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VERTICAL DISTRIBUTION AND METABOLISM IN ANTARCTIC MESOPELAGIC FISHES

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Abstract—1. Vertical distributions, oxygen consumption rates and activities of intermediary metabolic enzymes were examined in several species of Antarctic mesopelagic fishes as part of the AMERIEZ (Antarctic Marine Ecosystem Research at the Ice Edge Zone) program to study ice-edge biology in the Scotia–Weddell Sea region.

2. Sixteen mesopelagic fish species were captured, nine in sufficient numbers to determine their vertical distribution. Seven of the nine exhibited a diel vertical migration.

3. Oxygen consumption rates ($\dot{V}O_2$) declined with increasing depth of occurrence and ranged from 0.159 μl O_2/mg wet weight/hr in a fish living at the surface to 0.016 μl O_2/mg wet weight/hr in a fish living at 500 m.

4. Activities in white skeletal muscle of lactate dehydrogenase (LDH) and citrate synthase (CS), representing the anaerobic and aerobic pathways of intermediary metabolism, declined in a similar manner to oxygen consumption rate with depth.

5. Comparison of Antarctic and California mesopelagic fishes reveals a similar $\dot{V}O_2$ at normal habitat temperature. When extrapolated to the same temperature Antarctic fishes show the elevated $\dot{V}O_2$ commonly called "cold adaptation".

6. Cold adaptation is reflected in the activity of the aerobic pathway (CS) but not in the anaerobic (LDH).

INTRODUCTION

The pelagial south of the Antarctic Convergence undergoes seasonal fluctuations in surface temperature between −1.87°C and 0°C near the continent and −1°C to 4°C further north (Gordon *et al.*, 1982). Beneath, the water column varies between 0.25°C at 1000 m to −1.5°C at 100 m near the continent and between 2°C and 0°C at the same depths closer to the Convergence (Gordon *et al.*, 1982). Ice typically covers 50–60% of the sea surface between the continent and the Polar Front at its midwinter maximum (Zwally *et al.*, 1983) shrinking to less than 10% in summer. In addition, there are the radical seasonal changes in daylength associated with high latitudes. We may characterize the Antarctic pelagial as a system with very cold minimally fluctuating temperatures in both the horizontal and vertical planes, in concert with dynamic, predictable change in sea-ice cover and daylength.

The development of a distinct Antarctic pelagic region probably occurred at the Oligocene–Miocene boundary with the opening of the Drake Passage and the subsequent development of the Circum-Antarctic current and Antarctic Convergence (Clarke, 1983). Thus, species living within the Antarctic pelagial have been in as isolated an environment as is possible in a contiguous ocean for approximately 20 million years (Knox, 1970). It is to be expected that the extreme cyclicity in primary production, sea-ice cover and daylength as well as the need to carry on all life processes at temperatures close to freezing would have resulted in a characteristic set of adapted physiological and behavioral traits, perhaps similar to that seen in coastal species (see Clarke, 1983, for review).

It is the purpose of this article to review the metabolic characteristics of one element of the Antarctic pelagic fauna, the mesopelagic fishes, with respect to their patterns of vertical distribution. The traits are compared to those of fishes living in the Antarctic coastal system and the California borderland to discern any particular selective pressures operating in the Antarctic pelagial.

VERTICAL DISTRIBUTION OF FISHES

Sixteen mesopelagic fish species were captured in the Scotia–Weddell Sea region as part of the AMERIEZ (Antarctic Marine Ecosystem Research at the Ice Edge Zone) program (vic 60°S 40°W) during Nov–Dec 1983 (Table 1, Torres, *et al.*, 1984), nine in sufficient numbers to determine their vertical distribution. Three diel vertical patterns were in evidence (Fig. 1). The first (pattern I), exhibited by *Electrona antarctica*, *Gymnoscopelus braueri*, *G. opisthopterus*, *Krefftichthys andersoni*, *Protomyctophum bolini* and *Notolepis coatsi* consisted of a daytime center of distribution between 200 and 600 m shifting upward so that a substantive part of the population could be found in the upper 200 m at night. Only *Electrona antarctica* was captured by our nets between the surface and 100 m. However, at least two other species *K. andersoni* and *P. bolini*, were found in the stomachs of surface-feeding seabirds (Ainley, personal communication) leading us to conclude that at least these two species occasionally migrate into surface waters. The upward movement of pattern I fishes resulted in a displacement of approximately 20% of the total fish biomass into the upper 200 m at night. Pattern II was shown only by *Bathylagus*

Table 1. Species list and diel distribution pattern for all fishes captured in the Scotia–Weddell Sea Region (vic 60°S 40°W) Nov–Dec 1983 (Torres *et al.*, 1984)

Family	Genus-species	Diel habit
Bathylagidae	*Bathylagus antarcticus*	DVM
Gempylidae	*Paradiplospinus gracilis*	Insufficient data
Gonostomatidae	*Cyclothone* sp.	NM
	Cyclothone microdon	NM
Macrouridae	*Cyanomacrurus piriei*	Insufficient data
Melamphaidae	*Poromitra crassiceps*	Insufficient data
Microstomatidae	*Nansenia antarctica*	Insufficient data
Myctophidae	*Electrona antarctica*	DVM
	Electrona carlsbergi	Insufficient data
	Gymnoscopelus braueri	DVM
	Gymnoscopelus nicholsi	Insufficient data
	Gymnoscopelus opisthopterus	DVM
	Krefftichthys andersoni	DVM
	Protomyctophum bolini	DVM
Paralepididae	*Notolepis coatsi*	DVM
Scopelarchidae	*Benthalbella elongatum*	Insufficient data

DVM is an abbreviation for Diurnal Vertical Migration, NM for No Migration. *Cyclothone* sp. was described as *C. sumiae* in Kobayashi (1973).

antarcticus, which had a daytime population maximum between 400 and 1000 m and an upward displacement to a depth of 250 m at night (Fig. 1). Pattern III, typified by *Cyclothone microdon*, is one of no directed movement on a diel basis.

Vertical migration clearly dominates as a diel distribution pattern among the mesopelagic fishes of the Scotia–Weddell Sea region. Though quite common in mesopelagic fishes throughout the world ocean (e.g. Merret and Roe, 1974; Pearcy *et al.*, 1977; Nafpaktitis *et al.*, 1977; Gartner *et al.*, 1987) vertical migration has a special significance to the life history of polar species. Temperatures in the upper 100 m fall well below the freezing point of fish blood (−1.0 to −1.2°C, DeVries and Lin, 1977) for part of the year in all waters south of the polar front (Gordon *et al.*, 1982). Thus, at least *Electrona antarctica* is exposed to dangerously low temperatures as a consequence of its vertical migration throughout its geographic range (McGinnis, 1977). If we assume that the vertical migrations exhibited by Antarctic species are the result of maintaining position within an isolume as in other systems (see Longhurst, 1976, for review), the long nights of the austral winter would result in considerable periods of time spent near the surface in a supercooled state. The situation would be exacerbated by the presence of ice cover that would further decrease the amount of light reaching the sea surface, perhaps bringing isolumes and fishes up nearer surface waters. Some normally deep-living mesopelagic species including myctophids have been found close to the surface underneath the ice pack (Ainley *et al.*, 1986).

Electrona antarctica has been captured deep within the pack ice (Torres, personal observation) of the Weddell Sea. Thus, it is unlikely that the horizontal distribution of fishes is radically altered with the expansion and contraction of sea-ice cover that accompanies the changing austral seasons. It is probable that the cyclic environmental changes are accommodated within the life history strategy of vertically migrating fishes in some other way. Whether the

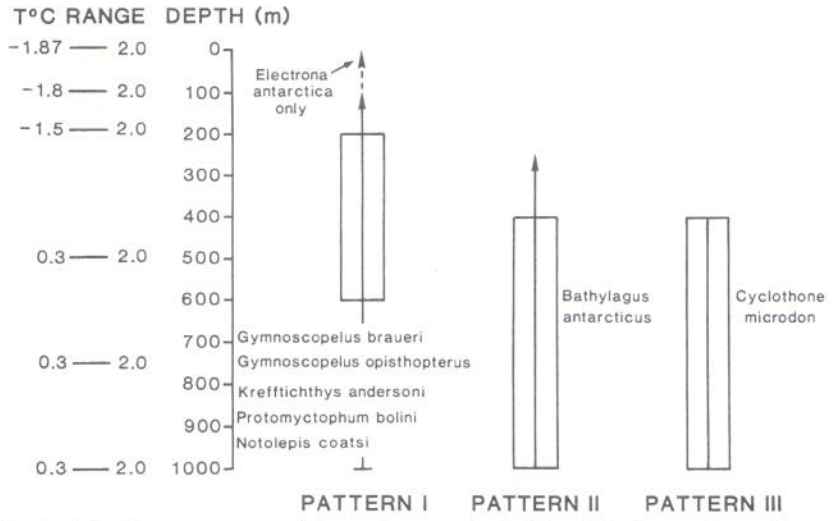

Fig. 1. Vertical distribution patterns of Antarctic mesopelagic fishes. Total range for each pattern is denoted by a vertical line; the superimposed box represents the region of maximum daytime numbers. Displacement of population due to vertical migration is from top of box to top of arrow. Temperature data from Gordon *et al.* (1982) for the Southern Ocean south of 60°S. Fish distributions from Torres *et al.* (1984) and unpublished data.

Table 2. Comparison of oxygen consumption in Antarctic pelagic and coastal fish species

Genus species	O_2 consumption at 0.5°C (μl/mg wet wt/hr)	Source
Pagothenia borchgrevinki	0.159	Wohlschlag, 1964
Notothenia rossii	0.091	Morris and North, 1984
Notothenia argustifrons	0.081	Morris and North, 1984
Electrona antarctica	0.042 ± 0.003 (47)*	Torres and Somero, 1988
Trematomus hansoni	0.038	Morris and North, 1984
Gymnoscopelus braueri	0.026 ± 0.003 (20)	Torres and Somero, 1988
Gymnoscopelus opisthopterus	0.022 ± 0.003 (15)	Torres and Somero, 1988
Bathylagus antarcticus	0.018 ± 0.002 (26)	Torres and Somero, 1988
Rhigophila dearborni	0.018	Wohlschlag, 1964
Cyclothone microdon	0.016 ± 0.002 (3)	Torres and Somero, 1988

Values for Torres and Somero are mean values (n and 95% CL supplied). O_2 consumption was measured at 0.5°C by Wohlschlag, and Torres and Somero, and at 3°C by Morris and North. Values from Morris and North were converted to 0.5°C using a Q_{10} of 2.0.

* $\pm$95% confidence limits (n).

accommodation is physiological, in the form of biological antifreezes, or behavioral is unknown at present.

OXYGEN CONSUMPTION RATES OF ANTARCTIC MESOPELAGIC FISHES IN COMPARISON WITH OTHER ANTARCTIC SPECIES

Oxygen consumption rates in Antarctic mesopelagic fishes fall in the low to intermediate range of values reported in the literature for coastal Antarctic species (Table 2). Values chosen for comparison were from studies on individuals of similar size (0.5–20 g, Morris and North, 1984) or habit (Wohlschlag, 1964). Many of the coastal species have a pelagic habit during their early life history (e.g., *Notothenia rossii*, *N. angustifrons* and *Trematomus hansoni*; Morris and North, 1984) and are thus most comparable at their smaller sizes.

The zoarcid *Rhigophila dearborni* is commonly found at depths greater than 400 m and exhibits a markedly depressed oxygen consumption relative to the shallower dwelling notothenioids. Wohlschlag (1963) attributed the low metabolic rates in *R. dearborni* to an absence or at least a very limited degree of metabolic cold adaptation. He observed that *Rhigophila* was the only representative of a primarily deep-sea marine family that had been examined up to that time, which might account for its unusually low metabolism.

We agree with Wohlschlag's conclusion that species' depth of occurrence influences their metabolism. However, its effect is less a result of relict phylogenetic influence than that of a suite of associated selective factors that must be accommodated within the adapted characteristics of a deeper-living species. To compare the metabolism of species from different geographic regions one must consider their depth of occurrence as an important part of their life habit.

DEPTH AND METABOLISM

Studies undertaken on a variety of organisms and at a variety of levels of organization demonstrate a marked decline in metabolic processes with increasing depth of occurrence. At the community level, microbial activity (Janasch and Wirsen, 1973), activity of electron transport systems (ETS) in microplankton (Packard *et al.*, 1971) and respiration of benthic sediment communities (Smith and Teal, 1973) all decline with increasing depth. Deeper-living ($\geqslant$150 m) individuals of larger species also show greatly reduced metabolic rates relative to surface dwellers. Broad-spectrum studies on trawl-captured midwater Crustacea (Childress, 1975) and fishes (Torres *et al.*, 1979; Fig. 2) show that species living at 1000 m may respire at a rate 2 orders of magnitude less than that of species living at the surface. The broad-spectrum studies on trawl-captured specimens are corroborated by elegant *in situ* work on the metabolism of deep-living species (Smith and Hessler, 1974; Smith and Laver, 1981) and by the examination of intermediary metabolic enzyme activity in mesopelagic species (Childress and Somero, 1979). Other lines of evidence including studies on excretory rates in midwater species (Hiller-Adams and Childress, 1983, Quetin *et al.*, 1980) and detailed examination of metabolism in individual deeper-living species (Gordon *et al.*, 1976; Quetin *et al.*, 1978) all support the trend that there is a general decline in metabolism with increasing depth of occurrence.

Inherent within a decline in metabolism with increasing depth in the water column is the potential influence of temperature and pressure. At this juncture, it appears unlikely that pressure contributes significantly to the decline of metabolism with depth. Existing evidence strongly suggests that the strategy employed by deeper-living species in adapting to pressure has been one of an insensitivity toward it both at the whole animal (Meek and Childress, 1973; Gordon *et al.*, 1976; Belman and Gordon, 1979) and the molecular level (Hochachka and Somero, 1984). In contrast, midwater species show a marked response to temperature (Childress, 1971, 1975, 1977; Torres *et al.*, 1979; Donnelly and Torres, 1988); where sufficient data exist to evaluate response to temperature with confidence, Q_{10}s are in the neighborhood of 2.0–3.0. Thus, temperature must be considered as a contributing factor to the decline in metabolism with depth. Unfortunately, it is difficult to separate the effect of temperature and the effect of species' depth of occurrence on metabolic rate where temperature decreases with depth. Temperature is a characteristic of a given depth as dictated by the permanent thermocline.

To assign a characteristic depth of occurrence for a species that inhabits a wide depth range one must arbitrarily choose between either of the two extremes

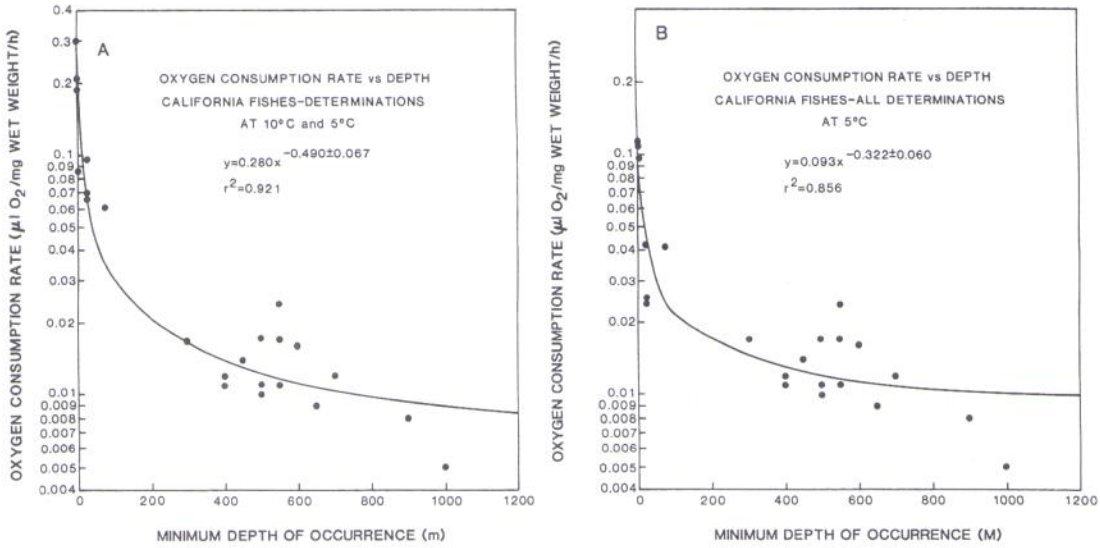

Fig. 2. (A) Oxygen consumption measured at 10°C for three fishes with MDO above 100 m, at 5°C for those below. (B) All fishes measured at 5°C. Slopes reported as b ± 95% CL.

(shallowest or deepest) or the center of distribution. Childress and Nygaard (1973) introduced the concept of "minimum depth of occurrence" to circumvent the problem, maintaining that this depth best reflects the food supply available to a species and that this criterion is as valid as any for the decision on what depth is most characteristic of a species. Minimum depth of occurrence is defined as that depth below which about 90% of a species population lives. The temperature within the water column that approximately corresponds to a species' minimum depth of occurrence is the temperature at which oxygen consumption rate is determined. It is this value for metabolic rate that is plotted vs depth to examine the trend of metabolism and depth.

Since in all but polar systems temperature declines with depth, and metabolism is measured at a species depth of occurrence, it is axiomatic that metabolism declines in deeper living species. What is interesting is that metabolism declines far more than would be expected on the basis of temperature alone (Fig. 2A). In the California Current the difference in metabolism between a fish living at the surface (0.300 μl O_2/mg wet wt/hr) and at 1000 m (0.005 μl O_2/mg wet wt/hr) is approximately 2 orders of magnitude. On the basis of temperature alone one would expect the fish living at 1000 m to respire at a rate about 50% of that of the surface dwelling species.

If the temperature at which metabolism is determined is held constant at 5°C for those species that have 5°C included within their bathymetric range there is still a decrease in the slope of the curve describing respiration vs depth (Fig. 2B). The trend of declining metabolism with depth of occurrence is unmistakably present but the constant temperature of 5°C no longer corresponds to species' minimum depth of occurrence. Thus, Fig. 2B decouples temperature from depth for the purposes of examining species physiological response to temperature. As such it has little meaning when applied to the field situation. To critically examine the influence of depth on metabolism it absolutely requires that temperature be constant with depth such as in the nearly isothermal situation found in polar oceans.

COMPARISON OF METABOLIC RATES OF ANTARCTIC AND CALIFORNIA MESOPELAGIC FISHES

It is clear that a comparison of metabolic rate in mesopelagic fishes from Antarctic and California waters must consider the observed decline in metabolism with depth of occurrence. Equally obvious is the fact that an evaluation of the influence of temperature on the decline must include information on fishes living in an isothermal or nearly isothermal sea. Thus, the Antarctic pelagial provides a natural experimental system because of its minimally varying temperature with depth (Fig. 1).

Curves describing the relationship between metabolism and depth in both systems are shown side by side in Fig. 3. Metabolism of Antarctic fishes was determined at a constant temperature of 0.5°C, California fishes at a temperature of 10°C for these with a depth of occurrence above 100 m, 5°C for those below (as in Fig. 2A). The relationship between depth and metabolism is similar in both systems, with a reduction in slope (-0.490 to -0.371) and elevation of the curve (0.287 to 0.162) in the transition from California to Antarctic waters. The resemblance is more striking on a log–log plot (Fig. 4), revealing another interesting facet in the comparison between California and Antarctic species; despite the differences in temperature between the two systems (10–5°C in California Species vs 0.5°C for Antarctic species), respiratory rate is very similar at any given depth. This suggests compensation for low temperature in the metabolism of Antarctic species, i.e. cold adaptation.

Comparisons between metabolism in temperate and polar species usually invoke a relation between

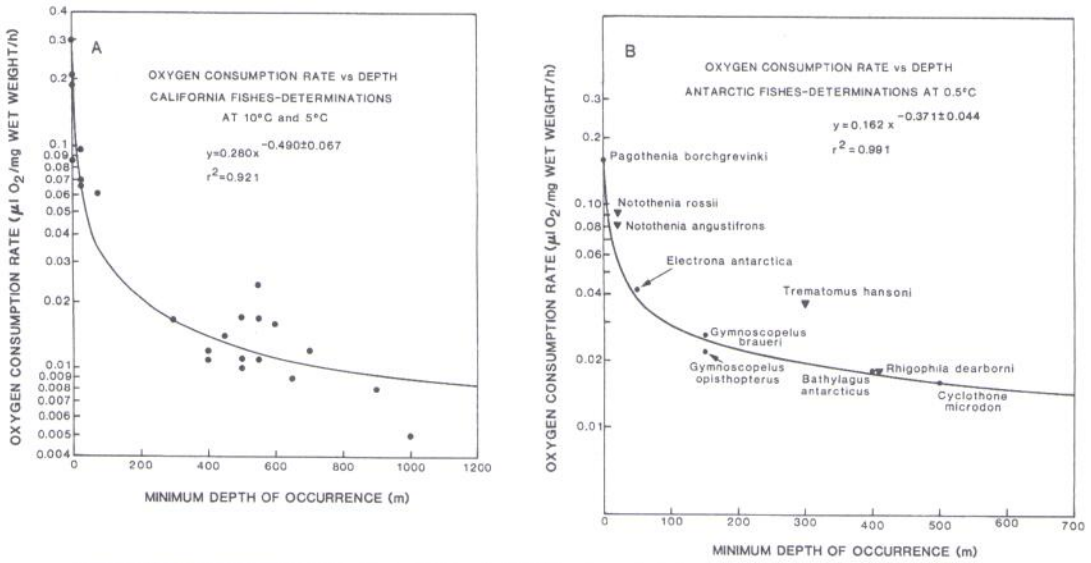

Fig. 3. Comparison of oxygen consumption in California and Antarctic mesopelagic fishes. (A) Oxygen consumption vs MDO in California fishes determined at 10°C and 5°C (as in Fig. 2A). (B) Oxygen consumption vs MDO in Antarctic mesopelagic fishes, all determinations at 0.5°C. Regression was calculated using only those fishes represented in the graph by filled circles; fishes denoted by inverted triangles are for reference only. Data from Table 2. Slopes reported as b ± 95% CL.

metabolism and temperature derived for the temperate group from a data set or from the literature (e.g. Winberg, 1956) and extrapolate it to low temperature, e.g. 0°C. In the same spirit, we may compare the rates of California species temperature corrected to 0.5°C (Fig. 4) to the rates of the Antarctic species. At any given depth, the metabolism of Antarctic species is approximately twice that of California species corrected to the same temperature. Thus, in the sense of Scholander *et al.* (1953) and Wohlschlag (1957, 1963, 1964). Antarctic mesopelagic fishes are cold-adapted relative to their California counterparts. However, in an ecological sense it is perhaps more interesting that rates from both regions are directly comparable. Caloric expenditure on routine metabolism in both regions is similar despite substantial differences in productivity cycles in the surface ocean and differences in water column temperature structure.

COMPARISON OF INTERMEDIARY METABOLIC ENZYME ACTIVITY IN ANTARCTIC AND CALIFORNIA SPECIES

The relation of metabolism to depth in California and Antarctic fishes as well as trends between systems may be further examined by comparing activity of intermediary metabolic enzymes in white skeletal muscle (Fig. 4A, B). White muscle comprises the largest fraction of body mass, and enzymatic activities in white muscle have been shown to reflect clearly the metabolic potential of this tissue, and of the intact fish (Childress and Somero, 1979). The enzymes analysed, lactate dehydrogenase (LDH, lac-

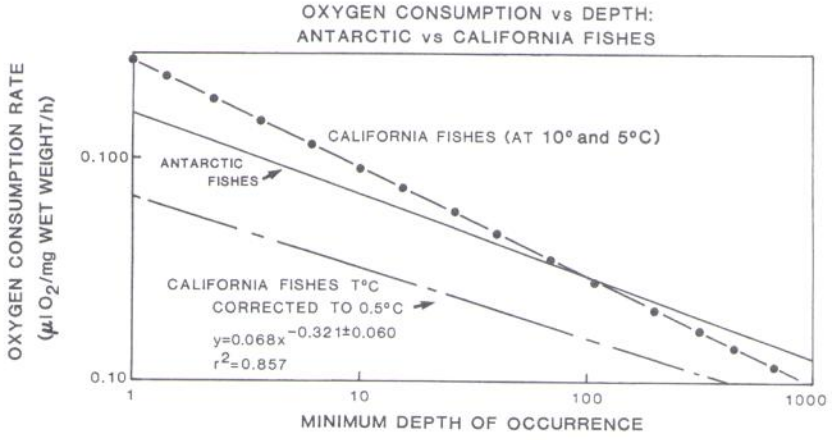

Fig. 4. The influence of temperature on oxygen consumption vs depth. California and Antarctic curves from Fig. 3 plotted on log–log axes. California curve temperature corrected using a Q_{10} of 2.0.

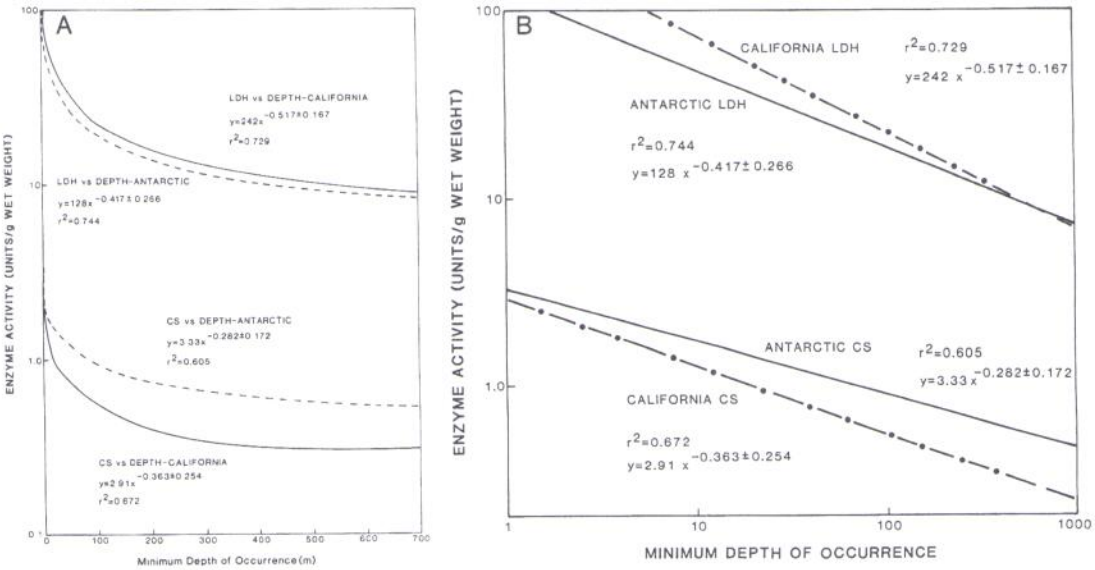

Fig. 5. LDH and CS activity of white skeletal muscle as a function of depth in California and Antarctic mesopelagic fishes. (A) Plotted on semi-log axes. (B) Plotted on log–log axes. Unites of enzyme activity are μmoles of substrate converted to product per minute.

tate: NAD^+ oxidoreductase) and citrate synthase [CS, citrate: oxaloacetate-lyase (COA-acetylating)], were selected as representative of anaerobic and aerobic potential, respectively. LDH is the terminal enzyme in anaerobic glycolysis in vertebrate tissues. CS is located within the mitochondrion and is positioned at the beginning of the citric acid cycle; it serves as a quantitative index of citric acid cycle activity (Lehninger, 1975). To be directly comparable, enzyme activities were analysed at the same temperature (10°C) in both systems.

It is clear from both the semi-log and log–log plots shown in Fig. 5 that enzyme activity declines with depth in a manner analogous to oxygen consumption rate. This is excellent corroborative evidence at the molecular level for the trend observed in whole animal metabolism. More interesting though, is the between-system comparison of enzyme activity vs depth. Anaerobic capability as indicated by LDH activity in Antarctic and California species is very similar when measured at the same temperature. Comparison of the two LDH curves using analysis of covariance (ANCOVA) shows that they are not significantly different ($P > 0.05$, F test) in their residual variance, slope or elevation. Visually, this is most obvious on the semi-log plot in Fig. 5A. It suggests that the compensation for temperature observed in oxygen consumption rate is not mirrored in increased LDH activity.

CS activity in Antarctic species is consistently above that of California species when measured at the same temperature. The difference in activity is somewhat less than would be expected on the basis of differences in extrapolated oxygen consumption rate (Fig. 4). If the two CS curves are compared using ANCOVA they are not significantly different in variance ($P > 0.40$) or in slope ($P > 0.50$). However, there is a trend toward higher elevation in the Antarctic CS vs depth curve. The trend does not reach the 0.05 significance level ($0.20 > P > 0.10$) but it is suggestive. A cold-adapted oxygen consumption rate, if it is to be reflected in enzyme activity would most likely be reflected in an elevation of an important step in the aerobic pathway.

If all available data on CS activity and oxygen consumption rate (with appropriate corrections) are plotted as in Fig. 6 the relation between the two becomes more obvious. There is an unmistakable correlation between CS activity and $\dot{V}O_2$ although with the present data set, not an exceptionally tight one ($r^2 = 0.470$). If one considers the array of investigators and techniques represented in Fig. 5 (see legend), and the fact that CS activity, like aerobic respiration rate, varies as a function of body size in fishes (Somero and Childress, 1980), the correlation that does exist is more impressive. With an expanded data base it is possible that CS activity could be used in the future as a means of estimating $\dot{V}O_2$. In this manner we may be able to estimate the oxygen consumption rate of species that are difficult to retrieve alive, e.g. the hatchet fishes.

CONCLUSIONS

Mesopelagic fishes living in waters south of the Antarctic convergences show marked similarities to their counterparts living in the California borderland. Vertical migration is an important foraging strategy in both systems (Pearcy *et al.*, 1977; Table 1). All fish families represented in the Antarctic pelagial are also present in California waters. Metabolic rates are similar, with Antarctic fishes exhibiting a somewhat higher oxygen consumption rate at equivalent temperature, an increase that we are attributing to cold adaptation. Both groups show a decline in oxygen consumption with depth of occurence that is mirrored in two enzymes of intermediary metabolism: LDH and CS. Within the perspective afforded by our

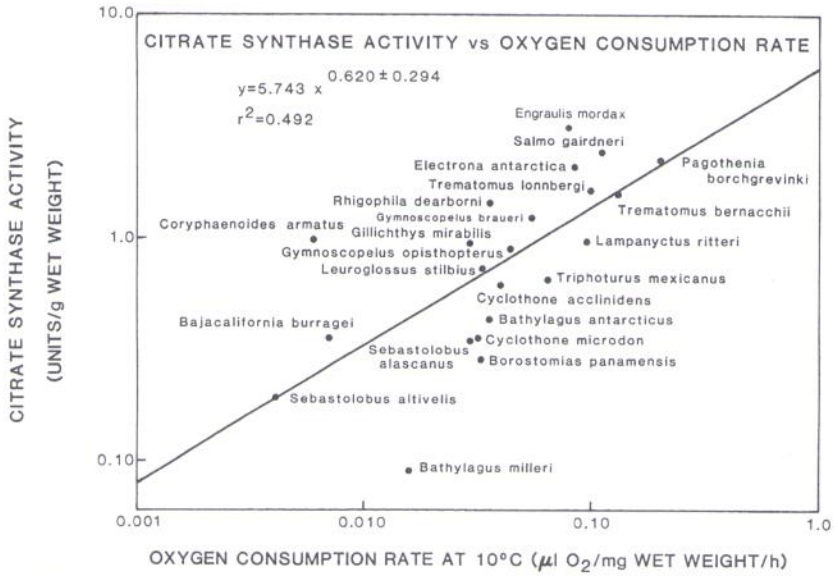

Fig. 6. CS activity vs oxygen consumption rate in a variety of fishes from different habitats. All oxygen consumption measurements corrected to 10°C using a Q_{10} of 2.0. Oxygen consumption rates come from the following sources: *Engraulis mordax*: Kaupp, unpublished datum; *Salmo gairdneri*, *Pagothenia borchgrevinki*, *Rhigophila dearborni*, *Gillichthys mirabilis*, *Trematomus bernacchii*, *Trematomus lonnbergi*: Wohlschlag, 1964; *Electrona antarctica*, *Bathylagus antarcticus*, *Gymnoscopelus braueri*, *Cyclothone microdon*, *Gymnoscopelus opisthopterus*: Table 2; *Lampanyctus ritteri*, *Leuroglossus stilbius*, *Triphoturus mexicanus*, *Borostomias panamensis*, *Bajacalifornia burragei*, *Bathylagus milleri*: Torres *et al.* (1979); *Cyclothone acclinidens*: Smith and Laver (1981); *Sebastolobus altivelis*: Smith and Brown (1983); *Sebastolobus alascanus*: Siebenaller (1984); *Coryphaenoides armatus*: Smith (1978). All values for CS activity from Childress and Somero (1979), Torres and Somero (1988) or are unpublished data of G. N. Somero.

data, similarities outweigh differences in the fishes of the two systems.

Differences in the physical and biotic characteristics of the pelagial in the two regions lie mainly in the potentially life-threatening cold temperatures in the upper 100 m of the water column and in the severe seasonality present in the primary production of the Antarctic system. These are potentially ameliorated by the mesopelagic distributions of the fishes and by their position in the trophic pyramid. The water column below 100 m provides a stable ice-free refugium for mesopelagic fishes that while considerably colder than the water column of the California borderland, (Gordon *et al.*, 1982; Scripps Institution of Oceanography, 1965) is not life-threatening. The highly pulsed primary production of the Antarctic (Heywood and Whitaker, 1984) imposes rigorous constraints on feeding by the herbivorous zooplankton prey of mesopelagic fishes, but since most of the zooplankton have multi-year life cycles (Everson, 1984) they should be able to provide meals for fishes throughout the year. Light levels during winter months are greatly reduced, perhaps enough to limit visual predation, but attenuated light is a characteristic of the mesopelagic environment throughout the world ocean. Mesopelagic fishes are in a sense "preadapted" to a life of cold and darkness, the Southern Ocean is simply one end of a continuum that extends from the equator to the pole.

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