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Exercise metabolism in two species of cod in arctic waters

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Abstract The northern range of Atlantic cod (*Gadus morhua*), overlaps the southern range of the Greenland cod (*Gadus ogac*), in the coastal waters of Western Greenland. The availability of a temperate water species (*G. morhua*) in the same area and oceanographic conditions as a polar species (*G. ogac*) presented us with the ideal circumstances to test the hypothesis of metabolic cold adaptation (MCA) since many of the problems associated with MCA studies (adaptation of the animals beyond their normal temperature range or mathematical extrapolation of data to common temperatures) could thus be avoided. We therefore used a swim tunnel to measure oxygen consumption in fish at 4°C over a range of swimming speeds and following exhaustion, monitored the size of the oxygen debt and time of oxygen debt repayment. There were no significant differences in standard (60–72 mg O_2 $kg^{-1} \cdot hr^{-1}$), routine (76 mg O_2 $kg^{-1} \cdot hr^{-1}$), active (137 mg O_2 $kg^{-1} \cdot hr^{-1}$), or maximal (157 mg O_2 $kg^{-1} \cdot hr^{-1}$) metabolic rate, metabolic scope (2.5) or critical swimming speed (2.2 $BL \cdot s^{-1}$) between the two species. Following exhaustive swimming, however, the half-time for oxygen debt repayment in *G. ogac* (43 min) was almost twice that of *G. morhua* (25 min). Despite its circumpolar distribution, therefore, there was no evidence of MCA in *G. ogac*.

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Introduction

Metabolic rate in poikilothermic animals such as fish is dependent on the temperature of the ambient water. Krogh (1914) proposed the concept of metabolic cold adaptation (MCA) to explain the observation that many species of fish living in polar oceans remained active at temperatures that rendered other animals sluggish or torpid (McDonald et al. 1987). The concept of MCA appeared to be supported by research conducted in 1950–60's which showed that standard or resting metabolic rates in Antarctic and Arctic fishes was as high as some tropical fishes (Scholander et al. 1953; Wolschlag 1962). Holeton (1974), was the first to challenge the concept of MCA when he failed to find any evidence of elevated resting metabolism in 10 of 11 polar species he examined. He suggested that the previous measurements of metabolism were artifactually high as a result of stress or hypoxia induced by the measurement process. Further research utilizing more sophisticated techniques has failed to resolve the controversy as recent studies and reviews have variously supported (Brett and Groves 1979; DeVries and Eastman 1981; Wells 1987; Forster et al. 1987; MacDonald et al. 1987, 1988) or rejected (Clarke 1983, 1991) the concept of MCA.

One of the problems involved in conducting MCA studies is the necessity of comparing metabolic rates of polar fish species with metabolism of fish from different latitudes. This complicates MCA assessment because measurements made on fish of dissimilar sizes or at different temperatures must be corrected mathematically by extrapolation. In addition, many of the species that have been compared are of different eco-type, sluggish bottom dwelling fish vs. more active pelagic fish, which further confounds the issue (readers are directed to MacDonald's et al.'s (1987) review for a more detailed consideration of these issues). Therefore, in order to clearly assess the MCA concept as it applies to

metabolism, it is necessary to measure oxygen consumption ($\dot{V}O_2$) in polar and non-polar fish under conditions where variables such as temperature, size, and activity are similar. The location of The Arctic Station at Qeqertassuaq/Godhavn afforded us the opportunity to make these measurements because the northern range of the temperate water Atlantic cod (*Gadus morhua*) overlaps the southern range of the Arctic and sub-arctic Greenland cod (*Gadus ogac*) off the western shore of Greenland (Leim and Scott 1966) where the laboratory is situated. While a previous study conducted in conjunction with this one (Steffensen et al. 1994) reported on standard metabolic rate in *G. morhua* and *G. ogac*, this report focuses on their active metabolism and swimming performance. Biochemical studies have suggested that in muscle of Antarctic fishes there is no MCA of the potential for anaerobic metabolism or aerobic metabolism of carbohydrates (Crockett and Sidell 1990). The enzyme activity in the aerobic and lipid catabolizing pathways, however, is higher than in temperate water counterparts. This suggests that at similar cold temperatures, anaerobic exercise performance in an MCA fish should be better than that of temperate water fish of similar ecotype. In addition, since there is no evidence for MCA in anaerobic pathways, one might also expect that polar fish would be less capable of using anaerobic metabolism to support swimming and would therefore incur a smaller oxygen debt during exhaustive exercise.

The purpose of this study was to test the concept of MCA by measuring metabolism and swimming performance in temperate and polar fish of similar size under identical conditions. Regression of the swimming speed-$\dot{V}O_2$ curve to its origin (0 $cm \cdot s^{-1}$) provides an estimate of standard metabolic rate (SMR) that can be compared with Steffensen et al.'s (1994) report of metabolism in resting fish under similar conditions. In addition, we wanted to evaluate the metabolic scope for activity and ability to repay an oxygen debt in polar and non-polar fish.

Materials and methods

The work took place in June (1990), at the University of Copenhagen's Arctic Station (Godhavn, Greenland). Specimens of *G. ogac* and *G. morhua* were caught at the same location and water temperature by jigging with hook and line. Following capture, they were maintained for the next three weeks in a holding pen in the harbor or in plastic tubs located at the research station. Water temperature during this period ranged from 3–8°C, and salinity was 32 ppt. In order to avoid problems associated with specific dynamic action (SDA), fish remained unfed for at least one week before being used in an experiment.

Measurement of swimming $\dot{V}O_2$ was performed in a Blazka type respirometer (8 cm dia. × 40 cm length) which was submerged in an aerated water bath at 4.0°C. Water PO_2 was monitored by pumping a subsample of water from the respirometer, past a Radiometer PO_2 electrode mounted in a flow-through cuvette thermostatted at 25°C to increase its response time. A stainless steel counter-current heat exchanger mounted between the pump and O_2 probe gradually altered the water temperature as it flowed towards or away from the O_2 electrode. Swimming speed, corrected for blocking effects (Bell and Terhune 1970), was calculated from a previously determined regression of motor controller power output on water velocity (TAD digital anemometer).

Experimental protocol

In order to avoid systematic errors, O_2 consumption measurements were made on individuals of either species, chosen at random. The fish's fork length and mass were recorded before placing it in the swimming tube and setting the water speed to 0.5 body lengths per second ($BL \cdot s^{-1}$). The oxygen electrode was calibrated with zero solution and air saturated water, the water bath covered (to reduce visual stimulation) and oxygen consumption ($\dot{V}O_2$) measurements were begun while the fish was acclimating to the chamber.

An A-D board (Data Translations DT2801) mounted in an Olivetti PC computer was used to monitor the swimming chamber's water temperature, PO_2, and motor controller power output (swim chamber velocity). The computer was programmed (Labtech Notebook) to automatically collect and analyze data over a ten minute measurement cycle. During the first four minutes of the cycle a computer-actuated water pump flushed the respirometer with aerated water from the surrounding water bath. The pump was then shut off, and after a one minute delay, the PO_2 of the chamber was recorded every ten seconds for the next five minutes. While the chamber was flushing in preparation for the next set of measurements, the program transferred the stored data set (time and PO_2) into a spreadsheet program (Lotus 1–2–3) and performed a linear regression of PO_2 on time. The resulting slope was used in the following formula to calculate $\dot{V}O_2$:

$$\dot{V}O_2 = \text{slope} \times VOL_{resp} \times M^{-1} \times \alpha$$

where $\dot{V}O_2$ (mg $O_2 \cdot kg^{-1} \cdot hr^{-1}$) = O_2 consumption, slope (mm $Hg \cdot hr^{-1}$) = $dPO_2 \cdot dtime^{-1}$, α (mg O_2 mm $Hg^{-1} \cdot l\,H_2O^{-1}$) = solubility of O_2 in water at a given temperature and salinity, VOL_{resp} (l) = volume of the respirometer minus the volume of the fish, and M (kg) = mass of the fish. The slope, regression coefficient, minimum and maximum PO_2, average temperature, calculated $\dot{V}O_2$, and average swimming velocity were printed, stored on disk, and the next 10 minute measurement cycle begun. In general, a regression coefficient (R^2) of less than 0.95 was indicative of some fault in the O_2 measuring system or an abrupt change in behavior during the measurement period. Faults in the measurement occurred infrequently and were usually a result of a reduction in water flow over the probe due to air bubble formation or debris in the inflow tube. These conditions were quickly corrected without disturbing the fish. $\dot{V}O_2$ calculations resulting from a regression with an $R^2 < 0.95$ were eliminated from the analysis.

All fish were acclimated to the swimming chamber for 8 to 12 h before $\dot{V}O_2$ measurements at higher swimming speeds were begun. Fish were judged to be acclimated when the $\dot{V}O_2$ at the acclimation swimming speed (0.5 $BL \cdot s^{-1}$) had remained constant (±5%) for at least 4 h. The O_2 probe calibration was then rechecked and the water velocity increased to the 0.75 $BL \cdot s^{-1}$. Oxygen consumption was monitored for two measurement periods (20 min), before water velocity was increased by 0.5 $BL \cdot s^{-1}$ and the next measurement cycle commenced by flushing the chamber, as described above. Water velocity was increased in 0.5 $BL \cdot s^{-1}$ increments until the fish was exhausted. We judged this to have occurred when, twice, the fish was unable to maintain its position in the forward end of the swimming section and allowed itself to be pushed against the screen in the rear of the chamber where it remained for more than 30s.

Following the second swimming failure, the water velocity was reduced to pre-exercise speed and O_2 consumption measurements continued until, $\dot{V}O_2$ returned to pre-exercise levels. In some cases, exhaustion occurred within 5 minutes of the onset of a swimming trial at the new velocity when the chamber was being flushed. Since we were unable to measure $\dot{V}O_2$ at this time, maximum swimming speed (U_{crit}) and $\dot{V}O_2$ was reported as the swimming speed and $\dot{V}O_2$ of the previous successfully completed trial. If, however, the fish failed to complete a trial once $\dot{V}O_2$ measurement had begun, the U_{crit} was prorated by the proportion of time spent swimming at the final speed using the equation described by Brett (1964):

$$U_{crit} = u_i + (t_i / t_{ii} \times u_{ii})$$

where u_i = highest velocity maintained for the entire swimming period ($cm \cdot s^{-1}$); u_{ii} = the velocity increment ($cm \cdot s^{-1}$); t_i = amount of time spent swimming at the "exhaustion" velocity (min), t_{ii} = the prescribed swimming period (min).

The water velocity to which the fish was acclimated was high enough to mix the water in the chamber but not so high that it required much swimming effort on the fish's part to maintain station in the tube. Since activity was not consistent or controlled during this period, $\dot{V}O_2$ measured for one hour immediately prior to the first step in the activity measurements is referred to as "routine metabolism". The term "active metabolism" is applied to the average $\dot{V}O_2$ measured during the highest swimming speed cycle. In most cases, $\dot{V}O_2$ continued to increase for the first 5 minutes following the reduction of water velocity after the fish became exhausted. This $\dot{V}O_2$ is referred to as "maximum metabolism". Standard metabolic rate was calculated by extrapolating the swimming speed-$\dot{V}O_2$ relationship back to 0 $BL \cdot s^{-1}$. Finally, metabolic scope was defined as the ratio of maximum metabolic rate to standard metabolic rate.

Data analysis

In order to arrive at a power-performance curve for the species, oxygen consumption at each speed was averaged for each individual, and the results for all conspecifics pooled. A linear regression of log $\dot{V}O_2$ on relative swimming speed ($BL \cdot s^{-1}$) was performed and the slopes and elevations of the resulting line compared with a modified Student's t-test (Zar 1974). The extrapolation of the resulting equation to 0 $BL \cdot s^{-1}$ was used as the estimate of SMR for the species. Interspecific comparisons of the mean values reported in Table 1 were made with a non-parametric Mann-Whitney U-test (Zar 1974). In all cases the fiducial level of significance was taken to be $P < 0.05$.

A curve stripping program (JANA; Lexington, Ky) was used to derive a best-fit multi-exponential equation to describe the rate at which oxygen consumption decreased during the post-exercise recovery period (Scarabello et al. 1992). In order to combine data for each fish, $\dot{V}O_2$ during recovery was normalized by dividing by the $\dot{V}O_2$ at U_{crit} (i.e. active $\dot{V}O_2$). Data for each ten minute period was averaged and used to calculate the oxygen-debt repayment curve for each species. Oxygen debt was judged to have been repaid when the curve intercepted the 95% confidence limits surrounding the average routine metabolism for the species.

Results

There were no significant differences among any of the measured metabolic rates (routine, active, or maximum), maximum swimming velocity, or metabolic scope between the two species (Tables 1 and 2, Fig. 1). In both *G. morhua* and *G. ogac*, $\dot{V}O_2$ increased from approximately 65 mg $O_2 \cdot kg^{-1} \cdot hr^{-1}$ (routine) to 137 mg $O_2 \cdot kg^{-1} \cdot hr^{-1}$ at which point the fish stopped swimming due to exhaustion. In 4 of the *G. morhua* and 2 of the *G. ogac*, metabolism continued to increase in the first five minutes of the post-exercise period resulting in a maximum $\dot{V}O_2$ which reached approximately 160 mg $O_2 \cdot kg^{-1} \cdot hr^{-1}$.

The linear regression of swimming speed in (SPD, $BL \cdot s^{-1}$) on log $\dot{V}O_2$ yielded the equation:

$$\log \dot{V}O_2 = 0.120\ SPD + 1.862\ (r = .84)$$

for *G. morhua* (Fig. 1a), and

$$\log \dot{V}O_2 = 0.153\ SPD + 1.782\ (r = .89)$$

for *G. ogac* (Fig. 1b). Neither the slopes nor the elevations of the two lines were significantly different.

During recovery from exercise (Fig. 2), $\dot{V}O_2$ in both fish remained elevated for 1–3 h before returning to pre-exercise (routine) values. The equation describing the decrease in $\dot{V}O_2$ during recovery from exercise was

$$Y = 0.41\, e^{-0.0286(t-10)} + 0.77\, e^{-0.0011(t-10)}\ (r = 0.94)$$

for *G. morhua* (Fig. 2a), and

$$Y = 0.60 e^{-0.0467(t-10)} + 0.62 e^{-0.004(t-10)}\ (r = 0.95)$$

Table 1 Mass, length, maximum swimming speed, $\dot{V}O_2$, and metabolic scope measured in the *Gadus morhua*

Fish	Mass (gm)	Length (cm)	U_{crit}		Oxygen Consumption				Scope (max/smr)
			($BL \cdot s^{-1}$)	($cm \cdot s^{-1}$)	SMR	Routine	Active	Max	
					($mg\ O_2 \cdot kg^{-1} \cdot hr^{-1}$)				
1	160	26.0	2.22	57.7	76.2	66.4	144.0	199.7	2.6
2	103	23.0	2.24	51.5	62.6	79.0	161.0	161.0	2.6
3	184	27.0	1.25	33.8	43.9	69.0	116.0	126.0	2.9
4	126	25.0	2.50	62.5	80.9	85.2	131.0	144.0	1.8
5	190	27.0	2.50	67.5	70.1	82.5	136.5	169.0	2.4
6	150	26.5	2.75	72.9	63.2	74.3	135.0	145.4	2.3
Mean	152	25.8	2.24	57.6	66.2	76.1	137.3	157.5	2.4
SEM	14	0.6	0.21	5.3	5.3	3.1	6.1	10.4	0.2

Table 2 Mass, length, maximum swimming speed, $\dot{V}O_2$, and metabolic scope measured in the *Gadus ogac*

Fish	Mass (gm)	Length (cm)	U_{crit}		Oxygen consumption				Scope (max/smr)
			($BL \cdot s^{-1}$)	($cm \cdot s^{-1}$)	SMR	Routine	Active	Max	
					($mg\ O_2 \cdot kg^{-1} \cdot hr^{-1}$)				
1	175	25.0	1.87	46.8	59.1	70.3	110.0	152.0	2.6
2	220	26.0	2.20	57.2	65.3	79.1	149.0	155.9	2.4
3	160	25.0	2.50	62.5	76.0	90.6	161.0	200.1	2.6
4	260	28.5	2.25	64.1	50.0	61.4	123.0	133.3	2.7
5	100	20.5	2.25	46.1	73.4	87.0	144.0	157.6	2.1
6	165	25.5	2.25	57.4	54.7	68.0	139.5	149.4	2.7
Mean	180	25.1	2.22	55.7	63.1	76.1	137.8	158.1	2.5
SEM	22	1.1	0.08	3.1	4.2	4.7	7.5	9.1	0.1

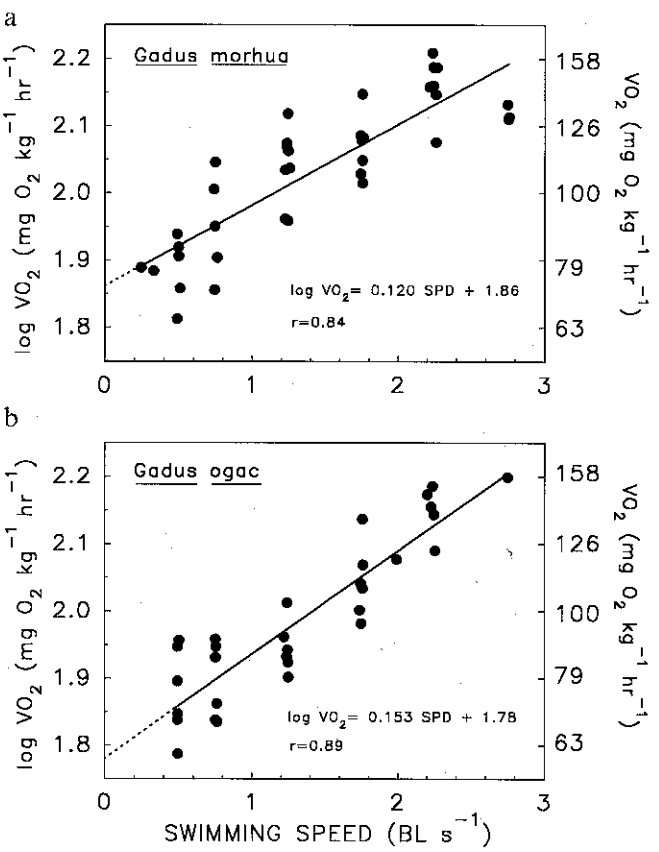

Fig. 1 Log rate of oxygen consumption of *G. morhua* (a) and *G. ogac* (b) plotted against swimming speed

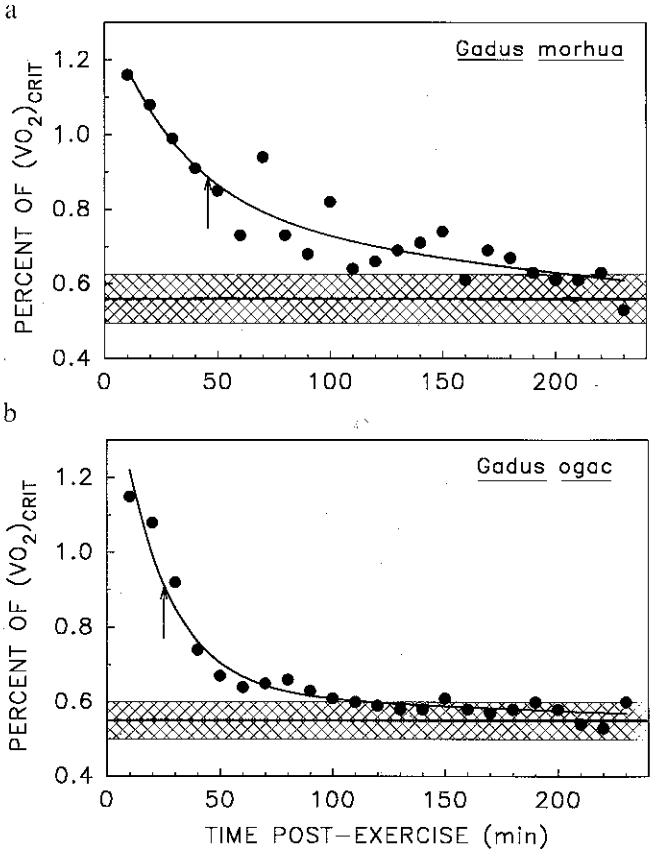

Fig. 2 Oxygen consumption as a fraction of maximum VO_2 during recovery from exhaustive swimming exercise. The routine metabolic rate is given by the heavy horizontal line and the 95% confidence limits represented by the cross-hatched area. The time required to repay 50% of the oxygen debt is indicated by the arrows

for *G. ogac*, where Y = percent of $(\dot{V}O_2)_{crit}$ and t = time (sec). Interestingly, the half-time for oxygen debt repayment in *G. morhua* (43 min) was almost twice that of *G. ogac* (25 min).

Discussion

Although the geographical distributions of *G. morhua* and *G. ogac* overlap, the life histories of the two species is quite different. Atlantic cod tend to live longer (20 yrs vs 11 yrs), grow larger (> 1.0 m vs 0.7 m), mature later (6–10 yrs vs 2–3 yrs), and have a much higher fecundity (Morin et al. 1991). *G. morhua* are found in a water temperature range from −0.5°C to 13°C and can live in waters as warm as 19°C (Leim and Scott 1966). In contrast, *G. ogac* actively feeds in ice-covered waters

(0°C) and has not been caught in waters warmer than 10°C.

In spite of the difference in geographical distribution and temperature preferences, the metabolic rates and swimming performance of both species of cod were strikingly similar. Although results of our companion study (Steffensen et al. 1994) reported that directly measured SMR in Greenland cod was higher than SMR in Atlantic cod, this finding was not supported by results of this study. Based on the swimming speed-$\dot{V}O_2$ regression equations, SMR in Atlantic cod (72.8 mg $O_2 \cdot kg^{-1} \cdot hr^{-1}$) was higher than in Greenland cod (60.5 mg $O_2 \cdot kg^{-1} \cdot hr^{-1}$) although the difference was not significant. It is important to note that although these two studies appear to contradict each other, the small difference (10%) reported by Steffensen et al. (1994) does not approach the 200% difference in SMR that has often been used as evidence for MCA in polar fishes (Holeton 1974; Brett and Groves 1979; Forster et al. 1987). It is quite likely that increases in spontaneous activity at low swimming speeds due to excitement and stress associated with the swimming trials, obscured small differences in SMR that were recorded in totally undisturbed fish.

When water velocity in the swim tube was increased, the rate of increase in $\dot{V}O_2$ (slope Fig. 1a) in *G. morhua* was identical to an earlier study by Soofiani and Priede (1985) conducted at 10°C and is quite low when compared with rates of increase reported in other fish (Beamish 1978). Interestingly, two previous studies on swimming performance in Atlantic cod at 10°C (Soofiani and Priede 1985, Butler et al. 1989) reported lower U_{crit}s than were obtained in this study at 5°C (2.24 $BL \cdot s^{-1}$). The maximum velocity recorded in cod by Soofiani and Priede (1985) was 1.95 $BL \cdot s^{-1}$ which was accompanied by an active $\dot{V}O_2$ of 183 mg $O_2 \cdot kg^{-1} \cdot hr^{-1}$, while Butler et al. (1989) found U_{crit} in *G. morhua* to be only 1.1 $BL \cdot s^{-1}$. These differences are probably a result of the longer swimming trial speed (30 or 60 minutes) which would tend to reduce U_{crit} and the higher acclimation temperature which would increases metabolic rate (Q_{10} effect).

It is often assumed that fish cease exercising during swimming trials as a result of exhaustion. In our study however, it was clear that their oxygen consumption during exercise was sub-maximal as the highest $\dot{V}O_2$ (maximum $\dot{V}O_2$-Table 1) was usually recorded during the first 10 minutes of recovery and ranged from 0% to 39% (mean 15%) higher than active $\dot{V}O_2$. This is similar to Soofiani and Priede (1985) who reported that maximum $\dot{V}O_2$ in *G. morhua*, chased (*not* swum in a tunnel) to exhaustion, was 40% higher than active $\dot{V}O_2$ recorded during swimming at U_{crit}. In their case, however, the peak in $\dot{V}O_2$ did not occur until 1–2 h after activity had ceased. Factors that contribute to the elevated metabolism following exhaustive exercise are the repletion of glycogen and creatine phosphate stores (Scarabello et al. 1992), correction of ion and fluid volume shifts that occurred during exercise (Wood 1991), and a "non-specific" stress reaction to forced exercise (Scarabello et al. 1991).

Regardless of the differences in $\dot{V}O_2$'s discussed above, the metabolic scope of Atlantic cod in the two studies are in good agreement and range from 2–3 which is quite low in comparison to rainbow trout (*Oncorhynchus mykiss*) which have metabolic scope of 7.5 at 4°C (Wieser 1985). Metabolic scope has also been reported to be relatively low (3–5) in the cryopelagic Antarctic fish, *Pagothenia borchgrevinki* (Forster et al. 1987).

Oxygen debt following cessation of exercise clearly reflects the fact that swimming activity was supported in some degree by anaerobic metabolism. The double exponential equations describing the curves in Fig. 2 indicate that oxygen debt repayment is a two-fold process consisting of a fast component and a slow component. Studies in rainbow trout (Scarabello et al. 1991) concluded that the fast component represents the "alactic" component (Margaria et al. 1933) involved in the resynthesis of ATP and phosphocreatine (PCr), while the second, slower component, results from a combination of lactate resynthesis to glycogen, and/or lactate oxidation (Scarabello et al. 1991).

Without measuring metabolites, it is difficult to specifically discuss details of anaerobic metabolism in this study. However, since previous work (Beamish 1968) indicates that *G. morhua* are not unusual in their ability to clear lactate following exhausting exercise, the rapidity of the oxygen debt repayment would suggest that both species were limited in their capability of using anaerobic metabolic pathways for maintaining swimming motion. This results from the low temperature at which the swimming trials were conducted. While it seems clear that *maximum* rates of glycolysis and PCr utilization are temperature independent (Brett 1964, Weiser et al. 1985, 1986), lactate accumulation and PCr hydrolysis are not, and are much more limited at 4°C than at 12 or 20°C (Weiser et al. 1986). In juvenile roach (*Rutilus rutilus*) for instance, lactate concentration increased only 15-fold at 4°C versus 33-fold at 20°C (Via et al. 1989).

The differences in the size of the O_2 debt (area under the curve) and the time needed to repay it (Fig. 2) suggests that *G. ogac* was more limited than *G. morhua*. This would tend to support Crockett and Sidell's (1990) assertion that anaerobic pathways are reduced in polar fish as has been reported in the Antarctic teleost, *Pagothenia borchgrevinki*. Exhaustive swimming in this species resulted in a moderate production of lactate (Davison et al. 1988) and a small oxygen debt that was repaid within an hour (Forster et al. 1987).

In conclusion, based on the results of this study, there is no evidence of MCA in aerobic metabolism in

Greenland cod. This is somewhat surprising given the circumpolar distribution of this species and its limited availability in waters warmer than 4°C (Nielsen 1992). However, it is clear from Table 1 and 2 and Fig. 1 and 2 that there is no difference between the two species with regard to standard, routine, active or maximum metabolism. Further, swimming performance and metabolic scope were virtually identical. The only differences noted were in the size of, and recovery from, O_2 debt. However, without measurements of metabolites it is difficult to make any firm conclusions as to the role of post-exercise oxygen consumption in supporting or contradicting the concept of MCA in *G. ogac*.

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