Metabolic rates of midwater crustaceans as a function of depth of occurrence off the Hawaiian Islands: food availability as a selective factor?

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Abstract. During July of 1983, 1986, and 1987, we measured rates of oxygen consumption of 234 individuals of 17 species of midwater crustaceans (orders Decapoda, Mysidacea, and Euphausiacea) off the Hawaiian islands at depths from the surface to greater than 1200 m. The routine metabolic rates declined with increasing depths of the species' occurrence to an extent greater than could be accounted for by depth-related changes in body size or water temperature. Most species appeared able to regulate their oxygen consumption down to the lowest oxygen partial pressures found in their depth range (20 mm Hg O_2), but did not regulate to such low oxygen partial pressures as did similar midwater crustaceans off California, where oxygen levels reach as low as 6 mm Hg. Metabolic rates of the shallower-living, but not the deepest-living Hawaiian crustaceans were significantly higher than those of Californian crustaceans. This is interpreted as indicating that the metabolic rates of midwater crustaceans are not adapted specifically to differing levels of primary production and that the decline with depth of metabolic rates in these species is not the result of food limitation at depth. The data are, however, consistent with the hypothesis that lower metabolic rates at depth are due to the relaxation of selection pressures relating to visual predation near the surface.

Introduction

The decline in routine aerobic metabolism of midwater crustaceans and fishes with increasing depth has been well documented (Childress 1971, 1975, 1977, Torres et al. 1979, Smith and Laver 1981, Donnelly and Torres 1988, Ikeda 1988, Torres and Somero 1988). A number of depth-related factors, including changes in temperature, pressure, and body size may contribute to this decline. However, the decline is greater than can be accounted for by these parameters (Childress 1975, Torres et al. 1979, Ikeda 1988, Torres and Somero 1988). In midwater fish-

es, the activities of enzymes of intermediary metabolism decline with depth in parallel with the decline in metabolic rates, indicating that the decline in metabolism with depth is determined at the subcellular level (Childress and Somero 1979, Somero and Childress 1980, Siebenaller and Yancey 1984, Torres and Somero 1988). These findings suggest that a decrease in locomotory abilities may be the basis for metabolic decline with depth. This interpretation has been supported for at least one deep-living species by the finding that the low metabolic rate of the bathypelagic species *Gnathophausia ingens* is related primarily to a lower capacity for active swimming than that found in surface-living crustaceans (Cowles and Childress 1988).

Various hypotheses regarding the selective factors responsible for the decline in metabolic rate with depth in midwater species have been proposed. The most often cited hypothesis is that the reduction in metabolic rate is due to selection for energy conservation because of low levels of available food at depth (Childress and Nygaard 1973, 1974, Childress 1975). A more recent hypothesis proposes that the reduction is due to relaxation at greater depths of factors selecting for energetically expensive robust bodies and rapid swimming abilities due to the prevalence of visual predation at shallower depths (Childress et al. 1980, Childress and Mickel 1985, Childress et al. 1990 a, b).

These hypotheses can be tested by comparing metabolic rates of midwater species from regions of differing biological and hydrographic characteristics. Most previous studies have been done in areas of high productivity, such as the California Current off Southern California. A site from the central Pacific gyre would provide a logical site for comparison, since the predictions of the two hypotheses regarding these two sites are opposite. From the food-limitation hypothesis, one could predict that species from the less productive central gyre would have lower metabolic rates, while the visual-predation hypothesis would predict that central gyre species would have higher metabolic rates due to the greater clarity and increased light penetration into the oligotrophic gyre water.

In this paper, we examine the decline in aerobic metabolism with depth in midwater crustaceans off Oahu, Hawaii, which is located in the North Pacific Central Gyre, and compare the observed decline with the decline accountable for by the known changes in the water column with depth. In addition, we compare the metabolic characteristics of this assemblage with those of a previously studied assemblage off California to evaluate the hypotheses regarding selective factors responsible for the decline.

Materials and methods

Capture and maintenance

Midwater crustaceans were collected off the northwestern coast of Oahu (Latitude 21° 20′N; Longitude 158° 20′W) from depths of 100 to 1200 m using the R.V. "New Horizon" during July of 1983, 1986, and 1987. The gear used was an opening and closing Tucker Trawl with a 3.3 m-square mouth, equipped with a thermally protecting cod end (Childress et al. 1978), and towed at 2.5 knots. Seventeen species, all of a generally shrimplike form but from the orders Decapoda, Mysidacea, and Euphausiacea were collected and studied on shipboard (Table 1). Species were identified using descriptions of Ziemann (1975), Chace (1986), Walters (1975), and Clarke (1962). Immediately after capture, the crustaceans were transferred from the thermally protecting cod-end to 1-liter aquaria of 5°C seawater. They were maintained at this temperature until used in an experiment, within 2 to 3 d of capture.

Measurement of metabolic rates

Each crustacean was placed individually in a closed chamber with a volume of between 100 ml and 1.1 liters. The volume chosen depended on the size of the crustacean and the experimental temperature. The chamber water was filtered through 0.45 μm membrane filters, and 20 mg per liter each of streptomycin and penicillin were added to the chamber to control microbial growth. The change in oxygen partial pressure over time was then measured continuously using Clark-type oxygen probes (Mickel et al. 1983) and a computer-based data-logging system (Cowles 1987). Control runs were conducted at each temperature, using the same chamber water after a run to measure background microbial respiration. Most experiments were continued until the crustacean had reduced the oxygen to such a low level that it was no longer capable of regulating its oxygen consumption. Runs generally lasted from 4 to 48 h. Each chamber was covered by a dark cloth during experiments to minimize disturbance. Runs were conducted at 5, 10, and 20°C.

The rate of change in oxygen level during the course of each experiment was used to calculate the average weight-specific oxygen consumption (MO_2) of each species at each temperature tested. Typically, measured rates were variable at first, as slight temperature differences in the chambers came to equilibrium and the crustaceans settled down after the disturbance of being placed in the chamber. Rates then remained relatively constant for an extended period, until a critical oxygen pressure (P_c) was reached, below which the animal was no longer able to regulate its oxygen consumption. Average MO_2 was measured over the range of oxygen levels in which oxygen consumption was relatively constant. This range varied by individual, but usually encompassed the range of 80 to 40 mm Hg O_2. The species' critical oxygen pressure was also noted. Each species' Q_{10} was calculated by comparing the average MO_2 of individuals studied at different temperatures.

Data analysis

Each species' depth range and minimum depth of occurrence (MDO), defined as the depth below which 90% of the population lives (Childress and Nygaard 1973, Childress 1977), was obtained from records in the literature and from our own observations. These data were combined with published reports of the temperature and oxygen profiles in the area (Murray and Riley 1969, Gordon 1970) to find the range of temperatures and oxygen levels encountered by each species. Each species' oxygen consumption at the temperature characteristic of its minimum depth of occurrence ($MO_{2\ MDO}$) was then estimated. If a directly measured rate was made at a temperature within one degree of the temperature at the species' MDO (T_{MDO}), that rate was used. If experimental temperatures had spanned the temperature at MDO, the MDO rate was interpolated between the two measured rates using the Q_{10} formula. If experimental temperatures did not span the T_{MDO}, the $MO_{2\ MDO}$ was calculated using the nearest measured temperature and a Q_{10} of 3. This Q_{10} is fairly high and slightly overestimates the effect temperature generally has on physiological functions such as oxygen consumption. We used this high Q_{10} in order to be conservative when correcting for temperature effects.

The best-fit power equation was calculated, relating respiratory rate to minimum depth of occurrence for the species assemblage. Each species' rate of oxygen consumption was then adjusted to 10 °C using the criteria given above, and MDO was again compared to MO_2 to estimate the fraction of the reduction in MO_2 with depth due to the decrease in temperature with increasing depth. MO_2 rates were then further adjusted to those expected for a 5 g individual, using the empirical relationship found between wet weight and MO_2 in the data set, and the relationship between depth and rate of oxygen consumption was again examined to see if the decrease in MO_2 with depth was influenced by changes in average body size. The range of depths in which the species were able to live aerobically was calculated by comparing depth ranges and P_c values for each species with the temperature and oxygen profiles of the water column.

Metabolic characteristics of the Hawaiian midwater crustaceans were compared to those off California (Childress 1975, Torres and Childress 1985). Only species from the orders Decapoda, Mysidacea, and Euphausiacea reported for the Californian assemblage were used, to provide comparability with the Hawaiian data. The Californian crustaceans had a similar range of minimum depths of occurrence (10 to 1200 m) and a similar ratio of vertical migrators to nonmigrators (5:10) as the Hawaiian assemblage. The relationships between $MO_{2\ MDO}$ and depth for the Hawaiian and Californian assemblages were compared by analysis of covariance (ANCOVA, Zar 1974), and by an extension of ANCOVA used to find the range over which Y values are significantly different between two regressions having different slopes (Zerbe et al. 1982). Confidence intervals given on slopes are 95% confidence intervals. Regression slopes were declared significant when their slopes differed from zero at the 5% confidence level (Student's t-test).

Results

Oxygen consumption rates of 17 species of Hawaiian midwater crustaceans were measured on shipboard (Tables 1 and 2).

All the species were oxyregulators, that is, they maintained a relatively constant rate of oxygen consumption with decreasing oxygen levels until a critical oxygen partial pressure (P_c) was reached (Fig. 1). Below this partial pressure their rate of oxygen consumption declined precipitously. Although anaerobic capacities were not specifically tested, most individuals became lethargic at oxygen pressures below their P_c, and mortality was com-

mon unless they were quickly transferred to oxygenated water.

The rates of regulated oxygen consumption of the vertical migrators were higher than those of the nonmigrators (Student's t-test, $P < 0.0001$, tested separately at each temperature). Mysid nonmigrators had the lowest rates. MO_2 generally increased with temperature, although not in all species at all temperatures. P_c also generally increased with temperature, especially between 10 and 20°C (ANOVA, $P < 0.01$). The P_c values for nonmigrators were generally lower than those of vertical migrators, although this difference was not significant (Student's

t-test). Comparison of the species' P_c values at different temperatures with their known depth ranges, environmental temperatures, and oxygen levels (Table 1, Fig. 2) showed that virtually all these species were able to live aerobically at all depths at which they are found, even within the oxygen minimum layer. The nonmigrators, which are resident in this layer, generally had P_c values at or well below environmental oxygen levels, while several vertical migrators, most notably the *Oplophorus* species, had P_c values quite close to oxygen levels encountered in the oxygen minimum layer at 5°C off Hawaii and may be close to being oxygen-limited at these daytime depths.
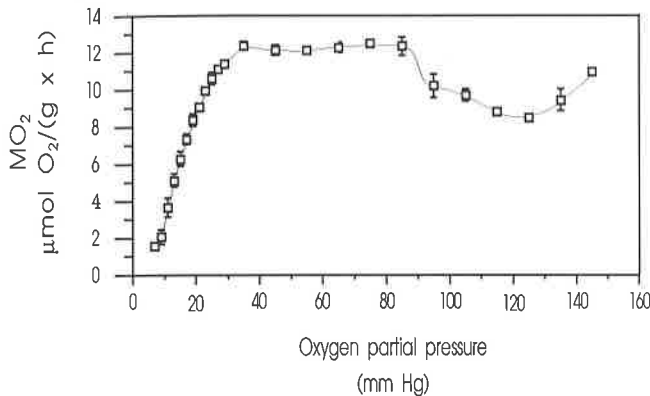

Fig. 1. Oxygen consumption (MO_2, μmol O_2 g^{-1} wet wt h^{-1}) for one individual at 20°C. Critical oxygen pressure for this individual was 35 mm Hg

Temperature effects

Vertical migrators appeared to exhibit normal metabolic responses to changes in temperature, at least in the 10 to 20°C range. Migrators' Q_{10} values between 10 and 20°C were between 1.2 and 4.6, and averaged 2.7 (Table 2). At 5°C, however, some of the vertically migrating oplophorids had higher rates of oxygen consumption than at 10°C, resulting in Q_{10} values as low as 0.4. This appeared to be due to increased routine activity levels at this temperature. Nonmigrators exhibited either low effects of temperature on metabolic rate between 5 and 10°C (Q_{10} was 0.3 to 1.1 for the *Acanthephyra* species and for the mysids, A–C and M–P in Table 2, respectively), or quite large effects (Q_{10} was 5.0 to 7.2 for the nonmigrating *Notostomus* and *Sergestes* species, E–F

Table 1. Crustaceans captured from midwater depths off Hawaii and analyzed in present study. MDO, Max. depth: minimum and maximum adult depths of occurrence, respectively; VM: vertical migrator (Y, yes; N, no). Species codes are used in Table 2. –: Experiments not performed

Species	Code	Wet mass (g)		MDO		Max. depth (m)	VM	No. individuals studied at:		
		mean	range	(m)	T (°C)			5°C	10°C	20°C
Order Decapoda										
Familiy Oplophoridae										
Acanthephyra acutifrons	A	8.64	1.06–31.07	600	5.5	1200	N	6	5	–
Acanthephyra curtirostris	B	2.29	0.62– 4.49	650	5.5	950	N	10	6	–
Acanthephyra smithi	C	3.84	1.26– 8.54	175	20.0	900	Y	4	13	4
Janicella spinicauda	D	0.35	0.28– 0.39	30	25.0	500	Y	–	3	6
Notostomus elegans	E	22.54	6.32–38.76	600	5.5	800	N	9	5	–
Notostomus gibbosus	F	10.40	0.86–27.65	800	4.5	1200	N	12	7	–
Oplophorus gracilirostris	G	2.58	0.48– 5.66	60	24.0	650	Y	2	6	8
Oplophorus spinosus	H	2.92	1.17– 4.46	140	21.0	750	Y	5	5	4
Systellaspis debilis	I	1.22	0.55– 1.80	110	22.0	900	Y	7	9	7
Family Sergestidae										
Sergestes (Sergia) bisulcatus	J	2.54	1.89– 3.26	225	17.5	900	Y	5	5	5
Sergestes (Sergia) fulgens	K	1.06	0.60– 1.27	150	20.0	625	Y	4	4	1
Sergestes (Sergia) tenuiremis	L	2.61	1.17– 4.06	550	6.0	800 +	N	4	6	3
Order Mysidacea										
Family Lophogastridae										
Gnathophausia gigas	M	1.01	0.96– 1.06	800	4.5	4000	N	3	–	–
Gnathophausia gracilis	N	2.45	1.01– 4.91	800	4.5	1100 +	N	8	–	–
Gnathophausia ingens	O	5.11	0.45–15.24	400	10.0	900	N	20	6	–
Gnathophausia zoea	P	3.99	0.87– 6.72	600	5.5	900	N	10	5	–
Order Euphausiacea										
Thysanopoda cornuta	Q	5.88	2.99– 8.78	1000	4.0	1000 +	N	2	–	–

Table 2. Oxygen consumption data (MO_2, μmol O_2 g^{-1} wet wt h^{-1}), Q_{10}, and critical oxygen pressures (P_c, mm Hg) for Hawaiian crustaceans (code designations given in Table 1). SE: standard error; min: minimum. In calculated MO_2 column, MDO are rates corrected to species minimum depth of occurrence, and 10°C, 5 g rates are MDO rates corrected to that expected for a 5 g individual at 10°C. See "Results – Depth effects" for equations used for these correction factors. -: experiments not performed

Code	5°C				10°C				20°C				Q_{10}		Calculated MO_2	
	MO_2		P_c		MO_2		P_c		MO_2		P_c		5–10°C	10–20°C	MDO	10°C, 5 g
	mean	(SE)	mean (SE)	min.	mean	(SE)	mean (SE)	min.	mean	(SE)	mean (SE)	min.				
A	1.66	(0.35)	29.5 (9.7)	15	1.71	(0.28)	28.9 (10.7)	17					1.1	–	1.62	3.06
B	1.82	(0.25)	28.1 (7.2)	14	1.88	(0.27)	28.9 (6.0)	16					1.1	–	1.82	2.30
C	7.31	(0.73)	27.0 (2.9)	19	4.70	(0.53)	27.3 (11.0)	11	11.21	(1.65)	25.5 (2.7)	21	0.4	2.4	11.21	3.73
D			–	–	5.05	(1.39)	–	–	15.44	(1.29)	37.0 (2.1)	29	–	3.1	26.74	2.73
E	1.34	(0.16)	16.5 (3.1)	10	2.99	(0.55)	22.8 (6.2)	10					5.0	–	1.34	2.80
F	0.48	(0.04)	14.2 (2.7)	7	1.28	(0.24)	28.0 (3.0)	12					7.0	–	0.48	0.76
G	13.08	(1.52)	35.0 (5.2)	30	10.63	(1.40)	40.5 (5.5)	31	23.19	(1.60)	47.7 (2.7)	37	0.7	2.2	35.98	7.77
H	8.43	(0.71)	32.9 (4.7)	20	5.08	(1.60)	18.2 (5.3)	6	23.46	(5.74)	53.0 (10.3)	43	0.4	4.6	23.46	3.80
I	2.41	(0.24)	24.2 (4.1)	14	4.33	(0.54)	35.0 (5.0)	13	7.80	(0.84)	43.5 (4.5)	31	3.2	1.8	9.71	2.72
J	2.57	(0.51)	26.3 (4.3)	16	4.65	(1.20)	39.2 (4.5)	26	7.41	(1.60)	74.8 (3.6)	66	3.3	1.6	6.60	3.41
K	3.74	(0.43)	26.2 (2.0)	24	6.87	(1.35)	39.8 (2.1)	34	19.92		87.0	87	3.4	2.9	19.92	4.07
L	1.50	(0.24)	25.4 (1.5)	23	4.03	(1.10)	31.9 (5.4)	18	4.78	(2.11)	54.6 (5.0)	50	7.2	1.2	1.68	1.89
M	0.69	(0.14)	17.2 (3.6)	14	–		–	–					–	–	0.69	0.71
N	0.91	(0.17)	26.8 (8.1)	10	–		–	–					–	–	0.91	1.52
O	2.16	(0.22)	13.4 (1.0)	9	1.52	(0.20)	15.4						0.5	–	1.52	1.42
P	1.62	(0.30)	19.5 (8.9)	11	0.91	(0.08)							0.3	–	1.31	2.26
Q	1.66	(0.43)	19.8 (5.2)	15	–								–	–	1.49	2.55

and J–L in Table 2). Few of the nonmigrators survived exposure to 20°C water. It should be pointed out that many of these nonmigrators live in water of around 5°C or below, and in nature rarely if ever encounter water even as warm as 10°C. Their responses to temperatures at 10°C and above are thus not expected to be adaptive.

Depth effects

Species' mean rates of oxygen consumption at the temperatures of their minimum depths (MO_2 $_{MDO}$) declined sharply with increasing minimum depth of occurrence. The best-fit power equation relating minimum depth of occurrence (MDO) to MO_2 $_{MDO}$ was:

$$MO_2\ _{MDO} = 5409\ MDO^{-1.277 \pm 0.276}. \qquad (1)$$

This is a highly significant relationship ($P < 0.001$). By Eq. (1), a species having a minimum depth of occurrence of 50 m would be expected to have a metabolic rate at that depth of 36 μmol O_2 g^{-1} wet wt h^{-1}, while a species at 500 m would have a MO_2 $_{MDO}$ of only 1.9, or 5.3% of the 50 m rate. By a MDO of 1000 m, MO_2 $_{MDO}$ declines to 0.80, only one-fiftieth the rate at 50 m.

Depth-related changes in temperature and in body size may be responsible for part of this decline. To correct for the influence of changes in temperature with depth, all MO_2 data were corrected to 10°C using Q_{10} values calculated as outlined in the "Materials and methods – Data analysis". The possible influence of changes in size with depth was less clear. The best-fit relationship between minimum depth of occurrence and wet weight (wt, g) indicated a slight tendency toward larger body size with depth, although the trend was not significant. The relationship between body wet weight (wt, g) and metabolic rate corrected to 10°C ($MO_{2,\ 10°C}$) was:

$$MO_{2,\ 10°C} = 3.667\ wt^{-0.224 \pm 0.465}. \qquad (2)$$

Although this relationship was not significant over the size range studied, the power of the relationship, -0.22, was very similar to the approximately -0.25 normally found in much larger data sets for this type of allometric relationship. Although neither the changes in body size with depth nor the change in MO_2 with size were significant, both tended in a direction which would produce lower metabolic rates at depth. We therefore took the conservative approach of correcting all rates to those expected for a 5 g individual, a weight intermediate among the size ranges of crustaceans studied.

After correcting for depth-related temperature changes by normalizing all data to 10°C, and for any possible influences of size by normalizing to 5 g, the best-fit relationship between minimum depth of occurrence and metabolic rate ($MO_{2,\ 10°C,\ 5\ g}$) was:

$$MO_{2,\ 10°C,\ 5\ g} = 20.769\ MDO^{-0.353 \pm 0.260}. \qquad (3)$$

($P < 0.02$). The decrease in aerobic metabolism with increasing depth of occurrence is thus significant, even when differences in temperature and body size are taken into account. By this equation, a species having a MDO of 500 m would have a metabolic rate less than half that
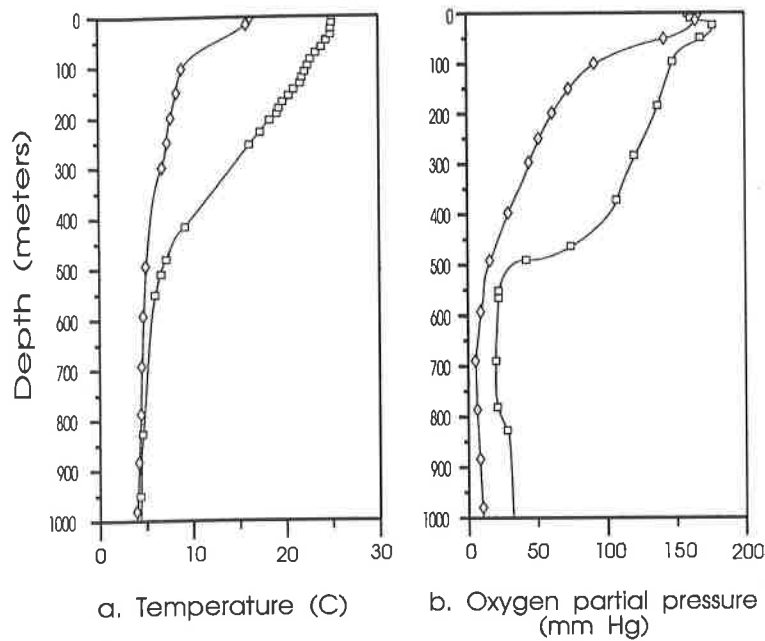
Fig. 2. Temperature and oxygen profiles off Hawaii (□) and California (◇). Hawaii data are from June data of Gordon (1970), California data from Childress (1969a). Oxygen data were converted to mmHg using the table in Murray and Riley (1969)
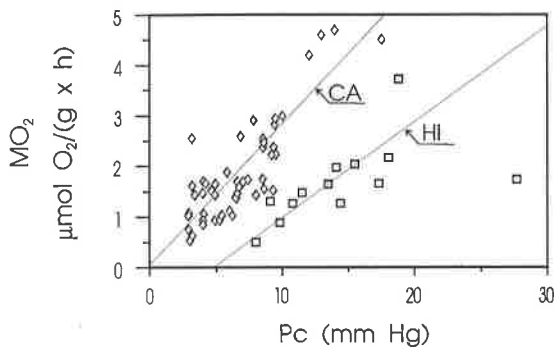
a. Temperature (C)

b. Oxygen partial pressure (mm Hg)

Fig. 3. *Gnathophausia ingens.* Critical oxygen pressures (P_c) and minimum rates of regulated oxygen consumption (MO_2) for individuals from populations off Hawaii (□) and off California (◇). Rates of oxygen consumption are indistinguishable between the two sites, but Hawaiian population has a significantly higher critical oxygen pressure. The Hawaiian outlier to extreme right is illustrated for completeness, but was not included in analysis as it is more than two standard deviations above mean for the rest of the Hawaii data. All measurements made at 5.5 °C
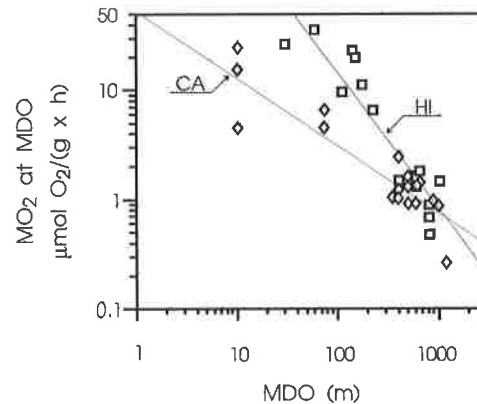
Fig. 4. Regulated oxygen consumption ($MO_{2\ MDO}$) at temperature of minimum depth of occurrence, as function of minimum depth of occurrence (MDO) for Hawaiian (□) and Californian (◇) midwater crustacean assemblages. Relationship off Hawaii: $MO_{2\ MDO} = 5409\ MDO^{-1.277 \pm 0.276}$. Relationship off California: $MO_{2\ MDO} = 58.90\ MDO^{-0.628 \pm 0.155}$. $MO_{2\ MDO}$ for Hawaiian assemblage is significantly higher than that of Californian assemblage down to depth of 500 m

of a species at 50 m after correcting for temperature and size differences, while the metabolism of a species living at 1000 m would be only one-third of that at 50 m.

Comparison with crustaceans off California

These Hawaiian species had significantly higher critical oxygen pressures at temperatures characteristic of the oxygen minimum layer than did a similar assemblage of crustaceans in the more severe oxygen minimum layer off California. P_c for the Californian species at 4 to 7.5 °C averaged 9 mm Hg (Childress 1975), while P_c for the Hawaiian species at 5 °C averaged 24 mm Hg, a highly significant difference. At warmer temperatures characteristic of waters above the oxygen minimum layer, howev-

er, there was no significant difference between the P_c values of species from the two sites, although the California species still averaged lower. Two species, *Acanthephyra curtirostris* and *Gnathophausia ingens*, were found at both sites. Both species had a significantly higher P_c off Hawaii (28.1 vs 8.3 for *A. curtirostris* and 13.4 vs 6.0 for *G. ingens*, Fig. 3), while no significant difference could be found between the metabolic rates of the two species between the two sites. P_c for *G. ingens* increased with metabolic rate in a parallel manner for both Hawaii and California, but P_c for the Hawaiian specimens was higher than that of the Californian specimens at any given MO_2 (Fig. 3).

As with the Hawaiian assemblage, the rate of aerobic metabolism in the Californian crustaceans decreased sharply with depth. The best-fit curve relating the de-
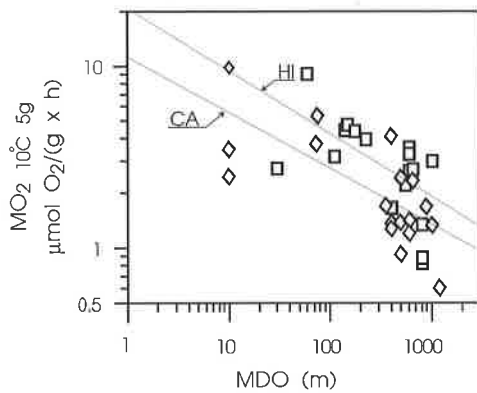
Fig. 5. Regulated oxygen consumption ($MO_{2\ 10°C\ 5g}$), corrected to 10°C and to 5 g wet wt, as function of minimum depth of occurrence (MDO) for Hawaiian (□) and Californian (◇) midwater crustacean assemblages. Relationship off Hawaii: $MO_{2\ 10°C\ 5g} = 20.769$ $MDO^{-0.353\pm0.260}$. Relationship off California: $MO_{2\ 10°C\ 5g} = 10.556\ MDO^{-0.302\pm0.155}$. Slopes of the two regressions are indistinguishable, but the Hawaii relationship has a significantly higher $MO_{2\ 10°C\ 5g}$ at any given depth (ANCOVA)

crease in metabolism to minimum depth of occurrence for the Californian crustacean assemblage was:

$$MO_{2\ MDO} = 58.90\ MDO^{-0.628\pm0.155}. \qquad (4)$$

This is also a highly significant relationship ($P < 0.01$). Metabolic rate for these Californian species declines less sharply with depth, however, than for the Hawaiian species (Fig. 4, analysis of covariance, $P < 0.01$). Further analysis of these two equations (Zerbe et al. 1982) indicates that the metabolic rates for the Hawaiian species are significantly higher than those for the Californian species down to a depth of 500 m. Below this depth there is no significant difference in metabolic rates between the two regions.

As discussed in subsection "Depth effects" above, temperature and wet weight are factors which may potentially affect these species' metabolic rates. To compensate for differences in water temperature and body size between Hawaii and California, the California data were also corrected to an intermediate temperature of 10°C, using a Q_{10} of 3, and 5 g wet weight. The resulting best-fit relationship between depth (MDO) and metabolic rate ($MO_{2,\ 10°C,\ 5g}$) for the Californian species was

$$MO_{2,\ 10°C,5\ g} = 10.556\ MDO^{-0.302\pm0.155}. \qquad (5)$$

The relationship was still highly significant. An analysis of covariance comparison of Eq. (5) with Eq. (3) revealed that the slopes of the relationships between temperature-corrected MO_2 and depth between Hawaii and California are indistinguishable, but that the Hawaiian relationship has a significantly higher Y-intercept, indicating higher metabolic rates for the Hawaiian species (Fig. 5). It should be pointed out that the higher metabolism for the Hawaiian assemblage is primarily due to the shallower-living species – at greater depths there is no apparent difference between the metabolism of the Hawaiian and Californian assemblages (Fig. 4). Fig. 5, in a comparison between the two populations, also reveals no apparent

temperature compensation which, if present, would have resulted in lower 10°C metabolic rates in the shallower-living Hawaiian species than in their Californian counterparts, which live in cooler water.

Discussion

As with crustaceans from other midwater habitats studied (Childress 1975, Donnelly and Torres 1988), this Hawaiian assemblage of midwater crustaceans appears to function primarily aerobically at all depths. Most of the nonmigrators, which remain resident in the oxygen minimum layer, were well able to regulate their oxygen consumption even at the low oxygen levels characteristic of their environment (Table 2). Vertical migrators, which had higher metabolic rates and are found in the oxygen minimum layer only during the daylight hours, had P_c values quite close to or slightly above the environmental oxygen pressure (PO_2) at the 5°C temperature characteristic of the oxygen minimum layer. They may thus be close to oxygen limitation, at least during the day when they are found in the oxygen minimum layer. The mean P_c values of vertical migrators, however, were sharply lower at 5 and 10°C than 20°C (Student's t-test, $P < 0.0001$), reflecting an adaptation for continued aerobic metabolism in the cool waters of the oxygen minimum layer. This trend in in vivo P_c parallels the finding by Sanders and Childress (1990 a) that the oxygen affinity of haemocyanin from several of these species (*Acanthephyra smithi, Oplophorus gracilirostris* and *Systellaspis debilis*) is temperature-dependent and increases at low temperatures. While some species at 5°C had mean experimental P_c values which were slightly above environmental PO_2 levels found in the oxygen minimum layer, none of them were significantly so. Given the possibility of slightly elevated activity due to capture and experimental procedure, the laboratory P_c values may sometimes be higher than in situ values. The minimum P_c values reported in Table 2 indicate that all the vertical migrators, with the possible exception of *O. gracilirostris*, are capable of living aerobically in the oxygen minimum layer. Given the limited anaerobic capacity of *O. gracilirostris*, we believe that this discrepancy is due to elevated rates of oxygen consumption in captivity, and that this species too must live aerobically in the oxygen minimum layer.

Comparison of the oxygen regulatory capabilities of these species with those of similar species from an area with much higher oxygen levels in the water column (Donnelly and Torres 1988) implies that, at least at the higher temperatures for which Donnelly and Torres have comparable data, these Hawaiian species are not strongly adapted to life at low oxygen levels, as their P_c values are in the same range as those from the higher oxygen region. This contrasts with midwater crustaceans from the very low O_2 minimum layer off California where the animals regulate their oxygen consumption to much lower values and are clearly adapted to very low oxygen levels (Childress 1968, 1969 a, b, 1971, 1975).

Donnelly and Torres (1988) report that the decline in aerobic metabolism with depth in the Eastern Gulf of

Mexico is no greater than that due to the decrease in temperature. However, their study lacked very deep-living species. In contrast, the present study, as well as that of Childress (1975) for a crustacean assemblage off California, found a clear decrease in metabolic rate with increasing depth beyond that attributable to changes in temperature or body size. The failure of Donnelly and Torres to find a decline in MO_2 with depth beyond that due to changes in temperature is probably due to the restricted depth range of the species which they studied. As they note, most of their species have MDO values of less than 300 m, which makes it difficult to obtain a sufficient depth range to test for relationships between depth and MO_2.

Comparison with assemblage of midwater species off California

Comparison of the metabolic characteristics of these Hawaiian species with those of a similar assemblage off California (Childress 1975) provides an opportunity to evaluate the selective factors responsible for the metabolic adaptations observed. The physical environment off California differs in several important ways from that off Oahu. The surface water is about $10\,C°$ cooler, and the oxygen minimum layer is much more pronounced than off Hawaii (Fig. 2). At 700 m, in the middle of the oxygen minimum layer, oxygen tension off California is a low as 5 to 6 mmHg, while off Hawaii oxygen is > 20 mmHg. Temperatures at depth are quite similar at both sites, around $5\,°C$ at 600 m. The coastally influenced waters off California have a euphotic zone (defined by light attenuation to 1% of surface levels) to only 30 to 66 m depth (Owen 1974, Cullen and Eppley 1981, Smith et al. 1987). Total light attenuation coefficients, calculated from data in these references using the formula cited in Raymont (1980), range from 0.07 to 0.15. The clear, central oceanic water off Hawaii, on the other hand, allows deep light penetration, as shown by a euphotic zone penetrating to 90–120 m (Cullen and Eppley 1981, Hayward et al. 1983, Hayward and McGowan 1985). The corresponding total light attenuation coefficients for the Hawaiian water are low, ranging from 0.04 to 0.06, indicating deep light penetration and low backscatter from particulates. Biotic properties differ also between the two locations, with the California waters being characterized by higher primary productivity (0.162 to 0.392 g C m^{-2}, Cullen and Eppley 1981, Smith and Eppley 1982) and zooplankton biomas (30 to 400 ml 1000 m^{-3}, Reid 1962, Loeb et al. 1983, Owen 1974). Hawaiian waters have lower surface primary production (0.054 g C m^{-2} d^{-1}, Cullen and Eppley 1981) and low zooplankton biomass (25 ml 1000 m^{-3}, Reid 1962). Productivity is also much more variable both temporally and spatially off California than off Hawaii (Childress et al. 1990 a).

The effect of the well-developed oxygen minimum layer on aerobic metabolism off California is reflected in the very low critical partial pressures found in the California species. That the low P_c of the California species is the result of selection for this trait at this site, rather than

simply of individual variation or differences in behavior, is shown by the fact that the haemocyanin of *Gnathophausia ingens* off California has a higher in vitro oxygen affinity than that of the same species off Hawaii (Sanders and Childress 1990 b). This again underscores the fact that these midwater crustaceans are adapted to live aerobically throughout their depth range, even to the point of selection for blood pigments of higher oxygen affinity in populations living in regions of lower oxygen tensions.

Several different selective factors have been postulated for the decrease in metabolic rate with increasing depth in midwater species, such as that observed in both the Hawaiian and the Californian assemblages. One hypothesis is that the reduction in metabolic rate is related to selection for energy conservation due to the decrease in biomass (Vinogradov 1968), and therefore lower food levels, at greater depths (Mauchline 1972, Childress and Nygaard 1973, 1974, Marshall 1979, George 1981, Vinogradov and Tseitlin 1983, Bailey and Robison 1986). Another points out that energy conservation may be expected to be adaptive at all depths, and proposes that the high metabolic rates of shallow-living species are due to strong selective forces working in directions which preclude certain energy-conserving adaptations. In particular, long-distance visual predator-prey interactions may select strongly for robust bodies and strong swimming abilities in shallow waters, but be relaxed at depth due to the low light levels (Childress et al. 1980, Childress and Mickel 1985, Childress et al. 1990 a). At these greater depths, the weakening of the factors which select for robust bodies and strong swimming abilities at the surface may allow the evolution of more energy-conserving characteristics, which could be reflected in lower metabolic rates.

A comparison of the metabolic characteristics of midwater assemblages off Hawaii and California provides an opportunity to evaluate the predictions of these two hypotheses. The central oceanic waters off Hawaii are less productive, and support less zooplankton biomass than the cooler, more productive waters of the California Current. If depth-related reductions in metabolic rate are due to decreases in food availability per se, one would predict that the metabolic rates of Hawaiian species at any given depth would be lower than those of the species living in the more zooplankton-rich waters off California. The fact that just the opposite is true, especially in the top few hundred meters, suggests that food limitation is an inadequate explanation for the depth-related decline in metabolic rates. We thus turn to the second hypothesis to evaluate its predictions in regard to these data.

The distance at which an object can be distinguished in the water by an eye of given acuity is a function of two variables: total illumination and contrast. Several factors combine to produce higher levels of illumination in the upper water column off Hawaii. At the subtropical Hawaiian location, midday surface incident light is brighter and the sun shines more nearly perpendicularly into the water than off California, minimizing surface reflection and increasing light penetration. Further, the low extinction coefficients of the Hawaiian water provide little absorption or scattering of the light, allowing deeper

light penetration and higher light levels in the upper midwater. This increased illumination would tend to increase the "reactive distance", or distance at which a predator or prey organism could be distinguished and reacted to. Contrast, the proportional difference between the target radiance and the background radiance, would also be greater off Hawaii. Contrast between the perceived object and its background also decreases with increasing distance due to "veiling" by downwelling scattered light, a sort of visual "noise" which is probably the most important factor limiting underwater visibility in daylight (Lythgoe 1988). Particulates in the water are the most important source of light scatter (Lythgoe 1988), and their greater abundance off California, as suggested by the higher attenuation coefficients there, would further decrease reactive distances. Reactive distances off Hawaii, given objects the same size, shape, and color, would thus be greater than off California due both to higher levels of illumination and to increased contrast. The predator-prey interaction hypothesis thus explains the higher metabolic rates observed in shallower-living species off Hawaii as a result of the more energy-consuming, robust bodies necessary because of the long-range, visual predatory pursuits possible in the well-lit, clear water.

While the higher metabolic rates observed in shallow-living species off Hawaii than off California fit well the predictions of the predator-prey interaction hypothesis, consideration must also be given to the lack of any significant difference found between the two sites in the unadjusted metabolic rates of the deeper-living species (Fig. 4). Downwelling daylight is potentially visible down to 1000 m in very clear ocean water (Clarke and Denton 1962) and presumably would be brighter off Hawaii than off California at greater depths. However, by a depth of 500 m, light intensity in even the clearest ocean waters (attenuation coefficient, $k = 0.033$/m) is quite low, less than 10^{-1} μW m^{-2} on a sunny day (Clarke 1971). Attenuation coefficients in Hawaiian waters ($k = 0.04$ to 0.06/m) are higher, and would reduce these light levels to between 10^{-5} and 10^{-9} μW cm^{-2} at 500 m. Bioluminescence for mesopelagic species generally ranges between 10^{-5} and 10^{-9} μW cm^{-2} (as measured at 1 m distance), and has been recorded at intensities of up to 10^{-2} μW cm^{-2} (Clarke 1961, Nicol 1978). Such intensities would be plainly visible above downwelling light levels by 500 m off Hawaii, even at midday. The much lower light levels off California due to the higher attenuation coefficient, and at both sites at night, would make these intensities visible at even shallower depths. Clarke and Denton (1962) report bioluminescence being plainly detectable during the day at depths of 400 m and below. Bioluminescence may thus become more important than downwelling light to visual predator-prey interactions at greater depths, especially at night and in less clear water. A similar effect was reported by Boden (1961) for light reception of upward-pointing photometers placed at fixed depths in the water. He found that as the light levels dropped near sunset, light intensity at his deeper station (200 m) dropped less than expected until the decrease was apparently obscured by bioluminescence. Alternatively, in the low light levels at depth, the visual reactive distances may become short enough that alternative cues, such as chemoreception or detection of near-field sound by the lateral line system of fish predators and by similar systems found in some shrimp (Denton and Gray 1988), may become more important. In any case, differences in the visual environment between Hawaii and California are probably minimal at depths ≥ 400 m. The observed lack of difference between the metabolic rates of the deep-living species is thus also compatible with the predator-prey interaction hypothesis.

In summary, the routine rate of aerobic metabolism in this assemblage of Hawaiian midwater crustacean species declines sharply with increasing depth. While part of this decline is due to temperature, a significant unexplained decline remains after correction for temperature. Of the two major alternate hypotheses for the selective factors producing the observed decline, the relaxation at depth of factors which at the surface select for metabolically-expensive, robust bodies and fast swimming abilities appears to best fit the data.

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