Deep-Sea Research, Vol. 37, No. 6, pp. 929–949, 1990.
Printed in Great Britain.

0198–0149/90 $3.00 + 0.00

Metabolic rates of benthic deep-sea decapod crustaceans decline with increasing depth primarily due to the decline in temperature

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(*Received* 28 *September* 1989; *in revised form* 5 *January* 1990; *accepted* 22 *January* 1990)

Abstract—The oxygen consumption rates of 11 species of benthic deep-sea decapod crustaceans were measured at a variety of temperatures to test the hypothesis that the metabolic rates of benthic crustaceans decline with increasing depth of occurrence only to the extent explained by the decline in temperature with depth. The species were captured at depths between 150 and 2000 m off Southern California using an epibenthic beam trawl equipped with a thermally protecting cod-end to bring the animals to the surface uncontaminated by sediment and at the depth temperature. The data, combined with those for six species of shallower-living crustaceans from California waters, showed a significant decline in oxygen consumption rate with increased species' depths of occurrence, when the measurements were made at temperatures appropriate to each species' depth range. There was no significant relation between wet weight and depth of occurrence in these species. When the data were adjusted to 10°C using a moderate temperature effect factor (corresponding to Q_{10} values of 2–2.3 depending on the species and temperature range), the significant relationship between oxygen consumption rate and depth was lost, indicating that the observed decline with depth was due to the decline in temperature with depth. When the relationship between metabolic rate and depth of occurrence for the most active (carideans and penaeid) species were compared (ANCOVA) with that for the rest of the species, the active species had significantly higher rates.

By combining this data set with data from the literature for a wide variety of shallow-living benthic decapod crustaceans, it was possible to create a data set of 35 species in which the effects of temperature, minimum depth of occurrence and body mass could be separated by multiple linear regression. This demonstrated highly significant effects of size and temperature, but no significant effect of depth for the entire data set and for the data set excluding penaeids and carideans. In contrast, the carideans showed a significant effect of depth on metabolic rate. This is discussed in terms of the adaptive and selective factors responsible for the well-known decline in metabolic rates of midwater crustaceans and fishes, an effect which does exceed the effect of temperature. It is suggested that the typical pattern for deeper living animals may be that metabolic rates on average vary as a function of depth due primarily to variation in temperature, except for the visually orienting pelagic groups (cephalopods, crustaceans and fishes). For those benthic forms which are particularly visually oriented and/or partially pelagic some significant depth-related decline in metabolism beyond that due to the decline in temperature is expected.

INTRODUCTION

AMONG the first biological rates measured on deeper living organisms were metabolic rates. CHILDRESS (1971b, 1975) showed that deeper living pelagic crustaceans had rates of

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oxygen consumption that declined rapidly with depth in the first kilometer. Although there were changes in the composition of these organisms as a function of depth (CHILDRESS and NYGAARD, 1973) this accounted for little of the decline. Temperature, pressure and size also were estimated to account for only a fraction of the decline with depth, leaving at least half of the decline unexplained. The pattern of metabolic rate declining with depth to a greater extent than can be explained by temperature also has been found for midwater fishes off California (TORRES *et al.*, 1979) and midwater crustaceans off Hawaii (COWLES, 1987). Studies on Antarctic midwater fishes (TORRES and SOMERO, 1988) and crustaceans (IKEDA, 1988) show that deeper living species have lower metabolic rates even in this essentially isothermal water column. The one study that has failed to show such a decline (DONNELLY and Torres, 1988) studied only species from a restricted mesopelagic vertical range which, as they note, probably explains their results. It appears that overall metabolism is slower in deeper living pelagic animals, since ammonia excretion also declines with increasing depth in crustaceans (QUETIN *et al.*, 1980; IKEDA, 1988). The metabolic rates measured in these studies of many different species have been confirmed by more detailed laboratory studies on particular species (e.g. CHILDRESS, 1971a; MEEK and CHILDRESS, 1973; GORDON *et al.*, 1976; QUETIN and CHILDRESS, 1976; BELMAN and GORDON, 1979; MICKEL and CHILDRESS, 1982a; ADAMS and CHILDRESS, 1983; TORRES and CHILDRESS, 1983, 1985) and *in situ* (SMITH and LAVER, 1981; SMITH, 1982, 1985). *In situ* studies have shown that the metabolic rates of deep-living benthopelagic fishes are also reduced as compared to shallower living benthopelagic species (SMITH and HESSLER, 1974; SMITH, 1978). Thus, it is well established that deeper living pelagic crustaceans and fishes generally have metabolic rates reduced below what would be expected of surface living species at the same temperatures.

The study described in this paper was undertaken to determine whether the metabolic rates of benthic crustaceans decline with depth beyond what can be explained by the concomitant decline in temperature or increase in size of individuals with depth. To carry out this study a new trawl had to be devised and constructed to obtain the desired specimens alive (CHILDRESS, 1985). We describe here the metabolic rates of 11 species of benthic crustaceans living down to a depth of 2000 m.

MATERIALS AND METHODS

Capture and maintenance

The specimens used in these studies were captured using an epibenthic beam trawl and thermally protecting cod-end, both designed and fabricated for these studies (CHILDRESS, 1985). The trawl itself has a 0.9 m high by 2.4 m wide mouth and is constructed of nominal 1 in. stretched mesh netting. It is supported about 0.2–0.3 m above the bottom by a frame that rides on 0.45 m wide runners. The net captures active benthic organisms without the sediment and other benthic material that could crush or asphyxiate them. The thermally protecting cod-end fitted to the trawl is much like previous such devices (CHILDRESS *et al.*, 1978) except that it is actuated by an air-charged piston which keeps the cod-end valves closed during deployment and recovery, but opens it at the greater pressures at depth. This system has successfully recovered live crustaceans and fishes from soft sediment down to depths of 2000 m.

Once the trawl was brought on board, the catch was emptied into a tub. The live animals were quickly transferred to buckets of cold water. They were then kept at temperatures

which approximated those at the depth at which they were captured for about 24 h before being used for metabolic rate measurements.

All the crustaceans used in this study were captured in basins of the Southern California continental borderland. The shallowest group of species (*Calastacus quinqueseriatus*, *Crangon communis*, *Pandalus jordani*, *Pandalus platyceros* and *Sicyonia ingentis*) was captured in the Santa Barbara Channel. All of these species survived for extended periods in captivity when they were kept at temperatures typical of their normal depth of occurrence and 1 atm pressure. The next deeper group of species (*Pandalopsis ampla*, *Paralomis multispina* and *Stereomastis sculpta*) was captured in Santa Catalina Basin, fauna described by SMITH (1983). *P. multispina* individuals survived and fed for up to several months in captivity when kept at 4°C and 1 atm, but only three were captured. *S. sculpta* survived for several weeks under the same conditions but was even rarer. *P. ampla* was much more abundant but few individuals survived more than a few days. The deepest group (*Crangon* cf. *abyssorum*, *Glyphocrangon vicaria* and *Munidopsis verrilli*) was captured in San Clemente Basin. *C.* cf. *abyssorum* is very similar to *C. abyssorum*, the only crangonid described from these depths off Southern California (SCHMITT, 1921; BUTLER, 1980) except that it has three instead of two median dorsal spines. *C.* cf. *abyssorum* was abundant and lived for a week or so at 1 atm and 3°C. *M. verrilli* lived a comparable period. *G. vicaria* was very abundant in the trawls, but was moribund at 1 atm and could only be kept alive under pressure. We maintained them for the short period before they were used in experiments, at 200 atm and 3°C in a flowing water pressure aquarium system (QUETIN and CHILDRESS, 1980).

Metabolism measurements

All of the animals except *G. vicaria* and *S. sculpta* were measured at 1 atm using methods similar to those described previously (CHILDRESS, 1971b; MICKEL and CHILDRESS, 1982b). Briefly, the crustaceans were placed in sealed, water-jacketed glass chambers with 50 mg streptomycin sulfate per liter added. The oxygen partial pressure was monitored with a Clark-type O_2 electrode. The water in the chambers was mixed and the stirring needs of the electrodes accommodated by enclosing the tips of the electrodes in a plastic vial with a magnetic stirring bar and having only a few holes for exchanging water with the rest of the chamber. The chambers were sufficiently large in relation to the crustaceans that 12–24 h were required to exhaust the oxygen.

Metabolic rates of *G. vicaria* and *S. sculpta* were measured under pressure. Six of the 11 *G. vicaria* runs were made at 200 atm using O_2 electrodes in pressure vessel respirometers (MICKEL and CHILDRESS, 1982b). The other eight and *S. sculpta* were run in a flowing water pressure (120 atm) respirometer system similar to the ambient pressure one used by ANDERSON *et al.* (1987). *G. vicaria* appeared to maintain normal body posture in the pressure respirometers. Since there was no obvious difference in the rates at the two pressures, they were combined for the purposes of this report. After each run the animal was removed and the chamber was resealed. After adding the minimum quantity of water necessary, a control rate of oxygen consumption was measured. This control was always very low (less than 5% of the total rate) and was subtracted from the total measured rate. The rates reported are those recorded after the crustacean had been in the respirometer for several hours and before oxygen became limiting. Usually the average rate between 30 and 70 torr was taken as the representative metabolic rate. All rates are presented

standardized to wet weight, measured when the specimens were removed from the respirometers, using the motion-compensated shipboard balance (CHILDRESS and MICKEL, 1980). Wet weight was used to standardize the data instead of dry weight or protein because it represents the metabolic rate of a living animal. Using other forms of standardization can lead to serious errors of interpretation concerning whole animal rates (CHILDRESS, 1977b; CHILDRESS and SOMERO, 1979).

Data analysis

All statistical analyses were executed using the Statview SE+ program (Abacus Concepts, Berkeley, CA) or the Fastat program (Systat, Evanston, IL). Simple linear and multiple linear regressions as well as ANCOVA were used. All regressions were carried out on ln transformed data to avoid obvious linearity problems in scatter plots of data. Rejection of a null hypothesis required $P \leq 0.05$. In addition to capture depth, the species' depth distributions were characterized by a "minimum depth of occurrence" (MDO), which is the depth below which 90% of the species is found in the Southern California region as determined from the literature and our own experience (CHILDRESS and NYGAARD, 1973). Ten meters was taken as the minimum depth for any animals which live at that depth or shallower to avoid distortions due to using ln transformed data in regressions. To test hypotheses concerning whether metabolic rate was significantly related to depth of occurrence, beyond the effects of temperature and body size, two different approaches were taken.

The first used only data from California (our own data with some from the literature) and because it was all collected in one region, where depth and temperature are closely related, multiple regression methods could not be used. In this treatment, for each species the metabolic rate determined at the temperature most closely approximating that at the species' minimum depth was normalized to 10 g and 10°C to remove the well-known effects of these parameters. The adjustment to 10 g was made using an equation of the form: $\ln (\mu l\ O_2\ mg\ wet\ wt^{-1}\ h^{-1}) = \ln a - 0.20 \ln (wet\ wt)$. The $\ln a$ value was calculated in each case by entering the measured average rate and the average wet weight. This $\ln a$ was then used with ln 10 in the above equation to estimate a species' rate at a 10 g wet weight. Ten g was chosen because it was intermediate among the sizes of animals tested so that less than an order of magnitude difference existed in either direction. The factor −0.20 was chosen because it represents an intermediate value among measured scaling coefficients (BRIDGES and BRAND, 1980). Rates were adjusted to 10°C in the same way using the equation: $\ln (\mu l\ O_2\ mg\ wet\ wt^{-1}\ h^{-1}) = \ln a + 0.55 \ln (°C)$. The factor 0.55 derives from the temperature effect observed in the deep-sea hydrothermal vent crab (MICKEL and CHILDRESS, 1982b) and is a moderate value within these data (Table 3). It corresponds to a Q_{10} of 2–2.3 depending on the temperature range. If the species was measured at 10°C and this temperature is within the species depth range, then we took the 10°C value and only adjusted for weight. The coefficients used for both adjustments were reasonable, moderate values, which, if anything, are likely to be too low, not too high. This is a conservative approach since the use of higher values would further reduce the relationship to depth. The temperatures used as the basis of these calculations were always ones measured within the temperature range of a species. This is important because the temperature response of a species outside its adapted range is not a suitable basis for comparing metabolic rates.

The second approach was to combine our data with data from the literature for shallow

living species from other regions and temperatures. The added shallow living animals had been measured at temperatures between 5 and 27°C. This data set allowed us to use multiple linear regression techniques on nonadjusted data to separate the "effects" of depth, temperature and wet weight. This data set was also partitioned in several different ways to separate different taxonomic groups.

RESULTS

Oxygen consumption rates

The mean metabolic rates which we measured are shown in Table 1. These data and those taken from the literature, normalized to the temperature at the minimum depth for each species and to 10°C and 10 g wet weight, are presented in Table 2. There was no significant relation between depth and mean animal size (Kendall rank correlation, $S = -1.3$, $P = 0.26$). Although most species were represented by too few individuals and too small a size range at a given temperature to show significant relations between metabolic rate and size (F-test of regression coefficient, $P > 0.05$), *P. platyceros* at 15°C and *S. ingentis* at 10°C had significant regressions ($P < 0.05$) against size. At a 90% significance level *P. ampla* at 3°C and *P. platyceros* at 10°C also showed metabolism–size relationships.

There is obvious variability in rates due to the habits of each species. For example, the carideans, which are active animals, appear to have generally higher rates at all temperatures. The observed temperature effects are not easily summarized (Fig. 1). In most cases they are low to moderate (most were between Q_{10} values of 1.5 and 2.5). When the deepest living species were measured outside their normal temperature range there was generally little effect of temperature on rate. Shallower living species generally showed larger effects of temperature either within or outside their normal temperature range. The relation

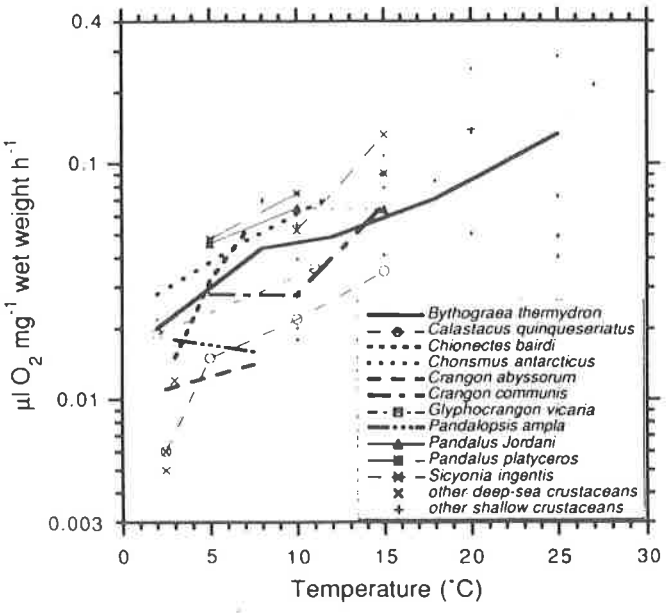

Fig. 1. The mean metabolic rates, adjusted to a 10 g wet weight, of a variety of benthic crustaceans plotted as a function of temperature. The sources for each species are those cited in Table 2. The other deep-sea and other shallow data are for the remaining species in Table 2.

Table 1. *Oxygen consumption rates* (μl O_2 mg^{-1} wet wt h^{-1}) *of benthic decapod crustaceans from greater depths off Southern California. Measurements on* Glyphocrangon vicaria *were made at* 100 *and* 200 atm *hydrostatic pressure. Superscripts following the species names indicate the source (listed below) used for the identification of the species and the estimation of the minimum depth of occurrence off Southern California*

Family genus and species	Depth of capture (m)	Minimum depth (m)	*T* (°C)	Wet wt (g)	Mean values *N*	μl O_2 mg^{-1} h^{-1} ± S.D.	Mean values Wet wt
Axiidae							
Calastacus quinqueseriatus[1]	400	292	2.5	3.17–3.25	2	0.0063, 0.0071	3.21
			5.0	1.08–4.81	5	0.018 ± 0.011	3.13
			10.0	1.42–1.93	5	0.030 ± 0.0039	1.73
			15.0	0.72–1.65	4	0.049 ± 0.021	1.38
Crangonidae							
Crangon cf. abyssorum[1,2]	1990	1250	2.0	0.97–1.48	9	0.016 ± 0.011	1.28
			7.5	0.89–1.50	2	0.014, 0.027	1.20
Crangon communis[1,2,3]	260	91	5.0	2.11–7.3	5	0.032 ± 0.011	4.69
			10.0	1.27–4.13	5	0.034 ± 0.0092	2.91
			15.0	1.39–4.40	6	0.088 ± 0.021	2.14
Galatheidae							
Munidopsis verrilli[1]	1990	1525	2.5	2.60–8.64	2	0.0054, 0.0088	5.62
Glyphocrangonidae							
Glyphocrangon vicaria[4]	1990	1250	2.0	4.99–19.20	11	0.021 ± 0.008	9.71
			11.0	8.26–10.70	3	0.036 ± 0.0061	9.85
Lithodidae							
Paralomis multispina[1]	1200	1100	3.0	6.46–10.10	3	0.012 ± 0.0027	7.64
Pandalidae							
Pandalopsis ampla[1,2]	1200	1000	3.0	1.88–11.96	8	0.020 ± 0.012	5.96
			7.5	5.01–13.24	7	0.016 ± 0.0080	9.55
Pandalus jordani[1,2,3]	300	124	5.0	8.13–14.51	6	0.045 ± 0.017	12.08
			10.0	7.69–17.91	11	0.062 ± 0.021	12.67
			15.0	8.39–13.33	6	0.062 ± 0.027	12.18
Pandalus platyceros[1,2,3]	180	91	5.0	0.74–50.4	11	0.041 ± 0.013	25.40
			10.0	0.71–105.3	18	0.059 ± 0.020	40.89
			15.0	12.66–50.5	6	0.073 ± 0.016	32.26
Sicyoniidae							
Sicyonia igentis[1,3]	160	10	10.0	9.48–23.65	5	0.044 ± 0.018	19.26
			15.0	10.60–36.89	4	0.117 ± 0.112	19.03
Polychelidae							
Stereomastis sculpta[5]	1200	1000	2.5	16.76	1	0.0045	16.76

1. SCHMITT (1921). 2. BUTLER (1980). 3. WORD and CHARWAT (1976). 4. WICKSTEN (1979). 5. WICKSTEN (1980).

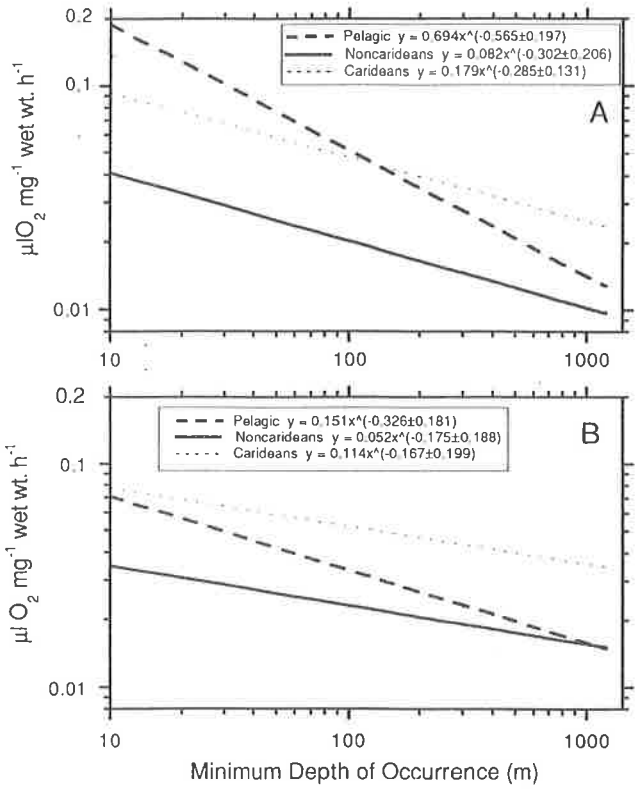

Fig. 2. The decline in oxygen consumption rate as a function of depth for two groups of California benthic decapod crustaceans (species from this study in Table 1 and species from the literature listed in caption of Table 3) and California pelagic crustaceans studied by CHILDRESS (1975). (A) Rates adjusted to temperatures at the minimum depth plotted as a function of minimum depth. Coefficients for all three lines are significantly different from zero (Table 3). (B) Rates adjusted to a temperature of 10°C and a wet weight of 10 g. Only the line for the pelagic crustaceans has a coefficient significantly different from zero.

between temperature and metabolic rates based on the individual measurements is given for various subsets of the data in Table 3. These all show similar, moderate temperature effects on metabolic rates. When one regresses the metabolic rates measured at the temperature closest to the temperature of the capture depth (Table 1) as a function of the minimum depth (Table 3), one finds a significant relationship showing that the metabolic rates of benthic crustaceans decline significantly with increasing depth. The major question addressed by the remaining analysis of these data is the extent to which this decline is a result of the effects of temperature and body weight or the result of other depth-related changes in metabolic properties.

Metabolism vs depth-adjusted data

For this approach we took the 11 species that we studied and added six shallow living species from the literature (*Callianasa californiensis*, *Cancer magister*, *Crangon franciscorum*, *Pleuroncodes planipes*, *Pugettia producta* and *Upogebia pugettensis*; citations in Table 2) to represent a full range of depths. When these are adjusted for temperature so that the estimated metabolic rate at the minimum depth is regressed against the minimum

Table 2. Oxygen consumption rates (μl O_2 mg^{-1} wet wt h^{-1}) of benthic decapod crustaceans from various depths and regions. For the purposes of our analyses, those species which come near the surface are shown as having a minimum depth of 10 m. **The estimates of the metabolic rates for* 10 g *specimens at* 10°C *were made using equations in the source publications. †The estimates of the metabolic rate for* 10 g *specimens at* 10°C *were made from the minimum depth metabolic rates shown using the equations described in the Results section*

Genus and species	Depth (m, min)	T (°C)	Wet wt (g)	μl O_2 mg^{-1} wet wt h^{-1} (min depth)	μl O_2 mg^{-1} wet wt h^{-1} (10 g, 10°C)	Source
Penaeidae						
Macropetasma africanus	10	20.0	0.325	0.228	0.036*	Cockcroft and Wollridge (1985)
Penaeus esculentus	10	25.0	16.0	0.067	0.034*	Dall (1986)
Penaeus japonicus	10	27.0	12.8	0.205	0.124†	Kulkarni and Joshi (1980)
Sicyoniidae						
Sicyonia ingentis	10	14.0	19.03	0.112	0.106	This study
Caridea						
Chorismus antarcticus	25	2.0	3.0	0.037	0.063*	Clarke (1983)
Crangon cf. *abyssorum*	1251	3.2	1.28	0.021	0.026†	This study
Crangon communis	166	8.5	2.91	0.031	0.026†	This study
Crangon crangon	10	20.0	1.2	0.393	0.092*	Van Donk and De Wilde (1981)
Crangon franciscorum	10	18.0	1.0	0.134	0.061†	Nelson *et al.* (1985)
Crangon vulgaris	10	13.0	0.25	0.15	0.051†	Hagerman (1970)
Glyphocrangon vicaria	1250	3.0	9.71	0.026	0.050†	This study
Notocrangon antarcticus	120	2.0	1.0	0.031	0.053†	Clarke (1983)
Palaemon elegans	10	20.0	1.00	0.22	0.094†	Dalla Via (1985)
Pandalopsis ampla	1000	4.0	5.96	0.023	0.034†	This study
Pandalus jordani	124	9.0	12.7	0.059	0.065†	This study
Pandalus platyceros	91	10.0	40.9	0.059	0.078†	This study

Astacidea						
Nephrops norvegicus	10	15.0	23.5	0.035	0.033*	Alcaraz and Sarda (1981)
Thalassinidea						
Calastacus quinqueseriatus	290	8.0	2.43	0.026	0.022†	This study
Callianasa californiensis	10	10.0	7.0	0.022	0.020†	Thompson and Pritchard (1969)
Callianasa jamaicense	10	25.0	5.84	0.055	0.029†	Felder (1979)
Upogebia pugettensis	10	10.0	6.0	0.060	0.055†	Thompson and Pritchard (1969)
Anomura						
Galathea strigosa	10	10.0	32.05	0.020	0.028*	Bridges and Brand (1980)
Munidopsis verrilli	1525	2.8	5.62	0.006	0.013†	This study
Pagurus bernhardus	10	10.0	8.35	0.040	0.040*	Bridges and Brand (1980)
Paralomis multispina	1100	3.5	7.64	0.013	0.022†	This study
Pleuroncodes planipes	10	20.0	3.0	0.064	0.019*	Quentin and Childress (1978)
Stereomastis sculpta	1000	4.0	16.8	0.006	0.011†	This study
Brachyura						
Bythograea thermydron	2500	12.0	65.0	0.034	0.043*	Mickel and Childress (1982)
Callinectes sapidus	10	25.0	125.8	0.127	0.139*	Lewis and Haefner (1976)
Cancer magister	10	10.0	700	0.017	0.028*	Prentice and Schneider (1979)
Chionectes bairdi	20	3.0	350	0.0056	0.038*	Paul and Fuji (1989)
Corystes cassivelaunus	10	10.0	14.65	0.017	0.018*	Bridges and Brand (1980)
Ebalia tuberosa	40	8.0	1.17	0.155	0.079†	Schembri (1979)
Ovalipes punctatus	10	20.0	39.0	0.072	0.069*	Du Preez (1983)
Panopeus herbstii	10	25.0	10.0	0.040	0.009*	Dimock and Groves (1975)
Pugettia producta	10	15.0	86.5	0.069	0.085†	Weymouth *et al.* (1944)

depth (Table 3) there is still a significant relationship between oxygen consumption rate and depth. The significant relationship is little affected by adjusting the data to correspond to a 10 g wet weight (Table 3). However, when the data are adjusted to 10°C, the slope ceases to be significant (Table 3). The metabolic rates as a function of depth of the more active group (caridenas and penaeid) are significantly higher than those of the other species (ANCOVA, $P = 0.032$ for data adjusted to 10°C and 10 g). For comparison, the fitted lines for the nonadjusted data for both groups are shown, along with the relationship found for midwater crustaceans (Fig. 2A; CHILDRESS, 1975). The lines for the same data sets adjusted to 10°C and 10 g are shown in Fig. 2B. These two figures clearly illustrate the difference between the two benthic groups in absolute rates and show that both decline much more slowly with depth than do the pelagic crustaceans. The conclusion from this analysis is that deeper living benthic crustaceans do have lower metabolic rates than shallower ones and this difference is due primarily to the decline in temperature with depth, not to other depth-related factors.

Table 3. *Regression equations relating metabolic rate* (μ O_2 mg^{-1} wet wt h^{-1}) *to temperature and depth for the California benthic decapod crustaceans studied in this report* (*Table* 1) *and previously* (*Table* 2: C. californiensis, C. magister, C. franciscorum, P. planipes, P. productus *and* U. pugettensis)

X parameter Data subset	$Y = aX^b$				
	N	a	$b \pm 95\%$ C.I.	F-test ($P =$)	R^2
Temperature					
All carideans by individuals	114	0.0097	0.689 ± 0.149	<0.0001	0.43
C. communis by individuals	16	0.0066	0.874 ± 0.462	0.0059	0.54
C. quinqueseriatus by individuals	16	0.0030	1.007 ± 0.327	<0.0001	0.76
G. vicaria by individuals	13	0.0154	0.346 ± 0.306	0.03	0.36
P. platyceros by individuals	35	0.0158	0.548 ± 0.292	0.0006	0.31
P. jordani by individuals	23	0.0297	0.262 ± 0.452	0.24	0.06
B. thermydron by means	4	0.0095	0.550	0.0096	0.92
Minimum depth by species, all California species					
Closest measured T to minimum depth	17	0.103	−0.261 ± 0.170	0.0052	0.42
Adjusted to T at minimum depth (Table 2)	17	0.103	−0.263 ± 0.155	0.0026	0.47
Adjusted to 10 g wt and T at minimum depth	17	0.129	−0.316 ± 0.157	0.0007	0.57
Adjusted to 10 g wt and 10°C (Table 2)	17	0.066	−0.141 ± 0.274	0.071	0.20
Minimum depth by species for California carideans and *S. ingentis*					
Adjusted to T at minimum depth (Table 2)	8	0.179	−0.285 ± 0.131	0.0018	0.82
Adjusted to 10 g wt and T at minimum depth	8	0.236	−0.350 ± 0.201	0.0053	0.75
Adjusted to 10 g wt and 10°C (Table 2)	8	0.114	−0.167 ± 0.199	0.086	0.41
Minimum depth by species for California crustaceans other than carideans and *S. ingentis*					
Adjusted to T at minimum depth (Table 2)	9	0.082	−0.302 ± 0.206	0.011	0.63
Adjusted to 10 g wt and T at minimum depth	9	0.100	−0.348 ± 0.189	0.0033	0.73
Adjusted to 10 g wt and 10°C (Table 2)	9	0.052	−0.175 ± 0.188	0.063	0.41
Minimum depth by species for California midwater crustaceans (data set from CHILDRESS, 1975)					
Closest measured T to minimum depth	27	0.694	−0.565 ± 0.197	<0.0001	0.59
Adjusted to 10 g wt and 10°C	26	0.151	−0.326 ± 0.181	0.001	0.57

Metabolism vs depth—multiple regression using nonadjusted data

The data set used for the multiple regression analysis of the relationship of oxygen consumption rate with depth, temperature and wet weight (Table 2) consists of data from two Antarctic crustaceans, one Arctic crustacean, numerous shallow living decapods and crustaceans from this study at the temperatures of their minimum depths. The hydrothermal vent crab data were not used in this analysis. (The data adjusted to 10 g and 10°C were also not used in this analysis but are presented in Table 3 as an aid to the reader.) There is no significant relationship between depth and wet weight in this data set (Kendall rank correlation, $S = -0.069$, $P = 0.95$). The results of multiple regressions on various partitionings of this data set are presented in Table 4. These partitionings included the entire data set, the entire set minus all carideans and penaeids, all carideans and penaeids, and the carideans alone. Temperature was a highly significant variable in all cases, and the magnitudes of its coefficient were generally larger than that used in the earlier analysis, supporting the conservative nature of that analysis. Wet weight was significant in all except the caridean grouping and the wet weight coefficients were comparable to that used for the weight adjustments in the earlier analysis, again supporting the conservative nature of that analysis. Depth was not a significant variable in any of the groupings except the carideans, where it was highly significant. The conclusion here is that temperature and size have strong relationships with metabolic rate but depth of occurrence is independently important only for the carideans.

Table 4. Multiple linear regression equations relating metabolic rate at minimum depth (μl O_2 mg wet wt^{-1} h^{-1}) to temperature, minimum depth of occurrence, and mean size for benthic decapod crustaceans studied in this report and in various reports from the literature (Table 2). Only those X parameters which approached significance in three-way tests ($P \leq 0.1$) are shown. The P values for depth in the first two regressions are 0.23 and 0.5, respectively. The data were linearized for the multiple regressions by log transformation

Data subset *X* parameter	$Y = aX^b$					
	N	*a*	*b* ± 95% C.I.	*P*	R^2	*F*
All crustaceans in Table 2 except *B. thermydron*						
	35	0.0098		<0.0001	0.68	34.3
Mean wet wt			−0.260 ± 0.117	<0.0001		20.5
Temperature			0.912 ± 0.264	<0.0001		49.7
All crustaceans in Table 2 except carideans, penaeids and *B. thermydron*						
	20	0.0039		<0.0001	0.68	17.8
Mean wet wt			−0.201 ± 0.185	0.0349		5.3
Temperature			1.154 ± 0.264	<0.0001		28.7
All carideans and peneids in Table 2						
	15	0.0418		<0.0001	0.89	28.6
Mean wet wt			−0.157 ± 0.127	0.020		7.4
Temperature			0.558 ± 0.314	0.0024		15.3
Minimum depth			0.145 ± 0.155	0.064		4.2
Carideans from Table 2						
	11	0.0607		<0.0001	0.95	78.6
Temperature			0.501 ± 0.117	0.0007		28.3
Minimum depth			−0.234 ± 0.099	0.0006		29.8

Comparison with the hydrothermal vent crab

An examination of metabolic rates adjusted to 10 g and 10°C (Table 2) shows that *B. thermydron* has a metabolic rate near the middle of all of the brachyurans, below the shallow living carideans, and about the same as or above that of the deeper living carideans. Figure 1 presents this comparison in a different way, plotting the mean rates of the vent crab at 272 atm and various temperatures with all of the species–temperature means from this study (Table 1) and the single species–temperature means from shallow living species (Table 2), all adjusted to 10 g wet weight. At all of the temperatures above 2°C, the vent crab data appear to be intermediate in value both to our values and to those from the literature. At 2°C, *B. thermydron* appears to have a higher rate than any of the deep-sea shrimps except *G. vicaria*, but is lower than the two Antarctic shrimps.

DISCUSSION

The results of both methods of data analysis indicate that benthic crustaceans are not a homogeneous group. The carideans are active animals with large eyes and often swim off the bottom, sometimes for extended times (PEARCY, 1970). Their metabolic rates are higher than those of other benthic crustaceans at all depths and, unlike those of other benthic crustaceans, do decline with increasing depth beyond the effects of temperature, although the effect of temperature is considerably larger than other effects of depth. Even so, the rates of the benthic carideans decline with depth much more slowly than do those of pelagic crustaceans. Thus, it may be that these benthic shrimp are showing the effects of a life habit split between the pelagic and benthic environments. The remaining group of benthic crustaceans does not show a significant decline with depth beyond the effect of temperature, suggesting that for completely benthic crustaceans the metabolic rates decline as a function of depth primarily due to changes in temperature with depth.

Animal size is also an important factor affecting metabolic rate, but it did not change significantly with depth for the group of benthic crustaceans which we studied. Studies on two species of benthic echinoderms from 1200 m also have indicated that their metabolic rates are comparable to those of shallow living species at comparable temperatures (SMITH, 1983). Although many physiological and biochemical adaptations are undoubtedly necessary to deal with the high hydrostatic pressures at depth (SIEBENALLER and SOMERO, 1989), we find no evidence in these results that these or other depth-related adaptations have resulted in substantial modifications in the metabolic rates of deeper living animals. Thus, for completely benthic crustaceans, aerobic metabolism is one biological process that appears to proceed at as great a rate in the deep sea as in shallower environments at comparable temperatures. Understanding the full significance of these findings requires some knowledge of the hypotheses put forward to explain the decline in metabolic rate with depth of pelagic fishes and crustaceans, so we provide below a brief summary of the previous research on this topic before returning to a consideration of the data at hand.

Review of the variation in metabolic rates as a function of depth of occurrence

The decline in metabolic rates with depth observed with pelagic fishes and crustaceans is well documented (see Introduction). The studies cited establish that this decline is greater

than that expected due to either lower temperature at greater depths or increased size of the animals living there.

One possible explanation for the decline in rates with depth was that there were depth-related changes in the composition of pelagic fishes and crustaceans so that deeper living ones were structurally reduced. However, while total protein content of midwater fishes declines with increasing depth to some extent, this decline is much less than the decline in metabolic rate (CHILDRESS and NYGAARD, 1973; CHILDRESS and SOMERO, 1979; SIEBENALLER and YANCEY, 1984). In contrast, the activities of enzymes indicative of aerobic and anaerobic metabolism in the muscles of midwater fishes decline much faster than does protein content with increasing depth of occurrence, paralleling the metabolic rates in rate of decline (CHILDRESS and SOMERO, 1979; SIEBENALLER and YANCEY, 1984; TORRES and SOMERO, 1988). This shows that the lower metabolic rates of deeper living species are laid down at the subcellular level and these changes do not result from an overall decline in protein content with depth but rather a specific and greater decline in enzymes which generate ATP. Studies showing decreased metabolic enzyme acivities in white muscle but not in heart or brain tissue of the deeper living fishes (CHILDRESS and SOMERO, 1979; SOMERO and CHILDRESS, 1980; SULLIVAN and SOMERO, 1980) indicate that the lower metabolic rates of these species are the result of greatly reduced locomotory abilities in the deeper living species, rather than the result of a general organism-wide reduction in tissue metabolic rates. Studies on the swimming costs and capacity of the deep-living mysid crustacean *Gnathophausia ingens* have recently indicated that its lower metabolic rate is due to reduced locomotor abilities (COWLES and CHILDRESS, 1988) as compared to those of shallower living pelagic crustaceans. Thus, the lower metabolic rates found with increasing depth of occurrence in pelagic fishes and crustaceans apparently reflect reduced locomotor abilities of the deeper living species.

The one measurement of the locomotor abilities of a deep-sea pelagic benthopelagic fish (*Antimora rostrata*), sometimes cited to question the reduction in locomotor abilities and metabolism with depth in fishes, serves as a good example to demonstrate the expected relationship between metabolic power and swimming speed (COHEN, 1977; MARSHALL, 1979). Cohen found that a 27 cm fish maintained a speed of 1.45 body lengths s^{-1} for 4.2 min while being chased by the submersible *Alvin* and concluded that this was not a greatly reduced swimming ability compared to shallower living species. On this basis, he suggested that the metabolic rates of deep living fishes might not be as reduced as had been suggested. However, since the power required to swim at increasing speed is roughly proportional to the velocity cubed (WEBB, 1975), swimming speed is not a sensitive indicator of metabolic power, since relatively small changes in swimming speed require large changes in metabolic power. Thus, a comparable sized rainbow trout with a maximum sustainable aerobic speed of about 2.6 body lengths s^{-1} (DOBSON *et al.*, 1987) would require about 6 times the power that the observed *Antimora* required. This estimated difference in aerobic power would be made even greater if the *Antimora* were, as seems likely under the conditions, swimming above its maximum sustainable speed and using some anaerobic power as well. Thus, Cohen's observations generally support a large difference in aerobic power between shallow and deep living pelagic fishes.

In fact the difference in aerobic power of these two species is even greater than the 6-fold minimum suggested. The measured citrate synthase activity, an indicator of aerobic power, in *A. rostrata* white muscle at 10°C is 0.37 units g^{-1} (SULLIVAN and SOMERO, 1980), while that of a 27 cm rainbow trout would be about 1.98 units g^{-1} (SOMERO and CHILDRESS,

1990). Since the measurements of swimming performance were made more than 10°C apart, the actual difference in citrate synthase acivities at the environmental temperatures would be expected to exceed a factor of about 12 assuming a Q_{10} of 2 for the enzyme.

The adaptive value of the decline in metabolic rate and locomotor abilities in midwater fishes and crustaceans was originally proposed to be the conservation of energy in the food-poor depths (CHILDRESS, 1971b; SMITH and HESSLER, 1974; SMITH, 1978) (food limitation hypothesis). However, the study of the growth rates and energy budgets of deeper living pelagic species (CHILDRESS and PRICE, 1978, 1983; CHILDRESS and MICKEL, 1980) showed that these species use more total energy in their life histories than do the shallower living vertically migrating species. This results from the larger sizes of the deeper living species as compared to the shallower ones. Thus, although the deeper living species are of lower energy concentration (CHILDRESS and NYGAARD, 1973, 1974), have lower metabolic rates, and have comparable lifespans as compared to the vertically migrating species, their total energy usages throughout their life histories appear to be much higher because they attain much larger sizes. That is, these mechanisms do not result in an actual energy saving but rather in reducing the cost of large size in the deeper living species. Thus, while conservation of metabolic energy may be of adaptive value to these species, another selective factors(s) must be driving the major changes with depth, since taken as a whole the life histories of the deeper living species are not energy conserving as compared to shallower living congeners (CHILDRESS and MICKEL, 1980).

We have suggested that, instead of food limitation, changes in visual predator–prey interactions with depth may be the critical variable allowing the evolution of lower metabolic rates and locomotor abilities in deeper living pelagic fishes and crustaceans (CHILDRESS *et al.*, 1980; CHILDRESS and MICKEL, 1985) (visual interactions hypothesis). The pelagic habitat is fundamentally different from benthic and terrestrial habitats in that it is three-dimensional and relatively homogeneous (MCFALL-NGAI, 1990). These differences greatly reduce the possibilities for refuge and crypsis in the pelagic environment. One consequence of this situation is that shallower living, visually orienting organisms are generally strong swimmers, which allows them to more successfully interact with predators or prey in a situation in which they can be detected at a considerable distance and the only refuge is to gain further distance or perhaps in some cases orient to gelatinous animals (ROBISON, 1986). With increasing depth, light intensity falls rapidly and the distances over which predator and prey can visually detect each other decline greatly. This means that there should be relaxation of selection for strong swimming abilities at greater depths since predators and prey need move only very short distances to successfully capture prey or escape predation. Further, sustained rapid swimming can have little adaptive value to an organism which can perceive only a very short distance in front of itself. In addition, it is possible that the presence of abundant mechanically stimulated luminescent organisms at depth may act to select against very active swimming by the micronekton, the "burglar alarm effect" (BURKENROAD, 1934; PORTER and PORTER, 1979). In addition, the eyes of pelagic decapods are progressively reduced at greater depths, suggesting less reliance on vision in deeper living pelagic crustaceans (MURRAY and HJORT, 1912; HILLER-ADAMS and CASE, 1988). Thus the visual interactions hypothesis appears a plausible explanation for the observed pattern of metabolic rates in pelagic fishes and crustaceans.

Both hypotheses can be subjected to tests by seeking out situations in the ocean where the variable of interest (food or vision) is different. For the food limitation hypothesis it has been suggested that one could examine the metabolic rates of deep living species which

are exposed to very different food concentration. Four attempts to take this approach have been made, although all face the problem that food availability was not quantified, but was assumed to be related to abundance of potential food items as broadly defined by the biomass of the next lower trophic level or the rate of primary production. The first was the measurement of the metabolic rates of deep-sea hydrothermal vent crabs that live in the presence of very high concentrations of their various food items around the hydrothermal vents (MIKEL and CHILDRESS, 1982b). This study concluded that the metabolic rates of the vent crab were comparable to those of shallow living brachyuran crabs but there were no data on deep living benthic crustaceans for comparison. A later analysis of the published metabolic rates of the vent crab with much published data on shallow living crustaceans and some preliminary data from this present study suggested that the metabolic rate of the vent crabs was about the same as non-vent deep-sea crustaceans and shallow living crustaceans, at comparable temperatures leading to the suggestion that metabolic rates of benthic crustaceans did not reflect the food availability in their environment (CHILDRESS and MICKEL, 1985).

A second test was the comparison of the chemical compositions of midwater fishes from the relatively rich California Current with those of a closely matched group of species from the much more sparsely populated North Pacific Central Gyre (BAILEY and ROBISON, 1986). These workers concluded that lipid content reflected food availability but protein content did not. Since protein content of midwater fishes is correlated with their metabolic rates (CHILDRESS *et al.*, 1980) it is likely that fishes from the two areas have comparable metabolic rates. The third sort of test has been to compare the metabolic rates of benthopelagic crustaceans with those of shallower living bathypelagic crustaceans (SMITH, 1985; CHILDRESS *et al.*, 1989). These crustaceans have comparable metabolic rates which, if one assumes that the generally higher biomasses near the bottom are indicative of higher food availability, would lead one to reject the food limitation hypothesis.

In the fourth sort of test, COWLES (1987) measured the metabolic rates of midwater crustaceans off the Hawaiian Islands and compared these rates with those published for the more productive region off California (CHILDRESS, 1975). Even after correcting for the temperature differences in the two regions, he found that above 400 m the Hawaiian species had higher metabolic rates while below that depth the rates were not significantly different. He interpreted these data to reject the food limitation hypothesis and to support the visual predator–prey hypothesis. He suggested that the higher metabolic rates of shallower living species off Hawaii also supported this hypothesis since the higher levels of illumination and greater water clarity off Hawaii should increase the distances over which visual interaction can take place there, therefore favoring greater muscle power and the associated greater metabolic rates.

Another possible test of these hypotheses, suggested by CHILDRESS and MICKEL (1985), is that animals without image-forming eyes would not be expected to show a change in locomotor abilities with increasing depth, because ambient light level would not affect their interactions with predators or prey in a fashion favoring a stronger locomotor response at higher light levels. Therefore, metabolic rates of sightless animals at greater depths would show only temperature effects if the visual interaction hypothesis is correct. If the food limitation hypothesis is correct, one would expect such deeper living species to have much lower metabolic rates than shallower living ones unless the abundance of their food source is not changing in parallel to total plankton biomass. There has not so far been an outright test of this hypothesis, although the limited data available on three species of

deeper living gelatinous organisms (SMITH, 1982; CHILDRESS and MICKEL, 1985; YOUNGBLUTH *et al.*, 1988; CHILDRESS *et al.*, 1989) suggests that their metabolic rates do not decline greatly with depth.

Another possible, although more complicated, test of the factors responsible for the metabolic decline of pelagic fishes and crustaceans with depth is the comparison of the rates of benthic animals from different depths. Such a data set for crustaceans would allow a more complete comparison of the metabolic rate of the hydrothermal vent crab with that of other deep-sea benthic crustaceans to determine whether the metabolic rates of benthic crustaceans reflect food availability in their environment. The data previously available have been used to suggest that the metabolic rates do not (MICKEL and CHILDRESS, 1982b; CHILDRESS and MICKEL, 1985). If this conclusion were supported by a more extensive data set which also showed no decline with metabolic rate with depth beyond the effect of temperature, then both hypotheses could be rejected as applying to the deep benthic fauna. The conclusion concerning food availability perhaps could be generalized to pelagic organisms, but the refuge provided by the bottom makes it very different from the pelagic realm in terms of the susceptibility of benthic organisms to visual detection. One could reasonably argue that the presence or absence of a decline with depth would reflect the importance or nature of visual predator–prey interactions in the benthic environment.

Benthic metabolic rates

The comparison of the metabolic rates of the hydrothermal vent crab, *Bythograea thermydron*, with the deep living benthic crustaceans studied here indicates that its metabolic rate is about the same as the more active species. This is appropriate since many observations of its behavior indicate that it is a relatively active species. Since *B. thermydron* lives at very high population densities in very rich communities (HESSLER and SMITHY, 1983) one would expect it to be exposed to high food levels, yet its metabolic rates do not appear to be greatly elevated relative to other deep-sea crustaceans. This suggests that the metabolic rates of benthic marine crustaceans do not evolutionarily respond to food availability to a substantial degree.

The responses to pressure of the deeper living crustaceans studied here strongly suggest that these animals, like *B. thermydron* (MICKEL and CHILDRESS, 1982a, 1982b), are generally stenobaric as indicated by the often poor survival of deeper living species as compared to shallower ones. However, the degree of this is highly variable. The most stenobaric of those studied was *G. vicaria*, a member of an exclusively deep-sea family, which could not survive at 1 atm pressure for more than a few hours and showed few signs of life at 1 atm pressure other than scaphognathite beating. The response of this species to low pressure was notably different from that of *B. thermydron* in that *G. vicaria* was flaccid with a notable lack of muscular tension or responsiveness at low pressure while the vent crab showed muscle tetany with responsiveness present but impaired by the contracture of its muscles. This suggests that pressure can differentially affect the inhibitory and stimulatory nerves of crustaceans, and these effects are not necessarily consistent among all crustaceans.

The temperature effects observed in the deeper living species in this paper are also notably different from those observed in *B. thermydron*, which shows a moderate effect of temperature over its very wide normal temperature range. In contrast, the deeper living species studied here, all of which live over very narrow temperature ranges, show little

increase in metabolic rates at higher temperatures. This kind of observation may be typical of deeper living, stenothermal crustaceans since it has also been observed in a variety of deep living midwater species (TORRES and CHILDRESS, 1985; COWLES, 1987). The significance of this lack of temperature effect is unclear at this time. Since it was measured outside the temperature ranges of the species, it is unlikely to have adaptive significance but it may reflect some aspect of the temperature adaptation of these stenothermal species.

The carideans are a group which has distinctive habits and these appear to be reflected in their metabolic adaptations to depth. As a group the eyes of benthic carideans increase in size with increasing depth, with the deep living members of the genera *Crangon*, *Glyphocrangon* and *Pandalopsis* having especially large eyes (HILLER-ADAMS, 1987). These changes probably increase the photic sensitivity of the eyes of the deeper living carideans, but other accompanying changes probably result in a loss of acuity. In contrast, although the eyes of noncaridean deep-sea species have not been studied in detail, it is obvious that they are, if anything, reduced in comparison with those of shallow living relatives. Thus one difference between these groups appears to be the extent of their reliance on vision. The other major difference is in behavior, since all of the carideans studied here appear to be relatively active, being capable of strong, pleopod propelled swimming although they are generally considerably denser than seawater. The ability to carry out such swimming requires more muscle power than does locomotion on the bottom. When compared with more completely benthic crustaceans, it does not seem surprising that they have a greater decline in metabolic rate with depth since the carideans are active, visually orienting animals.

This brings the discussion to where this report started out, with a consideration of the decline in metabolic rate with depth in midwater crustaceans and fishes. The data presented here indicate that the benthic environment is different in this regard. In particular, the shallow living pelagic species have high metabolic rates as compared to the deep living pelagic species. This shows that the difference between these two groups is not due to the rates at depth, but rather that for some reason the shallower living pelagic crustaceans have elevated metabolic rates and, as we have seen earlier, elevated locomotor abilities compared to the deeper living ones. The obvious difference here is the unique combination at shallower depths in the pelagic realm of higher illumination and therefore greater ability to see distant objects with the lack of any refuge except distance or perhaps in some cases gelatinous animals (B. ROBISON, personal communication). In contrast the benthos is always available as a refuge and in addition benthic species have a greater variety of possibilities for crypsis. That this leads to very different amounts of muscle power has been shown in comparisons of enzyme activities of pelagic and benthic fishes as well as comparisons of the scaling of these enzyme activities (SOMERO and CHILDRESS, 1980, 1990; CHILDRESS and SOMERO, 1990). Thus we suggest that the data presented here support the hypothesis that the decline in metabolic rate with depth in pelagic crustaceans is a result of the presence of very high locomotor capacities in shallow living pelagic fishes and crustaceans as a result of selection by visual predator–prey interactions in a habitat where the only refuge is distance.

Acknowledgements—We would like to thank the captain and crew of the R.V. *New Horizon* for their help in capturing the crustaceans used in this study and in helping us learn how to use the epibenthic beam trawl. The epibenthic beam trawl and pressure actuated cod-end could never have been successfully constructed without the

design assistance and fabrication work provided by the UCSB physics department machine shop under the supervision of H. R. Stuber. A Kuris provided help and advice in identifying the crangonid shrimps. The construction of the epibenthic beam trawl and the pressure-activated cod-end were funded by National Geographic Society grant 2146. The research described in this paper was funded by National Science Foundation grants OCE 85-00237 and OCE 86-10514 to JJC. We thank E. Thuesen for critically reading this manuscript.

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