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Oxygen consumption in four species of teleosts from Greenland: no evidence of metabolic cold adaptation

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Abstract Standard metabolic rate of Greenland cod or uvak, *Gadus ogac*, polar cod, *Boreogadus saida*, Atlantic cod, *Gadus morhua*, and sculpin, *Myxocephalus scorpius*, caught in the same geographical area on the west coast of Greenland was measured at 4.5 °C, the temperature at which the fish were caught. The present data does not support the Metabolic Cold Adaptation theory in the traditional sense of the standard metabolic rate being 2–4 times higher for Arctic fishes than for temperate species. The standard metabolic rate of the two exclusively Arctic species of teleosts was only 10% and 26% higher, respectively, than the two species that occur in temperate as well as Arctic areas. The critical oxygen tension, with respect to oxygen consumption, of resting uvak was between 50 and 60 mmHg, and the lethal oxygen tension 20–25 mmHg at 4.5 °C, which is considerably higher than for Atlantic cod from a temperate area measured at the same temperature.

Introduction

In the early 1900's, work by Ege and Krogh (1914) and Krogh (1916) suggested that cold water ectothermic animals were likely to have a metabolic rate higher than temperate animals when corrected for differences in measurement temperature. Later work by Scholander et al. (1953) and Wohlschlag (1960) supported this idea and demonstrated that the resting metabolism of Antarctic nototheniid fishes were indeed higher (Wohlschlag 1960), and the term "Metabolic Cold Adaptation" (MCA) was coined to describe this phenomenon (Wohlschlag 1960).

More recently, however, the concept of MCA has been challenged on methodological grounds. The primary criticism has centered around whether previous measurements of elevated standard metabolic rates (SMR) were accurate reflections of true SMR and therefore support for MCA, or merely artifactually high VO_2 measurements resulting from stress or uncontrolled activity during the measurement period (Holeton 1974; Clarke 1983; Wells 1987).

The aim of the present study was to determine whether Arctic fishes are metabolic cold adapted, with respect to oxygen consumption, by comparing standard metabolic rate in four teleosts species, two of which are exclusively polar, (polar cod and uvak) and two of which are found in both polar and temperate regions (Atlantic cod and common sculpin). In order to avoid some of the problems that have flawed earlier work, all species were captured in the same geographical area, selected for similar size, and VO_2 measured at the same temperature (4.5 °C). This eliminated problems associated with different life histories (e.g. water temperature, salinity, diurnal rhythms) and the need to standardize results by applying temperature or large weight corrections to the VO_2 measurements. Finally by utilizing automated, computerized, intermittent respirometry (Steffensen 1989), and determining standard metabolic rates over long periods when there were no disturbances in the laboratory, we were assured of obtaining metabolic rates from virtually unstressed fish.

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Materials and methods

Locality and fish

The experiments were carried out at the Arctic Station in Qeqertarssuaq/Godhavn, Greenland (69.15 N, 53.34 W) in June/July 1990. The fish, Atlantic cod, *Gadus morhua* (111–186 g); common sculpin, *Macrocephalus scorpius* (106–165 g); and Greenland cod or uvak, *Gadus ogac* (143–223 g) were caught with fishing rod, long line, gill-net or fish trap, at water depths ranging between 0.5 and 10 meters in the vicinity of Godhavn. Two polar cod, *Boreogadus saida*, 48 and 58 g, were caught from a commercial fishing vessel with a shrimp trawl at a depth of 360 m, 1 nautical mile east of Godhavn.

The fish were starved for at least 5 days and kept in net pens in the Godhavn harbour, and in 400 l outdoor PVC containers with recirculating sea water. Due to lack of cooling facilities, the water temperature in the holding tanks was influenced by the ambient temperature. Tank temperature fluctuated between 4 and 7°, whereas the water temperature at the collecting sites in the ocean varied between 4 and 6 °C. Salinity was 32–34 o/oo.

The respirometer

Oxygen consumption was measured by computerized, intermittent, flow-through respirometry, as described by Steffensen et al. (1984). Flow-through respirometry with 5 min measuring periods alternating with 5 min flush periods, was used to avoid wash-out problems associated with this technique (Steffensen 1989).

Oxygen tension of the water, pO_2, was measured with Radiometer E-5046 oxygen electrodes mounted in Radiometer D-616 thermostatted cuvettes, and connected to Radiometer PHM 73 Acid-base analyzers. The output signal from the Radiometer was recorded by an Olivetti PC equipped with a Data Translation DT2801 AD interface board driven by the program Labtech Notebook.

Due to the relatively slow response of polarographic oxygen electrodes at low temperatures, the cuvettes housing the electrodes were supplied with 25.0°C water from a thermostatted bath heated with a Hetotherm DT heater. A counter-current heat exchanger warmed the water sample flowing to the electrode as the water from the respirometer was sucked through the heat exchanger and past the oxygen electrode by an Istmatec roller pump fitted with gas-tight Tygon tubing.

Two respirometers (Volume = 1.4 l), made of plexiglass and fitted with four ports, were used simultaneously. Two ports were used for recirculating water in the respirometer during the measuring period to assure mixing, and two for flushing the respirometer during the flushing period.

The respirometers rested in a bath maintained at 4.5 ± 0.1 °C with a Hetofrig cooler and a Hetotherm heater. In order to avoid disturbance from human activity in the room all experiments were started approximately at midnight and continued for 12–14 hours, during which VO_2 was determined every 10 min.

Determination of standard VO_2

The continual measurement of resting VO_2 in fish can often result in a surprisingly wide range of VO_2 values. This is most often due to spontaneous activity of the animal that temporarily drives VO_2 for several minutes. The most common approach to calculate a resting VO_2 is to simply average a series of values taken while the fish is "resting". While this may be an accurate reflection of SMR if the fish was perfectly quiet during the measurement period, it is usually an overestimate of SMR as it includes VO_2 measurements during spontaneous (and usually unrecorded) activity. In order to eliminate this problem, we have calculated SMR from a frequency histogram of VO_2. This generally results in a large peak in or around the SMR and a few data points scattered among higher VO_2's. By the appropriate choice of parameters, it is possible to fit two "normal" curves to the frequency distribution of the raw data. The first narrow curve is a reflection of the normal distribution of SMR data points, while the second wider curve is a reflection of the routine metabolism.

Hypoxia

Experiments on the respiratory response to hypoxia of 5 uvak was performed in the same respirometers, by eliminating the flushing cycles and allowing the water oxygen tension to decrease. Water oxygen tension in the respirometer therefore decreased as a result of the rate of oxygen consumption by the fish. Oxygen tension, pwO_2, and temperature were collected and stored every 10 sec via LabTech Notebook. The experiment was terminated when pwO_2 fell to 20–30 mmHg. Oxygen consumption was computed by a linear regression of the decrease in pwO_2 with respect to time for every 200 s. Prolonged closed respirometry is not ideal for determining the effect of hypoxia on the standard VO_2, since pCO_2 will increase 4–5 mmHg. Due to the lack of compressed nitrogen in Greenland, however, no other method for producing progressive hypoxia was available.

Comparison of data

Oxygen consumption of teleost with different body weights was compared by correcting VO_2 to a body weight of 100 g using the equation:

$$VO_{2(100)} = VO_{2(I)} * \left(\frac{BW}{100}\right)^{(1-A)}$$

where $VO_{2(100)}$ = oxygen consumption for a 100 g animal, $VO_{2(I)}$ = oxygen consumption of an animal with body weight = BW, and A = the mass exponent describing the relationship between metabolic rate and body weight. For mammals, a value of 0.67 is well accepted both theoretically and experimentally according to Heusner (1991). For fishes, however, it is more difficult to determine a general value for the mass exponent (Schmidt-Nielsen 1984). Winberg (1956) suggested a value of 0.8, and resting speckled trout (*Salvelinus fontinalis*) gave values between 0.80 and 0.86 over a temperature range of 5 to 20 °C (Job 1955). In the present study a value of 0.80 was chosen, which is identical to that used by Holeton (1974). For Antarctic fishes weight exponents are scarce, but values ranging from 0.60 to 0.90 has been reported (Morris and North 1984). The difference in the extrapolated VO_2 values using an exponent of 0.8 or a value within the above range is less than a few percent, and have no influence on the final conclusion.

The VO_2 determinations from Wohlschlag 1960; Holeton 1973, 1974; Saunders 1963, did not have to be corrected, since equations describing the relationship between VO_2 and body weight was reported.

Statistics

Statistics differences were determined using Student's 2-tailed unpaired t-test. Values are present as mean ± std. dev., with the number of animals, N, presented in parentheses. n.s indicates no significance, $P < 0.05$.

Results

Due to handling stress when the fish were transferred to the respirometer, oxygen consumption was normally elevated for several hours. Figure 1 shows an example of oxygen consumption of an uvak for 13 h, beginning at 11:32 PM when it was transferred from the holding tank to the respirometer. The elevated VO_2 for the initial two hours can partly be ascribed to handling stress as well as our presence in the laboratory.

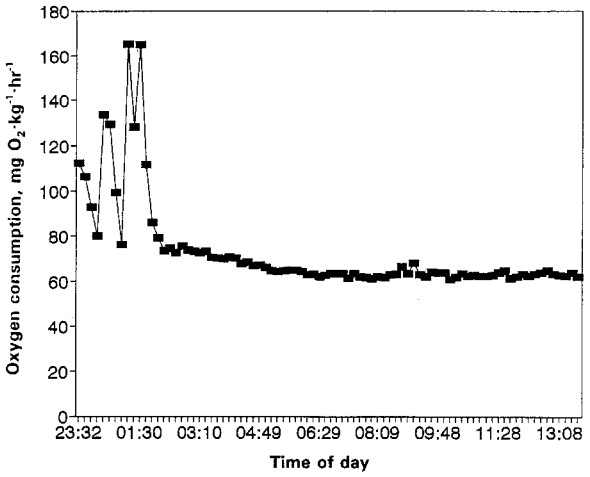

Fig. 1 An example of measurement of oxygen consumption of an uvak, *Gadus ogac*, starved for three days. Initially, after transfer to the respirometer, oxygen consumption was elevated due to handling stress. But after 2–3 h, and for the following 6 hours, VO_2 stabilized at a level considered to represent standard VO_2

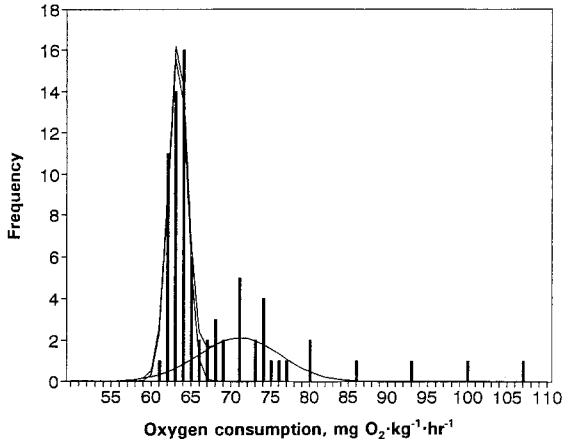

Fig. 2 An example of frequency distribution of VO_2 of uvak, and the fitted double normal distribution curve. The left narrow peak represent the standard VO_2, whereas the right wider peak represent routine oxygen consumption

An example of the technique used to determine standard metabolic rate by curvefitting two normal distribution curves to the frequency distribution of one night's determination of metabolic rate can be seen in Fig. 2. The tall narrow left peak represents the standard metabolic rate, while the peak on the right, caused by short periods of activity, can be considered routine metabolism.

A summary of measured standard metabolic rate of polar cod, uvak, Atlantic cod and sculpin, as well as SMR corrected to BW = 100 g, can be found in Table 1. Since there were only two determinations of oxygen consumption of polar cod, no statistics can be performed for this species. Oxygen consumption of uvak, however, was significantly higher than of Atlantic cod as well as of sculpin. Further, Atlantic cod had a significantly higher VO_2 than sculpin.

In Fig. 3 standard metabolic rates of polar cod, uvak, Atlantic cod and sculpin are compared to other teleosts (Arctic, Antarctic and temperate) measured at different temperatures and corrected to BW = 100 g. The lines are for those species in which VO_2 has been measured at two different temperatures. Calculated Q_{10} can be found next to the lines in Fig. 3.

VO_2 for polar cod at 1.0 °C obtained during an expedition to Igloolik, NWT, Canada, in the summer of 1992, are also shown on the graph (BS, I). The average VO_2 for 6 polar cod with a mean weight of 62 g was 78.8 mg $O_2 \cdot kg^{-1} \cdot hr^{-1}$ (Steffensen, Bushnell, Schurmann, Søeborg and Jensen, unpublished observations).

An example of determination of critical oxygen tension of uvak, defined as the pO_2 level at which it can no longer maintain oxygen consumption, and therefore changes from being an oxygen regulator to an oxygen conformer, is shown in Fig. 4. The horizontal line indicates standard metabolic rate for the fish determined at normoxia during the previous 9 hours. Critical oxygen tension was found to be between 50 and 60 mmHg. At oxygen tensions of 20–30 mmHg the uvaks lost equilibrium, and would eventually die. Hence it can be considered the lethal pwO_2.

Table 1 Measured oxygen consumption (VO_2(I)), and VO_2 corrected to a standard weight of 100 g (VO_2(100)). Values are mean VO_2 ± std. dev., (N) = Number of animals

	BW, g	VO_2(I), $mgO_2 \cdot kg^{-1} \cdot hr^{-1}$	VO_2(100), $mgO_2 \cdot kg^{-1} \cdot hr^{-1}$ Corr. to BW = 100 g
Polar Cod (2)	53.0 ± 7.1	95.6 ± 13.9	84.2 ± 14.5
Uvak (8)	180.9 ± 30.5	64.8 ± 4.5	72.8 ± 4.6
Atlantic Cod (8)	155.1 ± 27.9	61.0 ± 5.6	66.3 ± 4.7
Sculpin (9)	128.1 ± 21.5	45.4 ± 8.8	47.7 ± 8.1

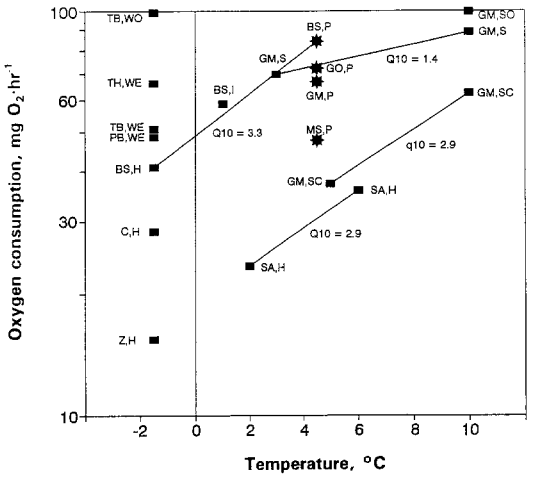

Fig. 3 Present (★) and literature values (■) of standard VO_2 for Arctic, temperate and antarctic teleosts at the different experimental temperatures. The present data as well as *Boreogadus saida* from Igloolik (BS,I) and *Gadus morhua* by Schurmann (GM, SC), have been extrapolated to a body weight of 100 g using a scaling factor of 0.80. See text for further details. Solid lines connect identical species measured at different temperatures. *Data labels*: C,H = Cottidae (Holeton 1974); BS;H = *Boreogadus saida* (Holeton 1974); Z;H = Zoarcidae (Holeton 1974); MS,P = *Myxocephalus scorpius* (Present study); GM,P = *Gadus morhua* (Present study); GO, P = *Gadus ogac* (Present study); BS,P = *Boreogadus saida* (Present study); BS,I = *Boreogadus saida* (Igloolik unpublished); GM,S = *Gadus morhua* (Saunders 1963); GM,SC = *Gadus morhua* (Schurmann unpublished); SA,H = *Salvelinus alpinus* (Holeton 1973): PB,WE = *Pagothenia* (*Trematomus*) *borchgrevinki* (Wells 1987 and Wohlschlag 1964); TB,WE = *Trematomus bernacchii* (Wells 1987); TH,WE = *Trematomus hansoni* (Wells 1987); TB,WO = *Trematomus bernacchii* (Wohlschlag 1960); GM,SO = *Gadus morhua* (Soofiani and Hawkins 1982)

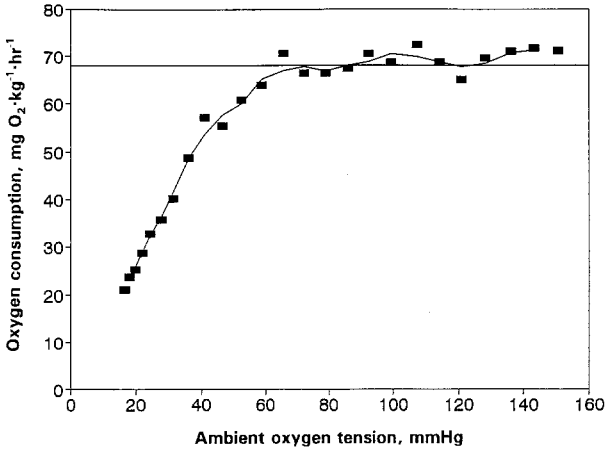

Fig. 4 An example of standard VO_2 of an uvak exposed to graded hypoxia. The horizontal line indicate standard VO_2 during the previous 9 hours. Critical pwO_2 was 50–60 mmHg. At a pwO_2 of approximately 20 mmHg the uvak lost equilibrium, and would eventually die if the respirometer had not immediately been supplied with oxygenated water. The solid line represent a 3 point moving average

Discussion

The major aim of this study was to obtain temperate and polar teleosts from the same locality and perform the experiments at the natural ambient temperature. This was done in order to avoid the possible errors that have confused results of the previous studies, namely temperature acclimation to temperatures that differed from that at which the fish were caught, and extrapolation of metabolic rates due to considerable size of temperature differences. For example, according to Holeton (1974), the data in Ege and Krogh (1914) and Krogh (1916), publications that initiated the dispute on Metabolic Cold Adaptation, have limited value because they were based on experiments with a single 9.3 g goldfish. This resulted in Q_{10} values that, even by the authors admission were considered "obviously erroneous".

To date no other studies investigating Metabolic Cold Adaptation in several species have been done at the same temperature, with similarly sized fish and from an area with both temperate and polar species present. Instead, most authors have used extrapolation of metabolic data from nonpolar species to low temperatures. The present study involves VO_2 measurements on both polar and temperate water species.

Polar cod, *Boreogadus saida*, prefer temperatures between 0–6 °C, but tolerate temperatures as high as 13.5°C (Craig et al. 1982). The polar cod in this study were caught at a depth of 350 meters at an unknown temperature, probably between 2 and 5 °C, but kept at the experimental temperature of 4.5°C. Atlantic cod from a temperate region, prefer a temperature of 12°C (Schurmann and Steffensen 1992), but are reported to tolerate up to 19°C, and have been found at temperatures as low as −0.5 °C (Leim and Scott 1966). Preferred and lethal temperatures for the circumpolar Greenland cod and common sculpin, *Myxocephalus scorpius*, are to our knowledge not known.

It was our intention to use fish of similar size in order to avoid scaling effect problems due to extrapolation of VO_2 beyond that size range studied. Extrapolation is extremely risky, and the best would be to avoid it. In the present study we tried to obtain fish of equal size, and as close to 100 g as possible. For comparison with other published values, however, we had to extrapolate to a 100 g fish as Holeton (1974).

The standard metabolic rates of uvak and Atlantic cod are in good agreement with values of 63.1 and 66.2 mg $O_2 \cdot kg^{-1} \cdot hr^{-1}$, respectively, found by extrapolating oxygen consumption values at different swimming speeds to zero activity (Bushnell et al. this volume). Further, as seen in Fig. 3 the values are in good agreement with literature values of Atlantic cod (GM,S) (From Saunders 1963) measured at other temperatures. Q_{10} for cod calculated from Saunders

measurements at 3 and 10 °C is 1.42, while Q_{10} for polar cod calculated from Holeton's value at −1.5 °C and our data from 4.5 °C is 2.95. Values for Arctic charr, *Salvelinus alpinus*, are also shown on Fig. 3 as SA, H (From Holeton 1973). Q_{10} for Arctic charr was 2.90.

Species with a sedentary behaviour and, hence lower standard metabolic rate, include Zoarcids and Cottidae (Z,H & C,H on Fig. 3). The common sculpin, MS,P in Fig. 3, is also a sedentary fish and has a considerably lower metabolic rate than the three other species in this investigation.

Oxygen consumption and oxygen transport of Arctic fishes is of physiological interest because the physical conditions such as low temperature, high oxygen concentration and partial pressure in Arctic waters are considerably more stable than in temperate or tropical areas. In the Sound between Denmark and Sweden, where large concentrations of Atlantic cod are common most of the year, water temperature fluctuates between 3 and 13 °C and oxygen saturation between 30 and 90% (personal observations). Fishes living in Arctic waters would therefore be expected to be less tolerant to hypoxia than fishes from temperate or tropical waters. The few observations we have from the uvak indicate that the critical pwO_2 was between 50–60 mmHg at 4.5 °C. Observations by Schurmann and Steffensen (in prep) show that Atlantic cod from Danish waters can maintain oxygen consumption at oxygen tension decreasing to approximately 25 mmHg at 5 °C and 35 mmHg at 10 °C. The lethal pwO_2 for uvak was between 20 and 30 mmHg which is approximately 3 times higher than the lethal pwO_2 of 7.5 mmHg at 5 °C found for the Atlantic cod (Schurmann and Steffensen 1992). The critical oxygen level for Atlantic cod increase with increasing temperature to 24 mmHg at 12 °C. Likewise Holeton reported that Arctic charr lost equilibrium at 2 °C at oxygen tensions of 22 to 28 mmHg (Holeton 1973). The high critical pwO_2 and lethal pwO_2 in uvak infer that polar fish are less hypoxia tolerant, but though have the mechanisms to respond. This is in agreement with Wells et al. (1989) who reported that *Pagothenia borchgrevenki* had the necessary mechanisms to respond to hypoxia in a way that is typical of teleosts that naturally inhabit oxylabile environments. Wells suggested that "the ability to make short-term adaptive changes in the oxygen delivery system in response to hypoxic exposure may be typical for vertebrates in general, rather than a feature seen only in those organisms which encounter environmental hypoxia on a regular basis".

It is clear from Fig. 3 that fishes from the Arctic, temperate, and Antarctic areas have quite scattered standard metabolic rates. The difference in VO_2 between species is unknown, but can probably be ascribed to different methods of measuring standard metabolic rate, as well as behavioral differences (sedentary versus pelagic fishes). It is difficult therefore to determine whether metabolic cold adaptation is indeed a fact or an artefact. We did not however, in the present study on Arctic and temperate species measured under similar conditions, find any evidence of metabolic cold adaptation in the traditional sense of a 2–4 times increase in standard VO_2. In the present study, VO_2 of polar cod and uvak normalized to a bw of 100 was only 26 and 11% higher than Atlantic cod. As we were only able to get two polar cod in Godhavn, and another six in Igloolik, we plan additional experiments on this species.

The importance of measuring VO_2 of long term adapted versus short term adapted species at a common temperature is also illustrated in Fig. 3. Here we have plotted VO_2 values of Atlantic cod that were measured at the same temperature as they were caught (10 °C) along with the VO_2s (at 5 °C) of Atlantic cod acclimated for three weeks to 5 °C (GM,SC – Schurmann unpublished observations – values are corrected to a 100 g fish). Interestingly the VO_2 of Atlantic cod collected and measured at 4.5 °C in Greenland is very similar to that of fish caught and measured at 10 °C in Denmark (66.3 and 62.5 mg O_2 hr^{-1}, respectively). Atlantic cod caught at 10°C, but measured at 5 °C after at least 3 weeks acclimation, however had a VO_2 of only 37.2 mg O_2 hr^{-1}. This does not indicate metabolic cold adaptation, but temperature compensation. If we had only been able to obtain uvaks in Greenland, and had compared their oxygen consumption with that of Danish cod at 5 °C we would have erroneously postulated that uvak were metabolically cold adapted.

The controversy surrounding Metabolic Cold Adaptation continues today. Torres and Somero (1988) recently reported that the metabolic rate of Antarctic mesopelagic fishes was approximately twice that of California species at equivalent temperatures, and thus ascribed it to be a well-developed compensation or adaptation for temperature in the Antarctic species. Another point of view is that of Clarke (1991), who believes that "the use of respiration rate to assess temperature compensation should be abandoned forthwith" Clark would rather like biochemical processes to be measured because they are simpler systems. Clarke's recent contribution to the controversy, however, is purely philosophical and ignores many previous and recent experiments. Among others it ignores Hochacka (1988), discussing coupled physical and biochemical properties of physiological systems affected by temperature. Especially the maintenance of a transmembrane potential at different temperatures in cells is discussed. In all cells the passive diffusion of ions through the membrane (a passive physical process) must be precisely balanced by the active transport of ions out of the cell against a concentration gradient (an active

biochemical process). Because temperature effects the two systems differently, the only way to maintain a proper balance between the two processes is either to decrease the membrane permeability or increase the ion pump capacity. Hochacka (1988) believes that polar fishes can maintain channel/pump flux ratios at unity by upward adjustments in functional pump densities, and that this presumably is why they have a higher-than-expected metabolic rate. Fish living at identical low temperatures could however also maintain channel/pump flux ratios at unity by downward adjustments in the functional channel densities of cell membranes. Organisms utilizing this strategy would be expected to have depressed metabolic rates, reduced scopes of activity, and reduced osmoregulatory capabilities. Deep sea fishes fits into this latter category by functioning at low temperatures, and have a lower metabolic rate as shown by Torres and Somero (1988).

At present a few Antarctic species appear to be candidates for being metabolically cold adapted. Among these are *Trematomus bernacchii* and *T. hansoni*. Since different experiments have produced quite different VO_2 values in these species (Wohlschlag 1960, 1964; Morris and North 1984; Wells 1987; Forster et al. 1987), we hope to be able to obtain *Trematomus* sp. and measure their standard metabolic rate with the present computerized respirometers in the near future. Hopefully we can then determine whether these Antarctic species really have an increased standard metabolic rate, or as Holeton (1974) suspected, that MCA is an artefact that can be ascribed to either disturbed fish and/or the measuring technique

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