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Oxygen consumption rates of midwater fishes as a function of depth of occurrence

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Abstract—Oxygen consumption was measured in 23 pelagic fish species whose minimum depth of occurrence ranged from zero to 1,000 m. Weight-specific respiratory rate declined rapidly with increasing minimum depth of occurrence. The decrease is partially due to environmental and compositional factors that covary with depth. Decreasing temperature accounts for 2% and the increased water content of deeper living species accounts for 30% of the observed decline. Other factors that might contribute to the decreasing oxygen consumption rate either had no significant effect (size, ash-free dry weight) or were considered to have small effects on the basis of existing evidence (pressure). The unexplained remainder of the decline appears to be an inherent characteristic of deeper living species that may be thought of as a decrease in aerobic metabolism per unit of muscle.

INTRODUCTION

RECENT investigations of a number of deep living (600 to 2,000 m) marine organisms have demonstrated a decline in metabolic processes with increasing depth of occurrence. The relationship has been demonstrated at the community level by studies of microbial degradation in the deep sea (JANNASCH and WIRSEN, 1973; JANNASCH, WIRSEN and TAYLOR, 1976) as well as in work on the respiratory activity of plankton (PACKARD, HEALY and RICHARDS, 1971) and benthic sediment communities (SMITH and TEAL, 1973). This decline is due both to the decline in biomass with depth and to lower metabolic rates of individuals of deeper living species. CHILDRESS (1969, 1971a, 1975) has shown that respiratory rates in crustaceans decline with depth, and CHILDRESS and NYGAARD (1973) predicted such a decline in fishes from their chemical composition. Fragmentary data for fishes support this prediction (CHILDRESS, 1971a, 1975; MEEK and CHILDRESS, 1973; SMITH and HESSLER, 1974; GORDON, BELMAN and CHOW, 1976), but data on a representative variety of midwater fishes of different taxa and vertical distributions have not been available. The present study was undertaken to fill this need.

MATERIALS AND METHODS

Collection of specimens

Most of the specimens were collected using midwater trawls from the *R. V. Oconostota* or *R. V. Velero IV* during 1974 and 1975. Sampling was in the San Clemente Basin off the coast of southern California. The entire catch from each haul was transferred into 3°C seawater and the most active fish were selected for measurements. These specimens were placed in buckets of seawater at the experimental temperature for from 30 min

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to 2 h before use. All suffered some mechanical damage during capture, but only those in the best condition were selected for study. Fishes in equivalent condition lived from one to three days in the laboratory.

Specimens of *Tarletonbeania crenularis* were captured at night in Monterey Bay using a dipnet and submersible light aboard the *R. V. Tage* in the fall of 1976. After capture, animals were placed in chilled (5 to 10°C) seawater and taken to the laboratory. Due to the method of capture (ROBISON, 1973) *T. crenularis* was in exceptionally good condition for experimentation. In the laboratory *T. crenularis* were maintained at either 8 or 13°C for approximately 2 h before being placed in respirometers. These temperatures correspond to day and night-time depths for this species.

Respiratory measurements

Oxygen consumption rates were determined by allowing individuals to deplete the oxygen in a sealed, water jacketed chamber filled with seawater. Temperature was maintained at either 5 or 10°C (± 0.1C°) by means of a refrigerated water bath. The oxygen partial pressure (PO_2) was monitored using a Clark polarographic oxygen electrode (CLARK, 1956) as the animal reduced the oxygen levels to low (0 to 40 mm Hg) partial pressures. Electrodes were calibrated using air- and nitrogen-saturated seawater at the experimental temperature (CHILDRESS, 1971b). The time required for consumption of oxygen to low levels varied from 2 to 10 h. Streptomycin and Neomycin (25 mg each l^{-1}) were added to the seawater to minimize microbial growth. To control for possible oxygen consumption by microorganisms, the animal was removed after selected runs, its volume was replaced with fresh seawater, and oxygen consumption was again measured for from 2 to 8 h. In all cases the microbial oxygen consumption was negligibly low.

The chambers were constructed from a length of glass tubing sealed permanently at one end with a piece of lucite and at the other with a removable plunger made from a disc of lucite with an O-ring about its circumference. The size of the individual chambers varied from 80 to 500 ml to accommodate a wide range of species. A magnetic stirring bar was used to insure mixing in the chamber and sufficient stirring for the oxygen electrode to function properly. A piece of Nitex screen isolated the fish from both the oxygen electrode and the stirring bar. The lowest possible stirring speed was used to avoid disturbing the animal. All experiments were run in the dark except for brief periods of observation under low light.

These observations revealed high activity levels for the first hour or two, presumably due to excitation from handling, and are identified as maximum rates in Table 1(b). After this initial active phase, the animals settled down to slow swimming movements and rhythmic opercular beats. These are labeled routine rates in Table 1. Observation of diurnal activity patterns was precluded by the structure of this study.

The fish treated in this study had generally suffered considerable trauma by capture and confinement, so the rates should be regarded as estimates of metabolism. They are not comparable to the carefully controlled respiratory measurements possible with animals that can be maintained for long periods in the laboratory. Despite the condition of these animals, agreement among individuals was good (see standard deviations in Table 1).

Conversion factors for dry weight, ash free dry weight, and protein-specific respiration were calculated using the chemical composition data reported by CHILDRESS and NYGAARD

Table 1a. Depth of occurrence of midwater fishes

Those values above the solid line represent fish whose oxygen consumption was measured at 5°C, those values below were measured at 10°C.

Family	Genus and Species	Symbol†	Minimum depth (m)	Wet wt. (g)
Alepocephalidae	Bajacalifornia burragei	5	1000	5.5 - 44.3
Anoplogasteridae	Anoplogaster cornuta	C	550	43.9 - 57.9
Astronesthidae	Borostomias panamensis	D	900	104.9 - 115.6
Bathylagidae	Bathylagus milleri	E	550	29.2 - 53.0
	Leuroglossus stilbius	H	25	5.1 - 12.0
Malacosteidae	Aristostomias scintillans	17	500	21.1
Melamphaidae	Melamphaes acanthomus	14	400	7.1 - 27.7
	Poromitra crassiceps	P	400	1.4 - 32.8
	Scopelogadus mizolepis bispinosus	Q	450	3.6
Moridae	Melanonus zugmayeri	16	550	15.5 - 47.5
Myctophidae	Diaphus theta	R	surface	0.9 - 4.4
	Lampanyctus regalis	S	500	2.9
	Lampanyctus ritteri	T	75	1.3 - 2.3
	Parvilux ingens	U	700	5.1 - 13.7
	Stenobrachius leucopsaurus	W	25	3.4 - 5.2
	Symbolophorus californiensis	[X]	surface	0.8
	Tarletonbeania crenularis*	Y	surface	3.29
	Triphoturus mexicanus	Z	25	0.6 - 1.7
Neoscopelidae	Scopelengys tristis	2	650	49.8
Oneirodidae	Oneirodes acanthias	3	900	3.7 - 4.7
Searsiidae	Sagamichthys abei	6	600	5.7
Stomiatidae	Stomias atriventer	11	300	17.1 - 26.6
Astronesthidae	Borostomias panamensis	D	300	62.2 - 132.7
Bathylagidae	Bathylagus ochotensis	13	surface	3.4
	Bathylagus wesethi	G	25	1.4 - 1.6
Clupeidae	Sardinops caerulea	[K]	surface	----
Melamphaidae	Melamphaes acanthomus	14	400	20.2 - 25.2
Myctophidae	Diaphus theta	R	surface	1.5 - 2.7
	Lampanyctus ritteri	T	75	1.3 - 2.9
	Stenobrachius leucopsaurus	W	25	3.8 - 5.0
	Tarletonbeania crenularis*	Y	surface	0.7 - 2.1
	Triphoturus mexicanus	Z	25	9.3
	Stomiatidae atriventer	11	300	9.3

*Oxygen consumption in *Tarletonbeania crenularis* was measured at 8°C and 13°C.
†Fish that have well developed gas filled swimbladders as adults have square brackets around their symbol.
‡Values from CHILDRESS and NYGAARD (1973).

Table 1b. Oxygen consumption rates of midwater fishes

Those values above the solid line represent fish whose oxygen consumption was measured at 5°C, those below were measured at 10°C.
The numbers in parentheses are (± Standard Deviation; *N*)

	Routine VO_2 $[\mu lO_2(mg\ ww)^{-1}h^{-1}]$	Predicted VO_2 ‡	Q_{10}	P_c (mm Hg)	Maximum VO_2	Conversion factors § $[\mu lO_2(mg^{-1}h^{-1})]$ Dry Wt.	AFDW	Protein
5	.005 (±.003; 3)	.010	-		.012	9.000	11.000	25.000
C	.024 (±.009; 3)	.027	-		.033	6.667	8.750	16.375
D	.017 (±.001; 2)	.015	-		.028	5.529	6.588	23.412
E	.011 (±.001; 3)	.026	-	< 4	.014	7.727	9.090	18.454
H	.024 (±.003; 3)	--			.112	5.333	6.042	14.542
17	.010	--	-		.014	-	-	-
14	.012 (±.001; 4)	.023	-		.024	8.000	11.083	23.166
P	.011 (±.001; 2)	.027	-		--	7.636	10.363	17.000
Q	.014	.023	-		.044	6.857	8.429	16.643
16	.017 (±.002; 4)	--	-	10	.037	-	-	-
R	.107 (±.02 ; 2)	--			.149	2.953	3.243	8.206
S	.011	.022	-		--	7.273	8.909	17.636
T	.041 (±.004; 2)	--	-		.044	3.415	3.756	8.634
U	.012 (±.002; 3)	.022	-		.022	11.083	14.666	29.417
W	.042 (±.004; 6)	--	-	12	.064	3.024	3.357	9.429
[X]	.060	--	-		--	-	-	-
Y*	.096	--	-	30	.220	-	-	-
Z	.025 (±.003; 3)	--	-		.061	3.480	3.840	10.880
2	.009 (±.000; 2)	.025	-	12	.013	6.556	7.111	19.222
3	.008 (±.005; 2)	.013	-		--	10.500	13.125	23.250
6	.016	.023	-		.029	7.875	9.938	16.500
11	.017 (±.002; 6)	.043	-		.031	5.235	6.059	16.941
D	.033 (±.005; 2)	--	4.1		.073	5.545	6.576	23.424
13	.084	--	-	<12	.127	-	-	-
G	.095 (±.012; 2)	.170			.195	5.989	7.421	11.895
[K]†	.300	.330	-		--	-	-	-
14	.038 (±.009; 5)	--	11.1		.069	6.000	8.289	17.342
R	.208 (±.020; 2)	.230	3.7		.238	2.952	3.240	8.221
T	.059 (±.005; 3)	.140	2.1	<12	.095	3.407	3.763	8.644
W	.070 (±.001; 3)	.230	2.9	20	.119	3.014	3.357	9.443
Y*	.186 (±.004; 2)	.280	5.9	35	.275	-	-	-
Z	.067 (±.012; 6)	.180	7.1		.109	3.478	3.851	10.896
11	.040	--	5.9		.104	5.225	6.075	16.950

*Oxygen consumption was measured in *T. crenularis* at 8°C and 13°C.
†This value for *Sardinops caerulea* from LASKER (1970).
‡Values calculated from CHILDRESS and NYGAARD (1973).
§Values derived from the data in CHILDRESS and NYGAARD (1973). They should be multiplied by the wet weight respiratory rate to convert it to the new form.
"AFDW" is an abbreviation for ash-free dry wt.

(1973). Simple regression lines were calculated with a programmable calculator using the least squares method. Ninety-five per cent confidence limits were calculated using the student's t distribution. The contributions of size, protein concentration, total protein content, and depth to the variation in respiratory rate were assessed using a stepwise multiple regression technique (BARR, GOODNIGHT, SALL and HELWIG, 1976).

Chemical composition

All of the specimens used for chemical composition studies were removed from the catch, identified, blotted with paper toweling, wrapped in two layers of heavy duty aluminum foil, frozen, and later analyzed for water, ash, protein, lipid, carbohydrate, total nitrogen, total carbon, and hydrogen using the methods described by CHILDRESS and NYGAARD (1973). The specimens were kept frozen for from one week to three months before analysis.

Depth distributions

The minimum depth of occurrence used here is that described by CHILDRESS and NYGAARD (1973). It is defined as the depth below which 90% of a population lives.

RESULTS

Our oxygen consumption rate for the mesopelagic predator *Anoplogaster cornuta* [0.024 μl O_2 (mg wet weight)$^{-1}$h^{-1}] agrees well with that measured by MEEK and CHILDRESS (1973) at 5.5°C [0.027 μl O_2 (mg wet weight)$^{-1}$ h^{-1}]. The results in Table 1b from fishes occupying a depth of 400 to 450 m [0.011 to 0.014 μl O_2 (mg wet weight)$^{-1}$h^{-1}] are also comparable to the rate of 0.012 μl O_2 (mg wet weight)$^{-1}$h^{-1} reported by CHILDRESS (1975) and BELMAN and GORDON (1978) for the Zoarcid eelpout *Melanostigma pammelas* (minimum depth of occurrence 450 m). Both *A. cornuta* and *M. pammelas* are exceptional animals in that they often come up in midwater trawls without apparent damage and may live for several weeks in the laboratory. Agreement between these reported laboratory measured rates and our shipboard rates for these species lends support to observations on the other species using this technique.

Oxygen consumption rate as a function of minimum depth of occurrence

Oxygen consumption rates appear to decrease with increasing minimum depth of occurrence (Fig. 1). The regression line in Fig. 1 was calculated using 10°C oxygen consumption values for all vertically migrating myctophids except *T. crenularis* (13°C) and 5°C values for all others. These temperatures approximate the environmental temperature range for all species. The difference in oxygen consumption rate between a fish living at the surface, such as *Sardinops caerulea* [0.30 μl O_2 (mg wet weight)$^{-1}$h^{-1}; LASKER, 1970] and a fish living at 1,000 m [*Bajacalifornia burragei:* 0.005 μl O_2 (mg wet weight)$^{-1}$ h^{-1}] approaches two orders of magnitude. Part of the decline in the wet weight specific rates is a result of the greater water content of deeper living fishes (BLAXTER, WARDLE and ROBERTS, 1971; CHILDRESS and NYGAARD, 1973). When ash-free dry-weight-specific respiration [R_D, μl O_2 (mg ash-free dry wt)$^{-1}$ h^{-1}] is plotted versus depth (x, m) there is a 30% decrease in the slope of the regression line ($R_D = 0.990\ x^{-0.344 \pm 0.068}$, $r = 0.916$, $N = 20$; cf. Fig. 1). Protein-specific respiration [R_p, μl O_2 (mg protein)$^{-1}$ h^{-1}] varies with depth in virtually the same manner as ash-free dry weight specific respiration ($R_p = 2.042\ x^{-0.337 \pm 0.049 - 0.049}$, $r = -0.940$, $N = 20$). This indicates a decrease in

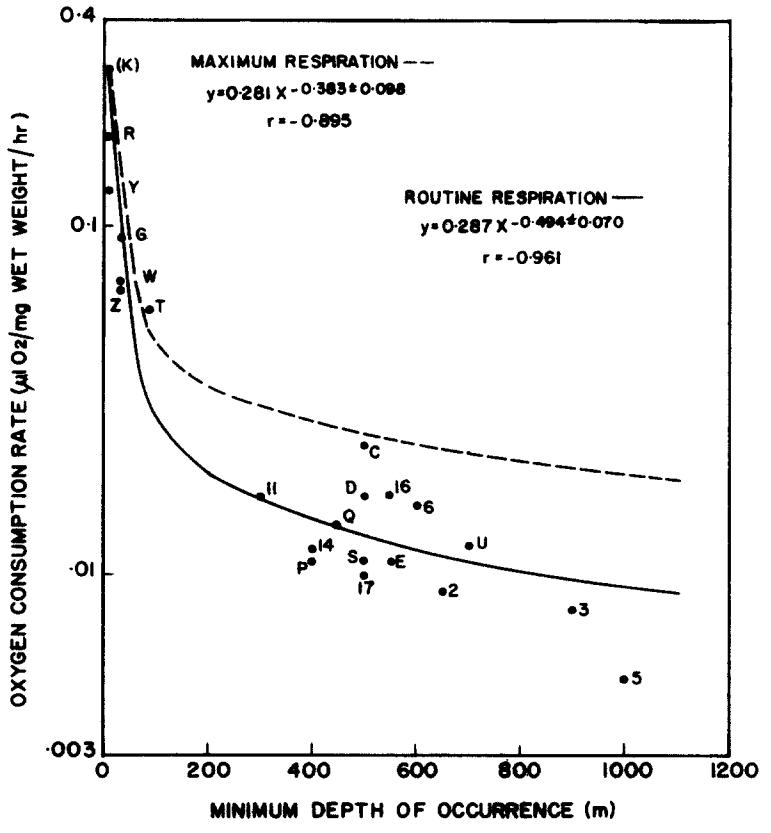

Fig. 1. Relationship between routine respiration (————) and maximum respiration (— — — —) rates and depth of occurrence. Symbols as in Table 1a. (k) from LASKER, 1970 (*Sardinops caerulea*).

oxygen consumption per unit protein and suggests that there is a decrease in the aerobic metabolism of muscle tissue in deeper living fishes. Our protein-specific respiratory rates (Table 1) are comparable to those reported for oxygen consumption of minced fish muscle tissue by GORDON (1972a, b, 1975), who found that the muscle of three myctophid species (*Myctophum nitidulum*, *Ceratoscopelus townsendi*, and *Triphoturus mexicanus*) had an oxygen consumption of about 0.370 μl O_2 $mg^{-1}h^{-1}$ over the range 5 to 15°C. This is similar to our data for myctophids (also including *T. mexicanus*) at 5°C (range: 0.354 to 0.396 μl $O_2 mg^{-1}h^{-1}$), although it is somewhat lower than our rates at 10°C (range: 0.510 to 0.730 μl O_2 $mg^{-1}h^{-1}$). There are no available data for comparison with our measurements on deeper living species. Both total protein (mg protein) and size (mg ash-free dry wt) of these fishes were tested for a possible influence on the trend toward lower respiratory rates at greater depths, but neither reached the level of statistical significance.

Two approaches were used to estimate the contribution of temperature to the respiratory decline. First, oxygen consumption was measured at 5°C in several of the fishes that undergo a diel vertical migration to near surface waters (Table 1) to compare them with deeper living fishes measured at that temperature. The means of the migrators' oxygen consumption rates at 5° are 73% higher than those of non-migrating species occupying

similar daytime depths (400 to 550 m; LAVENBERG and EBELING, 1967). This suggests that factors other than temperature are the major cause for the lower oxygen consumption rates. The slope of the regression between minimum depth of occurrence (x, m) and oxygen consumption rate at 5°C [R_5, μl O_2 (mg wet weight)$^{-1}$h^{-1}] is 30% less than that of Fig. 1 ($R_5 = 0.103\,x^{\pm 0.340 \pm 0.077}$, $r = -0.913$, $N = 19$). This reduction reflects the differences in oxygen consumption rates of the migrating species, expressed here at 5° and in Fig. 1 at 10°C. As this relationship does not distinguish between independent effects of depth and temperature, which covary in nature, the difference in slope is the maximum possible contribution of temperature. Its chief significance is that it shows a temperature-independent difference between the migrating and deeper living species, effectively eliminating temperature as the proximal cause for the observed decline.

We also used a stepwise multiple regression (BARR *et al.*, 1976) to assess the relative contributions of depth and temperature to the variance in respiratory rate of midwater fishes (i.e. the downward trend with depth of occurrence). In this case temperature alone contributes 2% of the observed decline, with the effect of depth held constant. Depth and temperature together explain 94.4% of the total variance in respiratory rate (r-square = 0.9441).

Also shown in Fig. 1 is a curve relating maximum oxygen consumption rate and depth of occurrence. There is no significant difference in the regression coefficients of maximum and routine rate curves, although the slope of the maximum rate line is somewhat less negative and higher with respect to the ordinate. This suggests that the maximum metabolic rates decline with respect to depth similarly to the routine rates.

Oxygen consumption as a function of temperature

Oxygen consumption was measured in 10 species of fish at two temperatures (Table 1b). Among these species only the vertically migrating myctophids encounter temperatures as high as 10°C within their vertical range. The Q_{10} values for these species range from 2.1 for *Lampanyctus ritteri* to 7.1 for *T. mexicanus*.

The Q_{10} of *Lampanyctus ritteri* (2.1), *Stenobrachius leucopsaurus* (2.9), and *Diaphus theta* (3.7) are within the range reported for other teleosts between 5 and 10°C (cf. WINBERG, 1956). *Tarletonbeania crenularis* and *T. mexicanus* have Q_{10} values of 5.9 and 7.1, respectively, which are unusually high. The large differences in metabolic rate between 5 and 10°C in all of these species, but particularly in *T. mexicanus* and *T. crenularis*, reflect large differences in muscular activity observed in the respirometers. All fishes were moderately active in the chambers at 10°C and quiescent at 5°C, resulting in a large disparity in the metabolic rates. This suggests substantial differences between the metabolic rates at daytime and nighttime depths.

The remaining species, with the exception of *Stomias atriventer* (300 m, 8°C) reside permanently at depths with ambient temperatures of 5 to 6°C. All showed profound increases in metabolic rate as a function of temperature, probably as a result of increased muscular activity. These species have resided in the stable low temperatures associated with deep water for periods measurable on the geological time scale. These data suggest that they have retained the physiological capability for sustaining an elevated metabolic rate for several hours in response to a rise in temperature.

Regulation of oxygen consumption

With the exception of *T. crenularis* (Myctophidae), *B. burragei* (Alepocephalidae), and *Oneirodes acanthias* (Oneirodidae) every species in Table 1 encounters oxygen partial

Table 2. Chemical composition of some midwater fishes.

Family	Alepocephalidae	Melamphaidae	Myctophidae
Genus and Species	Bajacalifornia burragei	Melamphaes acanthomus	Parvilux ingens
Symbol	5	19	U
Number analyzed	3	1	1
Wet weight (g)	6.7 - 47.4	13.5	13.7
H_2O (% wet wt)	87.5 ± 2.0*	87.5	19.0
Ash Free Dry Weight (% DW)	82.4 ± 1.7	72.2	75.0
Carbohydrate (% AFDW)	1.9 ± 0.2	1.2	1.5
Lipid (% AFDW)	32.1 ± 8.4	13.6	8.4
Protein (% AFDW)	43.6 ± 8.0	47.8	49.7
Carbon (% AFDW)	62.4 ± 2.0	-	-
Hydrogen (% AFDW)	9.6 ± 0.2	-	-
Nitrogen (% AFDW)	15.5 ± 1.9	-	-
Kcal/100 g wet weight	50.9	29.2	19.6

*Figures are: mean ± standard deviation.

pressures as low as 6 mm Hg somewhere within its vertical range. Observations on selected species shed some light on the ability of these animals to live at this low oxygen partial pressure. Values for the P_c (that PO_2 below which oxygen consumption ceases to be independent of external PO_2; PROSSER, 1973) were obtained for seven species at normal environmental temperatures (Table 1b). In only two of these cases (*B. milleri; T. crenularis*) does the P_c drop below the lowest environmental PO_2 encountered. However, all of these animals regulate their oxygen consumption down to a very low level ($\sim$ 12 mm Hg). It is possible that mechanical damage sustained in the net is responsible for some elevation of the P_c. Despite this fact, the P_c values shown in Table 1 are sufficiently low to enable these fish to live entirely aerobically at all depths but the core of the oxygen minimum layer (700 m; 6 mm Hg).

Chemical composition

Three species were analyzed for chemical composition (Table 2) to fill gaps in the data presented by CHILDRESS and NYGAARD (1973). Water content is high in these fishes (87.5 to 91% of wet weight), while lipid (0.8 to 4% of wet weight) and protein (5.5 to 6.5% of wet weight) are both low. Discussion of the implications of these data can be found in CHILDRESS and NYGAARD (1973).

DISCUSSION

Declining metabolic rates with increasing depth of occurrence are exhibited in communities of microplankton (PACKARD *et al.*, 1971) and benthic microbes (JANNASCH and WIRSEN, 1973; JANNASCH *et al.*, 1976) as well as in benthic sediment communities (SMITH and TEAL, 1973). The decline in community metabolism with depth results from a combination of reduced biomass at greater depths and lower weight-specific metabolic rates. Declining individual respiratory rates have been demonstrated by CHILDRESS (1969, 1971a, 1975) on a broad spectrum of crustacean species, by SMITH and HESSLER (1974) on two benthic fish species, and now in this study on a large number of midwater fishes. The phenomenon thus appears to be a general characteristic of life at greater depths.

Sustained muscular activity and the elevated metabolism it implies are necessary in surface waters, where avoidance of visual predators is a major problem. In addition, surface fishes can respond to low productivity with extensive horizontal movements. Such movement in deeper living species is less likely to be productive, because of the low biomass typical of mid-depths. For these fishes food gradients vary in the vertical plane. Deeper living fishes have thus apparently sacrificed muscular strength and mobility in exchange for lower metabolic rates. This trend is probably strongly selected against by predation in epipelagic forms, otherwise reduced energy expenditure would be more universally employed.

The marked change in the slope of Fig. 1 at about 150 m points to a depth-related phenomenon in addition to the general decrease of oxygen consumption rate with depth. The initial rapid decline is due to the large difference in respiratory rate between the vertical migrators (minimum depth of occurrence of from 0 to 75 m) and those fish residing permanently at intermediate depths, such as the melamphaids and some stomiatoid predators (*Borostomias panamensis, Stomias atriventer*). It is interesting that such a profound decline occurs, particularly because these two predators and several of the vertical migrators (*Bathylagus wesethi, Diaphus theta, Lampanyctus ritteri, Leuroglossus stilbius, Stenobrachius leucopsaurus*, and *Triphoturus mexicanus*) occupy similar daytime depths, even though they differ in minimum depth of occurrence. This difference in metabolic rate reflects a difference in the energy available to those fishes that feed in the upper mixed layer and those that remain largely below it. Vertically migrating fishes are largely free of the energy limitations imposed on the deeper species and are thus able to sustain higher metabolic rates. The energetic benefit (i.e. total energy gained minus energy used in maintenance) to the vertical migrator is determined by the metabolic cost of the migration itself and the probable increase in daily ration due to the migration into more productive shallower layers. Our data indicate that temperature has a large effect on the respiratory rates of the vertical migrators examined (Q_{10} values up to 7.1, Table 1b), suggesting that the trip to the surface costs substantial energy. This also implies that considerable gains in energy are made at the surface, because vertical migration is obviously a successful foraging strategy. Conversely, one may consider that the migrators in effect gain energy (cf. MCLAREN, 1963) by spending their days in relative torpor (BARHAM, 1971) in the colder waters below 200 m. This is perhaps a more realistic way of looking at the question because vertically migrating species are more similar to surface dwellers in terms of respiratory rate (Table 1b) and chemical composition (CHILDRESS and NYGAARD, 1973) than they are to deeper living species.

Both environmental and compositional factors are responsible for the observed decline in respiratory rate with depth. Estimates of their relative contributions are useful in

separating environmental and compositional effects from other adapted characteristics (e.g. behavioral and physiological). The maximum possible effect of temperature has been calculated from our data as 30% of the total decline, but this is too high because it confounds depth and temperature effects. The best estimate of temperature's contribution is the figure of 2% generated by the multiple regression. Possible acclimation to different thermal regimes (SCHOLANDER, FLAGG, WALTERS and IRVING, 1953) would not account for any of the decline, because any such effect would detract from and not contribute to the observed trend. Indeed, there is considerable doubt that any form of cold adaptation that implies a higher standard metabolism and its higher concomitant energy expenditure constitutes a selective advantage (cf. HOLETON, 1974). What is important here is not our estimate of temperature contribution to respiratory decline, because it is confounded with depth and life history parameters, but rather the fact that temperature is responsible for only a small fraction of the phenomenon.

Another variable that might contribute to a decline in respiratory rate with depth in the field is the low oxygen concentration of the deeper water in the basins off southern California. Our data and those of some previous investigators (CHILDRESS, 1969, 1971b, 1975; MEEK and CHILDRESS, 1973; GORDON *et al.*, 1976) indicate that species resident in the oxygen minimum (0.2 to 0.3 ml l^{-1}) can live totally aerobically there. Therefore, it is unlikely that low oxygen off southern California is an important factor in this decline.

Pressure effects on respiration are probably small. All literature (MEEK and CHILDRESS, 1973; GORDON *et al.*, 1976; BELMAN and GORDON, 1978) indicates that pressures within species' normal bathymetric range have no significant effect on fishes. Studies on muscle (GORDON, 1975) and enzymes (HOCHACHKA, SCHNEIDER and KUZNETSOV, 1970; HOCHACHKA, BEHRISCH and MARCUS, 1971; HOCHACHKA, SCHNEIDER and MOON, 1971; MOON, MUSTAFA and HOCHACHKA, 1971a, b, c) from fishes have had similar findings, while studies on crustaceans seem to indicate that responses to pressure are species-specific but relatively small (NAPORA, 1964; TEAL and CAREY, 1967; QUETIN and CHILDRESS, 1976; CHILDRESS, 1977). There is no reason to believe that pressure has an appreciably stronger effect on mesopelagic fishes.

Some of the decline in wet weight respiration with depth is accounted for by depth-related changes in the composition of these fishes (CHILDRESS and NYGAARD, 1973). In particular the oxygen consumption rate is reduced by about 30% by the increasing water concentration and the corresponding reduction in protein content in deeper living fishes. These compositional attributes of deeper living species function as a source of static lift (DENTON and MARSHALL, 1958; BLAXTER, WARDLE and ROBERTS, 1971; CHILDRESS and NYGAARD, 1973) allowing them to approach neutral buoyancy. Other buoyancy mechanisms among the species studied are gas filled swimbladders (*Symbolophorus californiensis*, CHILDRESS and NYGAARD, 1973; *Sardinops caerulea*, LASKER 1970) high lipid content (*Diaphus theta*, *Lampanyctus ritteri* and *Stenobrachius leucopsaurus*, BUTLER and PEARCY, 1972; CHILDRESS and NYGAARD, 1973) and constant swimming (*Tarletonbeania crenularis*, BARHAM, 1971; BUTLER and PEARCY, 1972; CHILDRESS and NYGAARD, 1973). The latter two mechanisms are restricted to fishes with minimum depths of occurrence above 300 m, species that have the highest respiratory rates (Table 1b). Most midwater species with functional gas filled swimbladders are killed by the rapid change in pressure during capture, including members of two important families, the hatchet fishes (Sternoptychidae), and the gonostomatids. The chemical composition of these species (CHILDRESS and NYGAARD, 1973) indicates that their oxygen consumption rates would

follow the curve shown in Fig. 1 despite their different buoyancy mechanisms.

Midwater crustaceans have fewer means of maintaining vertical position. Increased lipid content is responsible for their increasing buoyancy with depth until about 700 m, below which reduction in organic matter becomes more important (CHILDRESS and NYGAARD, 1974). Crustaceans also have higher weight specific oxygen consumption rates (wet weight, ash free dry weight and protein specific) than fishes ($\bar{x} = 45\%$ higher) at any given depth of occurrence (Table 1b; CHILDRESS, 1975). This difference is the reason for the difference between the rates predicted by CHILDRESS and NYGAARD (1973) and the observed rates (Table 1b). Oxygen consumption rate in midwater crustaceans declines with depth similarly to fishes (slope $= -0.564 \pm 0.050$ for crustaceans, -0.494 ± 0.060 for fishes) when compared on a wet weight basis. This suggests that both taxonomic groups are under comparable selective pressure to reduce energy expenditure at greater depths.

Both crustaceans and fishes exhibit a decreasing protein content (per cent wet weight) (CHILDRESS and NYGAARD, 1973, 1974) that is considerably less than the decrease in protein-specific respiration with increasing depth of occurrence. This indicates a selection for lower rates independent of and greater than selection for structural reduction of protein. It is a reduction in oxygen consumption per unit of muscle, and it implies a change in the nature of muscle metabolism with depth, which may be due to changes in the quality or quantity of enzymes involved in oxidative metabolism.

In summary, the decline of oxygen consumption rate with increasing depth of occurrence in midwater fishes is due to several factors of varying importance. Increasing water content accounts for 30% of the decline. Temperature is apparently a minor factor, with a total contribution of 2% to the trend. Size (mg ash-free dry weight) does not exert any significant influence, nor in all probability does pressure. The means by which these fishes achieve such low metabolic rates remain largely unexplained, but they probably involve low activity levels.

It appears that the conservation of energy is important in the evolution of deep-sea fishes. It has apparently resulted in the low respiratory rates described above, making a larger percentage of the limited available energy usable for growth and reproduction (TAYLOR and CHILDRESS, 1978).

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