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Low Temperature Limits Burst Swimming Performance in Antarctic Fish

I.A. Johnston^{1,2}, T.P. Johnson,^{1,2} and J.C. Battram

1 Introduction

The temperature of the Southern Ocean varies from $-1.86\text{ }^{\circ}\text{C}$ at high latitudes to around $5\text{ }^{\circ}\text{C}$ towards the Antarctic Convergence. Seasonal variations in temperature are less than $0.2\text{ }^{\circ}\text{C}$ close to the permanent ice shelf (Littlepage 1965), and only $2.5\text{ }^{\circ}\text{C}$ in the northern Antarctic (Everson 1970). There is evidence that these stenothermal conditions have existed relatively unchanged for several million years (Kennett 1977). Antarctic fish have therefore become highly specialized to cold conditions, and their upper lethal temperatures are often only $5\text{--}6\text{ }^{\circ}\text{C}$ (Somero and DeVries 1967). Shallow-water species synthesize a variety of glycopeptide or peptide antifreezes to prevent the growth of ice crystals in the blood down to $-2.7\text{ }^{\circ}\text{C}$ (DeVries 1988). The nature of other adaptations which confer cold tolerance are relatively poorly understood (Clarke 1983; Johnston 1990). For example, although brain tubulins from antarctic fish assemble *in vitro* to form microtubules at $-2.3\text{ }^{\circ}\text{C}$, they have broadly similar isoelectric points and amino-acid compositions to their mammalian counterparts which are cold-labile (Detrich and Overton 1988). The rates of molecular diffusion and enzyme reactions slow markedly at low temperatures. Thus, in the absence of compensating mechanisms, physiological processes would be expected to proceed more slowly in antarctic than in temperate or tropical fish. The rate of embryonic development would appear to confirm this prediction; this is exemplified by the time from fertilization to hatching in *Harpagifer antarcticus*, which is around 100 days at $0\text{ }^{\circ}\text{C}$, compared with 36–48 h in warm temperate fish at $25\text{ }^{\circ}\text{C}$ (Blaxter 1988; Johnston 1990). However, there is evidence that other processes, such as locomotion and respiration, show varying degrees of temperature compensation (Clarke 1983, 1987; Johnston 1990). During burst swimming, ATP utilization by the fast muscle fibres increases over 100-fold very rapidly. Since maximum speed is an important factor determining the success of prey capture and predator avoidance it is crucial to the survival of individuals, and presumably subject to high selective pressures. Larval stages are capable of much higher tail-beat frequencies and length-specific speeds than adult fish because of scaling effects (Blaxter 1986). Thus the escape behaviour of larvae is an ideal place to look for the limits to cold adaptation in polar species.

¹Gatty Marine Laboratory, Department of Biology & Preclinical Medicine, University of St. Andrews, St. Andrews, Fife, Scotland KY16 8LB, UK

²Pacific Gamefish Research Foundation, 74-425 Kealahou Parkway, 15 Kailua Kona, Hawaii 96740, USA

2 Materials and Methods

2.1 Fish

Harpagifer antarcticus (Hureau) were obtained from the South Orkney Islands, Antarctica and transported to St. Andrews where they were maintained in a cold aquarium at 0-0.5 °C (12 h light:12 h dark). They were fed three times a week on squid and live shrimps (*Crangon crangon*). Gravid fish were transferred to darkened nursery tanks with a gravel substrate 3-4 weeks prior to spawning. The eggs hatched in 101-105 days. Larvae were fed brine shrimp nauplii and natural plankton which included various copepod species. The larvae began to feed prior to the exhaustion of the yolk sac, which occurred after 12-16 days.

Fourteen-day larvae of the dolphin fish (*Coryphaena hippurus*), reared at 24-26 °C, were obtained from the Waikiki Aquarium, Honolulu, Hawaii.

2.2 Measurement of Burst Swimming Speed

Measurements of burst swimming speed were made in a water-jacketed perspex tank 50 x 50 x 2 cm deep which had a 1-cm-square grid glued to the bottom of the tank. Antifreeze solution was circulated through the water jacket in order to maintain a constant temperature. The water in the tank was circulated by using a small electric pump. Individual larvae were introduced into the tank and observed using a National Panasonic WVP-F10E video camera with a strobe-effect shutter (1/1000th s exposure). Light from a 20-W bulb was reflected off a semi-silvered mirror set at an angle of 45° in front of the camera lens. Sharp silhouettes were obtained by using a "Scotchlite" reflex reflector background beneath the tank. Larvae were observed until they settled in the field of view of the camera (5 × 5 cm). Burst swimming sequences were stimulated by touching the larvae close to the caudal fin with a 1-mm-diameter glass pipette. Burst swimming sequences were recorded at a rate of 50 frames/s. Those sequences beginning with a startle or C-response, i.e. involving a sharp flexion of the body following stimulation, were analyzed frame-by-frame. Several burst swimming sequences were recorded over a 30-40-min period and the fastest selected for detailed analyses. The recordings were played back using a 63.5-cm-wide screen monitor and the outline of the larvae and the calibration grid traced onto a transparent overlay. The first two frames were excluded from the analysis due to the considerable lateral movement of the head following initiation of the startle response. The "true" mean speed was calculated by aggregating the displacements of the snout frame by frame over the first ten frames following the C-start (200 ms) (Yin and Blaxter 1987). The maximum speed was estimated from the largest straight-line displacement of the snout between any pair of consecutive frames between frame 3 and frame 10. At the end of the experiments, the total length of each larvae was recorded.

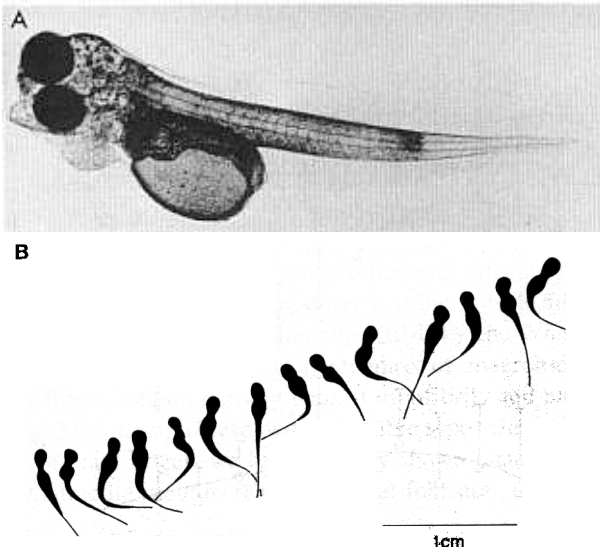


Fig. 1. **A** *Harpagifer antarcticus* larva at hatching. **B** Frame-by-frame tracing of an escape swimming sequence in response to tactile stimulation. Each successive frame is 20 ms apart

2.3 Results

An example of a C-start response in a newly hatched *Harpagifer antarcticus* larvae is shown in Fig. 1. All of the larvae were responsive to the probe at hatching. Escape swimming was characterized by large-amplitude body movements with a wavelength fractionally greater than one body length (Fig. 1). Frame-by-frame changes in speed during an escape response for 1-day-old yolk-sac larvae are shown in Fig. 2. Maximum speeds were attained after 40–60 ms and maintained for up to 240 ms (Fig. 2). Absolute true mean speed and maximum speed increased with length to 49 and 76 mm s⁻¹ in 9.2-mm end-of-yolk sac stage larvae. However, specific escape speeds calculated as body lengths s⁻¹ were similar in 1-day-old and 21–27-day-old *Harpagifer* larvae (Table 1). The escape speed of 21–27-day-old larvae also reached maximum values after 40–60 ms, but fell to around 40 mm s⁻¹ at 140 ms and were maintained at this level for up to 360 ms (not illustrated). Mean escape speeds (200 ms) and maximum speeds of 8-mm dolphin fish (*Coryphaena hippurus*) larvae in body lengths s⁻¹ were 2.4 times and 1.8 times higher than for equivalently sized *Harpagifer* larvae ($P < 0.01$); Table 1). The recording rate was not fast enough to accurately measure the tail-beat frequency of dolphin fish larvae at 25 °C, though in most cases it was close to 50 Hz over the first three to four strides, compared with around 15 Hz for *Harpagifer* larvae at 0 °C (Table 1).

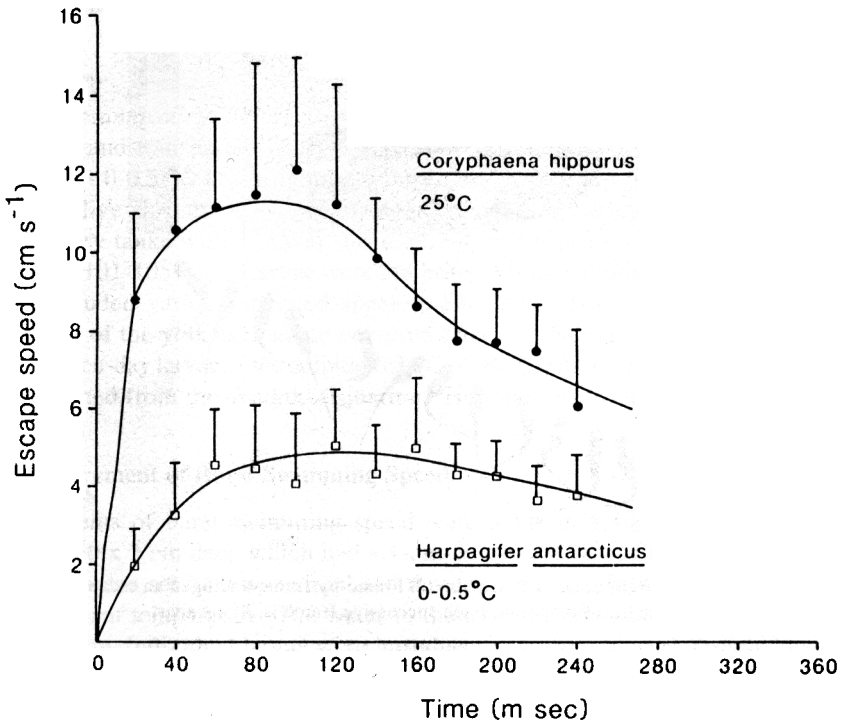


Fig. 2. Escape speeds of 1-day-old *Harpagifer antarcticus* larvae at 0 °C (n=9), and 14-day-old *Coryphaena hippurus* (14-day) larvae at 25 °C (n=9). Larvae were approximately 8 mm total length

Table 1. Burst swimming performance of fish larvae^a

Species	Stage	Total length (mm)	True mean speed (body lengths s ⁻¹)	Maximum speed (body lengths s ⁻¹)	Maximum tail-beat frequency (Hz)
<i>Harpagifer antarcticus</i>	Yolk sac 1 day	7.8 ± 0.6 (n = 9)	5.2 ± 1.0	8.2 ± 1.7	15.0 ± 2.1
<i>Harpagifer antarcticus</i>	End yolk sac 21-27 days	9.2 ± 0.5 (n = 7)	5.3 ± 0.3	8.3 ± 1.0	16.0 ± 1.7
<i>Coryphaena hippurus</i>	End yolk sac 14 days	8.0 ± 0.7 (n = 9)	12.6 ± 2.3	14.4 ± 2.4	30-50

^aValues represent mean ± SD.

3 Discussion

3.1 Swimming Behaviour

The larvae of *Harpagifer antarcticus* are relatively large and well advanced at hatching (see Fig. 1). The organization of the myotomal muscles in *Harpagifer* is typical of other fish larvae (Batty 1984; El-Fiky et al. 1987). Sustained swimming activity is supported by a thin layer of aerobic muscle fibres (2–4 μ diameter) situated immediately beneath the skin (Fig. 3). These fibres probably receive their oxygen supply directly across the skin, since functional gills are not present at this stage. In other species, the loss of these outer aerobic muscle fibres is correlated with the development of secondary gill lamellae (El-Fiky and Wieser 1988). Escape swimming behaviour is powered by the inner mass of anaerobic fibres (6–12 μ m diameter). These fibres contain densely packed myofibrils and have relatively few mitochondria (Fig. 3). Although these two larval fibre types are analogous to the slow and fast muscles of adult stages, we have recently shown that they contain different isoforms of the contractile proteins (Crockford and Johnston, unpubl. results).

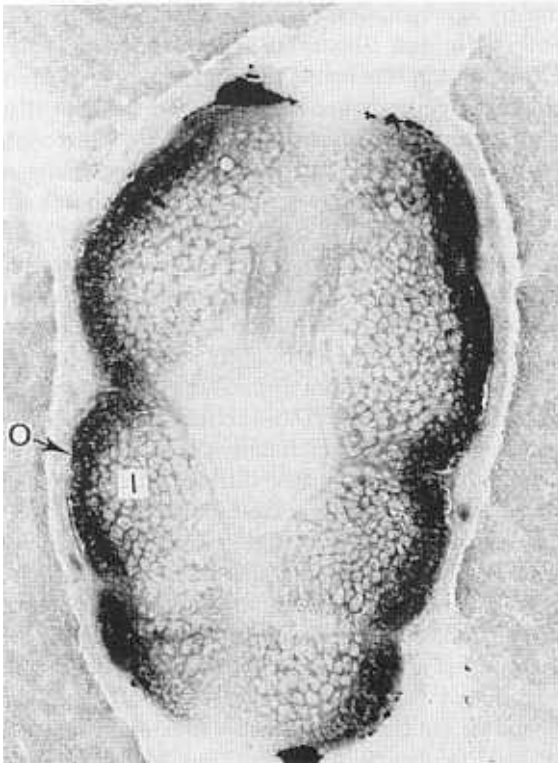


Fig. 3. Transverse frozen section through the trunk of a 1-day-old *H. antarcticus* larva stained for succinic dehydrogenase activity. Note the well-developed superficial layer of darkly stained aerobic muscle fibers (*O*) and the larger inner mass (*I*) of lightly stained anaerobic fibres

A variety of methods have been used to initiate startle responses in fish larvae, including electric shocks (Webb and Corolla 1981), natural predators (Webb 1981; Bailey and Batty 1984), acoustic stimuli (Blaxter and Batty 1985), and tactile stimuli (Yin and Blaxter 1987). Yin and Blaxter (1987) triggered C-starts either using a 0.2-mm-diameter probe or by attempting to suck the larvae into a 1.5-mm-diameter pipette. For cod, plaice, and herring, but not flounder, significantly higher maximum speeds and response rates were obtained using the pipette. Preliminary experiments with *Harpagifer* showed that touching and sucking with the pipette produced similar maximum speeds, suggesting it is the size of the probe which is important. The maximum swimming speed recorded between consecutive frames is dependent on the filming speed and is lower using conventional video (Bailey and Batty 1984; Blaxter and Batty 1985; Yin and Blaxter 1987) than when using cine film at 150–200 frames s^{-1} (Fuiman 1986). At 17 °C, northern anchovy larvae (8 mm length) accelerate over 8–16 ms to reach their prey, travelling a distance of about 0.4 mm (Hunter 1972). Thus maximum speed is likely to be the major performance component of larval behaviour determining the outcome of encounters with prey, whereas both speed and endurance will affect interactions with predators and nets (Webb and Corolla 1981). In the present study we have calculated the mean escape speed over 200 ms by aggregating the straight-line displacement of the snout over the first ten frames (Yin and Blaxter 1987). In order to evaluate interspecific differences in performance, it is essential to compare larvae of equivalent size, since the speed and tail-beat frequency are highly scale-dependent (Blaxter 1986). For example, speeds as high as 64 body lengths s^{-1} have been recorded at 28 °C, for newly hatched zebra danios which are only 2–3 mm long (Fuiman 1986). Data on swimming speeds for approximately 8-mm larvae analyzed in a similar manner are presented in Fig. 4. *Harpagifer antarcticus* larvae have mean escape speeds which are about half that for plaice and herring at 9–11 °C, and around 40% of that for anchovy and dolphin fish at 17–25 °C. Perhaps more significantly, the maximum tail-beat frequency in dolphin fish and plaice is around 30–50 Hz, compared with only 15 Hz in *Harpagifer* (see Table 1). Slightly larger post-larvae (1.07 cm) of the flying fish (*Hirundichthys affinis*) from tropical seas have been reported to achieve 35.9 body lengths s^{-1} for short periods (80–120 ms) at 20–25 °C (Davenport 1990). Unfortunately, comparisons of the maximum speeds achieved by adult stages are complicated by variations in body shape, different methods of analysis, and the limited and variable nature of the available data. Archer and Johnston (1989) carried out a detailed kinematic study of burst swimming in static water in juvenile (7–8 cm) *Notothenia neglecta*. They found that values for length-specific maximum swimming speed (8.7 body lengths s^{-1}) and tail-beat frequency (11.1 Hz) were lower than reported for temperate species of similar size (Archer and Johnston 1989). A modest burst swimming performance has also been reported for the cryopelagic antarctic fish *Pagothenia borchgrevinki* (Montgomery and Macdonald 1984), which at –1.5 °C and 23 cm total length had a maximum speed of only 4.9 body lengths s^{-1} at a tail-beat frequency of 5.7 Hz. Thus, although limited, the available data are consistent with the view that low temperature constrains burst swimming performance in polar fish, particularly for the early life stages.

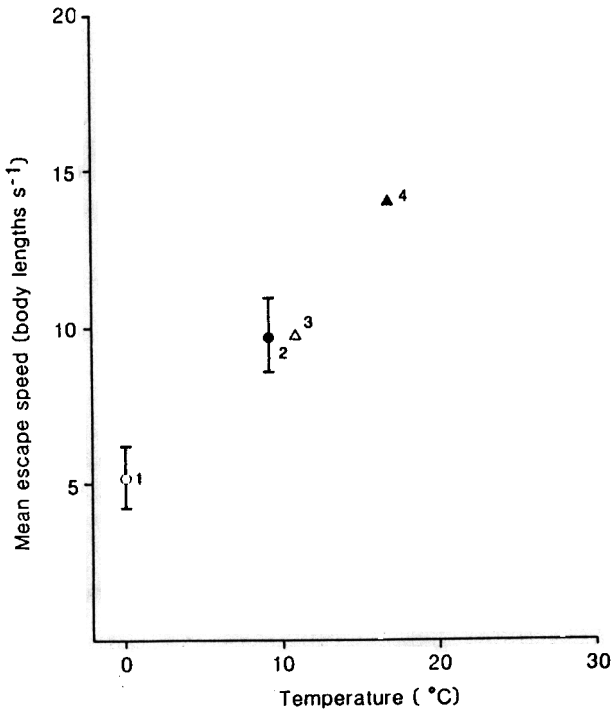


Fig. 4. Mean escape speeds of antarctic, temperate and tropical fish larvae, all 8 mm total length. 1 *Harpagifer antarcticus* (this study). 2 Baltic herring (*Clupea harengus*; Yin and Blaxter 1987). 3. Plaice (*Pleuronectes platessa*; Bailey and Batty 1984). 4. Northern anchovy (*Engraulis mordax*; Webb and Corolla 1981). 5. *Coryphaena hippurus* (this study)

3.2 Muscle Contractile Properties

During swimming, muscle fibres alternately shorten and lengthen and are physically stimulated during each tail-beat cycle. Under these conditions, power output is a complex function of the amplitude and frequency of the locomotory movements and the timing of nervous stimulation in relation to changes in muscle length (Johnston and Altringham 1988; Van Leeuwen et al. 1990). Although the power output of fish muscle has been measured under conditions simulating swimming (Altringham and Johnston 1990a), this approach has not yet been applied to the study of temperature adaptation. In teleosts, the temperature range over which isolated muscle fibres remain viable is strongly correlated with the habitat temperature (Fig. 5). Thus, myotomal fibres from the tropical species (*Thalossoma duperreyi*) develop little force below 10 °C, whereas conversely, fibres from the Antarctic species (*Pseudochaenichthys georgianus*) are inexcitable at this temperature (Fig. 5). Altringham and Johnston (1986) used skinned muscle fibres to determine the energy cost of maintaining tension under force-generating conditions. They found that whilst the force-temperature relation differed markedly between species, ATPase activity was remarkably similar. Thus, at 0 °C, the economy of contraction decreased markedly in the order antarctic > North Sea > tropical species. The

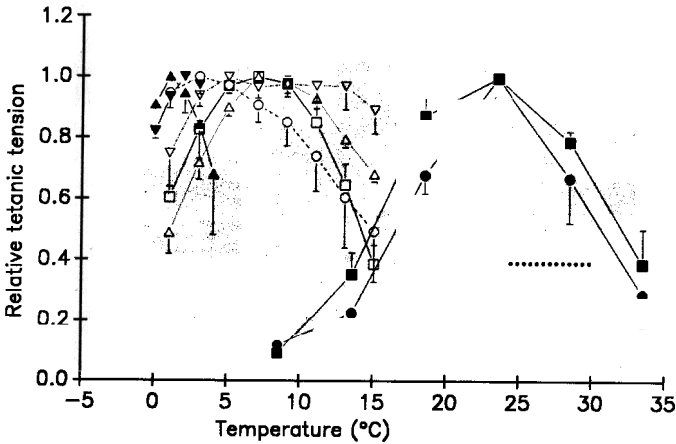


Fig. 5. The relationship between relative tetanic tension (normalized to the maximum at the normal habitat temperature) and experimental temperature for live, fast, myotomal and fin muscle preparations from antarctic, temperate and tropical marine teleosts. The symbols refer to the following species: Antarctic \blacktriangledown — \blacktriangledown *Trematomus lepidorhinus*, \blacktriangle — \blacktriangle *Notothenia neglecta*; Temperate \triangle — \triangle Saithe (*Pollachius virens*), \circ — \circ Dab (*Limanda limanda*), \square — \square Dragonet (*Callionymus lyra*), ∇ — ∇ Pogge (*Agonis cataphractus*); Tropical \blacksquare — \blacksquare Hawaiian Sergeant (*Abudefduf abdominalis*), \bullet — \bullet Saddle Wrasse (*Thalassoma duperryi*). Data represent the mean \pm SE. The normal environmental temperature range (Johnson and Johnston 1991)

economy of contraction of fibres from *Notothenia neglecta*, at normal body temperatures, is around twice as high as that of representative temperate species, and four times that of tropical species (Altringham and Johnston 1986). These results may be explained by (1) an uncoupling of ATPase activity and force generation at low temperatures in warm adapted species; or (2) an increase in the force produced per cross bridge cycle in the cold water species. The latter could be achieved through an increase in bound time (and hence the number of attached cross-bridges), and/or more force per cycle with no change in bound time. Experiments with skinned rabbit psoas muscle fibres show that at 5 °C, about two-thirds of the cross bridges are in the "force generating" state which suggests that both mechanisms are probably needed to explain increases in force with temperature within species (Brenner 1986). These adaptations in force generation are associated with changes in myosin structure (Johnston and Walesby 1977). Myosins from cold-water fish belong to an unstable type which rapidly aggregate on isolation, and are readily denatured by heat and urea (Connell 1961). However, the amino acid composition and subunit composition of these and mammalian myosins are similar (Connell 1958a, b; Rowleson et al. 1985). Johnston et al. (1975) reported that the -SH groups of myosin from the antarctic species, *Notothenia rossii*, reacted with 5,5'-dithio bis-2-nitrobenzoic acid 15 times faster than myosin from the Indian Ocean species *Amphiprion sebae*. This suggests that -SH groups in the cold-water species are more accessible, possibly reflecting a relatively open tertiary structure.

Studies with skinned fibres have shown, that, in contrast to force production, unloaded contraction velocity (V_{max}) shows no evidence for temperature compensation (Johnston and Brill 1984). Thus V_{max} is around 1 muscle lengths s^{-1} for the

antarctic species *Trematomus hansonii* at 0 °C and > 9 muscle lengths s⁻¹ in the tropical scrombroid (*Euthymus affinis*) at 28 °C (Johnston and Brill 1984; Johnston and Harrison 1985). Recently, similar results have also been reported for live muscle fibres (Johnson and Johnston 1991). The force-velocity (P-V) relationship becomes less curved as experimental and/or body temperature decreases, and this could provide a mechanism for partially compensating for the reduction in power output as both force and velocity decline (Johnston and Altringham 1985; Langfeld *et al.* 1989). For example, the change in curvature for fast muscles fibres from *Myoxocephalus scorpius* between 8 and 1 °C has been calculated to increase relative maximum power output by around 15% (Langfeld *et al.* 1989). This is because at a given load, a less curved force-velocity relationship yields a higher velocity, and thus a greater power output. However, such effects could only account for a modest temperature compensation of contraction velocity under load *in vivo*.

Twitch duration is greatly prolonged at low temperatures in tropical compared with cold-water species; this is largely due to differences in relaxation rate (Fig. 6). The mechanism underlying cold-adaptation of relaxation includes faster rates of calcium sequestration by the sarcoplasmic reticulum (SR). For example, at 0 °C, SR isolated from the fast muscle of *Notothenia rossii* accumulates Ca²⁺ at six times the rate of SR from the fast muscle of several tropical fish (McArdle and Johnston 1980). However, the degree of temperature compensation shown by relaxation is only partial, and on average, twitch duration is around four times shorter at the characteristic body temperature of Indo-West Pacific (23–26 °C) than antarctic (-1 to 1 °C) fish (Fig. 6). These results would suggest that maximum tail-beat frequency is limited by low temperature in polar species.

Altringham and Johnston (1990b) measured the power output of fast muscle fibres from cod (*Gadus morhua* L.) under conditions simulating swimming. They found that relative to isometric conditions, force, and the rates of rise and fall of force, are increased, and the duration of the contractile event is decreased. Therefore positive oscillatory work can be performed at somewhat higher frequencies than might be predicted from the time course of isometric contractions alone (Altringham and Johnston 1990b). Indeed, studies with isolated lizard (Marsh and Bennett 1985) and salamander (Else and Bennett 1987) muscles have shown a poor correlation between the time course of isometric twitches and limb cycling times, particularly at low temperatures. For example, during burst running in the salamander *Ambystoma tigrinum nebulosum*, the extension phase of the limb requires 203 ms at 10 °C, whereas the isometric twitch duration was in excess of 400 ms (Else and Bennett 1987). However, a much closer agreement between locomotory and muscle properties was found at preferred body temperatures (> 20 °C; Else and Bennett 1987). Similarly, the twitch duration of fast myotomal muscle in adult *Notothenia neglecta* is 114 ms at 1 °C (Johnson and Johnston 1990), and is comparable with the tail-beat cycle of 152 ms (Archer and Johnston 1989).

Modelling studies have shown that for anterior myotomes, positive work is produced throughout each tail-beat cycle, whereas net negative work is done in posterior myotomes (Hess and Videler 1984; Van Leeuwen *et al.* 1990). These differences result from systematic changes in the phase relation between length and force cycles (Johnston and Altringham 1988). Further complications result from the variable and complex orientation of fibres within myotomes, patterns of fibre

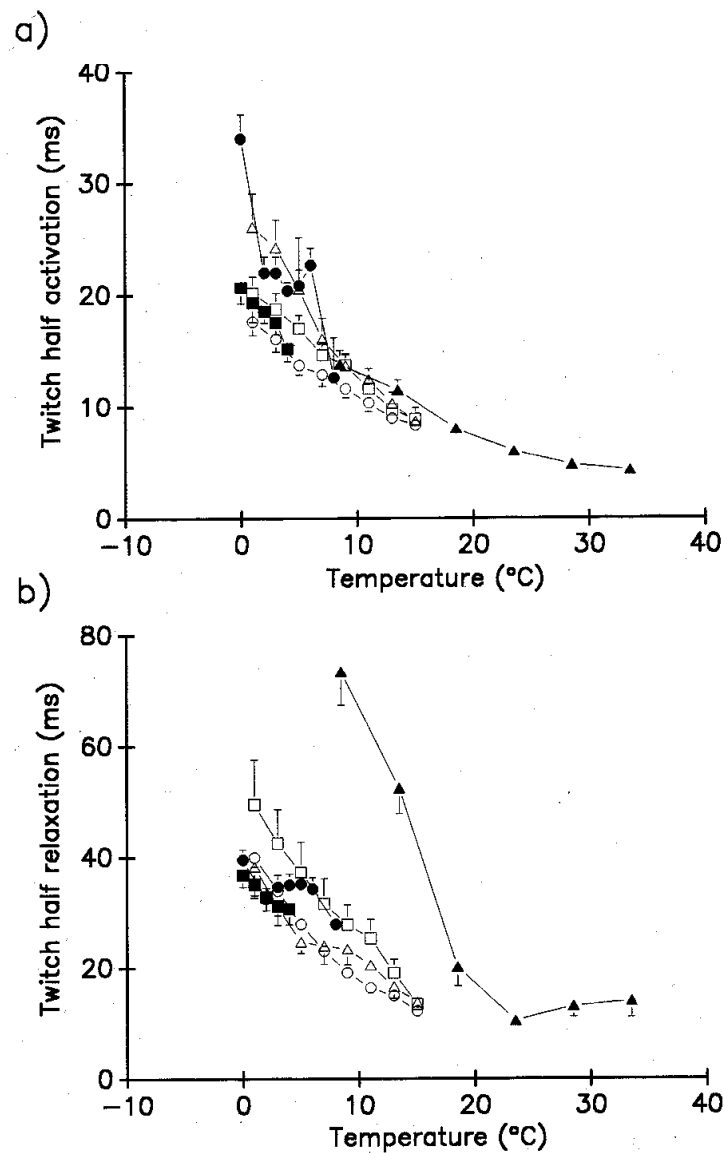


Fig. 6. The relationship between experimental temperature and (a) twitch half-activation time (ms) and (b) twitch half-relaxation time (ms), for live, fast myotomal muscle preparations from antarctic, temperate and tropical teleost marine species. The symbols refer to the following species: Antarctic ● icefish (*Pseudochaenichtys georgianus*), ■ *Notothenia neglecta*; temperate ○ saithe (*Pollachius virens*), △ dab (*Limanda limanda*), □ dragonet (*Callionymus lyra*); tropical ▲ saddle wrasse (*Thalassoma duperreyi*). Data represent mean \pm SE (Johnson and Johnston 1991)

recruitment and the passive properties of series and parallel elastic components. Although there is no simple relationship between whole animal performance and the properties of isolated muscle fibres, such studies have provided important insights into the mechanisms underlying cold adaptation of locomotion.

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