Exercise in the Cold: High Energy Turnover in Antarctic Fish

Peter L.M. van Dijk, Iris Hardewig, and Hans Otto Pörtner

Alfred Wegener Institute for Polar and Marine Research, Columbusstrasse, 27568 Bremerhaven, Germany

Introduction

Antarctic fishes inhabit one of the world's coldest marine habitats. At high latitudes the temperatures in the Southern Ocean are close to the freezing point of seawater at -1.86 °C and display little seasonal variation. The thermal conditions in the Antarctic have been relatively constant for several million years. The inhabiting fish fauna has therefore become highly specialized under the permanent cold conditions of this habitat which is reflected in a generally low upper lethal temperature of Antarctic fish at 5-6 °C [1]. In contrast to cold stenothermal polar fish, eurythermal boreal species must be able to survive a broader temperature range. While these species may be exposed to similarly cold water temperatures around 0 °C during winter, thermal conditions during summer require an elevated upper lethal temperature limit. On the other hand, eurythermal species are able to confine high cost metabolic activities like growth and reproduction to more favorable warmer seasons. Hence, acclimation to seasonal cold in eurythermal temperate species as opposed to adaptation to cold stenothermal conditions at high latitudes is associated with different requirements for the organism and may therefore result in distinct physiological features.

Recent histological and biochemical investigations suggest that, despite relatively low resting rates of metabolism, the capacity for aerobic energy production is enhanced in Antarctic species. Therefore, it may be more meaningful to investigate situations of high energy flux to determine whether metabolic cold adaptation does occur in Antarctic fish. The highest energy flux in fish is observed during burst swimming activity. Maximum speed is an important factor determining the success of prey capture and predator avoidance. Therefore, it is crucial for the survival of individuals and presumably subject to high selective pressures. In the following review we will summarize the available data on the ability of cold adapted fish to perform strenuous exercise and to recover from this

situation of high energy turnover. Special attention will be directed towards potential differences between seasonal cold *acclimation* of eurythermal temperate species as opposed to *adaptation* to the cold environment on the evolutionary time scale in Antarctic fish.

Effect of Temperature on the Ability to Perform Exercise

The actual activity pattern and the mode of locomotion observed in fishes depend upon the species' lifestyle. Two main types of swimming can be distinguished. The marathon-type of performance is powered mainly by red musculature and can be sustained for hours or even days. The maximal *sustainable* speed, which is the maximum speed that can be maintained for more than 200 min [2], is largely determined by the aerobic capacity of the red musculature of the fish. Maximal *swimming* speed is reached only for a short period of time during burst swimming when white musculature becomes active. The white muscle relies mostly on glycolytic energy production and therefore this fiber type is rapidly fatigued.

Acute cold exposure reduces the ability to exercise, but the negative effect of low temperature on aerobic and anaerobic swimming performance is compensated to various degrees during cold acclimation. While in goldfish acclimation to 5 °C leads to almost complete compensation of the maximal (anaerobic) swimming velocity compared to animals acclimated to 35 °C, killifish show only moderate compensation and no acclimatory effects were observed in trout [3,4].

Compensatory effects on the aerobic swimming capacity (maximal sustainable speed) have been observed in several species such as goldfish, carp and striped bass [5-7]. However, cold acclimation does not lead to complete compensation since warm acclimated fish are able to maintain higher swimming speeds than cold acclimated animals at their respective acclimation temperature (Table 1). Evolutionary adaptation to the polar environment, however, may have led to a higher degree of compensation as evidenced by a comparison of the maximal sustainable speeds from Antarctic and temperate fish. Maximum sustainable speeds of active pelagic *Pagothenia borchgrevinki* range between 1.8 and 2.15 bl sec^{-1} [8,9], while benthic *Notothenia coriiceps* can only maintain 0.8-1.0 bl sec^{-1} [10,11]. Table 1 shows that these values are well in the range of the maximum sustainable speeds of temperate fish species.

Burst swimming performance appears to be more constrained in polar fish, especially in larvae and juvenile animals as opposed to adult stages. No thermal compensation is observed in the startle response of cold adapted Antarctic fish larvae [12].

Table 1. Maximum sustainable swimming speeds in Antarctic and temperate fish. Fish swam at their respective acclimation temperature given in the Table

Species	V_{max} (bl sec^{-1})	Acclimation Temperature (°C)	Lifestyle	Source
Pagothenia borchgrevinki	1.8- 2.15	0	moderately active, pelagic	8,9
Notothenia coriiceps	0.8- 1.0	2	benthic	10,11
Gadus morhua	2.1 2.6	5 8	moderately active, pelagic	14
Morone saxatilis	1.9 2.8	9 25	migrator, pelagic	7
Oncorhynchus nerka	2.8 3.1	10 18	migrator, pelagic	15
Coregonus clupeaformis	1.4 1.7	5 12	moderately active, pelagic	16

Their maximum speed at 0 °C is 2 - 3 times lower than that of temperate and tropical larvae at their habitat temperatures as would be predicted from a Q_{10} of 2. Juvenile *N. coriiceps* show maximum swimming speeds lower than those of juveniles from a variety of temperate fish at higher temperatures [11]. Maximal velocities of adult *N. coriiceps* and *P. borchgrevinki*, however, are in the lower range of values for temperate fish [11,13]. It should be noted that maximum swimming speeds are influenced by several factors such as body shape, swimming mode and life style of a particular fish species. Therefore, comparisons between Antarctic and temperate fish species may be biased.

From the limited amount of data, one may conclude that cold compensation does occur for aerobic and to a lesser degree for anaerobic swimming performance in Antarctic fish. High speeds, however, are obviously not achievable at subzero temperatures, reflected in the generally slow movements and only moderately active life styles of Antarctic fish.

Energy Provision During Exercise

Aerobic Capacity

Sustained swimming is powered by slow aerobic muscle fibers that rely almost exclusively on aerobic energy provision. An increase of the maximum sustainable speed during cold adapation should therefore go along with an increase of the aerobic capacity. How do fish enhance their aerobic capacity in the cold? Several studies on temperate fish have shown a significant increase of the mitochondrial volume density in muscle cells during cold acclimation [17,18]. A similar trend is observed in Antarctic fish. Mitochondrial densities in slow fibers of several notothenioids are higher than those in temperate species at warm acclimation temperatures [19,20]. Besides a compensatory increase in oxidative capacity a second functional implication has been ascribed to changes in mitochondrial density. Increased number of mitochondria and concomitant reduction of the diffusion pathlength between capillaries or cytosolic compartments and these organelles may compensate for the reduced diffusion coefficients of metabolites and oxygen at low temperatures [17,21]. A recent study on diffusion limitations in fish muscle has shown, however, that diffusional fluxes of neither ATP nor phosphocreatine limit muscular function at low temperatures even in the absence of increased mitochondrial densities [22].

Only few studies have investigated the impact of cold acclimation or adaptation on the functional properties of mitochondria. There is some evidence that both cold acclimation and adaptation lead to an increase in mitochondrial aerobic capacity [23]. In the short-horned sculpin *Myxocephalus scorpius* a decrease of the acclimation temperature from 15 °C to 5 °C doubled maximal rates of pyruvate oxidation per milligram of mitochondrial protein [24]. A comparison of oxidative capacities of Antarctic, temperate and tropical fish showed only moderate cold compensation [25]. While respiration rates of mitochondria from tropical tilapia extrapolate to zero at around 2 °C, mitochondria of the Antarctic *N. coriiceps* still oxidize substrates at considerable rates at -1.5 °C. However, the aerobic capacity of tropical and temperate fish was considerably higher than that of Antarctic fish when compared at their habitat temperatures.

The mechanisms that underlie the increase of oxidative capacity of mitochondria are still the subject of investigation. Cristae density does not change during thermal acclimation of fish [17,21] and is probably not enhanced in Antarctic fish species [26].

A compensatory increase of mitochondrial enzyme activities after cold acclimation has been reported for many temperate fish like goldfish, carp and green sunfish [27-29] but may be absent in salmonid species like trout and lake whitefish [30,31]. Higher activities of oxidative enzymes per gram of tissue may be caused by an increased number of mitochondria, a higher amount of enzyme per mitochondrion or modulation of the specific activity of the individual enzyme molecule. Several studies of Wodtke [28,32] provide evidence that the activity of membrane bound mitochondrial enzymes - like cytochrome c oxidase (COX) and succinate dehydrogenase (SDH) - is enhanced by changes of the fluidity and lipid composition of the membranes during cold acclimation. While the increases of COX activity in seasonally cold acclimated fish range between 30 and 100% [27-29], *Gobionothoten gibberifrons* displays 5 times higher COX activities in the white muscle than a temperate zone fish with similar lifestyle [33]. Oxidative enzymes, located in the mitochondrial matrix as opposed to membrane bound enzymes, generally show only a moderate increase in cold acclimated or adapted animals. While COX and SDH are significantly enhanced in cold acclimated green sunfish, malate dehydrogenase remains unchanged [29]. Crockett and Sidell [33] found only 1.4 - 2.8 times increased citrate synthase activities in *Trematomus newnesi* and *G. gibberifrons* when compared to temperate species. Thus, a rise in mitochondrial density during cold acclimation or adaptation leads to increased activities of oxidative enzymes. The activity of membrane bound enzymes, such as COX and SDH, may be further increased by an activating effect of homeoviscous response of mitochondrial membranes.

Shifts in the saturation and fluidity of mitochondrial membranes during thermal acclimation have been documented for several species, such as goldfish and carp [32,34]. No data are available, however, on the membrane composition of mitochondria from Antarctic fish. Cytoplasmic membranes of Antarctic fish contain high percentages of polyunsaturated fatty acids and show up to 100% homeoviscous response [35]. Cold adapted organisms commonly show higher efficiencies of homeoviscous adaptation than eurythermal animals after cold acclimation [35]. Therefore, it can be assumed that mitochondrial membranes of Antarctic fish show at least the same degree of homeoviscous response as mitochondria from cold acclimated animals. At a given temperature a higher fraction of unsaturated fatty acids increases the permeability of membranes to ions especially to protons [36]. High rates of proton leakage through the inner mitochondrial membrane increase the oxygen consumption of mitochondria without a concomitant rise in ATP

synthesis. Therefore, lower ADP/O values may be expected in cold adapted animals when acutely exposed to warmer temperatures. We suggest that an increase of aerobic capacity in Antarctic fish tissues brought about by an increase of the number of mitochondria in combination with homeoviscous adaptation of mitochondrial membranes may set the upper temperature limit at which oxidative phosphorylation can work efficiently [37]. The low tolerance of Antarctic animals towards temperature elevation may be due to increased proton leakiness of the inner mitochondrial membranes at higher temperatures.

Anaerobic Capacity

During burst swimming total ATP turnover may increase over 100-fold compared to resting rates [12]. Oxidative metabolism alone is not able to meet these high rates of energy utilization. In fast twitch white muscles anaerobic glycolysis is the major source of energy during burst swimming in fish. High glycolytic rates lead to an accumulation of lactate and protons in the muscle tissue.

Rainbow trout acclimated to 5 °C or 18 °C accumulated the same amounts of lactate in the white muscle during exhaustive swimming [38]. These results are in contrast to data on roach [39,40] in which a change of acclimation from 20 °C to 4 °C leads to 50% reduction of lactate formation during exhaustive exercise. Data on changes of glycolytic enzyme activities are also contradictory. While trout and lake whitefish (*Coregonus clupeaformis*) show a compensatory increase of hexokinase and phosphofructokinase activities during cold acclimation [30,31], these enzymes are even less active in cold acclimated goldfish and striped bass [27,41]. Guderley [23] suggested that glycolytic enzymes may increase in species which do not change mitochondrial enzyme activity during cold acclimation (as in salmonids), while they may tend to decrease in species which exhibit a compensatory rise in oxidative enzyme activity.

A number of studies on capture and exercise stress in Antarctic notothenioids suggest that the anaerobic capacity of these animals is greatly reduced [42]. Exhaustive exercise induced only a minor increase of lactate in the white muscle of about 1-3 μmol g^{-1} in *N. coriiceps* and *P. borchgrevinki* [9,43]. Dunn and Johnston [43] examined maximal activities of glycolytic enzymes in *N. coriiceps* and concluded that the absence of lactate production is caused by a reduced glycolytic capacity in these fish. Enzyme profiles for several notothenioids show the same trend: generally, oxidative enzymes and creatine kinase show high degrees of cold compensation, while glycolytic enzymes do not [19,33]. The reduced

glycolytic capacity has been interpreted as a special adaptation to cold environment [43]. However, since absence of lactate formation has only been shown in notothenioids the question arises if indeed the low glycolytic capacity has an adaptional value or if it is rather a special phylogenetic trait of this fish family [9,44]. To shed light on this question we investigated the effect of exhaustive exercise on an Antarctic nonnotothenioid fish, the zoarcid *Pachycara brachycephalum* [45]. In this benthic sluggish fish we found relatively high amounts of lactate (11.5 ± 0.7 μmol g^{-1} muscle tissue), which is in the range found in flounder acclimated to 11 °C [46]. Based on these data, it may be concluded that a low glycolytic capacity is not a general phenomenon in Antarctic fish.

Interestingly, we did not find significant amounts of lactate in the plasma of *P. brachycephalum* after exhaustive exercise. In contrast to mammals, the bulk of lactate is retained in the white musculature of fish for glyconeogenesis in situ [47]. Nevertheless, significant increases in lactate concentrations are found in the plasma after severe exercise in temperate species. However, the muscle-to-blood gradient of lactate is dependent on the acclimation temperature [38]. Cold acclimated trout had lower blood lactate levels although intracellular concentrations were the same in both groups. The authors explain this phenomenon by a reduction of lactate diffusion from the intracellular space at low temperatures. It should be noted, therefore, that in cold adapted fish the onset of anaerobic metabolism must be established by the analysis of lactate levels in the muscle tissue rather than in the plasma, as is frequently done in temperate species.

Recovery from Exhaustive Exercise

During recovery from exhaustive exercise the restoration of pre-exercise conditions must be achieved within reasonable time to enable successive bouts of activity which may be crucial during predator-prey interactions. Despite only partial cold compensation of locomotory performance in fish, recovery processes seem to be largely independent of temperature [38,48]. Metabolic recovery from escape swimming occurred at identical rates in herring larvae reared at 5 and 12 °C [48]. In trout rephosphorylation of phosphocreatine and lactate clearance from blood and muscle occurred at the same rates in fish acclimated to 5 and 18 °C [38]. This shows that although resting levels of oxygen consumption are reduced in cold acclimated trout [49] the capacities for high power output during exercise and for postexercise recovery metabolism are largely compensated in cold acclimated animals. Again, the roach *Rutilus rutilus*

shows a different response to cold acclimation. While most other eurythermic species show perfect compensation of recovery processes, roach not only produce less lactate during burst activity at 4 °C, but also need about 4 times longer to regain pre-exercise lactate levels than their counterparts acclimated to 20 °C. Obviously, no compensatory mechanisms are functioning in this species despite an enhanced aerobic capacity [40].

In Antarctic fish the time required for recovery of blood composition and rates of oxygen consumption after exercise and capture stress is similar to temperate species. For most parameters this is essentially achieved within 8-24 h [8,9,42].

The rate of lactate clearance [45] in the eelpout *P. brachycephalum* (3.3 μmol g^{-1} h^{-1}) was even faster than that observed in flounder acclimated to 11 °C (0.62 μmol g^{-1} h^{-1}) and comparable to that observed in juvenile trout at 15 °C [46,50]. Also phosphocreatine is rephosphorylated within 3 hours [45], which is in the range of recovery times observed in trout [47].
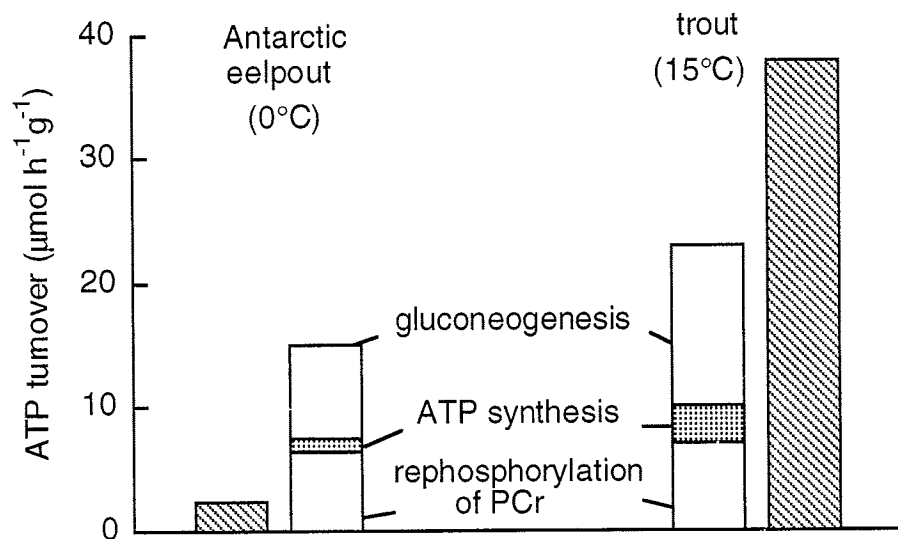

Fig. 1. The excess postexercise ATP production (on top of resting rates) during the first hour of recovery [45] from exhaustive [50] swimming in Antarctic eelpout *P. brachycephalum* at 0 °C and trout at 15 °C based on metabolite data (stacked bars) compared to resting levels of ATP turnover calculated from oxygen consumption rates (hatched bars)

A fast recovery from exhaustive swimming requires largely increased postexercise metabolic rates to pay off the oxygen debt. Based on metabolite data we calculated the ATP turnover necessary for gluconeogenesis, rephosphorylation of PCr and ATP synthesis during the first hour of recovery and compared the results with data on trout (Fig. 1). This comparison reveals that the ATP requirement during the first hour of recovery is about the same in trout at 15 °C and Antarctic eelpout at 0 °C! On the basis of the low resting metabolic rate in the latter (0.38 μmol O_2 g^{-1} h^{-1} compared to 6.3 μmol O_2 g^{-1} h^{-1} in trout; I. Hardewig, P. van Dijk and H.O. Pörtner, unpublished results; [50]) the factorial increase of ATP production required for recovery is much higher in eelpout. These data strongly suggest that Antarctic fish show metabolic cold adaptation. This adaption is not reflected in elevated resting metabolic rates, but becomes evident during situations of high energy turnover.

Conclusions

Antarctic fish have obviously developed mechanisms to compensate for the adverse effects of low temperatures on locomotory performance. Aerobic metabolic capacity and, accordingly, aerobic swimming velocities exhibit clear cold adaptation in Antarctic species. However, the increase of aerobic capacity may cause a high sensitivity towards temperature increases. This may be tolerated in cold stenothermal Antarctic species that do not experience large temperature variations in their habitat. Eurythermal organisms, however, must be able to maintain vital functions over a broad temperature range. A trade off between an increase in metabolic capacity and tolerance towards shifts in habitat temperature may have led to different degrees of cold compensation in stenothermal versus eurythermal species: While both groups generally appear to employ the same qualitative mechanisms to survive in the cold, the degree of cold compensation with respect to maximum rates of energy turnover during exercise and recovery seems to be more pronounced in stenothermal Antarctic fishes.

References

1. Somero GN, DeVries AL (1967) Temperature tolerance in some Antarctic fishes. Science 156:257-258
2. Beamish FWH (1978) Swimming capacity. In: Hoar WS, Randall DJ (eds) Fish physiology. Academic Press, New York, pp 101-187

3. Johnson TP, Bennet AF (1995) The thermal acclimation of burst escape performance in fish: an integrated study of molecular and cellular physiology and organismal performance. J Exp Biol 198:2165-2175

4. Johnson TP, Bennet AF, McLister JD (1996) Thermal dependence and acclimation of fast start locomotion and its physiological basis in rainbow trout (Oncorhynchus mykiss). Physiol Zool 69(2):276-292

5. Fry FEJ, Hart JS (1948) Cruising speed of goldfish in relation to water temperature. J Fish Res Bd Can 7:175-199

6. Rome LC, Loughna PW, Goldspink G (1984) Muscle fiber activity in carp as a function of swim speed and muscle temperature. Am J Physiol 247:R272-R279

7. Sisson JE, Sidell B (1987) Effect of thermal acclimation on muscle fiber recruitment of swimming striped bass (Morone saxatilis). Physiol Zool 60:310-320

8. Forster ME, Franklin CE, Taylor HH, Davison W (1987) The aerobic scope of an Antarctic fish Pagothenia borchgrevinki and its significance for metabolic cold adaptation. Polar Biol 8:155-159

9. Davison W, Forster ME, Franklin CE, Taylor HH (1988) Recovery from exhausting exercise in an Antarctic fish, Pagothenia borchgrevinki. Polar Biol 8:167-171

10. Johnston IA, Clarke A, Ward P (1991) Temperature and metabolic rate in sedentary fish from the Antarctic, North Sea and Indo-West Pacific Ocean. Mar Biol 109:191-195

11. Archer SD, Johnston IA (1989) Kinematics of labriform and subcrangiform swimming in the Antarctic fish Notothenia neglecta. J Exp Biol 143:195-210

12. Johnston IA, Johnson TP, Battram JC (1991) Low temperature limits burst swimming performance in Antarctic fish. In: di Prisco G, Maresca B, Tota B (eds) Biology of Antarctic fish. Springer Verlag, Berlin, pp 179-190

13. Montgomery JC, MacDonald JA (1984) Performance of motor systems in Antarctic fishes. J Comp Physiol 135:157-164

14. Beamish FWH (1966) Swimming endurance of some Northwest Atlantic fishes. J Fish Res Bd Can 23:341-347

15. Brett JR (1964) The respiratory metabolism and swimming performance of young sockeye salmon. J Fish Res Bd Canada 21:1183-1226

16. Bernatchez L, Dodson JJ (1985) Influence of temperature and current speed on the swimming capacity of lake whitefish (Coregonus clupeaformis) and cisco (C. artedii). Can J Fish Aquat Sci 42:1522-1529

17. Egginton S, Sidell BD (1989) Thermal acclimation of subcellular structures of fish muscle. Am J Physiol 256:R1-R10

18. Johnston IA (1993) Phenotypic plasticity of fish muscle to temperature change. In: Rankin JC, Jensen FB (eds) Fish ecophysiology. Chapman Hall, London, pp 322-340

19. Johnston IA (1987) Respiratory characteristics of muscle fibres in a fish (Chaenocephalus aceratus) that lacks haem pigment. J Exp Biol 133:415-428

20. Dunn JF, Archer SD, Johnston IA (1989) Muscle fiber types and metabolism in post-larval and adult stages of notothenioid fish. Polar Biol 9:213-223
21. Tyler S, Sidell BD (1984) Changes in mitochondrial distribution and diffusion distances in muscle of goldfish upon acclimation to warm and cold temperatures. J Exp Zool 232:1-9
22. Hubley MJ, Locke BR, Moerland TS (1997) Reaction-diffusion analysis of the effects of temperature on high-energy phosphate dynamics in goldfish skeletal muscle. J Exp Biol 100:975-988
23. Guderley H (1997) Temperature and growth rates as modulators of the metabolic capacities of fish muscle. In: Pörtner HO, Playle R (eds) SEB Series 66, Cold ocean physiology. Cambridge University Press
24. Guderley H, Johnston IA (1996) Plasticity of fish muscle mitochondria with thermal acclimation. J Exp Biol 199:1311-1317
25. Johnston I, Guderley H, Franklin CE, Crockford T, Kamunde C (1994) Are mitochondria subject to evolutionary temperature adaptation? J Exp Biol 195:293-306
26. Archer SD, Johnston IA (1991) Density of cristae and distribution of mitochondria in the slow muscle fibers of Antarctic fish. Physiol Zool 64:242-258
27. Sidell BD (1980) Responses of goldfish (Carassius auratus, L.) muscle to acclimation temperature: alterations in biochemistry and proportions of different fiber types. Physiol Zool 53:98-107
28. Wodtke E (1981) Compensation of the molar activity of cytochrome c oxidase in the mitochondrial energy-transducing membrane during thermal acclimation of the carp (Cyprinus carpio L.). Biochim Biophys Acta 640:710-720
29. Shaklee JB, Christiansen JA, Sidell BD, Prosser CL, Whitt GS (1977) Molecular aspects of temperature acclimation in fish: contributions of changes in enzyme activities and isozyme patterns to metabolic reorganization in green sunfish. J Exp Zool 201:1-20
30. Blier P, Guderley H (1988) Metabolic responses to cold acclimation in the swimming musculature of lake whitefish, Coregonus clupeaformis. J Exp Zool 246:244-252
31. Guderley H, Gawlicka A (1992) Qualitative modification of muscle metabolic organization with thermal acclimation of rainbow trout, Onchorynchus mykiss. Fish Physiol Biochem 10:123-132
32. Wodtke E (1981) The effects of acclimation temperature on the unsaturation of the main neutral and charged phospholipids in mitochondrial membranes of the carp (Cyprinus carpio L.). Biochim Biophys Acta 640:698-709
33. Crockett EL, Sidell BD (1990) Some pathways of energy metabolism are cold adapted in Antarctic fishes. Physiol Zool 63:472-488
34. Van den Thillart G, de Bruin G (1981) Influence of environmental temperature on mitochondrial membranes. Biochim Biophys Acta 640:439
35. Cossins AR (1994) Homeoviscous adaptation of biological membranes and its functional significance. In: Cossins AR (ed) Temperature adaptation of biological membranes. Portland Press, London, pp 63-76

36. Brand MD, Steverding D, Kadenbach B, Stevenson PM, Hafner RP (1992) The mechanism of the increase in mitochondrial proton permeability induced by thyroid hormones. J Biochem 206:775-781

37. Pörtner HO, Hardewig I, Sartoris FJ, van Dijk PLM (1997) Energetic aspects of cold adaptation: critical temperatures in metabolic, ionic and acid-base regulation. In: Pörtner HO, Playle R (eds) SEB Series 66, Cold ocean physiology. Cambridge University Press

38. Kieffer JD, Currie S, Tufts BL (1994) Effects of environmental temperature on the metabolic and acid-base responses of rainbow trout to exhaustive exercise. J Exp Biol 194:299-317

39. Wieser W, Koch F, Drexel E, Platzer U (1986) "Stress" reactions in teleosts: effects of temperature and activity on anaerobic energy production in roach (Rutilus rutilus L.). Comp Biochem Physiol 83A:41-45

40. Dalla Via J, Huber M, Wieser W, Lackner R (1989) Temperature related responses of intermediary metabolism to forced exercise and recovery in juvenile Rutilus rutilus (L.) (Cyprinidae: Teleostei). Physiol Zool 62:964-976

41. Sidell BD, Moerland TS (1989) Effects of temperature on muscular function and locomotory function in teleost fish. Adv Comp Env Physiol 5:115-156

42. Egginton S, Davison W (1997) Effects of environmental and experimental stress on Antarctic fishes. In: Pörtner HO, Playle R (eds) Cold ocean physiology. Cambridge University Press (in press)

43. Dunn JF, Johnston IA (1986) Metabolic constraints on burst-swimming in the Antarctic teleost Notothenia neglecta. Mar Biol 91:433-440

44. Egginton S (1997) A comparison of the response to induced exercise in red- and white-blooded Antarctic fishes. J Comp Physiol 167:129-134

45. Hardewig I, van Dijk PLM, Pörtner HO (1997) High energy turnover at low temperatures: recovery from exhaustive exercise in Antarctic and common eelpout (Zoarcidae). Am J Physiol, submitted

46. Milligan CL, Wood CM (1987) Muscle and liver intracellular acid-base and metabolite status after strenuous activity in the inactive, benthic starry flounder (Platichthys staelatus). Physiol Zool 60:54-68

47. Milligan CL (1996) Metabolic recovery from exhaustive exercise in rainbow trout. Comp Biochem Physiol 113A:51-60

48. Franklin CE, Johnston IA, Batty RS, Yin MC (1996) Metabolic recovery in herring larvae following strenuous activity. J Fish Biol 48:207-216

49. Beamish FWH (1964) Respiration of fishes with special emphasis on standard oxygen consumption. II. Influence of weight and temperature on respiration of several species. Can J Zool 42:177-188

50. Scarabello M, Heigenhauser GJF, Wood CM (1992) Gas-exchange, metabolite status and excess post-exercise oxygen consumption after repetitive bouts of exhaustive exercise in juvenile rainbow trout. J Exp Biol 167:155-169