otter trawl-14 (OTSB-14; Merret and Marshall 1981), all fitted with a 6 mm-mesh cod-end liner. The sampling design was intended to yield representative samples of the overall size range of each species that would offer both temporal (monthly samples) and spatial (broad depth range) continuity. Monthly samples were treated separately by month (from spring 1991 to fall 1993), and were never pooled. The depth range sampled was selected on the basis of information published in previous studies on the communities inhabiting the study area (Abelló et al. 1988; Cartes and Sardà 1992; Cartes 1993; Cartes et al. 1994a). The depth range, depth of maximum abundance for each species, and life habits are shown in Table 1 (after: Largardère 1977; Abelló et al. 1988; Cartes and Sardà 1992; Cartes 1993; Cartes et al. 1994a). Although the depth distributions of some of the species included extend down to nearly 2000 m, the overall maximum abundances for all species considered lay between 200 and 750 m (Abelló et al. 1988; Cartes and Sardà 1992; Cartes et al. 1994a; Company and Sardà 1997). Swimming behavior, catch methods and trophic aspects were chosen to establish the life habits described in the present study (after: Heegaard 1967; Burukovsky 1972; Lagardère 1977; Omori and Ohta 1981; Cartes 1991, 1993, 1995; Cartes et al. 1993, 1994b).

To show the overall size range sampled, Fig. 2 presents the size-frequency distribution of all 17 species studied. With the exception of *Geryon longipes* and *Paramola cuvieri*, individuals as small as 6 mm standard carapace length (CL) were captured. Mesopelagic species display diel vertical migration (Sardou et al. 1996), and

Table 1 Decapod crustaceans. Depth range, depth of maximum abundance, and number of individuals sampled of 17 species from western Mediterranean Sea (*Mes*, *Nek*, *Ben* mesopelagic, nekto-benthic and benthic species, respectively; *I* indeterminate individuals; *F* female; *M* males; *nd* no data)

Species	Species' code	Depth range (m)	Depth of max. abundance (m)	Habit	No. individuals measured	No. individuals sexed:		
						I	F	M
Suborder Dendrobranchiata								
Infraorder Penaeidea								
Family Aristeidae								
<i>Aristeus antennatus</i> ^a	Aa	176–2261	650	Nek	nd	nd	nd	nd
Family Solenoceridae								
<i>Solenocera membranacea</i>	Sm	3–871	350	Nek-Ben	6810	2	4899	1909
Family Sergestoidae								
<i>Sergestes arcticus</i>	Sa	180–2261	400	Mes	3174	0	1659	687
<i>Sergia robusta</i>	Sr	220–2261	550	Mes	1711	13	913	476
Suborder Pleocyemata								
Infraorder Caridea								
Family Pasiphaeidae								
<i>Pasiphaea sivado</i>	Ps	33–871	350	Mes	4156	20	982	1425
<i>Pasiphaea multidentata</i>	Pmu	128–2261	550	Mes	5491	2474	952	516
Family Processidae								
<i>Processa nouveli</i>	Pn	148–622	250	Nek-Ben	1672	0	730	537
<i>Processa canaliculata</i>	Pc	70–871	350	Nek-Ben	2617	0	1435	974
Family Pandalidae								
<i>Plesionika heterocarpus</i>	Ph	82–699	250	Nek	2831	12	1373	1446
<i>Plesionika edwardsi</i>	Pe	256–512	350	Nek	1790	8	834	598
<i>Plesionika gigliolii</i>	Pg	101–748	350	Nek	1601	2	828	523
<i>Plesionika martia</i>	Pm	165–871	600	Nek	3877	76	1671	1600
<i>Plesionika acanthonotus</i>	Pa	165–1749	650	Nek	928	68	492	368
Infraorder Astacidea								
Family Nephropidae								
<i>Nephrops norvegicus</i> ^b	Nn	66–871	450	Ben	nd	nd	nd	nd
Infraorder Palinura								
Family Polychelidae								
<i>Polycheles typhlops</i>	Pt	267–1949	750	Ben	881	4	605	272
Infraorder Anomura								
Family Galatheidae								
<i>Munida intermedia</i>	Mi	35–871	450	Ben	672	0	353	319
<i>Munida tenimana</i>	Mt	348–1949	650	Ben	1353	0	648	705
Infraorder Brachyura								
Family Homolidae								
<i>Paromola cuvieri</i>	Pcu	136–1149	350	Ben	41	0	15	26
Family Geryonidae								
<i>Geryon longipes</i>	Gl	439–1949	650	Ben	522	0	80	422

^a After Demestre (1990)

^b After Sardà and Leonart (1993)

Table 2 Cruises, trawl system, number of trawls, sampling frequency, season and depth range sampled (*OTMS*, *OTSB* Marietta-system otter trawl, semi-balloon otter trawl-14, respectively)

Cruise	Trawl system	No. of trawls	Sampling frequency	Sampling period	Depth range (m)
COM	Commercial bottom trawl	38	12 surveys (monthly)	Nov 1992–Oct 1993	300–800
RETRO I–IV	OTMS	37	4 surveys (seasonal)	Spring 1991 (RI), Autumn 1991 (RII), Winter 1992 (RIII), Summer 1992 (RIV)	330–1300
GII	OTMS	56	1 survey	Autumn 1991	230–610
ZONAP I	OTSB-14	24	1 survey	Spring 1992	219–1032

vertical size-structure differentiation of their populations (Cartes et al. 1994b). Thus, if a benthic trawl is used, sampling problems may occur. The size range sampled in this study (Fig. 2) indicates that juveniles of all species were sampled. For some species (*Solenocera membranacea*, *Pasiphaea multidentata*, *Processa canaliculata* or *Plesionika acanthonotus*), juvenile individuals were

well represented, but an undersampling for small-sized individuals occurred for some other species (*Pasiphaea sivado*, *Plesionika heterocarpus*, *P. edwardsi*). Estimation of growth parameters by modal progressions of size-frequency distributions is barely affected by undersampling a determinate size-group (Gayaniño et al. 1988).

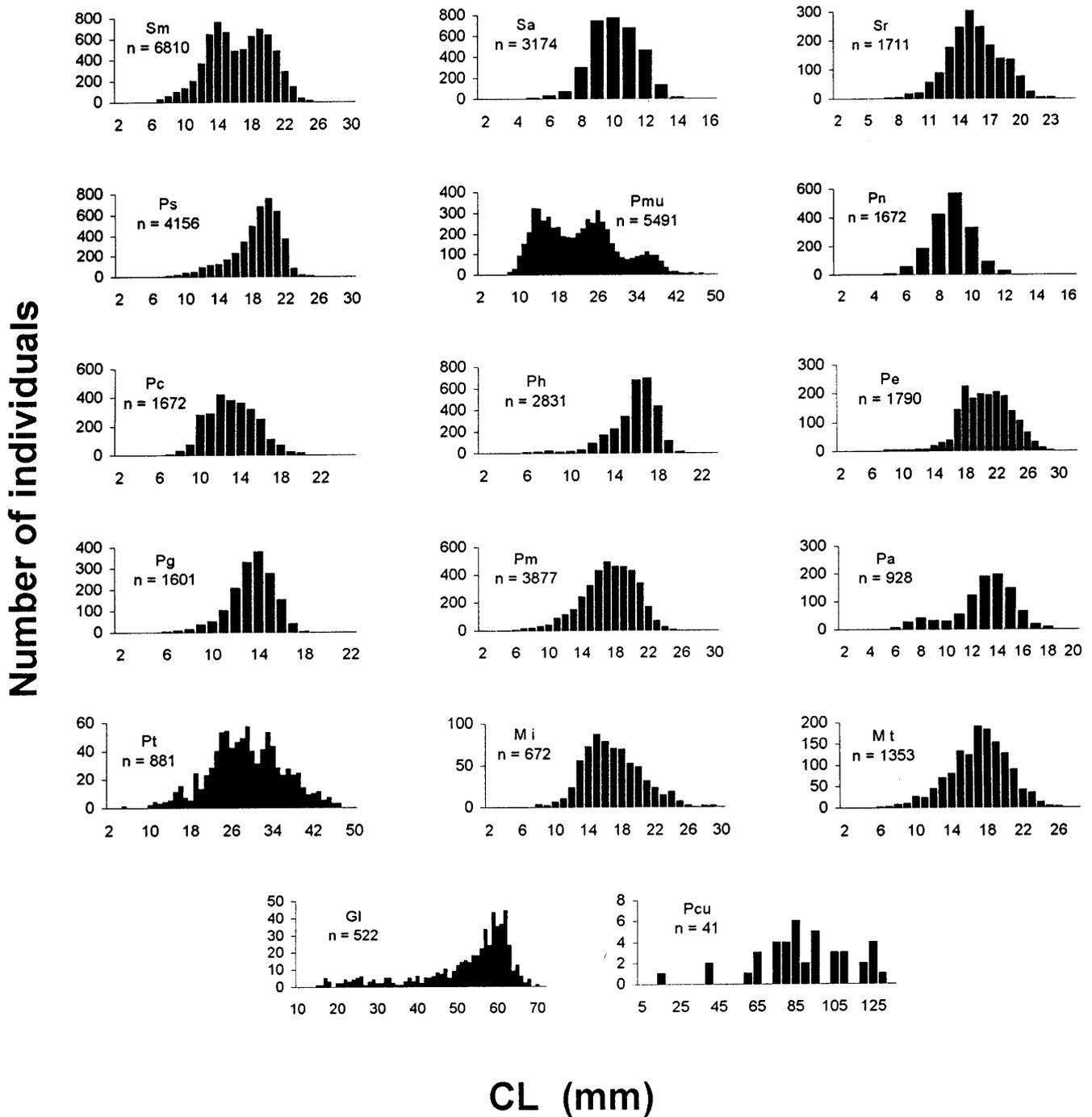


Fig. 2 Decapod crustaceans. Size-frequency histograms of 17 species from western Mediterranean Sea. Species' codes as in Table 1 (CL carapace length)

The specimens collected in each sample were separated by species, and the sex of each individual was determined to preclude possible size differences attributable to sexual dimorphism. All specimens were measured to the nearest 0.1 mm with a digital calliper. Standard carapace length was measured from the post orbital socket to the posterior median edge of the cephalothorax. Whenever necessary, a binocular microscope was employed to determine sex, which was established on the presence or absence of the male appendage on the second pair of pleopods (Zariquiey Alvarez 1968). Individuals were blotted dry and weighed to the

nearest 1 mg. The total number of specimens measured was 40 127 (breakdown in Table 1).

The size-weight relationship was calculated according to the power equation $y = a \cdot x^b$, where x = size (CL) in mm, y = weight in g, and b = the allometric coefficient (or slope). Analysis of variance (ANOVA) was used to test deviations in the value of the allometric coefficient from the theoretical value for isometric growth ($b = 3$). Only non-ovigerous females and ovigerous females with eggs removed were used in the calculations of the size-weight relationship. For each of the 17 species considered, three separate calculations of the size-weight relationship were made: the two sexes combined together with specimens of indeterminate sex (i.e. indeterminates+females+males), females and males. Von Bertalanffy growth parameters (von Bertalanffy 1934) were also calculated separately for females, males, and the two sexes com-

bined (including specimens of indeterminate sex) for 16 species in all. The growth parameters L_∞ (theoretical maximum individual size) and k (annual growth rate, or the rate at which individuals approach L_∞) were calculated by modal progression in the time-series of monthly size-frequency distributions. The calculations were performed with the ELEFAN statistical package according to the method of Pauly (1981) as modified by Gayanilo et al. (1988). This method was chosen because it affords the following advantages: (1) it is the most widely used method for decapod crustacean species, and thus contributes to the presentation of new data in a manner consistent with and comparable to those in the literature; (2) it includes an option for fitting the growth curve to a variable model taking seasonality into account (seasonal growth fluctuations are extremely marked in decapod crustaceans: Hartnoll 1983); (3) the model includes an index of the goodness of fit for the von Bertalanffy curve. Gayanilo et al. (1988) modified the von Bertalanffy growth function as follows:

$$L(t) = L_\infty \cdot [1 - e^{(-k(t-t_0) - (CK/2\pi) \cdot \sin(2\pi \cdot (t-tw+0.5)))}] , \quad (1)$$

where t_0 = age at size 0 and tw = period of slow growth, computerized in the ELEFAN software as the winter point ($WP = tw + 0.5$). WP values range between 0 and 1; values close to 0 or 1 indicate a slow-down in growth during the winter months; values close to 0.5 indicate that the slow-down in growth takes place in summer. C = the amplitude of the seasonality factor, which also ranges between 0 and 1; for values of C close to 0, the equation reduces exactly to the von Bertalanffy equation without seasonality; for values close to 1, the amplitude of the seasonality factor is maximal.

Since the parameters L_∞ and k are inversely correlated, the growth-performance index Φ was calculated to enable comparison of growth rates among the different species (Munro and Pauly 1983; Pauly and Munro 1984):

$$\log_{10} k = \Phi - 0.67 \cdot \log_{10} W_\infty , \quad (2)$$

where W_∞ = weight at size L_∞ , calculated using the power equation $W_\infty = aL_\infty^b$, with a and b calculated from the size-weight relationships for the specimens analysed in this study.

Also included in the "Discussion" are the von Bertalanffy growth-parameter values for the nektobenthic penaeid *Aristeus antennatus* and the benthic astacuran *Nephrops norvegicus* previously calculated by Demestre (1990) and Sardà and Leonart (1993), respectively, using the same methodology. The maximum age attained by each species was estimated on the basis of the monthly size-frequencies and the knowledge available on its overall biology (Company 1995).

Results

Relative growth

Table 3 shows the allometric size-weight relationships. Three separate, well-defined trends were observed, corresponding to the habits of the various species. Three of the four mesopelagic species (*Sergestes arcticus*, *Pasiphaea sivado*, and *P. multidentata*, which are all good swimmers) exhibited an increase in size relative to weight during growth. Although in most cases the allometric coefficient, b , was < 3 , the difference was not always significant. Allometric coefficients > 3 were recorded only for small *P. multidentata* individuals of indeterminate sex, for which the value of b was 3.13, although the difference was not significant. The mesopelagic species *Sergia robusta* was the sole exception, with a value of b of 3.03 for females, although once again the value was not significantly different from 3.

For species of the genus *Plesionika*, all of which are nektobenthic (i.e. benthic species of moderate locomotory ability and no diel migrational behaviour), b values were ~ 3 and generally did not differ significantly from the isometric value. Exceptions were the two smallest species, *P. gigliolii* and *P. acanthonotus*. Both female and male *P. gigliolii* had allometric coefficient values of < 3 . Female *P. acanthonotus* also had an allometric coefficient significantly lower than 3. As in *Pasiphaea multidentata*, individuals of indeterminate sex of the genus *Plesionika* displayed higher b values than females and males.

For strictly benthic species such as *Polycheles typhlops*, *Munida intermedia*, *M. tenuimana* and *Geryon longipes*, all b values were higher than 3, although not all the categories were significantly (so Table 3). These species underwent a slight increase in weight relative to size. The only exception was the species *Paramola cuvieri*, which however was represented by a very low number of specimens.

Figure 3 plots the trend of allometric coefficients (b values from Table 3) for the size-weight relationships of each species as a function of its life habit. The allometric species' index increased significantly from the mesopelagic to the benthic habit ($x = 2.382 + 0.276y$, $r = 0.615$, $p < 0.0000$). The mean allometric coefficients for species' habits also differed significantly (ANOVA, $p < 0.0001$), with a mean b of 2.63 for the mesopelagic, 2.97 for the nektobenthic, and 3.19 for the benthic habit.

No significant trend in relative growth (size-weight relationship) was found for shrimp species such as *Solenocera membranacea*, *Processa nouveli*, and *P. canaliculata*. These shrimps are quite good swimmers (authors' personal observations), but burrowing behaviour has also been described for them (Heegaard 1967; Lagardère 1977). They displayed different relative growth according to sex, with females of the genus *Processa* generally being heavier than males of equal size. For *S. membranacea* the reverse was true, with males relatively heavier. *S. membranacea* displays highly pronounced sexual dimorphism, with females attaining a larger maximum size than males. The present results indicate that *S. membranacea*, *P. nouveli* and *P. canaliculata* are both nektobenthic and benthic, i.e. of mixed habit.

Absolute growth

Table 4 shows the von Bertalanffy growth parameters for the 16 species of decapods for which these could be calculated. Data for *Paramola cuvieri* were not included because of the small number of specimens available. The growth-performance index, Φ , for *Aristeus antennatus* and *Nephrops norvegicus* were calculated from the von Bertalanffy growth parameters reported by Demestre (1990) and Sardà and Leonart (1993), respectively. The annual growth rate, k , for all species considered ranged from 0.07 to 1.11 (Table 3). Figure 4 reveals the rela-

Table 3 Decapod crustaceans. Size–weight relationships ($y = a \cdot x^b$, where x = size; y = weight; a = constant; b = allometric coefficient or slope) for 17 species including correlation coefficient (r), and significances (S) of slope where this differs from 3 for

ln-transformed data (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$) [I indeterminate individuals; F females; M males; (n) no. of individuals weighed]

Species	Sex	a	b	r	S	(n)
Family Solenocaridae						
<i>Solenocera membranacea</i>	F + M	0.000684	2.9081	0.964	0.0005***	(907)
	F	0.000221	3.3794	0.949	0.0000***	(246)
	M	0.000716	2.8859	0.959	0.0006***	(661)
Family Sergestoidae						
<i>Sergestes arcticus</i>	F + M	0.001395	2.3115	0.854	0.0000***	(160)
	F	0.010303	1.3991	0.722	0.0000***	(35)
	M	0.000790	2.5525	0.850	0.0008***	(145)
<i>Sergia robusta</i>	F + M	0.00478	2.9198	0.952	0.1959	(231)
	F	0.000367	3.0312	0.944	0.7999	(77)
	M	0.000470	2.9202	0.951	0.3018	(153)
Family Pasiphaeidae						
<i>Pasiphaea sivado</i>	F + M	0.000482	2.6844	0.955	0.0000***	(276)
	F	0.000239	2.9159	0.926	0.4000	(144)
	M	0.000366	2.7625	0.947	0.0584	(60)
<i>Pasiphaea multidentata</i>	I + F + M	0.000363	2.8413	0.988	0.0000***	(650)
	I	0.000156	3.1353	0.955	0.0684	(175)
	F	0.000775	2.6137	0.974	0.0000***	(161)
	M	0.000693	2.6508	0.977	0.0000***	(276)
Family Processidae						
<i>Processa noveli</i>	F + M	0.000517	3.0101	0.878	0.9579	(77)
	F	0.001227	2.5977	0.789	0.3616	(24)
	M	0.000317	3.2388	0.864	0.4531	(38)
<i>Processa canaliculata</i>	F + M	0.000182	3.3699	0.966	0.0000***	(154)
	F	0.000335	3.1358	0.974	0.1888	(53)
	M	0.000149	3.4462	0.966	0.0000***	(90)
Family Pandalidae						
<i>Plesionika heterocarpus</i>	I + F + M	0.000578	3.1024	0.989	0.0036**	(188)
	I	0.000135	3.8623	0.948	0.1211	(9)
	F	0.000784	2.9885	0.981	0.7952	(129)
	M	0.000618	3.0883	0.990	0.1701	(50)
<i>Plesionika edwardsi</i>	I + F + M	0.000595	3.0659	0.982	0.0165*	(453)
	I	0.000063	4.0010	0.923	0.4854	(4)
	F	0.000561	3.0893	0.979	0.0453*	(209)
	M	0.000929	2.9174	0.976	0.0533	(239)
<i>Plesionika gigliolii</i>	F + M	0.001324	2.8439	0.943	0.0096**	(285)
	F	0.002457	2.6012	0.888	0.0007***	(140)
	M	0.001390	2.9245	0.953	0.0211*	(144)
<i>Plesionika martia</i>	I + F + M	0.000363	3.1968	0.973	0.0000***	(370)
	I	0.000056	3.9579	0.938	0.2034	(7)
	F	0.000569	3.0408	0.965	0.4805	(208)
	M	0.000504	3.0806	0.965	0.2452	(149)
<i>Plesionika acanthonotus</i>	I + F + M	0.000575	3.1315	0.961	0.0446*	(192)
	I	0.000153	3.7074	0.773	0.6253	(7)
	F	0.002604	2.5502	0.928	0.0010***	(64)
	M	0.000879	2.9651	0.945	0.7126	(121)
Family Polychelidae						
<i>Polycheles typhlops</i>	I + F + M	0.000226	3.0309	0.959	0.6195	(210)
	F	0.000020	3.8210	0.937	0.0000***	(76)
	M	0.000238	3.0056	0.961	0.9402	(134)
Family Galatheidae						
<i>Munida intermedia</i>	F + M	0.000513	3.2265	0.966	0.0037**	(131)
	F	0.000416	3.3134	0.980	0.0012**	(55)
	M	0.000792	3.0617	0.949	0.6028	(76)
<i>Munida tenuimana</i>	F + M	0.000481	3.1472	0.967	0.0484*	(128)
	F	0.00493	3.1443	0.962	0.2183	(61)
	M	0.000463	3.1549	0.971	0.1149	(67)
Family Homolidae						
<i>Paromola cuvieri</i>	F + M	0.000572	2.9802	0.991	0.7986	(28)
	F	0.000607	2.9627	0.993	0.6779	(18)
	M	0.000048	3.5543	0.976	0.0855	(10)
Family Garyonidae						
<i>Geryon longipes</i>	F + M	0.000367	3.0966	0.988	0.0025**	(238)
	F	0.000306	3.1410	0.966	0.0192*	(203)
	M	0.000260	3.2048	0.975	0.1159	(35)

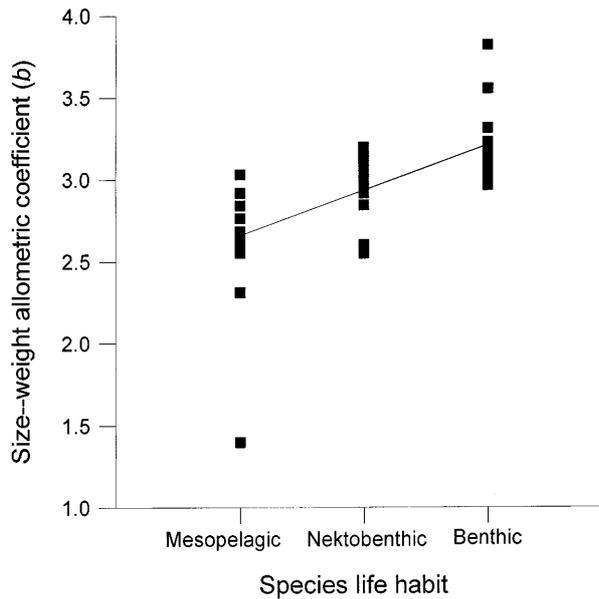


Fig. 3 Decapod crustaceans. Allometric coefficients (from size-weight relationship for each species) as a function of habitat. Linear regression parameters, correlation index, and significance level of slope (deviation from zero) are $y = 2.382 + 0.276x$, $n = 42$, $r = 0.62$, $p < 0.0000$

tionship between $\log L_{\infty}$ and $\log k$. The relationship between L_{∞} and k for all species studied combined was significant (females: $r = 0.699$, $p = 0.0012$; males: $r = 0.675$, $p = 0.0058$), indicating that the growth rates of all species were comparable. A comparison of k values on the basis of species' habit suggested that, on average, the strictly benthic species had lower k and higher L_{∞} values than the mesopelagic and nektobenthic species. As a result, the Φ values for the benthic species were quite close to the value calculated for the data set for all species combined (Table 4). Generally, mesopelagic and nektobenthic species were mainly situated in the upper left-hand portion of the plots in Fig. 4, with low L_{∞} and high k values. On the whole, the life spans of mesopelagic and nektobenthic species are shorter than the life spans of benthic species (Table 4). The strictly benthic species *N. norvegicus* (Nn), *Polycheles typhlops* (Pt), *Munida intermedia* (Mi), *M. tenuimana* (Mt), and *Geryon longipes* (Gl) are all in the lower right-hand portion of the plots in Fig. 4, i.e. with high L_{∞} but low k values compared to the other species. The only exceptions were the mesopelagic species *Pasiphaea multidentata* and the nektobenthic species *A. antennatus*, both of which also appeared in the lower right-hand portion of the plots (Fig. 4), with a high value of L_{∞} and moderately low value of k . Both species had the deepest distribution of its group (mesopelagic and nektobenthic, respectively) in this study.

Analysis of the changes in Φ with depth of maximum abundance for the various species revealed no significant trend for the species as a whole (Fig. 5). The slope did not differ significantly from 0 for either females or males (females, $p = 0.4112$; males, $p = 0.3289$), indicating no

general decrease or increase in absolute growth rates as a function of depth.

Nevertheless, certain trends were revealed within families. The two deepest-dwelling mesopelagic species in the families Sergestoidae and Pasiphaeidae (*Sergia robusta* and *Pasiphaea multidentata*) had higher values of Φ than species with shallower depth distributions (*Sergestes arcticus* and *P. sivado*; Table 4). In the family Pandalidae, the opposite trend was apparent, i.e. species with shallower depth distributions (*Plesionika heterocarpus* and *P. edwardsi*) had higher values of Φ than the species with the deeper depth range (*P. acanthonotus*). Accordingly, the k value for *P. heterocarpus* (0.9) was higher than that for the deepest-dwelling species, *P. acanthonotus* (0.55). Nevertheless, this did not represent an overall trend for the Pandalidae, since one of the species with a deeper depth distribution, *P. martia*, had a Φ that was only slightly lower than that of *P. heterocarpus* and *P. edwardsi* and that was similar to the Φ of the shallow-dwelling species *P. giglioli*. The growth-performance index for *Aristeus antennatus*, *Polycheles typhlops*, and *Geryon longipes* was higher than expected, having regard to their deep depth distributions (Tables 1 and 4), since deep-sea species are generally considered to have lower growth rates than species at shallower depths. These three species are commonly found at depths below 600 m, and their depth ranges can extend down to 2000 m.

Despite the above intra-family differences, overall the growth-performance index Φ indicated but low variability in the species studied ($\Phi = -0.151$ to 1.327; Table 4). Figure 6 graphically compares Φ values reported for various families of marine organisms (after: Pauly 1980; Munro and Pauly 1983) with the Φ values of female decapods in the present study. Female Φ data only were used because only data for that sex were available for all the species studied. Comparison revealed significant differences ($p < 0.0000$, one-way ANOVA), with mean Φ values of 0.00, 1.08, 1.58, 2.47, and 0.58 for the families Myctophidae, Penaeidae, Serranidae, and Scombridae and the decapod crustaceans in this study, respectively. Figure 6 shows the low growth rate for deep-water decapod compared to growth rates for shallow-water crustaceans (penaeids) and epipelagic fish species in the families Serranidae and Scombridae. Mesopelagic fishes of the family Myctophidae were the only group with a Φ value lower than the deep-water decapod crustacean species of the present study.

Discussion

Growth in mesopelagic species, which are generally not bound to the substratum and are good swimmers, tended to be manifested in a greater increase in size rather than in weight. The opposite occurred in the nektobenthic and benthic species, which tended to isometrical increases in size and weight or relatively greater

Table 4 Decapod crustaceans. Von Bertalanffy growth parameters (see “Materials and methods”) for 18 species in western Mediterranean Sea (*CL* carapace length; L_{∞} theoretical maximum individual size; k annual growth rate; *WP* winter point; Φ growth-performance index; *I* indeterminate; *F* females; *M* males; *nd* no data)

Species	Sex	CL (mm)		L_{∞}	k	WP	Φ	Estimated max. age
		min.	max.					
Family Aristeidae								
<i>Aristeus antennatus</i> ^a	I + F + M	nd	nd	nd	nd	nd	nd	
	F	nd	61.0	76.0	0.30	nd	0.857	5.0
	M	nd	38.0	54.0	0.25	nd	0.483	4.0
Family Solenoceridae								
<i>Solenocera membranacea</i>	I + F + M	4.9	26.8	29.0	0.65	0.01	0.542	
	F	6.3	26.8	28.5	0.65	0.97	0.519	2.5
	M	6.0	20.3	21.6	0.56	0.20	0.320	1.5
Family Sergestoidae								
<i>Sergestes arcticus</i>	I + F + M	5.0	13.7	17.0	0.80	0.80	-0.104	
	F	5.0	13.7	16.5	0.70	0.40	-0.151	1.0
	M	5.0	11.6	nd	nd	nd	nd	nd
<i>Sergia robusta</i>	I + F + M	7.0	22.5	24.3	0.64	0.88	0.292	
	F	9.0	22.5	24.8	0.64	0.85	0.301	2.0
	M	8.5	19.4	nd	nd	nd	nd	nd
Family Pasiphaeidae								
<i>Pasiphaea sivado</i>	I + F + M	7.0	24.3	29.5	0.55	0.11	0.162	
	F	10.0	23.2	26.0	0.55	0.20	0.057	2.0
	M	10.0	24.3	nd	nd	nd	nd	nd
<i>Pasiphaea multidentata</i>	I + F + M	6.5	46.7	50.0	0.80	0.70	0.833	
	F	21.0	46.7	48.5	0.85	0.95	0.807	3.5
	M	19.0	42.7	44.4	0.77	0.30	0.687	3.5
Family Processidae								
<i>Processa noveli</i>	F + M	6.0	12.0	13.5	1.10	0.10	0.119	
	F	6.0	12.0	13.5	1.11	0.10	0.154	1.0
	M	6.0	11.2	13.5	1.10	0.20	0.058	1.0
<i>Processa canaliculata</i>	F + M	6.7	20.0	23.0	1.10	0.44	0.610	
	F	6.8	20.0	23.0	1.10	0.40	0.622	1.0
	M	6.7	19.9	21.0	0.70	0.14	0.295	1.5
Family Pandalidae								
<i>Plesionika heterocarpus</i>	I + F + M	5.4	20.2	22.7	0.90	0.00	0.603	
	F	7.3	20.2	23.0	0.90	0.90	0.622	1.5
	M	7.2	19.4	22.4	1.00	0.60	0.621	1.5
<i>Plesionika edwardsi</i>	I + F + M	7.4	29.0	31.0	0.70	0.94	0.748	
	F	10.0	29.0	31.0	0.65	0.94	0.697	2.5
	M	10.6	27.2	32.0	0.80	0.40	0.840	2.5
<i>Plesionika gigliolii</i>	I + F + M	5.2	18.6	21.0	0.75	0.48	0.466	
	F	8.0	18.6	20.5	0.75	0.68	0.443	1.5
	M	6.8	16.0	20.0	0.55	0.40	0.259	1.5
<i>Plesionika martia</i>	I + F + M	5.0	26.7	30.1	0.50	0.90	0.561	
	F	9.8	26.7	30.4	0.39	0.86	0.440	2.5
	M	9.3	23.9	27.5	0.54	0.80	0.491	2.5
<i>Plesionika acanthonotus</i>	I + F + M	5.4	17.9	19.0	0.55	0.80	0.252	
	F	8.1	17.9	19.0	0.55	0.83	0.233	1.5
	M	7.8	16.2	18.4	0.50	0.00	0.129	1.5
Family Nephropidae								
<i>Nephrops norvegicus</i> ^b	F + M	nd	nd	nd	nd	nd	nd	nd
	F	nd	50.0	68.3	0.10	nd	0.581	6.0
	M	nd	65.0	85.0	0.07	nd	0.493	7.0
Family Polychelidae								
<i>Polycheles typhlops</i>	I + F + M	5.0	46.7	49.5	0.45	0.11	0.651	
	F	11.0	46.7	48.0	0.35	0.19	0.502	5.5
	M	10.3	30.0	32.0	0.50	0.10	0.399	2.5
Family Galatheidae								
<i>Munida intermedia</i>	F + M	7.2	28.7	30.5	0.32	0.36	0.509	
	F	7.8	27.2	29.0	0.25	0.05	0.320	2.5
	M	7.2	28.7	30.5	0.32	0.66	0.535	2.5
<i>Munida tenuimana</i>	F + M	6.0	26.0	29.5	0.40	0.50	0.478	
	F	6.8	25.1	27.5	0.40	0.09	0.411	2.5
	M	6.0	26.0	29.2	0.40	0.10	0.473	2.5
Family Geryonidae								
<i>Geryon longipes</i>	F + M	15.0	69.7	75.5	0.54	0.20	1.327	
	F	15.0	49.1	53.0	0.30	0.10	0.777	4.0
	M	16.4	69.7	75.0	0.50	0.20	1.290	6.0

^a After Demestre (1990)

^b After Sardà and Leonart (1993)

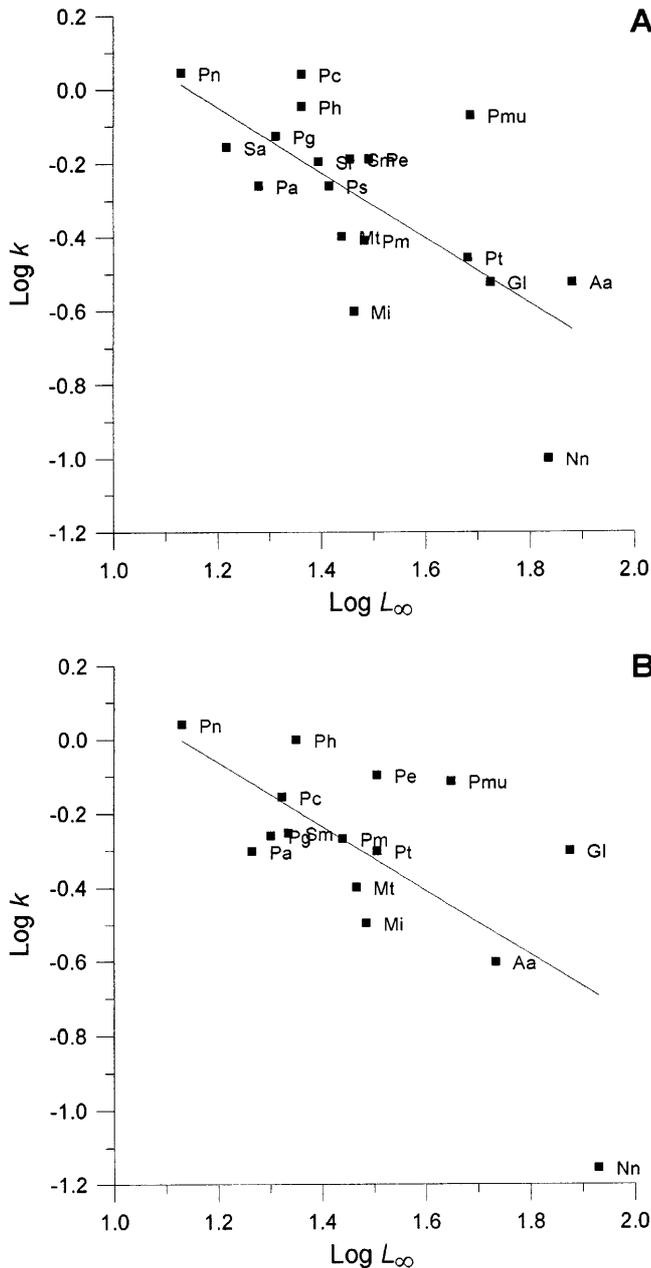


Fig. 4 Decapod crustaceans. Relationship between $\log L_{\infty}$ and $\log k$. Linear regression parameters are $y = 1.010 - 0.885x$ ($r = 0.70$, $p = 0.0012$) for females (A), and $y = 0.975 - 0.865x$ ($r = 0.68$, $p = 0.0058$) for males (B). Species' codes as in Table 1

increases in weight rather than in size. These results agree with those of Cartes et al. (1993), who linked a decreased CL:wet weight ratio to increased adaptation to the benthic habit. Therefore, amongst other factors, relative growth (size-weight relationship) would appear to be instrumental in prescribing the habits of decapod crustaceans. The results suggest that weight is a limiting morphological factor for decapod crustaceans with marked migratory behaviour, but not for nektobenthic or benthic species, in which weight does not appear to be a limiting morphological factor. The relative "heavi-

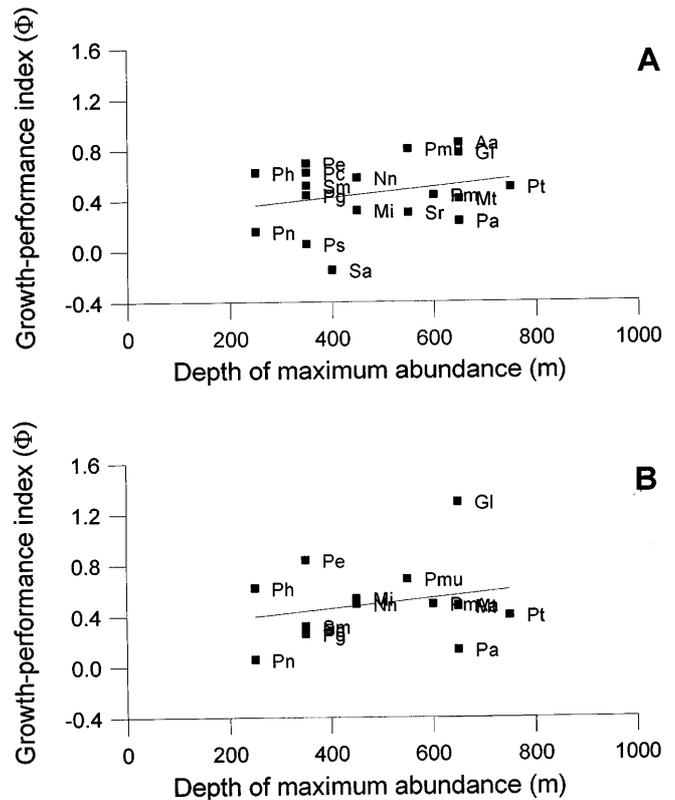


Fig. 5 Decapod crustaceans. Growth performance index, Φ , as a function of depth of maximum abundance for each species. Linear regression parameters are $y = 0.253 + 0.000x$ ($r = 0.24$) for females (A), and $y = 0.288 + 0.000x$ ($r = 0.23$) for males (B). Differences in slope (deviation from zero) were not significant for either females ($p = 0.3289$) or males ($p = 4112$). Species' codes as in Table 1

ness" of strictly benthic species may be an important adaptive factor, and strictly benthic species generally consist of lobsters and anomuran and brachyuran crabs. A laterally compressed body with a rudimentary rostrum are two further evolutionary morphological adaptations in mesopelagic crustaceans (Cartes et al. 1993), while a laterally uncompressed carapace and a long rostrum are common features in nektobenthic species such as *Aristeus antennatus* and the five species of the genus *Plesionika* (Burukovsky 1972; Sardà and Demestre 1989). In addition to morphological considerations, different metabolic and biochemical adaptations have been reported in species occupying different habitats, including very high lipid contents of mesopelagic species that may be useful in attaining neutral buoyancy in the water column (Childress and Nygaard 1974). Differences in oxygen consumption rates, organic matter content, and energy content between nektobenthic and benthic species of decapod crustaceans also have been reported (Company and Sardà 1998), with strictly benthic species generally having lower metabolic rates than nektobenthic species.

The growth rates of deep-sea organisms are generally considered to be lower than those of shallow-water organisms, and low water temperature and low food

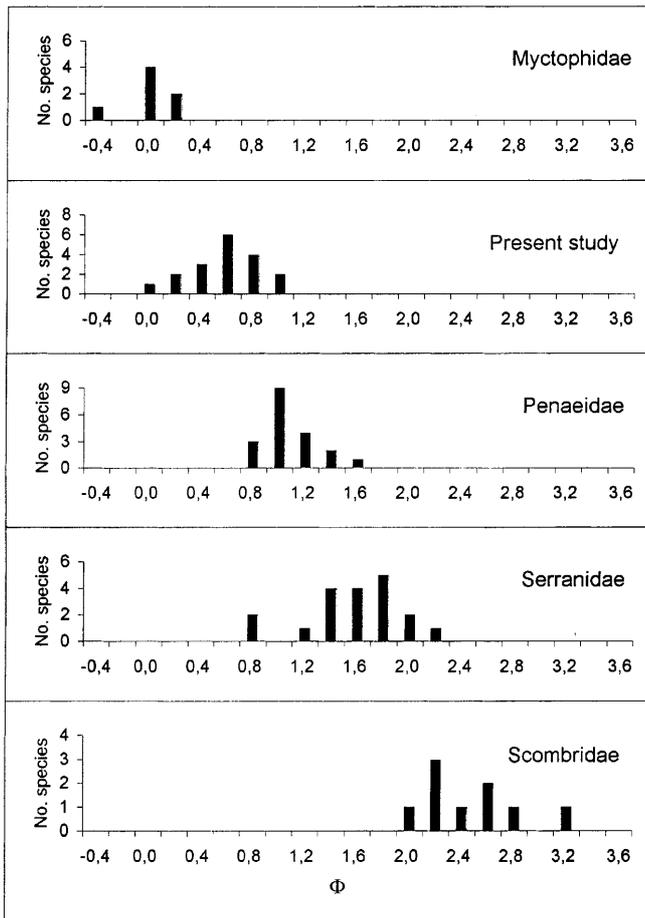


Fig. 6 Decapod crustaceans. Comparison between growth-performance index (Φ) for females of 18 species of deep-sea decapod crustaceans (*Present study*) and for three shallow-water families (Penaeidae, shrimps; Serranidae, Scombridae, fishes) and mesopelagic fish family Myctophidae (Data for Myctophidae, Penaeidae, Serranidae, and Scombridae from Pauly 1980 and Munro and Pauly 1983). Differences between families were significant ($p < 0.0000$, one-way ANOVA), with mean Φ values of 0.00, 0.58, 1.08, 1.58, and 2.47 for Myctophidae, the decapod crustaceans in present study, Penaeidae, Serranidae, and Scombridae, respectively

availability are held to be the major factors responsible for low growth rates (Mauchline 1972; Grassle and Sanders 1973; Gage and Tyler 1991). Using size-frequency data, Omori (1974) suggested that Atlantic bathypelagic species of decapod crustaceans such as *Acanthephyra pelagica* and *A. quadrispinosa* combine greater longevity with lower growth rates than epipelagic and mesopelagic species of the genera *Sergestes*, *Sergia*, *Acetes*, and *Lucifer*. The fishes of the family Macrouridae in the Northwestern Mediterranean Sea displayed the same pattern (Massutí et al. 1995). In contrast, Childress and Nygaard (1974) and Childress et al. (1980) reported that growth rates of bathypelagic fish species were comparable to those of epipelagic species and somewhat higher than those of mesopelagic species. These investigators postulated that the low metabolic rates of bathypelagic species (which do not undergo diel

vertical migrations of the same magnitude as mesopelagic species) may be one of the factors responsible for their high growth rates. The intra-family trend observed in the mesopelagic decapod crustaceans of the western Mediterranean Sea in the present study could correspond to the findings of Childress et al. (1980). Despite their larger size and longer life spans, the deepest-dwelling mesopelagic species (*Sergia robusta* and *Pasiphaea multidentata*) had higher Φ values than the shallower-dwelling species (*Sergestes arcticus* and *P. sivado*). No specific bibliography is available on diel migrational patterns along the depth gradient for pelagic crustacean megafauna in the Mediterranean Sea. We classified the pelagic species studied in the present work as mesopelagic, but the deepest-dwelling mesopelagic species (*Sergia robusta* and *P. multidentata*) have a maximum distribution depth of > 1000 m, and their biological characteristics are somewhat similar to those of the bathypelagic fishes investigated by Childress et al. The large size and rapid growth of bathypelagic fishes compared with mesopelagic fishes is also found in the deepest-dwelling mesopelagic species, *S. robusta* and *P. multidentata*. The nektobenthic–benthic species *Solenocera membranacea* and the nektobenthic species *Aristeus antennatus* are two species that belong to different families but occupy similar trophic habits (Cartes 1994, 1995) and appear to follow the same growth pattern as mesopelagic species. In contrast, the nektobenthic species of the genus *Plesionika* do not clearly follow the same growth pattern: the deepest-dwelling species, *P. acanthonotus*, had a lower Φ value than the shallower-dwelling species, *P. heterocarpus*. Despite these differences in intra-family growth rates, our overall findings indicate that, as a group, decapod crustaceans do not exhibit significant differences in growth rates, either as a function of habit (mesopelagic, nektobenthic or benthic) or depth of maximum abundance (see Figs. 4 and 5). The Φ values for the decapod crustaceans studied here were significantly different from those of the other families considered (Fig. 6), indicating that the decapod crustaceans we studied all had comparable growth rates. Generally, presuming growth to account for a large portion of an individual's energy budget, all species we examined displayed similar energy requirements for growth that were lower than those of shallow-water fish families (Serranidae and Scombridae) and higher than those of mesopelagic fishes (family Myctophidae). This indicates that growth patterns of decapod crustaceans are well-defined compared to those of other taxa. Environmental parameters may account for homogeneity in the absolute growth rates of crustacean decapods in the Mediterranean Sea compared to species with shallower distributions in tropical waters where water temperatures can be > 20 °C (Pauly 1980). Food and temperature are the two main environmental parameters affecting growth rates (Venner 1985). In crustaceans, the amount and/or quality of food and the water temperature influence the duration of the intermoult period and the moult size-increment, and both

cause an increase or decrease in growth rates, with faster growth rates at higher food concentrations and higher temperatures (Hartnoll 1983). The growth rates of tropical species such as the Penaeidae, Serranidae and Scombridae are higher than those of Mediterranean decapods, and food supply and/or temperature seems to be the factor(s) mainly responsible. There is a general decrease in water temperature with increasing depth in the major oceans of the world, with temperatures of $\sim 5^\circ\text{C}$ at 500 m (Mills 1983). The lower growth rates of the mesopelagic Myctophidae compared to those of Mediterranean decapods could also be related to water temperature, among other factors. Mediterranean deep waters are constant (13°C) all year-round, and are relatively oligotrophic compared to other oceans (Margalef 1985).

In conclusion, the size-weight relationship (relative growth) in decapod crustaceans in the Northwestern Mediterranean is a morphological parameter reflecting the species' habit, with weight increasing significantly more than size as species become more highly adapted to the benthic habit. In contrast, for decapod crustaceans as a whole, our results did not indicate significant variations in their absolute growth rates as a function of habit or depth of maximum abundance, despite slight differences within each family or group of species. Taking food availability and temperature to have the most influence on growth rates, the constant year-round temperature (13°C) in this region may contribute to the low interspecific variability in growth rates among Mediterranean decapod crustaceans compared to the interspecific differences reported for other oceans, in which steep depth-related temperature gradients may contribute to variability in growth rates.

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References

- Abelló P (1986) Anàlisi de les poblacions de crustacis decàpodes demersals al litoral català. Aspectes biològics del Braquiúrid *Liocarcinus depurator*. PhD dissertation. University of Barcelona, Barcelona
- Abelló P, Valladares FJ, Castellón A (1988) Analysis of the structure of decapod crustacean assemblages of the Catalan coast (North-West Mediterranean). *Mar Biol* 98: 39–49
- Anonymous (1997a) Report of the working group on *Nephrops* stocks. International Council for the Exploration of the Sea, Copenhagen (ICES 1997/Assess. 9)
- Anonymous (1997b) Report of the study group on life histories of *Nephrops*. International Council for the Exploration of the Sea, Copenhagen (ICES CM1997/K4, Assess 4)
- Aiken DE (1980) Molting and growth of lobsters. In: Cobb JS, Phillips BF (ed) *Biology and management of lobsters*. Vol 1. Academic Press, New York, pp 91–163
- Bertalanffy L von (1934) Untersuchungen über die Gesetzmäßigkeiten des Wachstums. 1. Allgemeine Grundlagen der Theorie. *Wilhelm Roux Arch EntwMech Org* 131: 613–653
- Bliss DE (ed) (1983) *The biology of Crustacea*. Academic Press, New York
- Burukovsky RN (1972) On the function of the rostrum in shrimps [In Russ]. *Trudy AtlantNIRO (Atlant nauchno-issled Inst morsk ryb Khoz Okeanogr)* 42: 176–179
- Caddy J (1987) Size-frequency analysis for Crustacea: moult increment and frequency models for stock assessment. *Kuwait Bull mar Sci* 9: 43–61
- Cartes JE (1991) Anàlisi de las comunidades y estructura trófica de los crustáceos decápodos batiales del Mar Catalán. PhD thesis. Universitat Politècnica de Catalunya, Barcelona
- Cartes JE (1993) Diets of deep-water pandalid shrimps on the Western Mediterranean slope. *Mar Ecol Prog Ser* 96: 49–61
- Cartes JE (1994) Influence of depth and seasonality on the diet of the deep-water aristeid *Aristeus antennatus* along the continental slope (400 to 2300 m) in the Catalan Sea (western Mediterranean). *Mar Biol* 120: 639–648
- Cartes JE (1995) Diets of, and trophic resources exploited by, bathyal penaeoidean shrimps from the Western Mediterranean. *Mar Freshwat Res* 46: 889–896
- Cartes JE, Company JB, Maynou F (1994a) Deep-water decapod crustacean communities in the Northwestern Mediterranean: Influence of submarine canyons and seasonal aspects. *Mar Biol* 120: 221–229
- Cartes JE, Sardà F (1992) Abundance and diversity of decapod crustaceans in the deep-Catalan Sea (Western Mediterranean). *J nat Hist* 26: 1305–1323
- Cartes JE, Sardà F, Company JB, Lleonorat J (1993) Day-night migrations by deep-sea decapod crustaceans in experimental samplings in the Western Mediterranean Sea. *J exp mar Biol Ecol* 171: 63–73
- Cartes JE, Sorbe JC, Sarda F (1994b) Spatial distribution of deep-sea decapods and euphausiids near the bottom in the northwestern Mediterranean. *J exp mar Biol Ecol* 179: 131–144
- Childress JJ, Nygaard M (1974) Chemical composition and buoyancy of midwater crustaceans as function of depth of occurrence off Southern California. *Mar Biol* 27: 225–238
- Childress JJ, Price MH (1983) Growth rate of the bathypelagic crustacean *Gnathopausia ingens* (Mysidacea: Lophogastridae). I. Dimensional and population structure. *Mar Biol* 50: 47–62
- Childress JJ, Taylor SM, Cailliet GM, Price MH (1980) Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off Southern California. *Mar Biol* 61: 27–40
- Cobb JS, Phillips BE (eds) (1980) *Biology and management of lobster*. Academic Press, London
- Company JB (1995) Estudi comparatiu de les estratègies biològiques dels crustacis decàpodes del talús de la Mar Catalana. PhD dissertation. University of Barcelona, Barcelona
- Company JB, Sardà F (1997) Reproductive patterns and population characteristics in five deep-water pandalid shrimps in the Western Mediterranean along a depth gradient (150–1100 m). *Mar Ecol Prog Ser* 148: 49–58
- Company JB, Sardà F (1998) Metabolic rates and energy content of deep-sea benthic decapod crustaceans in the Western Mediterranean Sea. *Deep-Sea Res* 45: 1861–1880
- Conan G (1985) Periodicity, and phasing of moulting. *Crustaceans Issues* 3: 73–99
- Demestre M (1990) Biología pesquera de la gamba *Aristeus antennatus* (Risso, 1816) en el mar Catalán. PhD dissertation. University of Barcelona, Barcelona
- Demestre M, Abelló P (1993) Growth and distribution of *Solenocera membranacea* (Risso, 1816) (Decapoda, Dendrobranchiata) in the Northwestern Mediterranean Sea. *Scientia mar* 57(2–3): 161–166
- Descouturelle G (1976) Influence de la température et de la sexualité sur la durée des stades d'intermue chez la crevette

- d'eau douce *Atyaephira desmaresti* Millet. Vie Milieu 25: 149–162
- Drach P (1939) Mue et cycle d'intermue chez les crustacés décapodes. Anns Inst océanogr, Paris (NS) 19: 103–392
- Emmerson WD (1980) Inducer maturation of prawn *Penaeus indicus*. Mar Ecol Prog Ser 2: 121–131
- Gage JD, Tyler PA (1991) Deep-sea biology: a natural history of organisms at the deep-sea floor. Cambridge University Press, London
- García S, Le Reste L (1987) Ciclos vitales, dinámica, explotación y ordenación de las poblaciones de camarones peneidos costeros. FAO DOC téch Pesca 203: 1–180
- Gayanilo FC Jr, Soriano M, Pauly D (1988) A draft guide to the Compleat ELEFAN. Software Project 2. International Center for Living Aquatic Resources Management (ICLARM), Manila
- Grassle JF, Sanders HL (1973) Life histories and the role of disturbance. Deep-Sea Res 20: 643–659
- Hartnoll RG (1983) Growth. In: Bliss DE (ed) The biology of Crustacea. Vol 8. Academic Press, New York, pp 214–282
- Heegaard P (1967) On behavior, sex-ratio and growth of *Solenocera membranacea* (Risso, 1816) (Decapoda, Penaeidae). Crustaceana 13: 227–237
- Hopkins TS (1985) Physics of the sea. In: Margalef R (ed) Key environments: Western Mediterranean. Pergamon Press, New York
- Lagardère JP (1977) Recherches sur la distribution verticale et sur l'alimentation des crustacés décapodes benthiques de la Pente Continentale du Golfe de Gascogne: analyse des groupements carcinologiques. Bull Cent Étud Rech scient Biarritz 11(4): 367–440
- Margalef R (1985) (ed) Key environments: Western Mediterranean. Pergamon Press, New York
- Massuti E, Morales-Nin B, Stefanescu C (1995) Distribution and biology of five grenadier fish (Pisces:Macrouridae) from the upper and middle slope of the Northwestern Mediterranean. Deep-Sea Res 42: 307–330
- Mauchline J (1972) The biology of bathypelagic organisms, especially Crustacea. Deep-Sea Res 19: 753–780
- Merret NR, Marshall NB (1981) Observations on the ecology of deep-sea bottom living fishes collected off northwest Africa (08°–270°N). Prog Oceanogr 9: 185–244
- Mills EL (1983) Problems of the deep-sea biology: an historical perspective. In: Rowe GT (ed) The sea. Vol 8. Wiley Interscience, New York, pp 1–79
- Morgan GR (1980) Population dynamics of spiny lobsters. In: Cobb JS, Phillips BF (eds) The biology and management of lobsters. Vol II. Academic Press, New York, pp 189–217
- Munro JL, Pauly D (1983) A simple method for comparing the growth of fishes and invertebrates. Fishbyte 1: 5–6
- Mytilineou CH, Castro M, Gancho P, Fourtouni A (1998) Growth studies on Norway lobster, *Nephrops norvegicus* (L.), in different areas of Mediterranean Sea and adjacent Atlantic. Scientia mar 62: 43–60
- Omori M (1974) The biology of pelagic shrimps in the ocean. Adv mar Biol 12: 233–324
- Omori M, Ohta S (1981) The use of underwater camera in studies of vertical distribution and swimming behaviour of a sergestid shrimp. *Sergia lucens*. J Plankton Res 3: 107–120
- Passano LM (1960) Molting and its control. In: Waterman TH (ed) The physiology of Crustacea. Vol 1. Academic Press, New York, pp 473–536
- Pauly D (1980) A new methodology for rapidly acquiring basic information on tropical fish stocks: growth, mortality and stock-recruitment relationship. In: Saila S, Roedel P (eds) Stock assessment for tropical small scale fisheries. Proceedings of an International Workshop, 19–21 September 1979. University of Rhode Island, International Center for Marine Research and Development, Kingston, Rhode Island, pp 154–172
- Pauly D (1981) Tropical stock assessment package for programmable calculators and micro-computers. ICLARM News 4: 10–13
- Pauly D, Munro JL (1984) Once more on the comparison of growth in fish and invertebrates. Fishbyte 2: 21–22
- Relini Orsi L, Relini G (1985) An attempt to assign von Bertalanffy growth parameters to *Aristeus antennatus* (Risso, 1816) (Crustacea, Decapoda) of the Ligurian Sea. Rapp P-v Réun Comm Explor scient int Mer Méditerr 29: 301–304
- Richard P (1978) Influence de la température sur la croissance et la mue de *Palaemon serratus* en fonction de leur taille. Aquaculture, Amsterdam 14: 13–32
- Sardà F (1985) Estudio de la edad, crecimiento y frecuencia de muda, en cautividad de *Nephrops norvegicus* (L.) del mar Catalán. Investigación pesq 49: 139–154
- Sardà F, Cartes JE, Company JB, Albiol T (1998) A modified commercial trawl used to sample deep-sea megabentos. Fish Sci 64: 492–493 (Nippon Suisan Gakk)
- Sardà F, Demestre M (1987) Estudio biológico de la gamba *Aristeus antennatus* (Risso, 1816) en el Mar Catalán (NE de España). Investigación pesq 51: 213–232
- Sardà F, Demestre M (1989) Shortening of the rostrum and rostral variability in *Aristeus antennatus* (Risso, 1816) (Decapoda:Aristeidae). J Crustacean Biol 9: 570–577
- Sardà F, Lleó J (1993) Evaluation of the Norway lobster (*Nephrops norvegicus*, L.) resource of the Serola bank off Barcelona (western Mediterranean). Scientia mar 57(2–3): 191–197
- Sardou J, Etienne M, Andersen V (1996) Seasonal abundance and vertical distributions of macroplankton and micronekton in the western Mediterranean Sea. Oceanol Acta 19: 645–656
- Sparre P, Ursin E, Venema SC (1989) Introduction to tropical fish stock assessment. Part I. Manual. FAO Fish tech Pap 306/1: 1–337
- Venner AM (ed) (1985) Factors in adult growth. Vol I. AA Balkema, Rotterdam
- Zariquiey Alvarez R (1968) Crustáceos decápodos ibéricos. Investigación pesq 32: 1–510