



## Oxygen consumption of East Siberian cod: no support for the metabolic cold adaptation theory

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Standard metabolic rate ( $R_S$ ) at 2° C of eight East Siberian cod *Arctogadus borisovi*, caught in West Greenland, body mass of  $601.5 \pm 147.6$  g (mean  $\pm$  s.d.), was  $40.9 \pm 5.9$  mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup> and  $59.0 \pm 6.6$  mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup> when extrapolated to a standardized 100 g fish.  $R_S$  was compared with three other Gadidae, to test the theory of metabolic cold adaptation (MCA). There was no evidence of MCA in the family. © 2001 The Fisheries Society of the British Isles

Key words: East Siberian cod; *Arctogadus borisovi*; Arctic; metabolic cold adaptation; oxygen consumption.

### INTRODUCTION

The classical studies of Ege & Krogh (1914) and Krogh (1914, 1916) suggested that polar ectotherms would have an elevated metabolic rate (metabolic cold adaptation, MCA) relative to temperate ectotherms when exposed to the same temperature. Work by Scholander *et al.* (1953) and Wohlschlag (1960, 1964) suggested that cold-water fishes tended to have a relatively higher metabolic rate than temperate and warm-water species. The theory was later criticized (Holeton, 1973, 1974; Clarke, 1980, 1983, 1991, 1993; Hop & Graham, 1995), and several authors claimed that there was no evidence for MCA (Wells, 1986, 1987; Bushnell *et al.*, 1994; Steffensen *et al.*, 1994; Clarke & Johnston, 1999).

A potential problem in comparative studies of MCA to date, is that the fish fauna of the Southern Ocean consist to a large part of notothenioids (Perciformes). Thus most comparative studies between polar, temperate and tropical species have related to ecology and only a few studies have concerned phylogeny (Scholander *et al.*, 1953; Clarke & Johnston, 1999). The only teleost order, besides the Antarctic zoarcids, with sufficient polar and non-polar data to test for MCA phylogenetically is the Gadiformes, the true cods (Clarke & Johnston, 1999).

Nielsen & Jensen (1967) revised the genus *Arctogadus* into two species, the Arctic cod *A. glacialis* (Peters), and the East Siberian cod *A. borisovi* Dryagin. The cod caught in the present study were classified as *A. borisovi* based on the presence of barbels on many specimens, on a total length ( $L_T$ ) range of 30–48 cm and that they appeared to be summer spawners, due to presence of ripe ovaries.

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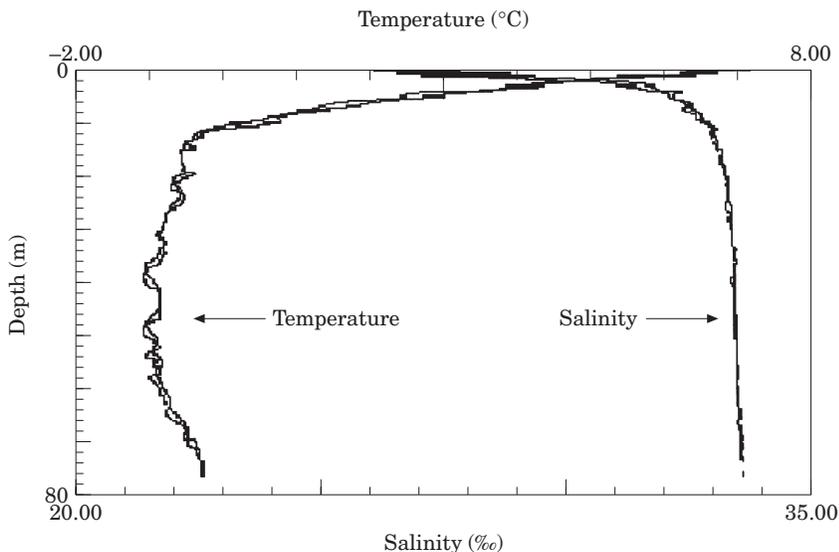


FIG. 1. Plot showing salinity and temperature with depth in the area where the East Siberian cod were caught. The data were collected with a Seabird Electronic SBE-25 Sealogger CTD.

The species is known from eastern Siberia eastward to Greenland, but as far as known has not caught around Uummannaq, Greenland. Species of *Arctogadus* have a strictly high Arctic distribution.

Both species of *Arctogadus* prefer a temperature of *c.* 0° C and they are often associated with partial ice cover (Nielsen & Jensen 1967; Süfke *et al.*, 1998), although two specimens of *A. borisovi* were caught in southern Greenland at a temperature of *c.* 3–4° C (Nielsen & Jensen, 1967). Observations shows that *A. borisovi* tolerates temperatures up to 7° C after several days of acclimation, but dies at *c.* 8° C (A. D. Jordan & M. Jungersen unpubl. obs.). Because of the low temperatures in which they live, the physiology of *Arctogadus* is of particular interest with respect to MCA.

The aims of the present study were to determine the standard metabolic rate ( $R_S$ ) of *A. borisovi* and compare it with values found for other species of Gadidae, to determine whether MCA is present in this family.

## MATERIALS AND METHODS

### LOCATION AND COLLECTION OF THE FISH

The experiment took place at the Arctic Station, University of Copenhagen, Qeqertarsuaq/Godhavn, Greenland (69°15'N; 53°34'W) in July 2000. East Siberian cod were caught at Qilaqitsoq near Uummannaq/Umanak (70°39'N, 51°54'W) at a depth of 20–50 m (Fig. 1). Water temperature of  $-1^{\circ}$  C and a salinity of 33–34‰ were recorded. They were caught by jigging with barbless hooks and placed in an insulated 385 l tub with aeration and transported to the Arctic Station. In the laboratory, the East Siberian cod were held in a 385 l insulated tub with continuous recirculating sea water at a temperature of 1–6° C (due to lack of cooling facilities) and a salinity of 28–34‰. Prior to experimentation all fish were starved for >8 days to avoid specific dynamic action (SDA).

### THE RESPIROMETER

The measurements of oxygen consumption were carried out with a computerized, intermittent-flow respirometry (Steffensen, 1989). A 50 l tank was filled with filtered

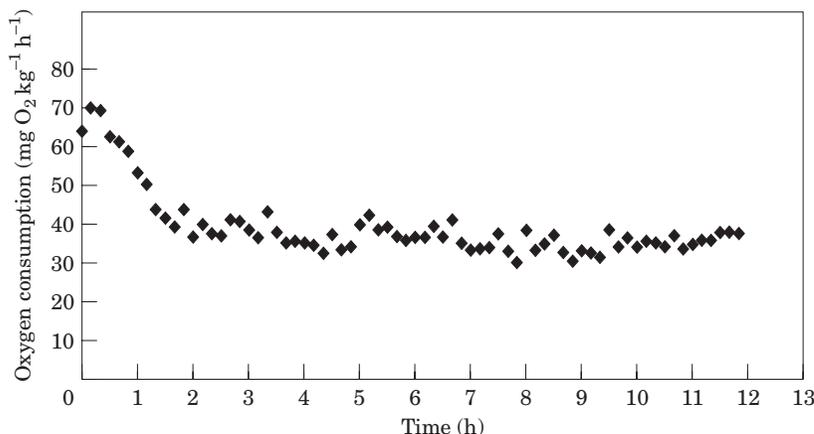


Fig. 2. Oxygen consumption of an East Siberian cod in the respirometer. Note the elevated values in the initial hours due to handling stress. Each point represents a 10 min period.

(63  $\mu\text{m}$ ) sea water and kept at a constant temperature of  $1.9 \pm 0.2^\circ\text{C}$  using a Hetofrig cooler and a Hetotherm heater and continuously circulated and aerated. The respirometer was immersed in a darkened tank. A cylindrical respirometer made of Plexiglas with a volume of 5240 ml was used. The respirometer was closed with an O-ring and wing nuts at both ends, and each end was fitted with two ports. Two ports were used for recirculating the water to avoid stratification in the chamber. The other two were used to flush the respirometer with oxygenated water and to remove accumulated excretory products. Water was collected continuously from the respirometer-recirculating shunt, at a flow of  $3\text{ ml min}^{-1}$  through gas tight Tygon tubing by an Ismatec roller pump.

Oxygen tension ( $PO_2$ ) was measured using Radiometer E-5046 oxygen electrodes mounted in Radiometer D-616 thermostatted cuvettes connected to Radiometer PHM 73 pH/blood gas analyser. An Acentia 900 N PC equipped with a Computer Boards PCM-DAS16D/16 AD interface board driven by Labtech Notebook was used for recording the output signal and controlling the flushing and closing of the respirometer.

Before the oxygen electrodes were placed in the cuvettes the water was warmed in a water bath maintained at  $24^\circ\text{C}$  with a Heto DT Hetotherm to increase the response time and signal from the polarographic oxygen electrodes.

## EXPERIMENTAL PROCEDURE

The size of the respirometer inhibited swimming activity. Oxygen consumption ( $\dot{V}O_2$ ) of each fish was measured over a period of 10–14 h at intervals of 10 min. Each measurement period started by flushing the respirometer for 3 min followed by a 2 min waiting period to allow for efficient mixing in the respirometer and the lag time of the water reaching the oxygen electrodes. During the next 5 min of the 10 min period, oxygen data were collected with a frequency of 1 Hz. After each period the oxygen consumption was automatically calculated from:  $\dot{V}O_2 = (a \cdot \text{vol} \cdot \beta) W^{-1}$  where  $a = (\Delta PO_2 / \Delta \text{min})^{-1}$ , vol = volume,  $\beta$  = oxygen solubility and  $W$  = body mass. The value was then stored and a new measuring period initiated.

In the first 2–4 h the  $\dot{V}O_2$  was elevated due to handling stress (Fig. 2). To exclude the high  $\dot{V}O_2$  values, all  $R_S$  values were obtained by curve fitting a normal distribution to the frequency distribution of the  $\dot{V}O_2$  values from the last 6 h of each experimental procedure, thus measuring  $R_S$  without the high values of the initial stress period.

In order to facilitate the comparison of results with previous experiments, all fish were corrected to a body mass of 100 g from:  $\dot{V}O_{2(100)} = \dot{V}O_{2(I)} (0.01 W)^{(1-A)}$  where  $\dot{V}O_{2(100)}$  = the corrected value of oxygen consumption for a 100 g fish,  $\dot{V}O_{2(I)}$  = oxygen consumption for a fish with body mass  $I$  and  $A$  = the scaling exponent. The value of  $A$ ,

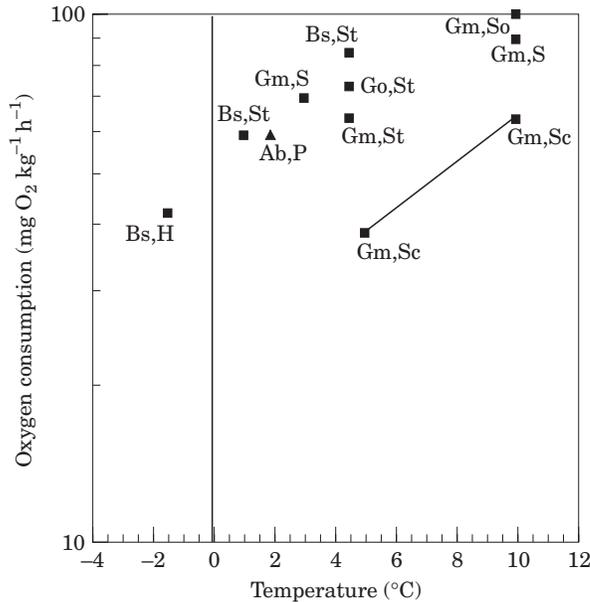


FIG. 3. Standard metabolic rate at different temperatures of four species of Gadidae. Bs,H=*Boreogadus saida* (Lepechin) (Holeton, 1974); Bs,St=*B. saida* (J. F. Steffensen, unpubl. data); Gm,S=*Gadus morhua* L. (Saunders, 1963); Bs,St=*B. saida* (Steffensen *et al.*, 1994); Go,St=*Gadus ogac* Richardson (Steffensen *et al.*, 1994); Gm,St=*G. morhua* (Steffensen *et al.*, 1994); Gm,Sc=*G. morhua* (H. Schurmann unpubl. data); Gm,So=*G. morhua* (Soofiani & Hawkins, 1982). The ▲ Ab,P is *A. borisovi* from the present study.

the relationship between metabolic rate and size, is controversial. On the basis of a review by Clarke & Johnston (1999), based on 138 earlier studies, a value of  $A=0.79$  was chosen for this study.

## RESULTS

The mean  $\pm$  S.D.  $R_S$  of East Siberian cod of mass  $601.5 \pm 147.6$  g was  $40.9 \pm 5.9$  mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>. When adjusted to a standard mass of 100 g  $R_S=59.0 \pm 6.6$  mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>.

These results were compared with other  $R_S$  values for three genera and four species of Gadidae derived from previous studies (Fig. 3). Temperature ranged from  $-1.8$  to  $+10.0^\circ$  C.

## DISCUSSION

Despite the fact that the theory of metabolic cold adaptation (MCA) arose out of erroneous measurements on oxygen consumption in ectotherms as criticized by Holeton (1973, 1974), Clarke (1980, 1983, 1991, 1993), and Hop & Graham (1995), and that most recent studies on the subject have shown no evidence of MCA (Wells, 1986, 1987; Bushnell *et al.*, 1994; Steffensen *et al.*, 1994; Clarke & Johnston, 1999), the theory has yet to be abandoned.

By comparing the present result with earlier calculations of  $R_S$  on other Gadidae species, the East Siberian cod showed no signs of being metabolic cold

adapted. The measured value of  $R_S$  for the East Siberian cod found in the present study lies within the range predicted from the oxygen consumption values of the other species of Gadidae (Fig. 3). The discrepancy of  $R_S$  values of Atlantic cod *Gadus morhua* L. (i.e. higher for cod collected and measured in Greenland compared to cod collected and measured in Denmark at the same temperature) was thought to be caused by genetic variance in the haemoglobin alleles-I (Karpov & Novikov, 1981). However, McFarland (1998) who studied  $R_S$  at various temperatures and acclimation times in different genotypes of Atlantic cod, found no significant differences. Hop & Graham (1995) measured the effect of long-term (5 months) v. short-term (2 weeks) acclimation on the oxygen consumption, and found that MCA was probably caused by insufficient acclimation time. Hence different acclimation time is a possible explanation for the differences in  $R_S$  among the Atlantic cod. Also it is likely that the low value of  $R_S$  found for the Atlantic cod caught in Denmark and measured at 5° C, is towards the limit of its temperature preference in Denmark, whereas this is a typical temperature for the Atlantic cod around Greenland.

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