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BIOCHEMICAL CHARACTERISTICS OF MACROURID FISHES DIFFERING IN THEIR DEPTHS OF DISTRIBUTION

JOSEPH F. SIEBENALLER,[1,*] GEORGE N. SOMERO,[2,*] AND RICHARD L. HAEDRICH[3,*]

[1]*School of Oceanography, Oregon State University, Marine Science Center, Newport, OR 97365;* [2]*Marine Biology Research Division, Scripps Institute of Oceanography, University of California—San Diego, La Jolla, CA 92093;* [3]*Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9, Canada; and,* **Marine Biological Laboratory, Woods Hole, MA 02543*

Abstract

Enzymic activities (units per gram wet weight of tissue) were measured in white skeletal muscle and brain tissue of five species of macrourid (rattail) fishes occurring over an approximately 5000 m depth gradient. Muscle protein and water contents were also determined. All species exhibited extremely low amounts of muscle enzymic activity for the glycolytic enzymes lactate dehydrogenase (LDH) and pyruvate kinase (PK), relative to values previously reported for shallow-living fishes. Malate dehydrogenase activity also was low, while citrate synthase (CS) activity was similar to levels found in shallow-living fishes. Interspecific differences among the rattails were large, especially for LDH activity which is a strong indicator of a fish's capacity for vigorous, burst swimming. *Coryphaenoides armatus*, a large rattail which is likely to be the most active swimmer among the species studied, had the highest enzymic activities and protein content, and, for LDH, PK, and CS, exhibited a significant scaling of enzymic activity with body mass. Scaling relationships were not observed for any other species. Brain enzymic activities were similar among all species. Muscle and brain enzymic activities also are reported for species belonging to four other deep-sea teleost families. The low levels of enzymes of energy metabolism found in skeletal muscle of these deep-sea fish species, and the interspecific variation in these activities are discussed in terms of the locomotory capacities and feeding strategies of these fishes. The potential usefulness of these types of enzyme data in estimating whole fish respiration rates is considered. We predict that the respiratory rates of the rattail species which have extremely low enzymic activity levels will be much lower than the respiratory rates previously measured for *C. armatus*.

Introduction

The macrourid (rattail or grenadier) fishes comprise the dominant component of the bathyal fish fauna in many areas of the ocean (*e.g.*, Marshall, 1965, 1973; Iwamoto, 1970). There are some 300 macrourid species, a number of which may have cosmopolitan distributions (Marshall, 1973; Iwamoto and Stein, 1974). The rattails are an important component of deep-sea food webs (Haedrich and Henderson, 1974; Pearcy and Ambler, 1974). In the area south of New England, rattail fishes may account for up to 80 percent of the slope megafaunal biomass (Haedrich and Rowe, 1977; Haedrich *et al.*, 1980). Because of their feeding habits, the rattails

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Abbreviations: CS, citrate synthase; LDH, L-lactate dehydrogenase; MDH, L-malate dehydrogenase; PK, pyruvate kinase.

are important in terms of energy input and energy dispersal in the deep sea (Haedrich and Henderson, 1974; Pearcy and Ambler, 1974; McClellan, 1976), and may play an important role in the maintenance of macrofaunal species diversity (Dayton and Hessler, 1972; see Grassle and Sanders, 1973, for a contrasting view).

Rattail species differ in their feeding strategies and, even within a species, small and large individuals may differ in their prey and location in the water column. Some rattail species are motile scavengers, and have been observed to come to bait (Isaacs, 1969; Isaacs and Schwartzlose, 1975). Analyses of gut contents (Haedrich and Henderson, 1974; Pearcy and Ambler, 1974; McClellan, 1976) and head morphology (McClellan, 1976) have provided insight into their feeding habits and sources of food. Smaller rattail species, *e.g.*, *Nezumia bairdii, Coryphaenoides* (=*Lionurus*) *carapinus*, and smaller individuals of other species, *e.g.*, *C.* (=*Nematonurus*) *armatus* and *C. rupestris*, feed primarily on benthic or bottom-associated invertebrates (Haedrich and Henderson, 1974; Pearcy and Ambler, 1974; McClellan, 1976). Larger species, such as *C. rupestris, C. armatus*, and *C.* (=*Chalinura*) *leptolepis* may rely more on pelagic organisms, at least once these species reach a certain size (Haedrich and Henderson, 1974; Pearcy and Ambler, 1974; McClellan, 1976). It is not clear whether such pelagic prey are encountered near the bottom or much higher in the water column; nonetheless, it is likely that these rattails make excursions into midwater.

Rattail fishes have received relatively little physiological study, and we presently have few data concerning the physiological correlates of feeding and locomotory patterns. Smith and Hessler (1974) and Smith (1978) have determined the respiration rates of two large, common rattail species *in situ*. *Coryphaenoides acrolepis* was studied in the San Diego Trough at 1230 m; *C. armatus* was studied at 3650 m in the northwest Atlantic. Both species had very low respiration rates, consuming oxygen at only approximately 4 percent of the rates shown by similar-sized, shallow-living related species at the same experimental temperature. Both species fell on a similar weight *versus* respiration rate curve.

The present experiments were initiated to obtain additional information about the metabolic characteristics of rattail fishes, including data on interspecific differences in muscle metabolism that relate to variations in feeding strategy and locomotory capacity. Our approach involved measurement of the activities of key enzymes of energy metabolism (glycolysis and the citric acid cycle) in white skeletal muscle. Recent studies (Childress and Somero, 1979; Sullivan and Somero, 1980; Siebenaller and Somero, 1982; Somero, 1982) have demonstrated that the levels of activity of these enzymes in white muscle correlate strongly with the feeding strategy and capacity for vigorous swimming in a wide spectrum of marine fishes. Active pelagic swimmers like tunas have up to 1000-fold higher levels of glycolytic enzyme activity per gram wet weight of muscle than sluggish deep-sea species (Sullivan and Somero, 1980). Such enzymic indices are useful even in fine-scale comparisons of congeneric fishes which differ in their depth distributions (Siebenaller and Somero, 1982). Thus, a shallow-living scorpaenid fish, *Sebastolobus alascanus*, had approximately twice as much activity for several enzymes of energy metabolism in muscle as did a deep-living, closely related species, *S. altivelis*. Interspecific differences in muscle enzymic activity also correlate well with measured variations in oxygen consumption rate among midwater species (Childress and Somero, 1979), a finding which suggests that muscle enzymic activity data may be useful in making predictions about *in vivo* metabolic rates. Lastly, glycolytic enzymes of white skeletal muscle exhibit a striking scaling relationship with body size (Somero and Childress, 1980). Larger individuals of a species contain much

higher levels of glycolytic enzymes per gram muscle than smaller individuals, a scaling function which appears to relate to the conservation of a stable capacity for burst locomotory performance in all sizes of individuals of a species (Somero and Childress, 1980). The presence of this type of metabolic scaling relationship, therefore, may provide some clue as to the importance of vigorous swimming activity in a species, and may indicate whether large and small members of a species have similar demands for intense locomotory performance.

Our comparisons of different-sized individuals of five macrourid species collected in the northwest Atlantic show that extremely large differences in muscle enzymic activity exist among species, and among different-sized individuals of the larger, more actively swimming species. However, there are no apparent differences in muscle enzymic activity among these species related to depth of occurrence *per se*. These data, plus observations made on several other deep-living fishes collected in the same trawls, are discussed in terms of interspecific differences in feeding behavior and metabolic requirements of life in the deep sea.

Materials and Methods

Specimens

Samples were taken with a 41-foot (12.5 m) Gulf of Mexico shrimp trawl, fished as in Haedrich *et al.* (1980), on cruise 93 of the R/V Oceanus in an area south of New England. Based on the distributional information described in Haedrich *et al.* (1980), samples were taken at appropriate depth intervals to obtain, at their depths of maximal abundance, the species used in this study. Sampling was conducted in late March and early April so that surface waters would be cold, and specimens would not be subjected to thermal shock. The fishes often had a heartbeat when brought to the surface, and were maintained in ice-cold seawater until frozen in a −80°C freezer at sea. Specimens were typically processed within an hour after the trawl was brought on deck. The samples were transported to the laboratory where they were maintained at −76°C.

A series of five macrourid species encompassing a depth range of 5000 m were obtained: *Nezumia bairdii*, *Coryphaenoides rupestris*, *Coryphaenoides* (=*Lionurus*) *carapinus*, *Coryphaenoides* (=*Nematonurus*) *armatus*, and *Coryphaenoides* (=*Chalinura*) *leptolepis*. The depth ranges and depths of maximal abundance of these species are reported in Table I. Specimens of the following deep-living species were also obtained and studied: *Halosauropsis macrochir* (Halosauridae), *Bathysaurus agassizi* (Bathysauridae), *Histiobranchus bathybius* (Synaphobranchidae), and *Dicrolene intranegra* (Brotulidae). The distributions of these species are given in Table III.

Enzymic activity determinations

The fish were measured and weighed. Tissue samples were dissected from the frozen specimens and weighed, and the frozen tissue was added to an appropriate volume of 10 m*M* Tris-HCl buffer (pH 7.5 at 10°C). For white skeletal muscle, the dilution was either 4:1 (volume:weight) or 8:1, depending on the viscosity of the homogenate. For brain, the dilution was 8:1. Tissues were homogenized on ice in a ground glass tissue homogenizer (Kontes Glass Co., Duall-23 model). The homogenate was centrifuged at 2500 × *g* for 10 minutes at 4°C. The supernatant was used without further purification for enzymic activity measurements. All activities are expressed as μmoles substrate converted to product per minute per gram wet weight of tissue at 10°C.

TABLE I

White skeletal muscle compositions and enzymic activity profiles of five macrourid fish species.

	N	Depth range* (m)	Depth of maximal abundance (m)	Mass [mean & range] (g)	% Water	Protein (mg/g)	Enzyme activity (units/g wet wt) [Mean ± S.D.] LDH	PK	MDH	CS
Nezumia bairdii	8	260–1965	600	54 24–102	81.2 ± 1.2 (8)	144.0 ± 16.5 (4)	6.9 ± 2.7	4.6 ± 2.2	17.5 ± 10.1	0.62 ± 0.15
Coryphaenoides rupestris	5	550–1960	1000	84 84–86	84.6 ± 0.6 (4)	142.1 ± 31.0 (3)	16.0 ± 5.8	5.4 ± 2.6	9.7 ± 0.5	0.58 ± 0.10
Coryphaenoides carapinus	11	1250–2740	2000	80 23–132	85.3 ±0.8 (4)	119.8 ± 22.5 (4)	4.7 ± 2.4	5.9 ± 2.2	6.8 ± 0.9	0.50 ± 0.19
Coryphaenoides armatus	13	1885–4815	2900	344 34–819	83.7 ± 2.4 (9)	177.1 ± 18.2 (4)	53.1 ± 28.9	7.2 ± 2.4	18.5 ± 3.5	0.79 ± 0.26
Coryphaenoides leptolepis	7	2288–4639	3500	456 90–960	82.3 ± 0.5 (7)	144.2 ± 16.5 (4)	4.3 ± 1.2	2.6 ± 0.3	6.9 ± 1.0	0.41 ± 0.14

* The depth ranges are from Haedrich *et al.*, 1980 and Haedrich, unpublished data.

The following enzymes were assayed in white skeletal muscle: L-lactate dehydrogenase (LDH, EC 1.1.1.27; L-lactate:NAD^+ oxidoreductase), pyruvate kinase (PK, EC 1.7.1.40; ATP: pyruvate phosphotransferase), L-malate dehydrogenase (MDH, EC 1.1.1.37; L-malate: NAD^+ oxidoreductase), and citrate synthase (CS, EC 4.1.3.7; citrate: oxaloacetate lyase (CoA-acetylating)). In brain tissue, LDH, PK, MDH and CS were assayed for some species. Assays were conducted as described in Somero and Childress (1980). For MDH appropriate controls were run to check for the decomposition of oxaloacetate during the course of the experiment.

Water and protein content of white muscle

Wet weights were determined on muscle samples, and the samples were then dried at 60°C and weighed after 24 hours, when they had dried to a constant weight. The percentage water was determined from the difference between the initial wet weight and the final dry weight. Protein concentration of white muscle was determined using the microbiuret method of Itzhati and Gill (1964). Homogenates were prepared in distilled water and diluted to 100:1 (volume:weight) with NaOH to give a final NaOH concentration of 1 *M*. Samples were used without centrifugation. Protein concentration was determined, after addition of the biuret reagent, from the difference in absorbance at 310 and 390 nm, using bovine serum albumin as a standard.

RESULTS

Macrourid white skeletal muscle

The enzymic activities, and water and protein contents of the white skeletal muscle of the five macrourid species are given in Table I. As a group, these species display lower enzymic activity, lower protein content, and higher water content

than do the shallower-living species which have been studied (*cf.* Childress and Somero, 1979; Sullivan and Somero, 1980). Lowered skeletal muscle enzymic activities have been observed for both midwater and benthopelagic fishes.

Within this group of rattails there is a wide variation of enzymic activity and protein content. This among-species variation is not correlated with depth of occurrence of the species. *Coryphaenoides armatus* displays strikingly higher levels of protein and enzymic activity per gram wet weight of muscle than do the other species. Also, for *C. armatus*, there is a statistically significant scaling of enzymic activity to body mass for CS, PK, and LDH (Fig. 1). The equations for these scaling relationships are: $A = 1.0\ W^{-0.59 \pm 0.005}$ for CS; $A = 1.83\ W^{0.24 \pm 0.13}$ for PK, and $A = 1.16\ W^{0.66 \pm 0.20}$ for LDH. The 95% confidence intervals are given for the

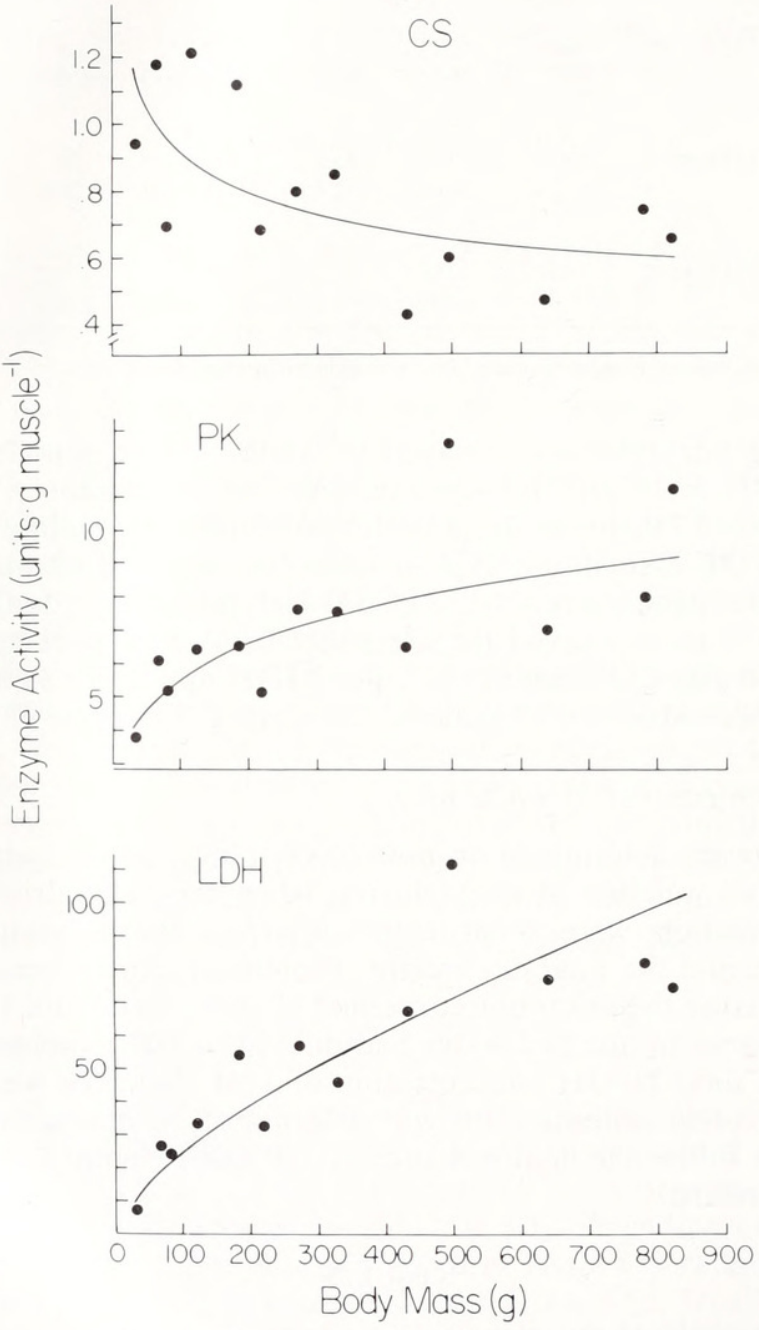

FIGURE 1. The scaling of enzymic activity in white skeletal muscle *versus* body mass for individuals of *Coryphaenoides armatus*. Citrate synthase (CS), pyruvate kinase (PK) and lactate dehydrogenase (LDH) displayed statistically significant scaling of activity *versus* body mass. The equations fitting these data are given in Results; the lines shown were fit by these equations.

TABLE II

Enzymic activity in brain tissue of three species of Coryphaenoides.

	Mass [mean & range] (g)	Enzyme activity (units/g wet wt) [Mean± S.D.]			
		LDH	PK	MDH	CS
Coryphaenoides rupestris	66 58–86	27.8 ± 4.3	22.0 ± 6.7	43.5 ± 9.1	2.0 ± 0.2
Coryphaenoides armatus	255 67–494	22.0 ± 3.7	13.3 ± 1.2	50.7 ± 5.5	1.4 ± 0.2
Coryphaenoides leptolepis	625 278–960	17.6 ± 2.6	13.8 ± 1.0	35.1 ± 4.2	1.3 ± 0.2

Four individuals of each species were used.

scaling exponents. "A" is the enzymic activity and "W" the wet weight of the entire fish in grams. None of the other macrourids showed detectable mass-related scaling of enzymic activity. For example, *C. leptolepis*, for which we had individuals ranging in mass from 90 to 960 grams, had a range of LDH activity of only 2.3 to 5.3 units per gram wet weight, with no size-related variation. The scaling patterns observed for white muscle enzymes of *C. armatus* agree with those noted for a variety of shallow-living fishes (Somero and Childress, 1980) in that the activities of the two glycolytic enzymes, LDH and PK, increase with rising body mass, while the activity of the citric acid cycle (=aerobically poised) enzyme CS displays lower activity per gram muscle in larger specimens.

Macrourid brain tissue

The activities of the four enzymes assayed in skeletal muscle also were measured in brain tissue of *C. rupestris*, *C. leptolepis*, and *C. armatus* (Table II). The values are somewhat variable, but generally similar among the three species. These activities are comparable to those reported for other fishes, both shallow- and deep-living (Childress and Somero, 1979; Sullivan and Somero, 1980; Siebenaller and Somero, 1982). We observed no scaling relationships for the brain enzymes, but this result may be due to the small sample size used in the study.

Muscle enzymic activities and compositions of other deep-sea families

The enzymic activities and water and protein contents of white skeletal muscle of representatives of four other deep-sea fish families are given in Table III. The enzymic activities in these species are low and within the range found for the macrourid species.

There is variation among these species, and wide variation between individuals of *Histiobranchus bathybius*. The protein and water contents of the muscle of this species were extremely variable, and some component of the tissue may have caused interference with the protein measurements. These data are not reported here.

The number of individuals and the size range of individuals which were taken in our sampling program are not adequate to permit us to address the question of mass-related scaling in these species.

TABLE III

White skeletal muscle compositions and enzymic activity profiles for species of four deep-living fish families.

	N	Depth range* (m)	Depth of maximal abundance (m)	Mass [mean & range] (g)	% Water	Protein (mg/g)	Enzyme activity (units/g wet wt) [Mean ± S.D.] LDH	MDH	PK	CS
Halosauropsis macrochir	3	1500–5179	2300	290 248–365	81.2 ± 0.4	90.7 ± 24.4	11.6 ± 1.7	3.6 ± 0.03	2.2 ± 0.4	0.40 ± 0.75
Bathysaurus agassizi	2	1500–2967	2000	625 433–817	80.9 ± 0.4	107.8 ± 11.0	35.4 ± 6.0	9.2 ± 1.8	11.0 ± 0.9	0.81 ± 0.21
Histiobranchus bathybius	2	1885–1093	2900	793 328–1258	—	—	53.0 ± 59.8	8.5 ± 7.8	12.3 ± 12.6	0.61 ± 0.52
Dichrolene intranegra	1	720–1960	1000	85	81.1	100.5	46.4	13.2	6.4	1.21

* Depth ranges are from Haedrich *et al.*, 1980, and Haedrich, unpublished data.

DISCUSSION

All of the species examined in this study have extremely low levels of LDH, PK, and MDH activity per gram of skeletal muscle compared to shallow-living fishes. For example, activities of LDH, the enzyme which appears to be the best index of a fish's capacity for intense, burst swimming (Somero and Childress, 1980), range between approximately 200 and 1000 units per gram in muscle of shallow-living, pelagic fishes; and 4 to 150 units per gram in deep-living fishes (Sullivan and Somero, 1980; Tables I and III). Citrate synthase, an indicator enzyme of the citric acid cycle, is present in only low activities in white muscle, a reflection of the anaerobic poise of this tissue (*cf.* Somero and Childress, 1980). CS activity varies only slightly among species, and only a small reduction in CS activity is noted in deeper-living fishes (Sullivan and Somero, 1980). MDH activity is intermediate between the two glycolytic enzymes (LDH and PK) and CS in terms of interspecific variation. MDH may play some role in cytoplasmic redox balance, albeit LDH is the dominant factor in this context, and it may also contribute to the shuttling of reducing equivalents between the cytosol and the mitochondria, and to the function of the citric acid cycle. Because of this variety of roles, MDH is less apt to be a strong indicator of burst swimming capacity than either LDH or PK. The results of the present study, like those of earlier comparisons of enzymic activities (Childress and Somero, 1979; Sullivan and Somero, 1980; and Siebenaller and Somero, 1982), indicate that reduction in the capacity for anaerobic glycolysis in muscle, *i.e.*, in burst swimming ability, is a major feature of adaptation to life in the deep sea.

There is wide variation of glycolytic activity in white muscle among the five rattail species, however, especially in the case of LDH. The highest levels of enzymic activity, and the only significant scaling relationships between enzymic activity and body mass, are found for *C. armatus* (Table I; Figure 1). At least larger-sized individuals of this species appear to make excursions into midwater to prey on pelagic organisms (Haedrich and Henderson, 1974; Pearcy and Ambler, 1974). The relatively high levels of glycolytic enzymes in white muscle of *C. armatus*, and the body-mass-related scaling noted for LDH and PK, may be reflections of a relatively high capacity for swimming compared to the other rattail species we

examined. *Coryphaenoides armatus* also had the highest muscle protein content of all the rattails studied.

The second-highest levels of LDH were found in *C. rupestris*. This species has a poorly ossified skeleton and weak musculature development (Marshall, 1973), but it has been reported to make excursions into the water column, and to feed on pelagic prey (Haedrich, 1974). *Nezumia bairdii* and *C. carapinus* feed on benthic invertebrates (Haedrich and Henderson, 1974; Pearcy and Ambler, 1974; McClellan, 1976). Although larger individuals of *C. leptolepis* may take pelagic prey (Pearcy and Ambler, 1974), this species has a poorly developed swimbladder and probably stays near the bottom (Marshall, 1973; Pearcy and Ambler, 1974). These species have very low levels of glycolytic enzymic activity in their white skeletal muscle, which may reflect a low potential for burst swimming correlated with this foraging habit.

The low levels of enzymic activity found in *C. leptolepis* relative to *C. armatus* demonstrate that body size does not contribute significantly to the interspecific differences noted in enzymic activity. Thus, large individuals of *C. armatus* had approximately ten times as much LDH activity and three times as much PK activity as similar-sized individuals of *C. leptolepis*. The finding that skeletal muscle LDH activity is low and very similar in all sizes of *C. leptolepis* examined indicates that this fish is unlikely to have much capacity for rapid burst locomotory activity. Burst swimming capacity would, in fact, decrease considerably with increasing body size for *C. leptolepis*, since a scaling relationship between body mass and LDH activity comparable to that found for *C. armatus* muscle is needed to conserve a constant burst swimming capacity as body size increases (Somero and Childress, 1980).

Smith (1978) measured respiration rates in *C. armatus* that were very low in comparison to those of shallow-living fishes at similar temperatures. Previously, Smith and Hessler (1974) measured a comparably low respiration rate for *C. acrolepis*. The respiration rate of *C. armatus* scaled with body mass according to the equation: $Y = 0.03\ W^{0.65}$, where Y is the oxygen consumption rate (ml/h) and W is the wet weight of the fish (g). The scaling we have determined for LDH activity in skeletal muscle of *C. armatus* is fit by a similar power function: $A = 1.16\ W^{0.66}$, where A is the LDH activity (units per g wet weight) and W is fish wet weight (g). The virtually identical scaling exponents indicate a linear relationship between oxygen consumption rate and LDH activity in this species.

Childress and Somero (1979) demonstrated an interspecific correlation between LDH activity and oxygen consumption rate for midwater fishes. A similar relationship of oxygen consumption rate and LDH activity for benthopelagic rattails is suggested by the scaling relationships for oxygen consumption and LDH activity of *C. armatus*, as discussed above, and the finding of similar levels of LDH activity in *C. acrolepis* and *C. armatus* (Sullivan and Somero, 1980; Table I). The *in situ* respiration rates of *C. acrolepis* and *C. armatus* were also similar (Smith and Hessler, 1974; Smith, 1978). However, the relationship of LDH activity and respiration in macrourids does not fall on the same curve as the data for midwater fishes. Also, for the midwater fishes examined by Childress and Somero (1979), MDH activity correlated with oxygen consumption rates. MDH activity in *C. armatus* does not scale as the same fractional exponent of mass as does oxygen consumption, and thus may not be a predictor of respiration rate in macrourid species.

Assuming a relationship between respiration rate and LDH activity in rattails, the very low activities of LDH observed in *N. bairdii*, *C. rupestris*, *C. carapinus*, and *C. leptolepis* are indicative of extremely low rates of oxygen consumption.

These four rattail species may have some of the lowest metabolic rates of any fishes. The body mass *versus* respiration rate relationship described by Smith (1978) for *C. acrolepis* and *C. armatus* may, therefore, overestimate the oxygen consumption rates of the other rattail species we have studied.

Despite the wide interspecific variation in the activities of skeletal muscle enzymes, relatively small interspecific differences were found in comparisons of brain enzymes (Table II). This finding agrees with previous reports of Childress and Somero (1979), Sullivan and Somero (1980) and Siebenaller and Somero (1982), who found no evidence for depth- or activity-related trends in brain enzymic activity. The general similarity in brain enzymic activities for both glycolytic and citric acid cycle enzymes among widely different fishes from shallow and deep-sea habitats suggests that the requirements of neural function are similar among different fishes.

The muscle enzymic activities of the representatives of the four other deep-sea fish families also are very low relative to shallow-living, actively swimming fishes (Table III; Sullivan and Somero, 1980). These low activities are again likely to be a reflection of a relatively low capacity for active swimming. Marshall (1973) considers the rattails, halosaurs and brotulids to be slow, intermittent swimmers. The low muscle enzymic activities found in *H. macrochir* and *D. intranegra* and the smaller rattails are consistent with this view. The low skeletal muscle activities of the bathysaur, *B. agassizi*, also suggest a similar locomotory capacity.

A high amount of variation between individuals was noted for the synaphobranchid fish, *Histiobranchus bathybius*. The wide variation in muscle enzymic activities could be a reflection of a strong scaling relationship like that noted for *C. armatus*; however, we captured too few specimens of *H. bathybius* to test this hypothesis. The finding that LDH activity in muscle of *H. bathybius* reached 95 units per gram in the larger specimen examined (mass = 1258 g) and 156 units per gram in a specimen studied by Sullivan and Somero (1980) (mass not known due to lack of a complete specimen), suggests that this species is capable of an active locomotory style.

In summary, our examination of five rattail fishes has revealed that depth of occurrence *per se* is not a factor in the differences in white muscle enzymic activities within this family of fishes. Rather, the differences in muscle enzymic activities appear to reflect interspecific variation in feeding habits. The large rattail, *C. armatus*, possessed the highest levels of glycolytic enzymes and the only scaling of these activities with body mass. Both traits are argued to be evidence for an active locomotory habit, at least relative to other rattail fishes. The extremely low muscle enzymic activities found in the species we examined are taken as evidence for very low whole organism respiration rates of these fishes. To the extent that whole organism oxygen consumption rate is linearly related to LDH activity of muscle (Childress and Somero, 1979), we propose that the four rattail species found to contain the lowest LDH activities have extraordinarily low respiratory rates, rates that are considerably lower than those which would be predicted by extrapolation using the respiration rate *versus* body mass relationship developed by Smith (1978) in his studies of *C. armatus*.

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