Aerobic metabolism of the anglerfish *Melanocetus johnsoni*, a deep-pelagic marine sit-and-wait predator

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Abstract—*Melanocetus johnsoni* (Teleostei:Melanocetidae), a bathypelagic marine sit-and-wait predatory fish captured off Hawaii, has an average aerobic metabolism of $0.486\,\mu$mol $O_2\,g^{-1}\,h^{-1}$, a rate much lower than that of more active species from similar depths but similar to that of other sit-and-wait predators. Larger individuals have a lower mass-specific metabolic rate than do small ones (the slope of the allometric relationship between wet mass and mass-specific metabolism is -0.46). This species, a resident of the oxygen minimum layer, is capable of regulating its oxygen consumption down to the lowest oxygen pressures encountered in its environment off Hawaii, and can also survive for hours under severely hypoxic or anaerobic conditions.

INTRODUCTION

Melanocetus johnsoni Günther (1864) is a bathypelagic ceratioid anglerfish found in all oceans (Fitch and Lavenberg, 1968) and commonly taken in deep-sea trawls. In the Central Pacific it is found mostly between depths of 500 and 1500 m (Pietsch and Van Duzer, 1980). Females range in size up to 13 cm in length, while males are reduced in size. Anglerfish are inactive sit-and-wait predators that attract their prey with a lure composed of a rodlike modified first dorsal fin spine, or illicium, tipped with a luminescent bulb, or esca, which attracts prey to the mouth. The body and mouth of *M. johnsoni* are a uniform black colour. The body is bulbous and poorly streamlined, in keeping with its apparently sluggish habits. After a meal the extremely distensible, rounded stomach may be much larger than the entire rest of the body (for example, we captured one 8.8 g specimen which had three snipe eels (*Nemichthys sp.*) totalling 12.3 g in its stomach). When undisturbed in the laboratory, this species remains quiescent or carries on a slow, languid sculling with the fins, in keeping with the known habits of shallower-living anglerfish.

As with many bathypelagic fish species, *M. johnsoni* is a stenothermal, cold-water species, and its integument is easily damaged by net abrasion. There have been few opportunities to retrieve it unharmed and to observe living, healthy specimens. We have been able, however, to capture a number of individuals in good condition and to study important characteristics of their physiology on board ship. In this paper we report on the metabolic characteristics of *M. johnsoni* captured in the Central Pacific off Hawaii, and compare its metabolism with that of other deep pelagic species.

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MATERIALS AND METHODS

Live female *M. johnsoni* were captured from 600 to 1000 m depths off the northwestern coast of Oahu (Latitude 21°20′N; Longitude 158°20′W) during July of 1983 and 1986. The gear used was a 3.3 m square opening and closing Tucker trawl equipped with a thermally protecting cod end (Childress *et al.*, 1978), towed at 2–2.5 knots. This apparatus has proved effective in capturing mesopelagic and bathypelagic species and bringing them to the surface in good physiological condition. Immediately after capture, the fish were transferred to 1–20 litre aquaria, depending on their size, and maintained at 5°C until use. Holding time varied from 0 to 48 h, with most fish being used within 24 h. During an experiment, each fish was placed individually in a closed glass chamber with a volume of 150–2200 ml, depending on the size of the fish, and held at a constant temperature of 5°C throughout the experiment. Chamber water was 0.45 μm-membrane filtered seawater to which 20 mg l^{-1} streptomycin and penicillin had been added to control microbial growth. The time-dependent change in oxygen partial pressure in the chambers, caused by the subject's metabolic uptake of oxygen, was then monitored over time using Clark-type oxygen electrodes (Mickel *et al.*, 1983) connected via an A/D board to an IMB-compatible computer (Cowles *et al.*, 1991). A magnetic stir bar spinning at moderate speeds within a perforated cage in the chamber kept the water well mixed and provided stirring for the electrode. The chamber was covered with a dark cloth during the experiment to minimize disturbance to the subject. Experiments lasted from 6 to 36 h, being terminated when the subject depleted the oxygen in the chamber to levels below the subject's critical oxygen pressure (P_c, = that pO_2 below which O_2 consumption is no longer independent of external pO_2; Prosser, 1973), as evidenced by a sharp decrease in its rate of oxygen uptake. The subject was then removed from the chamber, weighed on a shipboard balance (Childress and Mickel, 1980), and either preserved in formalin or maintained in an aerated aquarium for further observation.

The rate of change in oxygen level during the course of each experiment was used to calculate the subject's weight-specific rate of oxygen consumption (MO_2, μmole O_2 g^{-1} h^{-1}). Typically, rates were high and variable at first due to disturbance of the subject during transfer to the experimental chamber. Later the rate stabilized at a routine level, and remained stable until P_c was reached, at which time it dropped rapidly toward zero. The average MO_2 was calculated for all oxygen pressures clearly above P_c and for the range of oxygen pressures over which aerobic metabolism was relatively constant. P_c was calculated by regressing the declining metabolic rate against oxygen pressure (mm Hg) for those points that were clearly below the subject's P_c, and calculating where this best-fit line intersected the mean metabolic rate for the regulated range above P_c. The length of time the subject spent below P_c before being removed from the chamber, and whether the animal survived this period of hypoxia, were noted.

RESULTS

A total of eight specimens, ranging in wet mass from 1.2 to 99.9 g, were captured in good physical condition and analysed. All of those included in this analysis had empty stomachs, as determined by noting the lack of stomach distension or by examination of stomach contents after the experiment. We believe, therefore, that most of these fish had not eaten recently, though we cannot rule out the possibility that some may have regurgitated while
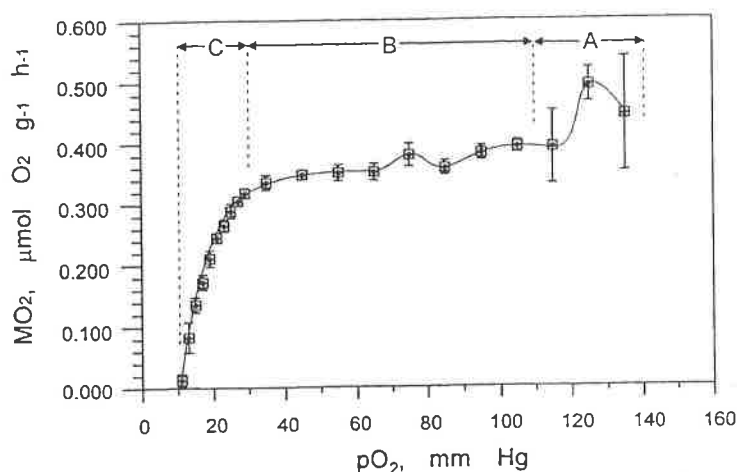
Fig. 1.   Pattern of aerobic metabolism in *Melanocetus johnsoni* subject number 191. Error bars are standard deviation. Region A: higher and variable metabolism on initial placement into the experimental chamber. Region B: regulated metabolic rate after subject has settled down to routine, undisturbed activity. Region C: sharply dropping metabolic rate at oxygen pressures below the subject's critical oxygen pressure (P_c). Based on 1072 records in an 8.27-h experiment.

being retrieved in the cod end; which could produce elevated metabolism in affected individuals due to post-digestive effects. All of the anglerfish were alive at the end of the experiment, and those that were kept for observation typically remained alive and active for several days more in the laboratory. Four of the eight individuals were not run long enough to establish their regulated rate of metabolism and P_c, or their aerobic pattern did not show a clear regulation of metabolism; while four other individuals did show clear regulation and a definite P_c. Only the individuals with clearly regulated aerobic metabolism and P_c were used for calculation of these parameters.

During the experiment the anglerfish swam slowly, using primarily the caudal fin with some auxiliary motions of the pectoral fins; or else hung motionless in the water. The fish's physical condition could be assessed by a gentle touch to the body at the end of the experiment. In healthy specimens this elicited a slow swimming response if the touch was to the lateral or posterior body, or often a fast strike if the touch was on or near the esca.

M. johnsoni is clearly capable of regulating its aerobic metabolism (Fig. 1). The average rate of regulated aerobic metabolism for these individuals was 0.486 μmoles O_2 g^{-1} h^{-1}, with a minimum of 0.259 and a maximum of 0.667 (Table 1). Individuals were able to regulate their metabolism down to a P_c of 22–35 mm Hg (Table 1). Although activity was not formally quantified, subjective observations and notes taken during the experiment indicate that the more active individuals had higher metabolic rates. Early in the experiment oxygen consumption was higher and more variable, presumably due to initial agitation and higher activity levels of the fish after the disturbance of being transferred to the experimental chambers. These initial rates, comprising the first several hours of each experiment, were discarded before calculation of regulated metabolism. Maximum observed aerobic factorial scope for any individual, including the initial period of elevated MO_2, was 3.5. This was for sustained metabolism, which lasted at least 20 min at each rate, and considered only metabolism at oxygen pressures above P_c. Since the subjects were not compelled to swim, this factorial scope must be regarded as a conservative estimate. The average aerobic factorial scope observed, which no doubt also underestimates true factorial scope, was 1.7.

Table 1. *Characteristics of aerobic metabolism measured from the Melanocetid anglerfish Melanocetus johnsoni and other deep living fish species off Hawaii. Individuals with missing data (—) were not run to P_c*

| Animal number | Wet wt g | $MO_2 \mu$mole O_2 g^{-1} h^{-1} | | | | P_c mm Hg | Minutes below P_c | Minutes below 20 mm Hg |
| | | Total above 30 mm Hg | | Regulated | | | | |
		range (mm Hg)	rate	range (mm Hg)	rate			
Melanocetus johnsoni								
25	99.9	30–79	0.259	30–80	0.259	22	224	204
35	58.3	70–110	0.330	—	—	—	—	—
39	13.9	30–99	0.667	33–99	0.667	33	286	232
41	4.5	90–130	0.321	—	—	—	—	—
135	2.1	71–123	0.377	—	—	—	—	—
136	11.8	30–117	0.726	30–80	0.665	26	94	74
190	1.2	102–130	1.184	—	—	—	—	—
191	49.6	30–137	0.378	30–110	0.353	25	152	130
Mean:			**0.530**		**0.486**	**26**	**189**	**160**
Oncirodes sp. (Oneirodidae): Sit-and-wait predator. MDO = 900 m								
23	53.4	130–140	0.214	—	—	—	—	—
Caulophrynid sp. (Caulophrynidae): Sit-and-wait predator. MDO = 900 m								
30	28.1	86–132	0.149	—	—	—	—	—
Chiasmodon niger (Chiasmodontidae): Roving predator. MDO = 750 m								
31	76.6	40–120	1.1	—	—	—	—	—
Stomias danae (Stomiatidae): Roving predator. MDO = 400 m								
175	13.8	40–140	1.3	—	—	—	—	—

The larger individuals had a significantly lower mass-specific rate of aerobic metabolism than did smaller individuals. The best-fit power relationship between wet mass (X, g) and rate of regulated aerobic metabolism (Y, μmole O_2 g^{-1} h^{-1}) was:

$$[Y = 2.144X^{-0.460\pm0.096}; n = 4]$$

The power of this relationship was highly significantly different from zero, and also significantly less than -0.25, the average slope often empirically found for such allometric relationships. Firm conclusions about allometric relationships in this species, however, should not be made until a broader dataset has been examined.

The P_c values measured, 22–35 mm Hg, were in the same range as the lowest environmental oxygen pressures (20–28 mm Hg) that would be encountered in the oxygen minimum layer in these waters at the depths at which *Melanocetus* is found (Cowles *et al.*, 1991). Though the subjects with higher metabolic rates generally tended to have higher P_c, the relationship between the rate of aerobic metabolism and P_c was not significant in this small dataset.

Besides being clear oxyregulators, the *M. johnsoni* in these experiments also exhibited a substantial capacity for survival in hypoxic conditions, surviving up to 4.75 h at environmental oxygen pressures too low to sustain regulated aerobic metabolism. They continued to live and respire, though at sharply reduced rates, long after pO_2 had dropped below 20 mm Hg, the lowest environmental pO_2 they would encounter in the water column (Table 1). None of these individuals died from the low oxygen pressures, so their true capacity for survival in hypoxia is clearly greater than that recorded in the table. Also, none of the subjects completely ceased the uptake of oxygen even at partial oxygen pressures far below their P_c, so their metabolism was at least partly aerobic down to the lowest oxygen levels detected.

Single individuals of several other deep-living fish species were also captured and studied for comparison (Table 1). In general, the roving predators (*Chiasmodon niger* and *Stomias danae*) had higher routine rates of aerobic metabolism, while the other anglerfish species (*Oneirodes* sp. and the caulophrynid angler) had comparable or lower rates.

DISCUSSION

This study supports the view that, besides the well-established decrease in the mass-specific rate of aerobic metabolism of midwater marine species with increasing depth of occurrence, a species' mode of living may also be an important determinant of its routine metabolic rate as suggested by Sullivan and Somero (1980). The routine metabolic rates measured for *Melanocetus* in this study are lower than any rates reported for shallower-living midwater fish species having a minimum depth of occurrence (MDO, depth below which 90% of the population are found) of less than 400 m (Childress and Nygaard, 1973; Torres *et al.*, 1979; Donnelly and Torres, 1988). *M. johnsoni*'s rate is also slightly below the rate predicted by the combined best-fit curve for fish species off California living at depths of 500–1000 m (Fig. 2, Torres *et al.*, 1979). *M. johnsoni* thus has a low metabolic rate even when compared with other fish species living at similar depths. This difference is most pronounced when comparing *M. johnsoni*'s metabolism with that of species presumed to be more active deep roving predators. *Anoplogaster cornuta*, for example, has been reported to have a routine metabolism of 0.89–1.25 μmole O_2 g^{-1} h^{-1} (Meek and Childress, 1973; Gordon *et al.*, 1976; Torres *et al.*, 1979; Donnelly and Torres, 1988) (some
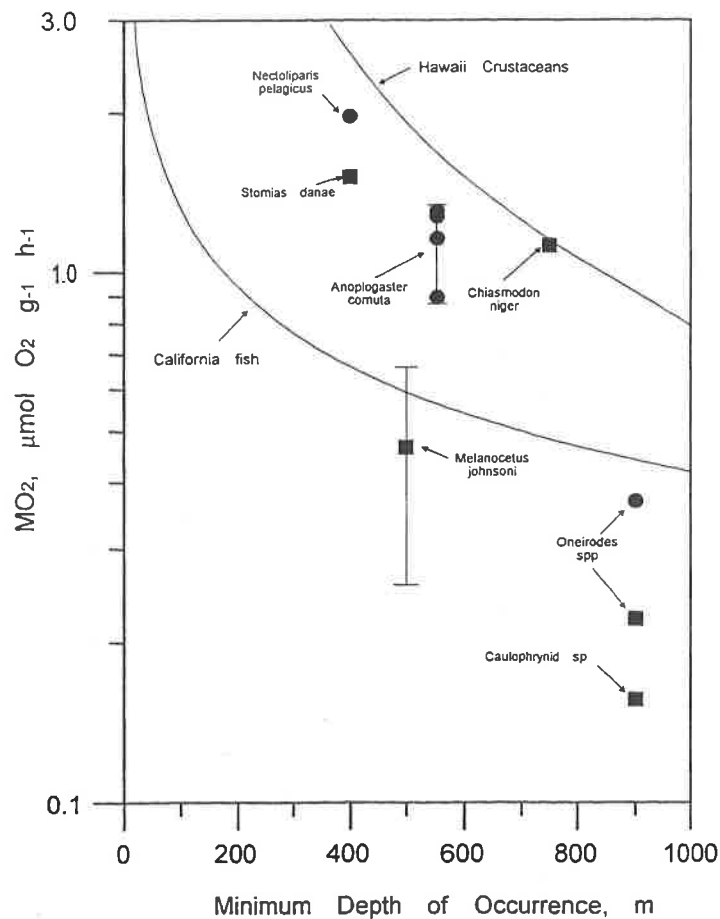
Fig. 2.   Range of rates of aerobic metabolism measured for *Melanocetus johnsoni*, compared with rates reported in the literature for other deep pelagic species, as a function of minimum depth of occurrence (MDO). Error bars = range. Squares = our own data; circles = data from the literature. Sources for estimates from literature: California fish: Torres *et al.*, 1979. Hawaii crustaceans: Cowles *et al.*, 1991. *Nectoliparis pelagicus*: Childress, 1975. *Anoplogaster cornuta*: Meek and Childress, 1973; Gordon *et al.*, 1976*; Torres *et al.*, 1979; Donnelly and Torres, 1988*. *Oneirodes acanthias*: Torres *et al.*, 1979. References marked with an asterisk were corrected to 5°C using Q_{10} calculated from the data or a Q_{10} of 2 if data for only one temperature were presented.

values corrected to 5°C using Q_{10} calculated from the data or a Q_{10} of 2 if rates were measured at only one temperature), which exceeds *M. johnsoni*'s mean rate by two to three times. Our own preliminary data on Hawaiian roving predators (Table 1) indicates a rate of around 1.1 μmole O_2 g^{-1} h^{-1} for *Chiasmodon niger* and 1.8 (at 10°C; 1.3 when corrected to 5°C) for *Stomias danae*. Other sit-and-wait predators, on the other hand, have similarly low rates to *M. johnsoni*: 0.365 μmole O_2 g^{-1} h^{-1} for *Oneirodes acanthias* (Torres *et al.*, 1979); 0.214 for a 53.4 g Hawaiian *Oneirodes* species, and 0.149 for a 28.1 g Hawaiian Caulophrynid angler (Table 1). *Melanocetus johnsoni* also has a lower rate of aerobic metabolism than do large pelagic crustaceans living off Hawaii at this depth (Cowles *et al.*, 1991) (Fig. 2), as do many deep pelagic fish. Most large pelagic crustaceans such as shrimps, euphausiids and mysids are negatively buoyant (Childress and Nygaard, 1974) and appear to swim actively at all times (Cowles and Childress, 1988; Cowles, 1994), which may contribute to a higher routine metabolism than is found in fishes. Several crustacean species, however, are neutral or positively buoyant and would not need to swim constantly

to maintain station in the water column (Childress and Nygaard, 1974; Sanders and Childress, 1988). These crustacean species tend to have lower metabolic rates than most other pelagic crustaceans, comparable to those of fish. *Notostomus gibbosus* from Hawaii, for example, has an aerobic metabolism of 0.48 μmole O_2 g^{-1} h^{-1} (Cowles *et al.*, 1991), while an unidentified *Notostomus* species from California has a rate of 0.334 (Childress, 1975).

Douglas *et al.* (1976) suggested on the basis of blood characteristics that fishes that migrate vertically into the oxygen minimum layer may function anaerobically while resident in the layer, and become aerobic only when they migrate upward to more oxygenated water. While *M. johnsoni* is not a vertical migrator, its metabolism clearly does not match this pattern since it is able to maintain its regulated rate of oxygen uptake down to the lowest oxygen pressures found in the oxygen minimum layer, at least off Hawaii. In this respect, it is similar to *Nectoliparis pelagicus* and *Melanostigma pammelas* (Childress, 1975; Gordon *et al.*, 1976) which are resident in the more strongly developed oxygen minimum layer off California and yet are able to regulate oxygen consumption down to environmental pO_2, and thus can live aerobically even within the oxygen minimum layer. It is not known whether ability to live aerobically even at low oxygen tensions is generally true for fishes resident in the oxygen minimum layer, nor whether it would also be true for individuals living in even more strongly hypoxic oxygen minimum layers such as are found in the eastern tropical Pacific.

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