Antarctic Science 1 (2): 97–108 (1989)

Review

Antarctic fish muscles — structure, function and physiology

IAN A. JOHNSTON

Gatty Marine Laboratory, Department of Biology & Preclinical Medicine, University of St. Andrews, St. Andrews, Fife KY16 8LB, Scotland

Abstract: The structure and function of swimming muscles in Antarctic fish is reviewed, the emphasis being on the highly endemic sub-order Notothenioidei. Adult stages of the vast majority of species swim at low speeds using large pectoral fins (labriform locomotion). This is supplemented with sub-carangiform swimming in pelagic juvenile stages and in the adult stages of some other species. The thrust for sustained activity is provided by the recruitment of slow muscle fibres. Slow muscle myofibrils typically occur in columns one fibril thick entirely surrounded by mitochondria. The resulting high volume density of mitochondria (30–60%), and short inter-mitochondrial spacing, is thought to represent an adaptation which serves to compensate for the detrimental effects of low temperature on enzyme reaction and diffusion rates. Sub-carangiform swimming is used to achieve burst speeds associated with prey capture and/or predator avoidance. Burst speeds require the recruitment of fast twitch fibres in the myotomes. In many demersal species the energy supply for burst swimming largely comes from phosphogen hydrolysis, and the capacity of fast twitch fibres for anaerobic glycogenolysis is severely reduced. Antarctic fish are characterized by delayed maturation, slow growth and low metabolic rates. The fast myotomal muscles of adult stages often contain few fibres less than 80 μm diameter, fibres 200–450 μm diameter forming the major size class in numerous species. It is therefore likely that hyperplasia ceases at a relatively early stage in development and that subsequent muscle growth involves hypertrophy of existing fibres. Studies of the contractile properties of isolated muscle fibres suggest that low temperature limits maximum swimming performance in Antarctic fish. Kinematic data suggest that this is most noticeable for juvenile stages, which have higher maximum tail-beat frequencies than adults.

Accepted 15 February 1989

Key words: metabolism, Notothenioidei, temperature adaptation.

Introduction

The dominant features of the Southern Ocean are temperatures close to the freezing point of sea-water (–1.86°C) and extreme seasonal variations in primary productivity. At high latitudes the sea is in permanent contact with ice and has an annual temperature variation of less than 0.2°C (Littlepage 1965), rising to only 2.5°C in the northern Antarctic (Everson 1970). The fish fauna is generally less diverse than that of the Arctic, with gadiformes, clupeiformes and salmoniformes either absent or poorly represented. Around 203 species, 86 genera and 28 families have been recorded from the Antarctic region (Andriashev 1987). The most numerous in terms of species and biomass belong to the sub-order Notothenioidei (order Perciformes). They are highly endemic, with 97% of species occuring south of the Antarctic Convergence (DeWitt 1971). Notothenioids are thought to have evolved from a bottom-living ancesteral stock which became isolated from temperate waters around 30–40 million years ago following the establishment of circum-Antarctic currents (Kennett 1977). Extant species lack a swim bladder and the vast majority are demersal and relatively sedentary as adults (Andriashev 1965). However, some species have become secondarily adapted to pelagic life, enabling them to exploit the abundance of mid-water prey (Andriashev 1965, DeVries & Eastman 1978, Eastman 1985).

The special nature of the environment, and a long period of isolated development, has resulted in the evolution of some unusual forms. The icefishes (family Channichthyidae) are unique among adult vertebrates in that they lack the respiratory pigment haemoglobin (Ruud 1954), and their muscles contain only minute traces of myoglobin (Hamoir & Gerardin-Otthiers 1980, Walesby *et al.* 1982). A common feature of polar fishes is their relatively slow growth rate, delayed sexual maturation, low fecundity, and the production of large yolky eggs (Marshall 1953). Among notothenioids, oogenesis usually takes two or more years, and there is a lengthened period of embryogenesis which results in the hatching of large advanced larvae with short larval, and pro-

https://doi.org/10.1017/S0954102089000167 Published online by Cambridge University Press

tracted pelagic juvenile stages (Everson 1970, Andriashev 1987). The basal metabolic rates of notothenioids are generally lower than for temperate fish (Holeton 1970, Clarke 1983). This is associated with a decrease in protein turn-over rates, which in turn is thought to reflect a complex interplay of abiotic (low temperature) and biotic factors (prey availability, reproductive strategy etc.) (Clarke 1987).

Diversity of activity patterns

Notothenioids exhibit a range of activity patterns and styles of swimming. However, continuously swimming filter-feeding fish are absent from the Antarctic. It may be that life styles with such high energetic cost are precluded by the low temperatures and extreme seasonality of production in the Southern Ocean.

Most demersal notothenioids are negatively buoyant and their weight in water is around 3–4% of their weight in air (Eastman & DeVries 1982). Typically, they have relatively large heads and reduced axial musculature, spending long periods on the bottom supported on the tips of stout pelvic and anal fins (Norman 1938). Most species in adulthood utilize a drag-based labriform mode of swimming at low speeds, which involves a sculling action of large fan-shaped pectoral fins. The pectoral fin muscles are well developed, constituting around 2–3% of body weight (Johnston & Harrison 1985).

Some species show a range of adaptations to increase buoyancy (Eastman & DeVries 1982). A few species, including *Pleuragramma antarcticum* (Boulenger), *Aethotaxis mitopteryx* (DeWitt) and *Dissostichus mawsoni* (Norman), have attained neutral or near neutral buoyancy, enabling them to become permanent members of the mid-water community (DeVries & Eastman 1978, Eastman & DeVries 1981, Eastman 1985). For example, *P. antarcticum* ('silverfish') have near neutral buoyancy and, in the absence of a swim bladder, static lift is provided by flotation sacs containing triacylglycerol (DeVries & Eastman 1978). Neural and haemal arches, spines and ribs are reduced and the scales are thin and weakly mineralized (Eastman & DeVries 1981, 1982). Silverfish use a sub-carangiform mode of swimming employing the tail at low speed, but do not swim continuously. In aquaria they have been observed to hover motionless for long periods (DeVries & Eastman 1978). Thus *P. antarcticum* relies on 'energy saving' buoyancy mechanisms rather than swimming ability to maintain a pelagic existence.

Cryopelagic species with intermediate densities such as *Pagothenia borchgrevinki* (Boulenger) are also well represented (Andriashev 1965). They use labriform swimming to maintain themselves in the water column (Montgomery & Macdonald 1984). Cryopelagic species are able to take refuge in the many millions of square miles of fast and drift ice, feeding on amphipods, and planktonic sub-ice calanoids and euphausids (Andriashev 1987).

Muscle fibre types

Sustained locomotory activity in fish is supported by the recruitment of slow twitch muscle fibres (Bone 1978, Johnston 1981, Altringham & Johnston 1988). Slow fibres have distinct M-lines, narrow diameters, contain abundant mitochondria and have a well-developed capillary supply (Bone 1978, Johnston 1981). They are multiply innervated (Bone 1964), responding to nerve stimulation with both junction potentials and overshooting action potentials (Altringham & Johnston 1988).

Maximum swimming speeds require the recruitment of fast twitch fibres (Bone 1978). These fibres have shorter contraction times and generate higher power outputs than slow fibres (Johnston 1983, Altringham & Johnston 1988). Fast fibres also have distinct M-lines but are distinguished from slow fibres by their larger average diameters, densely packed myofibrils, relatively few mitochondria and sparse capillary supply (Bone 1978, Johnston 1981). In the Acanthopterygii these fibres are polyneuronally innervated (Bone 1964), responding to nerve stimulation with overshooting action potentials (Altringham & Johnston 1988). The sarcoplasmic reticulum, an internal membrane system concerned with Ca^{2+}-cycling, is moderately well-developed in both fast and slow fibres (Akster *et al.* 1985). A range of fibre types with intermediate properties have been also described (Bone & Chubb 1978, Johnston 1983).

The myotomes of some species contain a superficial layer of pale muscle fibres. At the ultrastructural level these fibres are distinguished from fast and slow fibres by the absence of M-lines, their relatively few, large diameter myofibrils, poorly developed sarcoplasmic reticulum and low density of mitochondria (Bone *et al.* 1986, Kilarski & Kozlowska 1987). This class of fibre produce lower tensions and have slower contraction speeds than slow fibres (Bone *et al.* 1986). It is has been suggested that they are analogous to the tonic fibres of land vertebrates, having a role in maintaining posture (Bone *et al.* 1986, Kilarski & Kozlowska 1987).

Although the structural and contractile properties of fast and slow muscle fibres in Antarctic fish correspond to those in temperate species they do have a number of unusual properties. For example, histochemical methods for myosin ATPase activity are not able to differentiate different fibre types in Antarctic species (Davison & Macdonald 1985, Harrison *et al.* 1987, Dunn *et al.* 1989). All fibre types are inactivated at acid pH, and following alkaline preincubation they stain darkly for myosin ATPase activity (Harrison *et al.* 1987). The myosin from Antarctic fish is of a highly labile type which readily aggregates and loses its ATPase activity on isolation (Johnston *et al.* 1975). These properties are thought to reflect structural specializations for low temperature function (Connell 1961, Johnston & Walesby 1977), and may provide an explanation for the anomalous staining characteristics of myosin ATPase.

https://doi.org/10.1017/S0954102089000167 Published online by Cambridge University Press

The average diameter of muscle fibres in Antarctic fish is often much greater than for temperate species of similar size (Fig. 1). Slow fibres from the pectoral fin adductor muscles of six species of notothenioids were found to have average diameters of 50–70 μm (Dunn *et al.* 1989). Fibres containing abundant mitochondria with diameters in the range 100–200 μm form the predominant size class in the pectoral fin adductor muscles of numerous species including the icefishes, *Pseudochaenichthys georgianus* (Norman) and *Champsocephalus gunnari* (Lönnberg) (Fig. 1). Apparently the loss of respiratory pigments in channichthyiids has not resulted in a compensatory decrease in mean fibre diameter (Fig. 1). Increases in muscle mass during growth result from the production of new fibres from myosatellite cells (hyperplasia), and from the hypertrophy of existing fibres (Nag & Nursall 1972). In a study of temperate freshwater fish a general relationship was found between the ability of a species to maintain the production of new fibres and both its growth rate and ultimate size (Weatherley & Gill 1985). The fast myotomal muscle in the adult stages of a number of notothenioids contain relatively few small diameter fibres, suggesting muscle growth is largely achieved through fibre hypertrophy. For example, mean fibre diameter for the fast myotomal muscles of 30-cm *Notothenia rossii* (Fischer), which can reach >70 cm, was found to be around 160 μm (Smialowska & Kilarski 1981). Fibres of 100–220 μm diameter comprised 51% of the total, with few fibres having diameters <30 μm (Smialowska & Kilarski 1981). The trunk muscles of *Trematomus hansoni* (Boulenger) (31 cm) were found to contain no fast fibres less than 80 μm in diameter, with around 20% of fibres having diameters in the range 250–300 μm (Smialowska & Kilarski 1981). The low surface to volume ratio of muscle fibres in Antarctic fish may serve to reduce the energy cost associated with maintaining ionic gradients and help to contribute to the low basal metabolic rates observed in these fish (Hemmingsen & Douglas 1970, Morris & North 1984).

In general, slow muscle fibres in Antarctic fish have similar activities of aerobic enzymes, but higher volume densities of mitochondria than comparable temperate species (Johnston 1987). The myofibrils in some Antarctic species are arranged in ribbons one fibril thick, such that each is entirely surrounded by mitochondria (Fig. 2). This results in 30–60% of the fibre volume being filled with mitochondria even in relatively slow swimming species. High densities of mitochondria may serve to partially compensate for the detrimental effects of low temperature on enzyme reaction and diffusion rates. This is likely to be particularly significant for adenylates and for metabolites which cross the mitochondrial membrane such as malate and α-ketoglutarate. The diffusion constants in muscle for small molecules such as adenylates and lactate are about two orders of magnitude slower than for oxygen (Hill 1965, Sidell & Hazel 1987). High mitochondrial densities are also observed for temperate species acclimated to the cold (Johnston & Dunn 1987). For

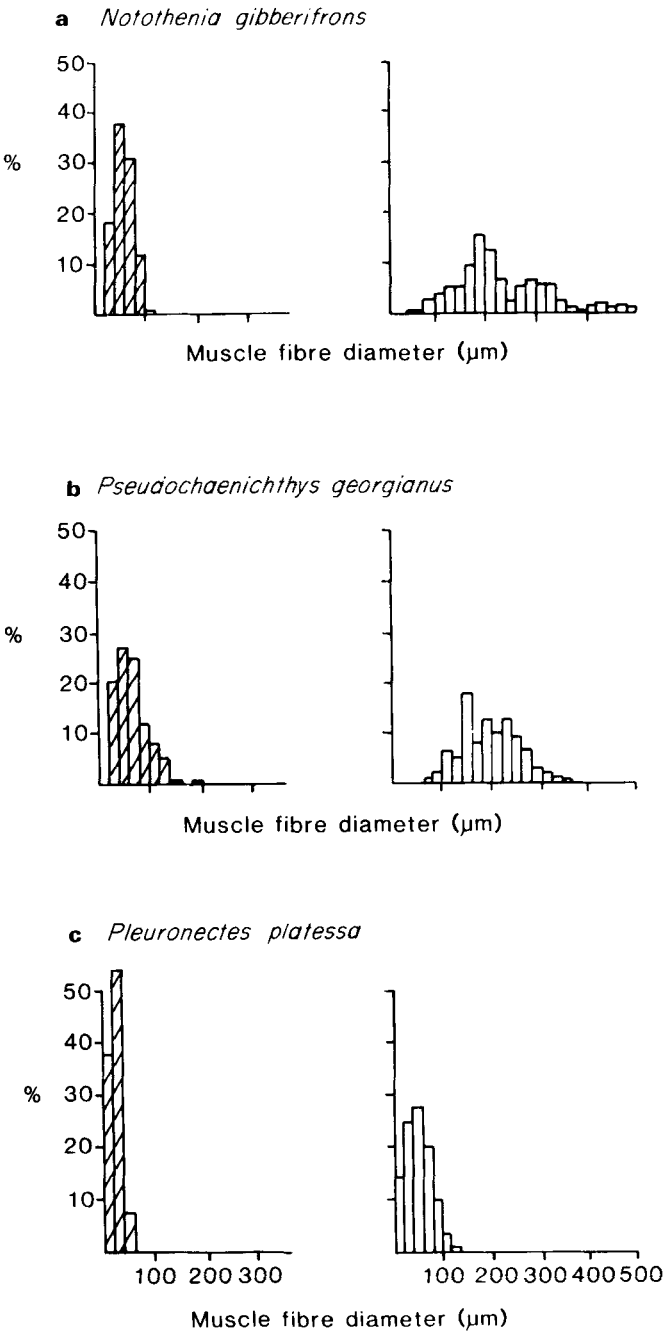


Fig. 1. Frequency distributions of muscle fibre diameters in demersal fish determined from frozen sections. **a.** *Notothenia gibberifrons* Lönnberg, 25–40 cm standard length (SL). **b.** *Pseudochaenichthys georgianus*, 28–55 cm (SL) (from Antarctica) and **c.** plaice, *Pleuronectes platessa*, 23–30 cm (SL) (from the North Sea). Shaded bars represent slow fibres isolated from either the pectoral fin adductor (Antarctic species) or myotomal muscles (plaice). Unshaded bars represent fast fibres isolated from dorsal myotomes. The data are adapted from Dunn *et al.* (1989) and unpublished reports.

https://doi.org/10.1017/S0954102089000167 Published online by Cambridge University Press

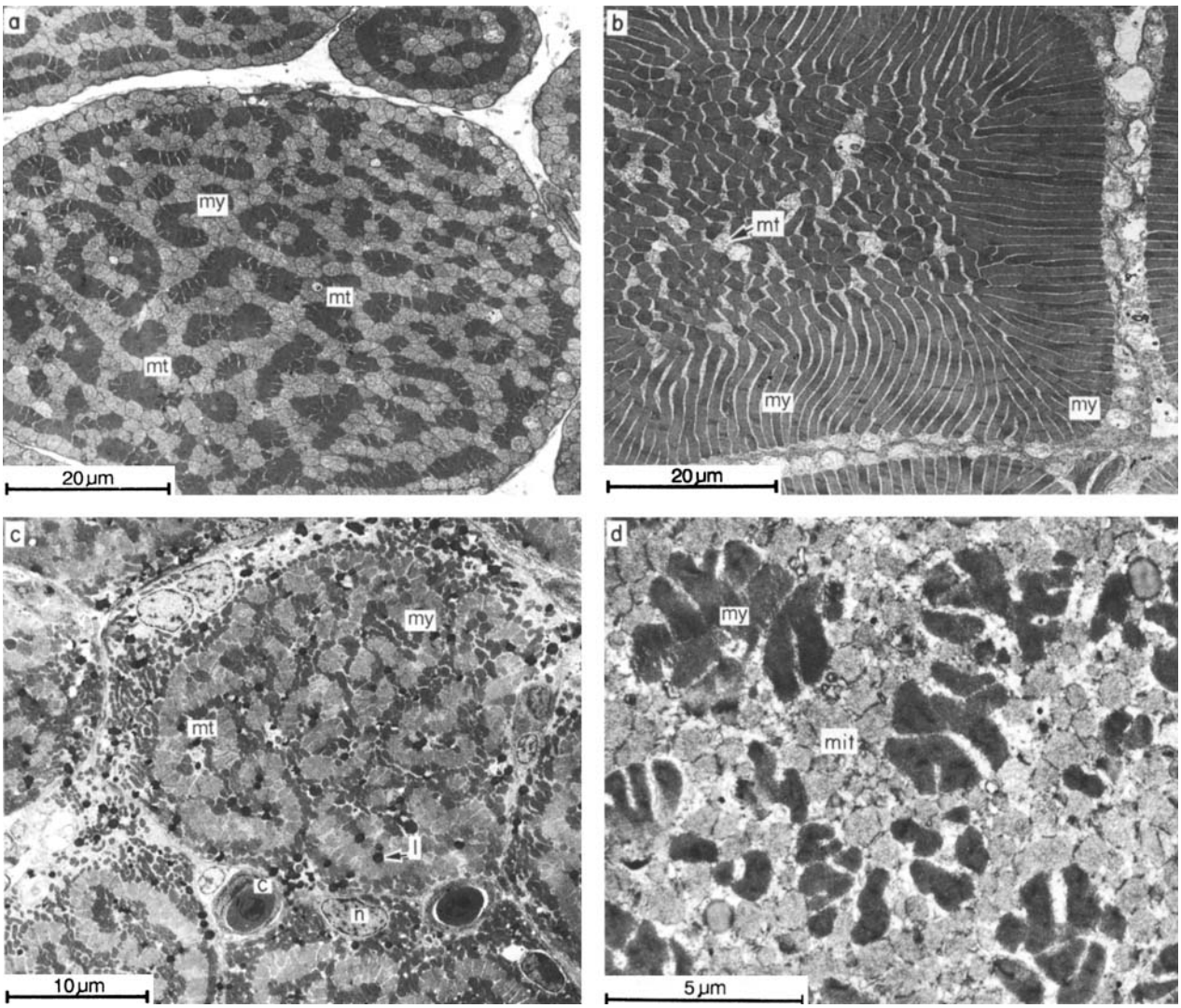


Fig. 2. Fine structure of fast and slow muscle fibres from Antarctic fish. The plates show electron micrographs of transversely sectioned muscle fibres. **a.** Slow myotomal fibres from *Pleuragramma antarcticum*; myofibrils are arranged in thin ribbons surrounded by mitochondria. **b.** Fast myotomal fibres from *Pleuragramma antarcticum*; note the low abundance of mitochondria and ribbon-shaped peripheral myofibrils. **c.** Slow fibres from the pectoral fin adductor muscle of the pelagic blue phase fingerling stage of *Notothenia neglecta*; there are numerous lipid droplets and mitochondria, the majority of myofibrils occur adjacent to mitochondria. **d.** Slow fibres from the pectoral fin adductor muscle of the demersal icefish, *Chaenocephalus aceratus* Lönnberg; myofibrils are large and irregular in cross-section and surrounded by mitochondria. l = lipid droplets, mt & mit = mitochondria, my = myofibrils, c = capillary, n = nucleus.

example, mean mitochondrial spacing was found to be 2.3 µm and 4.0 µm respectively, in 5°C-acclimated and 25°C-acclimated striped bass (*Morone saxatilis*) (Egginton *et al.* 1987).

Distribution of muscle fibre types

Studies of the relative proportions and distributions of fast and slow fibres in different muscles can provide valuable information on the activity patterns of different species. For example, species which are entirely dependent on labriform locomotion at cruising speeds, such as *Pagothenia borchgrevinki*, contain a low proportion of slow fibres in their myotomes (Davison & Macdonald 1985). The total amount of slow muscle in pectoral fin and myotomal muscles is also likely to be correlated with aerobic scope for activity.

The cryopelagic species *Pagothenia borchgrevinki* uses sub-carangiform swimming to launch itself into the water column (Macdonald *et al.* 1987). Sustained activity is powered

https://doi.org/10.1017/S0954102089000167 Published online by Cambridge University Press

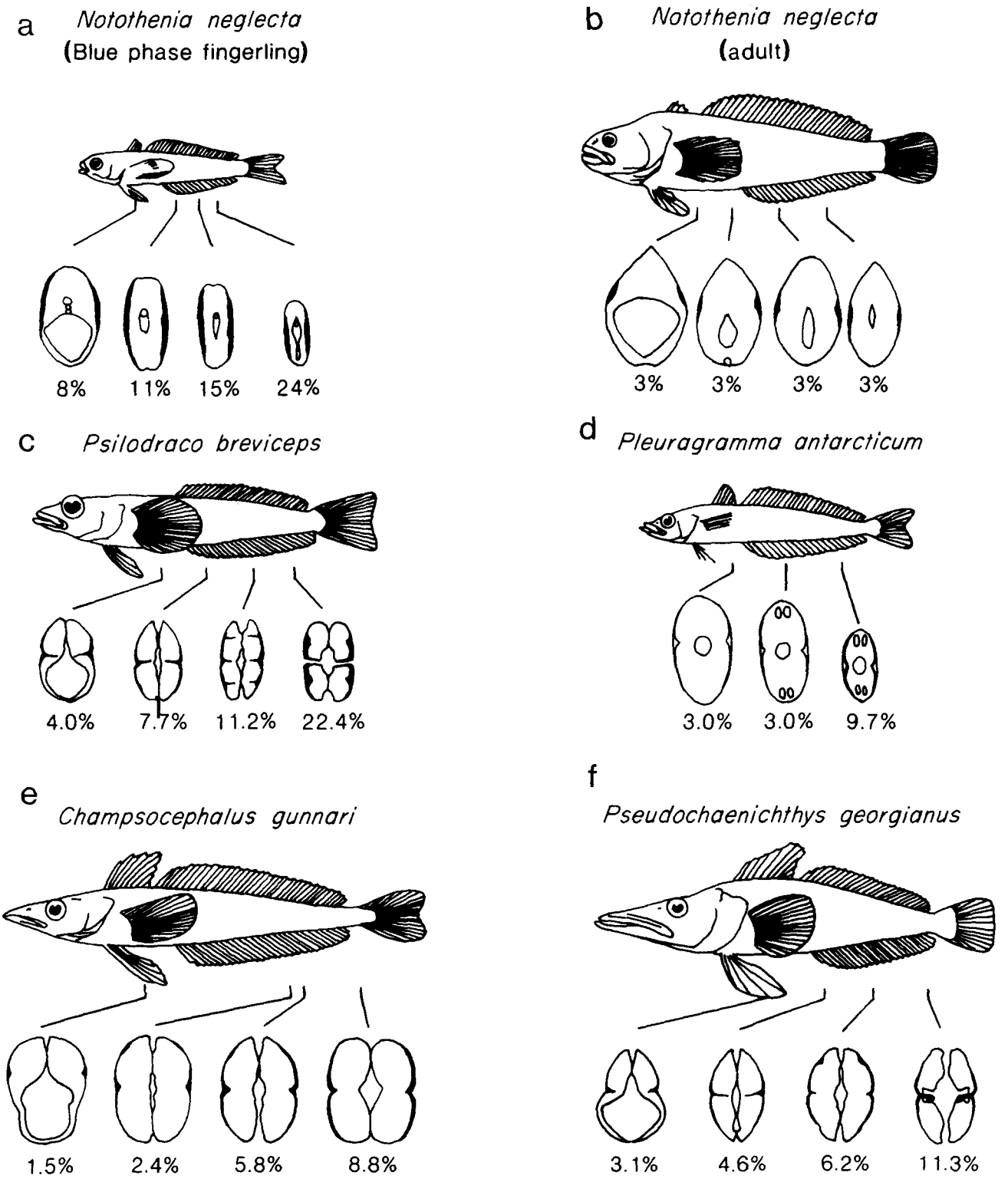


Fig. 3. Distribution of fast and slow muscle fibres in the myotomes of some Antarctic fish. Diagrams show the lateral body shape and distribution of fast (unshaded areas) and slow (shaded areas) muscle fibres, in cross-sections of the trunk. The numbers correspond to the cross-sectional area of the slow muscle as a percentage of total muscle cross-sectional area. **a.** Pelagic blue phase fingerling stage of *Notothenia neglecta*, 7–8 cm standard length (SL), **b.** demersal adult stage of *Notothenia neglecta*, 24–40 cm (SL), **c.** *Psilodraco breviceps* Norman, 11 cm (SL), **d.** *Pleuragramma antarcticum*, 12–13 cm (SL), **e.** *Champsocephalus gunnari*, 14 cm (SL), and **f.** *Pseudochaenichthys georgianus*, 17 cm (SL).

https://doi.org/10.1017/S0954102089000167 Published online by Cambridge University Press

by a single class of relatively small diameter slow fibres in the pectoral fin muscles (Davison & Macdonald 1985). In contrast, the pectoral fin adductor muscles of many demersal species, such as *Trematomus bernacchii* (Boulenger), also contain a significant proportion of larger diameter fast fibres (Davison & Macdonald 1985). These fibres may have a role in producing the few fast pectoral fin strokes used to lift the fish off the bottom (Davison & Macdonald 1985).

The myotomes of sedentary species, such as *Notothenia neglecta* (Nybelin), are almost exclusively composed of fast twitch fibres (Fig. 3). Slow fibres in the myotomes of *N. neglecta* have larger diameters, fewer mitochondria, and lower capillary densities than homologous fibres in the pectoral fin muscles (Table I). It has been suggested that slow myotomal fibres in labriform swimmers have a role in producing the slow bending movements of the trunk used to initiate changes in direction, and in generating low amplitude tail flicks (Archer & Johnston, in press). A layer of superficial fibres which stain weakly for myosin ATPase and succinic dehydrogenase activity has also been found in the myotomes of all notothenioids examined (Dunn *et al.* 1989). These fibres, which have many of the characteristics of tonic fibres, may hold the trunk in a fixed position during labriform locomotion and when the fish is resting on the sea bed.

The pelagic juvenile stages of demersal species are more active. In contrast to adults, the juvenile stages use a sub-carangiform mode of swimming at low speed (Johnston & Camm 1987, Dunn *et al.* 1989). The myotomes of fingerling *N. neglecta* contain a high proportion of slow muscle fibres consistent with a relatively high aerobic scope for activity (Fig. 3). These fibres have smaller diameters and three times the density of mitochondria compared with homologous fibres in adults (Table I).

Adult members of the mid-water fish community exhibit a variety of sustained swimming styles and activity patterns. The myotomes of *P. antarcticum* contain a relatively low proportion of slow fibres, even though it relies on sub-carangiform swimming at low speeds (Fig. 3). The gills of *P. antarcticum* are also poorly developed, according well with its relatively sluggish habit and suggesting a low aerobic scope for activity (Kunzmann 1987, Johnston *et al.* 1988). The pelagic icefish *Champsocephalus gunnari* is known to be more active. It has well-developed pectoral fins and a relatively modest proportion of slow myotomal muscle which suggests that it predominantly uses labriform swimming at sustained speeds. In contrast, the myotomes of adult *Psilodraco breviceps* contain a much higher proportion of slow fibres consistent with the use of both labriform and sub-carangiform locomotion at cruising speeds (Fig. 3). *P. breviceps* is known to undertake frequent vertical migrations to feed on planktonic prey (Permitin 1970). Its muscles suggest that it is a strong swimmer with a relatively high aerobic scope for activity.

Table I. Indices of capillary supply and organelle volume densities (%) for muscle fibre types in Antarctic fish. Values represent Mean ± SE m.ad.p: pectoral fin adductor muscle; f(d): fibre diameter (μm); $NA_{(c,f)}$: numerical density of capillaries per mm^{-2} muscle fibre cross-sectional area; $Vv_{(mit,f)}$: volume density of mitochondria (%); $Vv_{(mf,f)}$: volume density of myofibrils (%). Original data from 1. Johnston & Camm 1987, 2. Johnston 1987, 3. Fitch *et al.* 1984, 4. Johnston *et al.* 1988.

Parameter	f(d) (μm)	$NA_{(c,f)}$	$Vv_{(mit,f)}$	$Vv_{(mf,f)}$
Notothenia neglecta[1] (blue phase fingerling)				
m.ad.p: slow fibres	24.2±0.5	1727±511	35.6±2.7	52.5±2.6
myotomal: slow fibres	29.0±0.4	1225±103	37.0±1.6	38.6±1.0
myotomal: fast fibres	40.0±0.7	320±53	2.6±0.4	76.5±1.4
Notothenia neglecta[1] (adult)				
m.ad.p: slow fibres	47.5±0.8	498±59	34.3±2.3	54.4±2.2
myotomal: slow fibres	92.0±0.4	266±107	13.1±1.1	70.3±2.0
myotomal: fast fibres	120±6.2	100±34	1.4±0.5	86.3±0.5
Chaenocephalus aceratus (adult)				
m.ad.p: slow fibres[2]	—	—	50.1±2.0	35.0±19
myotomal: slow fibres[3]	58.9±3.1	544±38	30.0±1.2	68.0±1.0
Pleuragramma antarcticum[4] (adult)				
myotomal: slow fibres	34.0±0.7	1057±134	56.3±1.9	42.2±1.6
myotomal: fast fibres	128±4.4	60±29	6.3±1.0	81.3±1.1

Labriform locomotion

It has been suggested that pectoral fin drag-based mechanisms of propulsion represent an adaptation for slow swimming, where the efficiency of sub-carangiform locomotion is low (Blake 1979). The kinematics of labriform swimming have been studied for the cryopelagic species *Pagothenia borchgrevinki* (Montgomery & Macdonald 1984), and for the demersal species *Notothenia neglecta* (Archer & Johnston 1989). *P. borchgrevinki* swim for long periods just underneath the sea ice (Andriashev 1965). Labriform swimming speed is a linear function of pectoral fin beat frequency, reaching a maximum of 38 cm s^{-1} (1.8 body lengths s^{-1}) in 23 cm specimens, at a fin beat frequency of around 2 Hz (at −1.5°C) (Montgomery & Macdonald 1984). Adult *N. neglecta* are only intermittently active; 29 cm specimens have a maximum cruising speed of 0.8 body lengths s^{-1}, at a pectoral fin beat frequency of 1.0 Hz (at 1–2°C) (Archer & Johnston, in press). Juvenile specimens (7–8 cm) spend longer in the water column and can attain speeds of 1.4 body lengths s^{-1}, at a pectoral fin beat frequency of 1.7 Hz (Archer & Johnston, in press). The main power stroke in labriform swimming is the adduction phase (Fig. 4a, b). Successive fin rays are joined by a highly flexible membrane and they move both laterally backward and vertically upward producting a sinusoidal wave over each pectoral fin. Once adducted, the leading anterior edge of the pectoral fin continues to move dorsally against the side of the body, prior to the start of the abduction stroke (Fig. 4a). The abduction of the fin is a two-stage process. Initially the fin is abducted to a glide position

https://doi.org/10.1017/S0954102089000167 Published online by Cambridge University Press

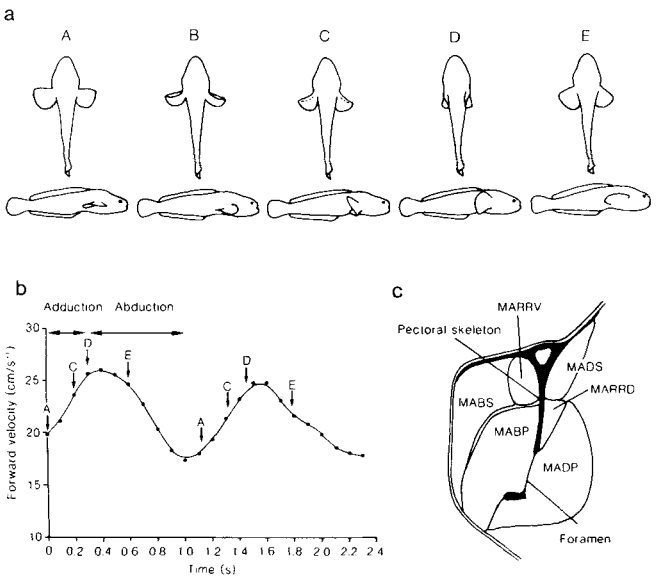


Fig. 4. Labriform swimming in adult *Notothenia neglecta*, 31 cm standard length. **a.** Diagrammatic representation of the pectoral fin-beat pattern. **b.** Forward velocity over two complete pectoral fin-beat cycles; A–C adduction time of the leading edge of the pectoral fin, A–D the complete adduction stroke, D–E abduction and E–A the glide period (adapted from Archer & Johnston, in press). Cross section through the pectoral muscle mass of *Notothenia neglecta* at the level of the foramen showing positions of the muscles. Abductor muscles: MABS = M. Abductor Superficialis, MABS = M. Abductor Profundis, MARRV = M. Arrector Ventralis. Adductor muscles: MADS = M. Adductor Superficialis, MADP = M. Adductor Profundis and MARRD = M. Arrector Dorsalis (adapted from Harrison *et al.* 1987).

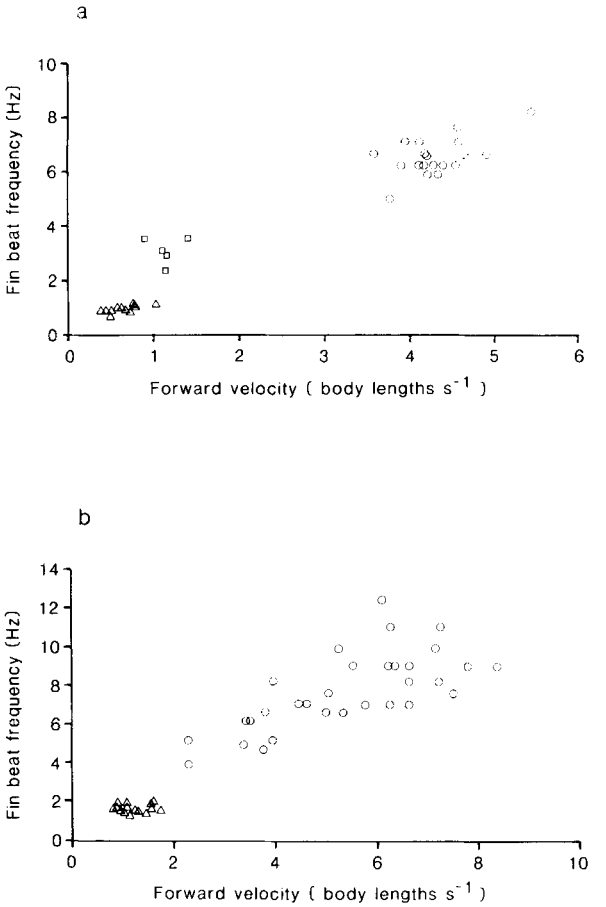


Fig. 5. Swimming behaviour in **a.** adult, 27–31 cm standard length and **b.** juvenile, 7–8 cm standard length, *Notothenia neglecta*, illustrating the length-specific speeds at which different swimming modes are utilized. Data points represent single steady swimming sequences. (From Archer & Johnston, in press.) △ = labriform swimming, O = sub-carangiform swimming, □ = mixed labriform and sub-carangiform swimming.

to provide lift corresponding to the main refractory period of the fin beat cycle. Immediately prior to adduction the leading edge of the fin moves anteriorly and ventrally again to begin the adduction stroke (Fig. 4a, Archer & Johnston, in press).

The muscular anatomy associated with the primary shoulder girdle in *Notothenia* is typical of the general percoid plan (Harrison *et al.* 1987). Two abductor and two adductor muscles are responsible for articulating the fin blade around the posterior border of the pectoral fin skeleton, whilst two arrector (= errector) muscles fan-out the fin (Fig. 4c). The adductor muscles constituting two thirds of the mass are pinnate with long superficial tendons serving to maximise force production per unit volume (Harrison *et al.* 1987).

Burst swimming

Adult *Notothenia neglecta* (Archer & Johnston, in press) and *Pagothenia borchgrevinki* (Montgomery & Macdonald 1984) operate a two-geared system in which there is a sharp division between the steady speeds that can be attained using labriform and sub-carangiform swimming. For example, in *N. neglecta* which are 29–31 cm long, intermediate speeds between 1.5 and 3.5 body lengths s^{-1} always involve unsteady swimming (Fig. 5). In contrast, because of the higher proportion of slow fibres in their myotomes, steady swimming sequences are observed at all possible speeds in juveniles (Fig. 5).

In all species sub-carangiform swimming is used for rapid acceleration and to achieve the burst speeds required to avoid predation, or to capture prey. Macdonald *et al.* (1987) observed that Antarctic cod *Dissostichus mawsoni* feeding on *Pagothenia borchgrevinki* do not initiate a strike until within about 20 cm of their prey. In contrast, the escape response of prey is usually elicited at several times this distance and consists of a fast start followed by a short sprint consisting of 3 or 4 tail beat cycles (Macdonald *et al.* 1987). During artificially induced escape responses, the

https://doi.org/10.1017/S0954102089000167 Published online by Cambridge University Press

maximum speed observed for *P. borchgrevinki* was 4.9 body lengths s^{-1} at a caudal fin beat frequency of 5.7 Hz (Montgomery & Macdonald 1984). Archer & Johnston (in press) trained *N. neglecta* to swim along a 4-m raceway, by associating an underwater flashing light with the appearance of food. Several fish were kept in the raceway at a time in order to create a competitive situation and to induce burst swimming. During burst swimming sequences the pectoral and pelvic fins are rapidly (0.22 s) adducted and held against the body, and the dorsal and anal fins are partially erected (Fig. 6). The maximum speeds and tail-beat frequencies attained by *N. neglecta* are shown in Table II. Interestingly, the comparatively modest maximum tail-beat frequency observed in small fish is partially compensated for by a greater tail-beat amplitude (Table II).

Muscle metabolism

During sustained activity energy is produced by aerobic metabolic pathways involving the catabolism of glucose, fatty acids and possibly amino acids (Hochachka 1985). Forster *et al.* (1987) reported that the maximum oxygen consumption of *Pagothenia borchgrevinki* was only 3–5 times higher than resting values. Similar aerobic activity has been reported for bottom-living temperate species (Jones & Randall 1978). However, in view of the low basal metabolic rate in *P. borchgrevinki*, the absolute maximal oxygen consumption is low, equivalent to 156 ml kg^{-1} h^{-1} for 50-g specimens (Forster *et al.* 1987).

The density of mitochondria in slow fibres varies with activity patterns and possibly with latitude (Johnston *et al.* 1988). In general, slow muscle fibres in haemoglobinless species have higher densities of mitochondria than comparable 'red-blooded' species (Johnston 1987, Dunn *et al.* 1989), but lower densities of mitochondrial cristae. Most of the enzymes involved in the production of ATP by oxidative phosphorylation are located on the inner mitochondrial membrane and matrix. The net result of changes in mitochondrial and cristae density is that slow muscles in channichthyids have similar activities of aerobic enzymes and rates of oxygen consumption as in sympatric 'red-blooded' species (Johnston & Harrison 1985, Johnston 1987). The observed reduction in average mitochondrial spacing in icefish slow fibres may compensate for the absence of myoglobin under certain conditions.

The two main pathways of energy production in fast muscle fibres are phosphagen hydrolysis and anaerobic glycolysis (Hochachka 1985). ATP production from creatine phosphate (PCr) is catalysed by a single near equilibrium enzyme, creatine phosphokinase (CPK). This pathway supplies the immediate requirements for ATP, but is ultimately limited by the pool size of PCr. In fatigued muscle adenylate kinase (AK) catalyses the conversion of 2ADP to ATP +

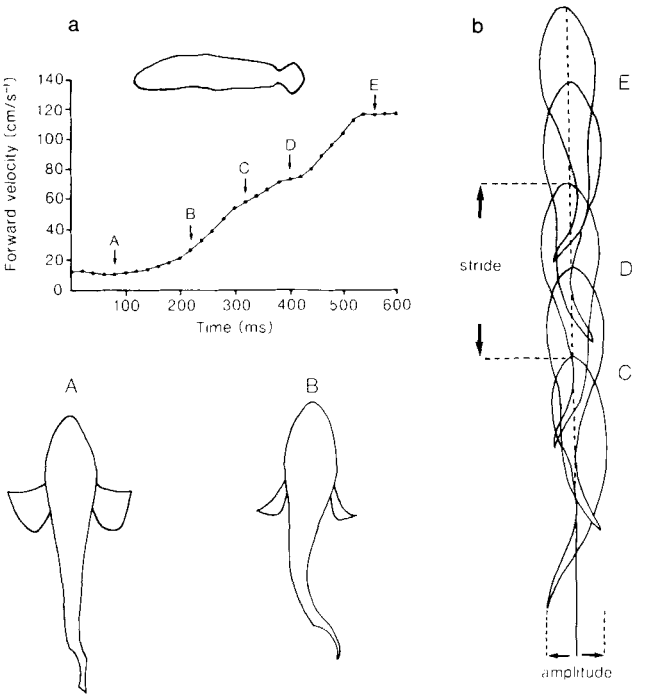


Fig. 6. Transition from labriform to sub-carangiform swimming in an adult *Notothenia neglecta*, 31 cm standard length, at the start of a burst swimming sequence. The lateral outline of the fish is shown as an insert in **a**. Acceleration was calculated over the first two strides, first stride B–D (0.31 L), second D–E (0.51 L). Tail-beat frequency 5.9 Hz, amplitude 0.24 L, pectoral fin adduction time (A–C), 0.24 s. (From Archer & Johnston, in press.)

Table II. Kinematics of swimming in static water in the Antarctic teleost *Notothenia neglecta*. Values represent Mean ± SE of the five fastest labriform and sub-crangiform swimming sequences at 1–2°C. The average standard lengths of adult and juvenile fish were 29.3 cm and 7.6 cm respectively. L is body length (cm). (From Archer & Johnston, in press.)

Labriform swimming				
Stage	Forward velocity (L/s)	Pectoral-fin adduction time (s)	Pectoral-fin frequency (Hz)	Stride length (L)
Adult	0.78±0.12	0.34±0.04	1.0±0.1	0.77±0.12
Juvenile	1.36±0.26	0.21±0.03	1.7±0.3	0.78±0.18
Sub-carangiform swimming				
Stage	Forward velocity (L/s)	Tail-beat frequency (Hz)	Tail-beat amplitude (L)	Stride length (L)
Adult	4.3±0.4	6.6±0.6	0.20±0.03	0.66±0.06
Juvenile	6.8±1.0	8.9±1.4	0.29±0.04	0.77±0.14

https://doi.org/10.1017/S0954102089000167 Published online by Cambridge University Press

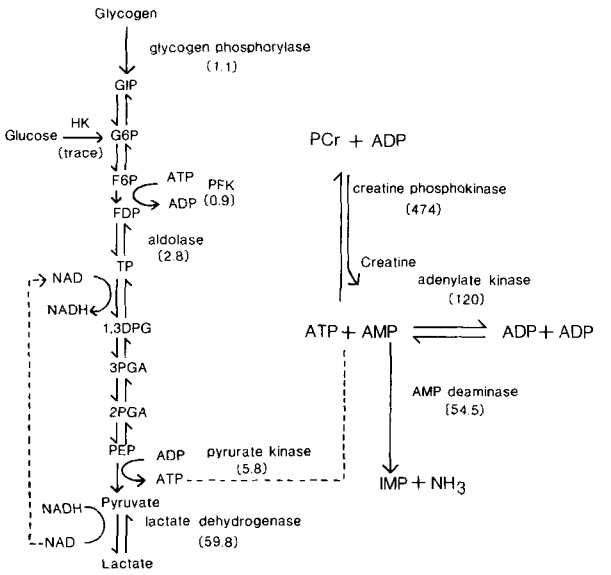


Fig. 7. Immediate energy supplying pathways in the fast muscle of adult *Notothenia neglecta*. The relative importance of each pathway for supplying ATP during burst swimming is indicated by the size of labelling, i.e. largest lettering indicates most important pathways. Numbers in parentheses are mean enzyme activities in μmol min^{-1} g^{-1} wet wt. Abbreviations: PCr = phosphocreatine, ATP = adenosine triphosphate, ADP = adenosine diphosphate, AMP = adenosine monophosphate, IMP = inosine monophosphate, NH_3 = ammonia, GIP = glucose-1-phosphate, G6P = glucose-6-phosphate, F6P = fructose-6-phosphate, FDP = fructose 1, 6-biphosphate, TP = triose phosphates, 1,3DPG = 1, 3-phosphoglyceric acid, 3PG = 3-phosphoglycerate, 2PG = 2 -phosphoglycerate, PEP = phosphenolpyruvate, HK = hexokinase, PFK = phosphofructokinase. (Adpated from Dunn & Johnston 1986.)

AMP (Fig. 7). Since the adenylate kinase reaction is close to equilibrium, the reaction product AMP must be removed before the reaction can proceed to completion. This results in the production of inosine monophosphate (IMP) and a decrease in the adenylate concentration. Dunn & Johnston (1986) found that the activities of glycolytic enzymes in the fast twitch fibres of *Notothenia neglecta* at 0°C, were low compared to those in temperate fish assayed at 15°C, whereas the activities of CPK, AK and AMP deaminase were similar or higher (Fig. 7). They also measured muscle metabolite concentrations before and after 3 min of vigorous exercise. Concentrations of metabolites associated with cellular energy status declined with exercise. At the same time, there was no change in the concentrations of most glycolytic metabolites measured (including glycogen, glucose and lactate), while PCr concentration decreased, and IMP concentration increased (Dunn & Johnston 1986). These observations suggest that the potential for ATP generation via PCr hydrolysis is enhanced in *N. neglecta*, whilst glycolytic capacity is relatively reduced. Similar enzyme activity profiles are found for the fast muscle of the demersal icefish (*Chaenocephalus aceratus*) (Johnston 1987). The reliance on PCr as the major fuel for burst swimming would be expected to limit endurance to relatively few tail-beat cycles. This accords well with field observations of behaviour in these species. Adults are ambush feeders and can be observed perching among rocks or partially burying themselves in soft mud in wait for prey organisms to approach (Daniels 1982). Davison *et al.* 1988 found that *Pagothenia borchgrevinki* subjected to forced exercise rapidly fatigue following the transition from labriform to sub-carangiform locomotion. The poor endurance of *P. borchgrevinki* was also related to an inability to produce lactate from anaerobic glycolysis, suggesting a similar pattern of energy metabolism to *N. neglecta* (Davison *et al.* 1988). Indeed, at exhaustion, lactate concentrations in fast muscles were within the range reported for most non-exercised temperate fish in the literature. Relatively high activities of glycolytic enzymes have been reported in the fast muscle of another Antarctic fish, *Notothenia gibberifrons* (Dunn *et al.* 1989). This suggests that the pattern of energy supply to fast muscles in *N. neglecta* and *P. borchgrevinki* is probably related more to the type of swimming activity elicited by prey capture and/or predator avoidance than to some special adaptation to low temperature.

Adaptations to low temperature

Precht (1958) has provided a useful classification of the patterns of temperature adaptation observed in ectotherms. He defined resistance adaptations as those which modify upper and/or lower lethal limits, thereby changing the temperature over which normal function is maintained. In contrast, capacity adaptations are those which modify rate processes in order to compensate for temperature effects over the normal thermal range of a species. The very existence of an abundant fish fauna permanently living at close to 0°C, is testament to a wide variety of resistance adaptations. Perhaps the best documented of these is the presence of glycopeptide and peptide anti-freezes which serve to inhibit the growth of ice crystals and lower the freezing point of body fluids below that of sea-water (DeVries 1988). The structures of membranes and proteins are also highly specialized for low temperature function (Johnston 1985). For example, brain tubulin sub-units from Antarctic fish assemble *in vitro* and remain stable at 0°C, whereas mammalian microtubules depolymerize at similar temperatures (Detrich & Overton 1988). The conduction of nerve impulses in warm-adapted animals is readily blocked by low temperature, whereas the peripheral nerves of Antarctic fish remain active at temperatures down to –5°C (Macdonald 1981). This is thought to reflect in part complex adaptations in the fatty acid composition of phospholipids which serve to

https://doi.org/10.1017/S0954102089000167 Published online by Cambridge University Press

reduce membrane fluidity (Cossins & Bowler 1987). Montgomery *et al.* (1983) found that the eye movements of *Girella tricuspidata*, a temperate fish living at 14°C, ceased when cooled to 5°C. Although vestibulo-ocular reflexes in McMurdo Sound fishes show clear resistance adaptations, the fastest eye movements measured in several Antarctic fish, at −1.9°C, were only around half as fast as those for the temperate fish at 14°C (Montgomery & Macdonald 1984). The extent to which Antarctic animals exhibit capacity adaptations to low temperature remains controversial, and is a central theme of current physiological research (Clarke 1987).

The suggestion that polar fishes have elevated basal metabolic rates (BMR) has received a lot of attention in the literature (see reviews by Clarke 1983 and Macdonald *et al.* 1987). Some degree of metabolic cold adaptation would be expected on theoretical grounds because of the need to maintain ionic gradients and protein turn-over etc. However, it is very difficult to define basal metabolism and to completely eliminate the effects of stress and activity. The balance of evidence is that the BMR of Antarctic fish is probably around two-fold higher than it would be for temperate species if extrapolated to the same low temperature (Forster *et al.* 1987). Since this is comfortably within the interspecific variation in BMR reported for Antarctic fish it is not possible to precisely quantify the effect (Clarke 1983). Of greater ecological importance is the fact that maintenance energy requirements in Antarctic fish are significantly lower than for temperate species at their normal body temperature (Clarke 1983).

Measurements of energy expenditure at rest provide little indication about maximum levels of performance. The power requirements of swimming rise exponentially with increasing speed (Webb 1975). During burst swimming, fast muscle fibres undergo rapid cycles of contraction and relaxation, increasing their rate of ATP utilization more than 100-fold. Fast motor systems therefore provide an ideal model for investigating any constraints on behaviour imposed by low temperature.

Studies to date have shown considerable variation in the degree of capacity adaptation observed between different elements of the neuro-muscular system. Force generation

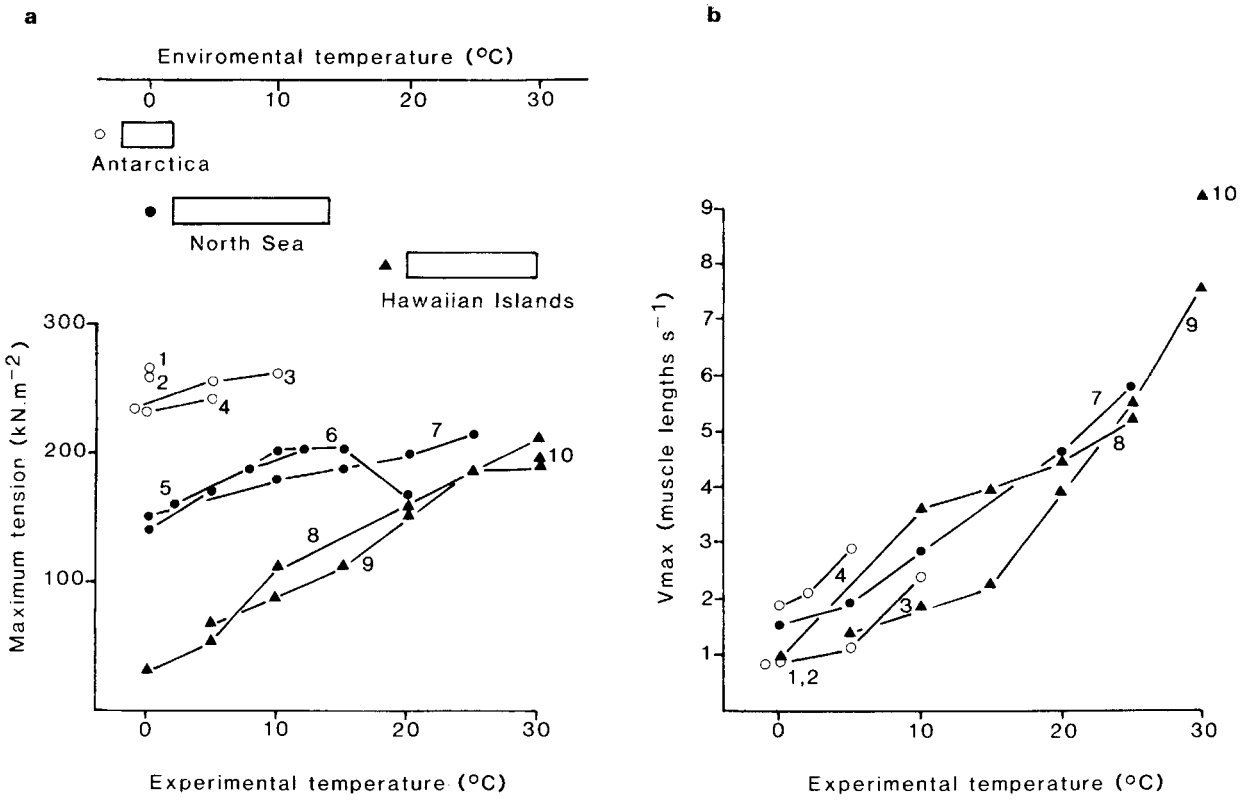


Fig. 8. Effects of temperature on the contractile properties of skinned fibres isolated from the fast myotomal muscles of marine fish. **a.** Maximum isometric tension and **b.** unloaded contraction velocity (Vmax) plotted against experimental temperature. Antarctic species from the South Orkney Islands: 1. *Trematomus hansoni*, 2. *Notothenia rossii*, 3. *Chaenocephalus aceratus*, 4. *Notothenia neglecta*. North Sea species: *Gadus morhua* L., *Myoxocephalus scorpius* L., *Platichthys flesus* L. Tropical species: 8. *Maikaira nigricans*, 9. *Carangus melampygus* Wakiya, 10. *Euthynnus affinis*. (From Johnston & Altringham 1988.)

https://doi.org/10.1017/S0954102089000167 Published online by Cambridge University Press

appears to be perfectly compensated to low temperature (Johnston & Brill 1984, Johnston & Altringham 1985, 1988). Maximally activated skinned fibres from Antarctic fish generate higher tensions at 0°C than similar fibres from temperate and tropical species when measured at their normal environmental temperatures (Fig. 8a). In contrast, the unloaded contraction speed of fibres is largely independent of adaptation temperature (Fig. 8b). McVean & Montgomery (1987) have reported that twitch contraction times, which are an important determinate of tail beat frequency, only show a partial capacity adaptation. This may reflect slower rates of relaxation and calcium pumping by the sarcoplasmic reticulum (SR) of cold water fish. For example, SR prepared from the fast muscle of *Notothenia rossii* accumulated calcium at six times the rate achieved by SR from a tropical fish at 0°C. However, assayed at their respective environmental temperatures, calcium pumping rates were around five times faster for the warm-water species (McArdle & Johnston 1980). All these results suggest that maximum swimming speeds in Antarctic fish are probably less than for temperate species. This is difficult to quantify due to the lack of comparative data on species with similar body shapes and ecologies. The maximum swimming speeds observed for the adult stages of *Notothenia neglecta* (Archer & Johnston, in press) and *Pagothenia borchgrevinki* (Montgomery & Macdonald 1984) are indeed towards the lower end of the range reported for temperate fish. Significantly, the maximum tail-beat frequency in juvenile *N. neglecta* is very modest, and only slightly greater than for adult stages (Archer & Johnston, in press). Since tail-beat frequencies are inversely related to body-length, any lack of temperature compensation should be most noticable for the early life stages. Measurements of the burst swimming speeds of fish larvae should prove a promising area of future research.

Acknowledgements

The author is grateful to the British Antarctic Survey for their continued support. This work was funded by an Antarctic Special Topics grant (GST/02/86) from the Natural Environment Research Council of the UK.

References

Akster, H.A., Granzier, H.L.M. & ter Keurs, H.E.D.J. 1985. A comparison of quantitative ultrastructural and contractile characteristics of muscle fibre types of the perch, *Perca fluviatilis* L. *Journal of Comparative Physiology*, **155B**, 685–691.

Altringham, J.D. & Johnston, I.A. 1988. Activation of multiply innervated fast and slow myotomal fibres of the teleost *Myoxocephalus scorpius*. *Journal of Experimental Biology*, **140**, 313–324.

Andriashev, A.P. 1965. A general review of the Antarctic fish fauna. *In* van Mieghem, I. & van Oye, P., *eds*. *Biogeography and ecology in Antarctica*. *Monographie Biologicae*, **15**. The Hague: Junk, 491–550.

Andriashev, A.P. 1987. A general review of the Antarctic bottom fish fauna. *In* Kullander, S.O. & Fernholm, B., *eds*. *Proceedings of the Vth Congress European Ichthyology, Stockholm 1985*. Stockholm: Swedish Museum Natural History, 357–372.

Archer, S.D. & Johnston, I.A. In press. Kinematics of labriform and subcarangiform swimming in the Antarctic fish, *Notothenia neglecta*. *Journal of Experimental Biology*.

Blake, R.W. 1979. The mechanics of labriform motion 1. Labriform locomotion in the Angelfish (*Pterophyllum eimekei*): an analysis of the power stroke. *Journal of Experimental Biology*, **82**, 255–271.

Bone, Q. 1964. Patterns of muscular innervation in the lower chordates. *International Reviews Neurobiology*, **6**, 99–147.

Bone, Q. 1978. Locomotor muscle. *In* Hoar, W.S. & Randall, D.J., *eds*. *Fish Physiology*, **7**. New York & London: Academic Press, 361–424.

Bone, Q. & Chubb, A.D. 1978. The histochemical demonstration of myofibrillar ATPase in elasmobranch muscle. *Histochemical Journal*, **10**, 489–494.

Bone, Q., Johnston, I.A., Pulsford, A. & Ryan, K.P. 1986. Contractile properties and ultrastructure of three types of muscle fibre in the dogfish myotome. *Journal of Muscle Research & Cell Motility*, **7**, 47–56.

Clarke, A. 1983. Life in cold water: the physiological ecology of polar marine ectotherms. *Annual Review of Oceanography and Marine Biology*, **21**, 341–453.

Clarke, A. 1987. The adaptation of aquatic animals to low temperatures. *In* Grout, B.W.W. & Morris, G.J., *eds*. *The effects of low temperatures on biological systems*. London: Edward Arnold, 313–348.

Connell, J.J. 1961. The relative stabilities of the skeletal muscle myosins of some animals. *Biochemical Journal*, **80**, 503–509.

Cossins, A.R. & Bowler, K. 1987. *Temperature biology of animals*. New York & London: Chapman & Hall, 339 pp.

Daniels, R.A. 1982. Feeding ecology of some fishes of the Antarctic Peninsula. *Fisheries Bulletin US*, **80**, 575–588.

Davison, W. & Macdonald, J.A. 1985. A histochemical study of the swimming musculature of Antarctic fish. *New Zealand Journal of Zoology*, **12**, 473–483.

Davison, W., Forster, M.E., Franklin, C.E. & Taylor, H.H. 1988. Recovery from exhausting exercise in an Antarctic fish, *Pagothenia borchgrevinki*. *Polar Biology*, **8**, 167–171.

Detrich, H.W. III & Overton, S.A. 1988. Antarctic fish tubulins: heterogeneity, structure, amino acid compositions and charge. *Comparative Biochemistry and Physiology*, **90B**, 593–600.

DeVries, A.L. 1988. The role of antifreeze glycopeptides and peptides in the freezing avoidance of Antarctic fishes. *Comparative Biochemistry and Physiology*, **90B**, 611–622.

DeVries, A.L. & Eastman, J.T. 1978. Lipid sacs as a buoyancy adaptation in an Antarctic fish. *Nature*, **271**, 352–353.

DeWitt, H.H. 1971. Coastal and deep-water benthic fishes of the Antarctic. *Antarctic Map Folio Series*, **15**. New York: American Geographical Society, 1–10.

Dunn, J.F. & Johnston, I.A. 1986. Metabolic constraints on burst-swimming in the Antarctic teleost *Notothenia neglecta*. *Marine Biology*, **91**, 433–440.

Dunn, J.F., Archer, S.D. & Johnston, I.A. 1989. Muscle fibre types and metabolism in post-larval and adult stages of notothenioid fish. *Polar Biology*, **9**, 213–223.

Eastman, J.T 1985. The evolution of neutrally buoyant notothenioid fishes: their specializations and potential interactions in the Antarctic marine food web. *In* Siegfried, W.R., Condy, P.R. & Laws, R.M., *eds*. *Antarctic nutrient cycles and food webs*. Berlin, Heidelberg: Springer-Verlag, 430–436.

Eastman, J.T. & DeVries, A.L. 1981. Buoyancy adaptations in a swim-bladderless Antarctic fish. *Journal of Morphology*, **167**, 91–102.

Eastman, J.T. & DeVries, A.L. 1982. Buoyancy studies of notothenioid fishes in McMurdo Sound, Antarctica. *Copeia*, **1982**, 385–393.

Egginton, S., Ross, H.F. & Sidell, B.D. 1987. Morphometric analysis of intracellular diffusion distances. *Acta Stereologica*, **6/III**, 449–454.

Everson, I. 1970. The population dynamics and energy budget of *Notothenia neglecta* Nybelin at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, No. 23, 25–50.

Fitch, N.A., Johnston, I.A. & Wood, R.E. 1984. Skeletal muscle capillary

https://doi.org/10.1017/S0954102089000167 Published online by Cambridge University Press

supply in a fish that lacks respiratory pigments. *Respiration Physiology*, **57**, 201–211.

FORSTER, M.E., FRANKLIN, C.E., TAYLOR, H.H. & DAVISON, W. 1987. The aerobic scope of an Antarctic fish, *Pagothenia borchgrevinki*. *Polar Biology*, **8**, 155–159.

HAMOIR, G. & GERARDIN-OTTHIERS, N. 1980. Differentiation of the sarcoplasmic reticulum proteins of white, yellowish and cardiac muscles of an Antarctic haemoglobin-free fish, *Champsocephalus gunnari*. *Comparative Biochemistry & Physiology*, **65B**, 199–206.

HARRISON, P., NICOL, J.M. & JOHNSTON, I.A. 1987. Gross morphology, fibre composition and mechanical properties of pectoral fin muscles in the Antarctic teleost, *Notothenia neglecta* Nybelin. *In* KULLANDER, S.O. & FERNHOLM, B., *eds*. *Proceedings Vth Congress European Ichthyology, 1985*. Stockholm: Swedish Museum Natural History, 459–465.

HEMMINGSEN, E.A. & DOUGLAS, E.L. 1970. Respiratory characteristics of the haemoglobin-free fish, *Chaenocephalus aceratus*. *Comparative Biochemistry & Physiology*, **33**, 733–744.

HILL, A.V. 1965. *Trails and trials in physiology*. London: Edward Arnold, 374 pp.

HOCHACHKA, P.W. 1985. Fuels and pathways as designed systems for support of muscle work. *Journal of Experimental Biology*, **115**, 149–164.

HOLETON, G.F. 1970. Oxygen uptake and circulation by a haemoglobin-less Antarctic fish (*Chaenocephalus aceratus* Lönnberg) compared with three red-blooded Antarctic fish. *Comparative Biochemistry & Physiology*, **34**, 457–471.

JOHNSTON, I.A. 1981. Structure and function of fish muscles. *In* DAY, M.H., *ed*. *Vertebrate locomotion*. *Symposia of the Zoological Society of London*, No. 48, London: Academic Press, 71–113.

JOHNSTON, I.A. 1983. Dynamic properties of fish muscle. *In* WEBB, P.W. & WEIHS, D., *eds*. *Fish biomechanics*. New York: Praeger, 36–67.

JOHNSTON, I.A. 1985. Temperature adaptation of enzyme function in fish muscle. *In* LAVERACK, M.S., *ed*. *Physiological adaptations of marine animals*. Cambridge: Cambridge University Press, 95–122.

JOHNSTON, I.A. 1987. Respiratory characteristics of muscle fibres in a fish (*Chaenocephalus aceratus*) that lacks haem pigments. *Journal of Experimental Biology*, **133**, 415–428.

JOHNSTON, I.A. & ALTRINGHAM, J.D. 1985. Evolutionary adaptation of muscle power output to environmental temperature:force-velocity characteristics of skinned fibres isolated from Antarctic, temperate and tropical marine fish. *Pflügers Archives*, **405**, 136–140.

JOHNSTON, I.A. & ALTRINGHAM, J.D. 1988. Muscle contraction in polar fishes: experiments with demembranated muscle fibres. *Comparative Biochemistry & Physiology*, **90B**, 539–548.

JOHNSTON, I.A. & BRILL, R. 1984. Thermal dependence of contractile properties of single skinned muscle fibres from Antarctic and various warm water marine fishes including skipjack tuna (*Katsuwonus pelamis*) and kawakawa (*Euthynnus affinis*). *Journal of Comparative Physiology*, **155B**, 63–70.

JOHNSTON, I.A. & CAMM, J.-P. 1987. Muscle structure and differentiation in pelagic and demersal stages of the Antarctic teleost *Notothenia neglecta*. *Marine Biology*, **94**, 183–190.

JOHNSTON, I.A. & DUNN, J. 1987. Temperature acclimation and metabolism with particular reference to teleost fish. *In* BOWLER, K. & FULLER, B.J., *eds*. *Temperature and animal cells*. *Society of Experimental Biology Symposium No. 41*, 67–93

JOHNSTON, I.A. & HARRISON, P.W. 1985. Contractile and metabolic characteristics of muscle fibres in Antarctic fish. *Journal of Experimental Biology*, **116**, 223–236.

JOHNSTON, I.A. & WALESBY, N.J. 1977. Molecular mechanisms of temperature adaptation in fish myofibrillar adenosine triphosphatases. *Journal of Comparative Physiology*, **119B**, 195–206.

JOHNSTON, I.A., CAMM, J.-P. & WHITE, M.G. 1988. Specialisations of swimming muscles in the pelagic Antarctic fish *Pleuragramma antarcticum*. *Marine Biology*, **100**, 3–12.

JOHNSTON, I.A., WALESBY, N.J., DAVISON, W., & GOLDSPINK, G. 1975. Temperature adaptation in myosin of Antarctic fish. *Nature*, **254**, 74–75.

JONES, D.R. & RANDALL, D.J. 1978. The respiratory and circulatory systems during exercise. *In* HOAR, W. S. & RANDALL, D.J., *ed*. *Fish physiology*, **7**. New York: Academic Press, 425–501.

KENNETT, J.P. 1977. Cenozoic evolution of Antarctic glaciation, the circumantarctic ocean and their impact on global paleoceanography. *Journal of Geophysical Research*, **82**, 3843–3876.

KILARSKI, W. & KOZLOWSKA, M. 1987. Comparison of ultrastructure and morphometrical analyses of tonic, white and red muscle fibres in the myotome of teleost fish (*Neomacheilus barbatulus* L.). *Zeitschrift für mikroskopische und anatomische Forschung*, **4**, 636–648.

KUNZMANN, A. 1987. Gill morphometrics of an Antarctic fish, *Pleuragramma antarcticum*. *In* KULLANDER, S.O. & FERNHOLM, B., *eds*. *Proceedings Vth Congress European Icthyology. 1985*. Stockholm: Swedish Museum Natural History, 467–468.

LITTLEPAGE, J.L. 1965. Oceanographic investigations in McMurdo Sound, Antarctica. *Antarctic Research Series*, **5**, 1–37.

MACDONALD, J.A. 1981. Temperature adaptation in the peripheral nervous system: Antarctic vs temperate poikilotherms. *Journal of Comparative Physiology*, **142**, 411–418.

MACDONALD, J.A., MONTGOMERY, J.C. & WELLS, R.M.G. 1987. Comparative physiology of Antarctic fishes. *Advances in Marine Biology*, **24**, 321–388.

MARSHALL, N.B. 1953. Egg size in Arctic, Antarctic and deep-sea fishes. *Evolution*, **7**, 328–341.

MCARDLE, H.J. & JOHNSTON, I.A. 1980. Evolutionary temperature adaptation of fish sarcoplasmic reticulum. *Journal of Comparative Physiology*, **135**, 157–164.

MCVEAN, A.R. & MONTGOMERY, J.C. 1987. Temperature compensation in myotomal muscle: Antarctic vs temperate fish. *Environmental Biology of Fishes*, **19**, 27–33.

MONTGOMERY, J.C. & MACDONALD, J.A. 1984. Performance of motor systems in Antarctic fishes. *Journal of Comparative Physiology*, **154**, 241–248.

MONTGOMERY, J.C. & MACDONALD, J.A. 1985. Oculomotor function at low temperature: Antarctic vs temperate fish. *Journal of Experimental Biology*, **117**, 181–191.

MONTGOMERY, J.C., MCVEAN, A.R. & MCCARTHY, D. 1983. The effects of lowered temperature on spontaneous eye movements in a teleost fish. *Comparative Biochemistry and Physiology*, **75A**, 363–368.

MORRIS, D.J. & NORTH, A.W. 1984. Oxygen consumption of five species of fish from South Georgia. *Journal of Experimental Marine Biology & Ecology*, **78**, 75–86.

NAG, A.C. & NURSALL, J.R. 1972. Histogenesis of white and red fibres of trunk muscles of a fish *Salmo gairdneri*. *Cytobios*, **6**, 227–246.

NORMAN, J.R. 1938. Coast fishes. Part III. The Antarctic zone. *Discovery Reports*, **18**, 1–104.

PERMITIN, YU. E. 1970. The consumption of krill by Antarctic fishes. *In* HOLDGATE, M.W., *ed*. *Antarctic ecology*. London: Academic Press, 177–182.

PRECHT, H. 1958. Concepts of the temperature adaptation in unchanging reaction systems of cold-blooded animals. *In* PROSSER, C.L., *ed*. *Physiological adaptation*. Washington DC: American Association for the Advancement of Science, 50–78.

RUUD, J.T. 1954. Vertebrates without erythrocytes and blood pigment. *Nature*, **173**, 848–850.

SIDELL, B.D. & HAZEL, J.R. 1987. Temperature affects the diffusion of small molecules through cytosol of fish muscle. *Journal of Experimental Biology*, **129**, 191–203.

SMIALOWSKA, E. & KILARSKI, W. 1981. Histological analysis of fibres in myotomes of Antarctic fish (Admiralty Bay, King George Islands). I. Comparative analysis of muscle fibre size. *Polish Polar Research*, **2**, 109–129.

WALESBY, N.J., NICOL, C.J.M. & JOHNSTON, I.A. 1982. Metabolic differentiation of muscle fibres from a haemoglobin-less (*Champsocephalus gunnari* Lönnberg) and a red- blooded (*Notothenia rossi* Fischer) Antarctic fish. *British Antarctic Survey Bulletin*, No. 51, 201–214.

WEATHERLEY, A.H. & GILL, H.S. 1985. Dynamics of increase in muscle fibers in fishes in relation to size and growth. *Experentia*, **41**, 353–354.

WEBB, P.W. 1975. Hydrodynamics and energetics of fish propulsion. *Bulletin of the Fisheries Research Board of Canada*, No. 190, 1–158.

https://doi.org/10.1017/S0954102089000167 Published online by Cambridge University Press