

KINEMATICS OF LABRIFORM AND SUBCARANGIFORM SWIMMING IN THE ANTARCTIC FISH *NOTOTHENIA NEGLECTA*

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Summary

1. The kinematics of labriform and subcarangiform swimming have been investigated for juvenile (7–8 cm) and adult (27–30 cm) stages of the antarctic teleost *Notothenia neglecta* Nybelin at 1–2°C.

2. Upper threshold speeds using the pectoral fins alone (labriform swimming) were 0.8 L s⁻¹ in adult fish and 1.4 L s⁻¹ in juveniles, where L is body length.

3. In adult fish, steady subcarangiform swimming is only used at speeds of 3.6–5.4 L s⁻¹ (tail-beat frequencies of 5.0–8.3 Hz). Intermediate speeds involve unsteady swimming. In contrast, juvenile fish employ subcarangiform swimming at a range of intermediate velocities between the maximum labriform and burst speeds (2.3–8.4 L s⁻¹ at tail-beat frequencies of 4.0–12.5 Hz). These differences in swimming behaviour are discussed in relation to changes in life-style and muscle fibre type composition between juvenile and adult fish.

4. Burst swimming speeds in *N. neglecta* have been compared with equivalent data from temperate species. It seems likely that low temperature limits swimming performance in antarctic fish. This is more noticeable in juvenile stages, which normally have much higher tail-beat frequencies than adult fish.

Introduction

The water temperature of the Southern Ocean has been close to or lower than 0°C for 5–10 million years (Kennett, 1977). Seasonal changes in temperature are less than 0.2°C at high latitudes (Littlepage, 1965), and only 2.5°C in the northern Antarctic (Everson, 1970). There are numerous examples of resistance or tolerance adaptations that allow antarctic fish to withstand these very low temperatures (Clarke, 1983; Macdonald *et al.* 1987). The presence of glycoprotein antifreezes in the body fluids of antarctic fish prevents the growth of ice crystals in the blood plasma at temperatures down to -2.7°C (DeVries & Lin, 1977). Membranes and proteins have structures which are specialized for function at around 0°C (Cossins & Bowler, 1987). For example, brain tubulin subunits from antarctic fish assemble *in vitro* and remain stable at the low ambient temperatures

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experienced by these fish, whereas homologous proteins from homeotherms depolymerize at similar temperatures (Dietrich & Overton, 1986). Many physiological processes, including Ca^{2+} pumping by the sarcoplasmic reticulum (McArdle & Johnston, 1980) and muscle tension generation (Johnston & Altringham, 1985), show partial or complete capacity adaptations relative to warm-water species (Clarke, 1987). However, not all rate processes exhibit temperature compensation: for example, the unloaded contraction velocity of skinned muscle fibres shows little variation at 0°C between tropical, temperate and antarctic fish (Johnston & Brill, 1984).

There have been relatively few studies of temperature adaptation at higher levels of organization (Macdonald *et al.* 1987). In several antarctic species the velocity of the fastest eye movements at -1.9°C are about half that of a temperate-water fish acclimated to 14°C (Montgomery & Macdonald, 1984). Eye movements of the warm temperate water fish extrapolate to zero velocity at $3-4^{\circ}\text{C}$ and cease at 5°C (Montgomery & Macdonald, 1984). Montgomery & Macdonald (1984) found evidence that the maximum swimming speed of the cryopelagic species *Pagothenia borchgrevinki* showed only slight capacity adaptation. The aim of the present study was to obtain a detailed kinematic analysis of sustained and burst swimming behaviour in pelagic and demersal stages of the antarctic fish *Notothenia neglecta* Nybelin. The results are discussed in relation to similar data from temperate and tropical species.

Materials and methods

Fish

Notothenia neglecta (Nototheniidae; Notothenioidei; Perciformes) were obtained from the South Orkney Islands, Antarctica, and transported to St Andrews, Scotland. Fish were maintained in tanks of filtered recirculated sea water at $+2^{\circ}\text{C}$ within an air-temperature controlled cold-room. When not being used for swimming analysis, fish were fed twice a week to satiation on a diet of chopped squid, herring or krill.

Four adult fish (total length 26.9–30.5 cm) and four juvenile fish (total length 7.1–8.1 cm) were used.

Methods

Fish were trained to swim along a 4 m long raceway, by association of an underwater flashing light with the appearance of food, as described by Wardle & Kanwisher (1974). Three to four fish were kept in the raceway at a time to stimulate a competitive situation and induce burst swimming sequences. Spontaneous swimming along the raceway was also filmed and analysed.

A video camera (JVC KY-2700 CVC) was positioned 170 cm above the base of the raceway to provide dorsal views of swimming sequences. Lateral views were obtained by filming through a window in the side of the raceway. A background illumination lighting system (Wardle, 1975; Videler, 1981), together with reflex

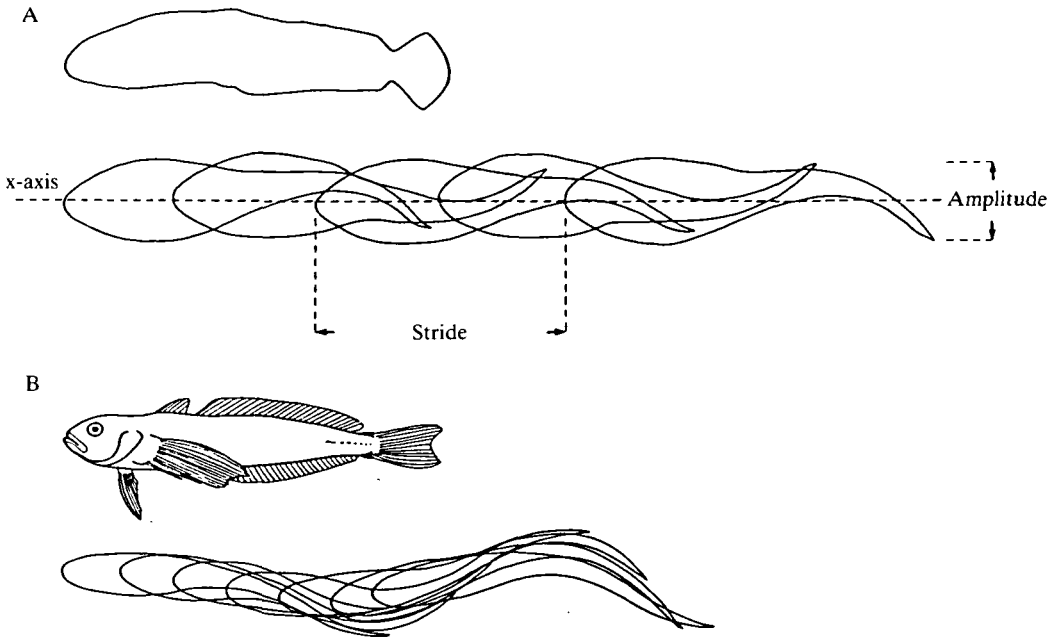


Fig. 1. Diagrams illustrating subcarangiform motion in *Notothenia neglecta*. (A) Adult: lateral and dorsal profiles during burst swimming. Tracings of dorsal profiles were made at positions of maximum amplitude of the tail during a two-stride sequence. Fish total length 30.5 cm, forward velocity 4.5 L s^{-1} (136 cm s^{-1}), tail-beat frequency 6.4 Hz, amplitude 0.19 L and stride 0.70 L. (B) Juvenile: lateral body profile when stationary, dorsal profile of body positions of 0.02 s intervals during a complete tail-beat cycle or stride. Fish total length 7.1 cm, forward velocity 7.0 L s^{-1} (50 cm s^{-1}), tail-beat frequency 8.3 Hz, amplitude 0.27 L and stride 0.85 L.

reflector material (Scotchlite 3M) on the base and side of the raceway, produced dark silhouettes of the fish against a bright background, while maintaining overall low light levels needed for the fish to perform.

Film analysis

Two distinct swimming modes were examined, labriform and subcarangiform motion. The transition from labriform to subcarangiform swimming was also examined in the adult fish.

Video recordings (50 frames s^{-1}) were analysed frame by frame, with a dubbed time interval of 0.02 s. A 5 cm grid was marked on the base and side of the raceway, the scale was accordingly corrected for the level at which the fish swam, and movement recorded with reference to the grid. Forward velocity was measured along an x-axis, the path of motion; x values of the tip of the head were obtained for each frame of a swimming sequence. Tail-beat frequency, tail-beat amplitude and stride length (the distance moved over one complete tail-beat cycle) were measured for each sequence of steady subcarangiform swimming (Fig. 1A).

Kinematic parameters recorded during labriform motion included pectoral fin

beat frequency, pectoral fin adduction time and the stride (the distance moved over one complete pectoral fin-beat cycle). Measurements of adduction time of the leading edge of the pectoral fin and amplitude of the fin beat were also possible in the adult fish.

Statistical analysis

Velocity in the x direction was estimated to be the mean value of five dx/dt values around $t = n$:

$$d_x/d_{t=n} = f\left(\frac{1}{12}x_{(n-2)} - \frac{2}{3}x_{(n-1)} + \frac{2}{3}x_{(n+1)} - \frac{1}{12}x_{(n+2)}\right),$$

where f is the number of frames per second (Videler & Wardle, 1978). Labriform swimming velocity was estimated at 0.04 s intervals ($f = 25$), analysis of subcarangiform motion was carried out at 0.02 s intervals ($f = 50$). Only steady swimming sequences with a standard error (s.e.) of mean forward velocity values of less than 5% were used for analysis of labriform and subcarangiform motion.

The five fastest subcarangiform swimming sequences and the five fastest sequences of labriform swimming were obtained for each fish. These provided mean fastest subcarangiform and labriform motion parameters for each fish ($N = 5$) and for each size group ($N = 20$).

Comparison of length-specific swimming velocity and kinematics was made between juvenile and adult fish. A nested two-way analysis of variance (Sokal & Rohlf, 1981) was carried out to determine the significance of variation between fish within each size and between size groups. Because of the low number of steady swimming sequences obtained for fish no. 6 and in order to obtain a balanced design for the nested two-way analysis of variance, one set of data from the adult fish was dropped. This provided data from three fish of each size group, with one missing term for fish no. 8.

Results

Description of the labriform stroke

Sustained low-speed swimming is achieved by using large, fan-shaped pectoral fins, in a drag-based, labriform mode of locomotion. The pectoral fin-beat pattern is similar to pattern A described for *Cymatogaster aggregata* (Webb, 1973).

The main power stroke involved in labriform motion is the adduction phase (Fig. 2A–D). Successive fin rays, joined by a highly flexible membrane, move both laterally backwards and vertically upwards, producing 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, before the abduction stroke commences. Abduction of the fin involves both laterally forward and vertically downward motion of the fin rays. Abduction occurs in two stages. Initially the fin is abducted to a glide position (Fig. 2E) and, just prior to adduction, the leading edge moves anteriorly and ventrally again to begin the adduction stroke (Fig. 2A).

Unlike in *C. aggregata*, the main refractory period of the fin-beat cycle in

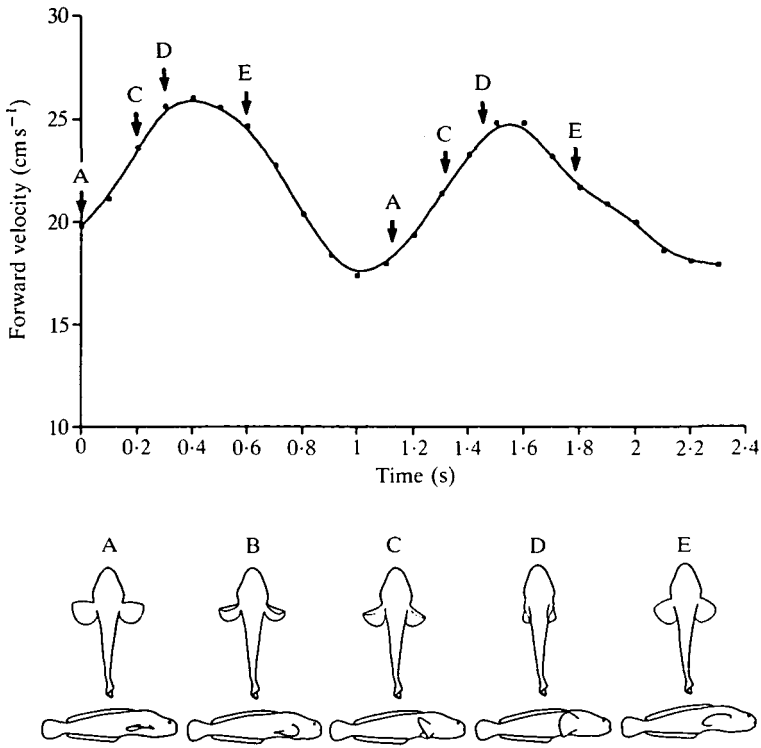


Fig. 2. Diagram illustrating labriform motion in adult *Notethenia neglecta*. The forward velocity over two complete pectoral fin-beat cycles, and a diagrammatic representation of the pectoral fin-beat pattern are shown. A–C, adduction time of the leading edge of the pectoral fin; A–D, the complete adduction stroke; D–E, abduction; and E–A, the glide period.

N. neglecta occurs when the fin is abducted, not adducted. This may in part be due to the negative buoyancy of *N. neglecta*, as the abducted pectoral fin provides lift during the glide period.

Labriform swimming kinematics

The kinematics of the five fastest labriform sequences observed for each fish are summarized in Table 1. One of the fingerling fish was only filmed once during a steady labriform swimming sequence and is therefore not included in the table. Fingerling fish no. 8 was only filmed four times during steady labriform motion, so the values listed for that fish are not necessarily the fastest speeds obtainable.

Forward swimming velocity was significantly different among individuals within each size group ($P \leq 0.05$). Despite this, a nested analysis of variance indicates that significant variation between size groups also occurred ($P \leq 0.01$). Juvenile fish accomplished length-specific speeds using labriform swimming ($1.36 \pm 0.26 \text{ L s}^{-1}$) that were nearly twice those obtained for the adult fish ($0.78 \pm 0.12 \text{ L s}^{-1}$) ($P \leq 0.01$). Pectoral fin-beat frequencies and pectoral fin adduction times were

Table 1. Kinematics of labriform swimming in the antarctic teleost *Notothenia neglecta*

Fish no. (L, cm)	Forward velocity ($L s^{-1}$)	($cm s^{-1}$)	Pectoral fin adduction time (s)	Leading edge adduction time (s)	Pectoral fin-beat frequency (Hz)	Amplitude (rad)	Stride length (L)
Adult fish							
1 (30.5)	0.70 ± 0.07	21 ± 2	0.35 ± 0.02	0.23 ± 0.02	1.02 ± 0.18	1.79 ± 0.10	0.68 ± 0.09
2 (29.5)	0.72 ± 0.09	21 ± 3	0.35 ± 0.04	0.21 ± 0.04	1.03 ± 0.11	1.83 ± 0.06	0.70 ± 0.11
3 (26.9)	0.85 ± 0.11	23 ± 3	0.34 ± 0.04	0.19 ± 0.03	1.02 ± 0.11	1.86 ± 0.09	0.80 ± 0.02
4 (30.2)	0.86 ± 0.09	26 ± 3	0.31 ± 0.02	0.20 ± 0.03	0.95 ± 0.09	1.82 ± 0.21	0.91 ± 0.07
Mean (L)	0.78 ± 0.12	23 ± 0.3	0.34 ± 0.04	0.21 ± 0.03	1.01 ± 0.13	1.83 ± 0.12	0.77 ± 0.12
Juvenile fish							
5 (8.1)	1.59 ± 0.12	13 ± 1	0.21 ± 0.02		1.72 ± 0.25		0.93 ± 0.13
7 (7.2)	1.23 ± 0.22	9 ± 2	0.23 ± 0.05		1.70 ± 0.29		0.73 ± 0.18
8* (7.1)	1.24 ± 0.26	9 ± 1.8	0.20 ± 0.02		1.70 ± 0.30		0.69 ± 0.16
Mean (L)	1.36 ± 0.26	10 ± 2	0.21 ± 0.03		1.71 ± 0.26		0.78 ± 0.18

* $N = 4$.Values represent mean \pm s.e.

Measurements are of the five fastest labriform sequences from each of four adult and three juvenile fish.

Table 2. Kinematics of burst swimming in the antarctic teleost *Notothenia neglecta*

Fish no. (L, cm)	Forward velocity (L s ⁻¹)	Forward velocity (cm s ⁻¹)	Tail-beat frequency (Hz)	Tail-beat amplitude (L)	Stride length (L)
Adult fish					
1 (30.5)	4.2 ± 0.2	128 ± 5.8	6.3 ± 0.2	0.20 ± 0.02	0.67 ± 0.05
2 (29.5)	4.2 ± 0.3	127 ± 9.8	6.1 ± 0.8	0.19 ± 0.04	0.70 ± 0.04
3 (26.9)	4.7 ± 0.5	127 ± 12.5	7.1 ± 0.9	0.21 ± 0.03	0.67 ± 0.06
4 (30.2)	4.1 ± 0.4	123 ± 11.6	6.9 ± 0.2	0.18 ± 0.02	0.59 ± 0.06
Mean (L)					
29.3 ± 1.6	4.3 ± 0.4	126 ± 9.7	6.6 ± 0.6	0.20 ± 0.03	0.66 ± 0.06
Juvenile fish					
5 (8.1)	6.2 ± 1.0	50 ± 7.8	10.0 ± 1.5	0.27 ± 0.01	0.63 ± 0.13
6 (7.9)	6.7 ± 1.0	53 ± 8.2	8.3 ± 0.9	0.29 ± 0.03	0.81 ± 0.12
7 (7.2)	6.8 ± 0.4	49 ± 3.3	8.2 ± 1.2	0.29 ± 0.04	0.83 ± 0.07
8 (7.1)	7.4 ± 1.3	53 ± 9.7	9.1 ± 1.5	0.31 ± 0.05	0.82 ± 0.12
Mean (L)					
7.6 ± 0.5	6.8 ± 1.0	51 ± 7.2	8.9 ± 1.4	0.29 ± 0.04	0.77 ± 0.14

Values represent mean ± s.e.
Five sets of measurements were made from each of four fish of each size range.

also significantly shorter in juvenile than in adult fish ($P \leq 0.01$). However, the length-specific distance moved forward during a fin-beat cycle, the stride, was not significantly different between the size groups (Table 1). The transparent nature of the juvenile pectoral fin made more detailed analysis of the pectoral fin-beat cycle difficult with the filming technique used.

Subcarangiform motion

Faster swimming speeds are achieved by employing a subcarangiform mode of locomotion. Pectoral and pelvic fins are adducted against the body, the dorsal and anal fins are partly erected (Fig. 1).

A summary of the burst swimming kinematics of each of the fish studied is included in Table 2. No significant differences in kinematic parameter were found among fish of the same size group.

The fastest length-specific sprint swimming speeds were significantly higher in juvenile fish than in adults ($P \leq 0.02$). The specific amplitude of the tail-beat was also significantly higher in the juvenile fish ($P \leq 0.02$). Higher tail-beat frequencies and strides were observed in the juvenile fish, although these were not significantly different at the $P \leq 0.5$ level (Table 2).

Labriform to subcarangiform transition

Several sequences of the transition from labriform to subcarangiform motion were analysed for adult *N. neglecta*. The response of fish provoked by flashing of the underwater light was analogous to fast starts described by Webb (1978) and

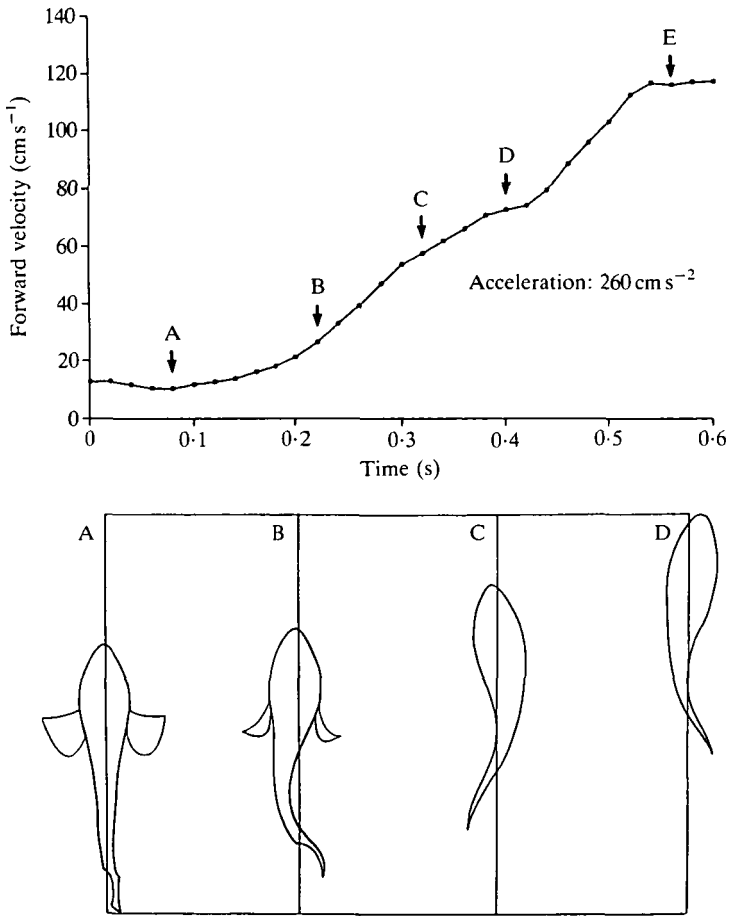


Fig. 3. Diagram of the transition from labriform to subcarangiform motion at the start of a burst swimming sequence, in an adult *Nothethenia neglecta*. Acceleration was calculated over the first two strides, first stride B–D (0.31 L), second D–E (0.51 L). Tail-beat frequency 5.9 Hz, amplitude 0.24 L. Pectoral fin adduction time (A–C) 0.24 s.

Weih's (1973). A preparatory stroke involving movement of the trunk into a 'C-start' position was coupled to rapid adduction of the pectoral fins. Caudal fin propulsive strokes of high amplitude accelerated the fish to a maximum velocity. In the majority of cases, a maximum velocity was only reached after at least two complete tail-beat cycles (Fig. 3). During a typical fast start, maximum velocity is reached at the end of kinematic stage 2 (the first propulsive stroke), with maximum acceleration occurring during stage 1 (Webb, 1978).

Fastest acceleration was observed during a transition sequence performed by fish no. 4 (total length 30.2 cm). Acceleration over two strides was 301 cm s⁻², tail-beat frequency was 7.14 Hz and amplitude 0.21 L. Full adduction time of the

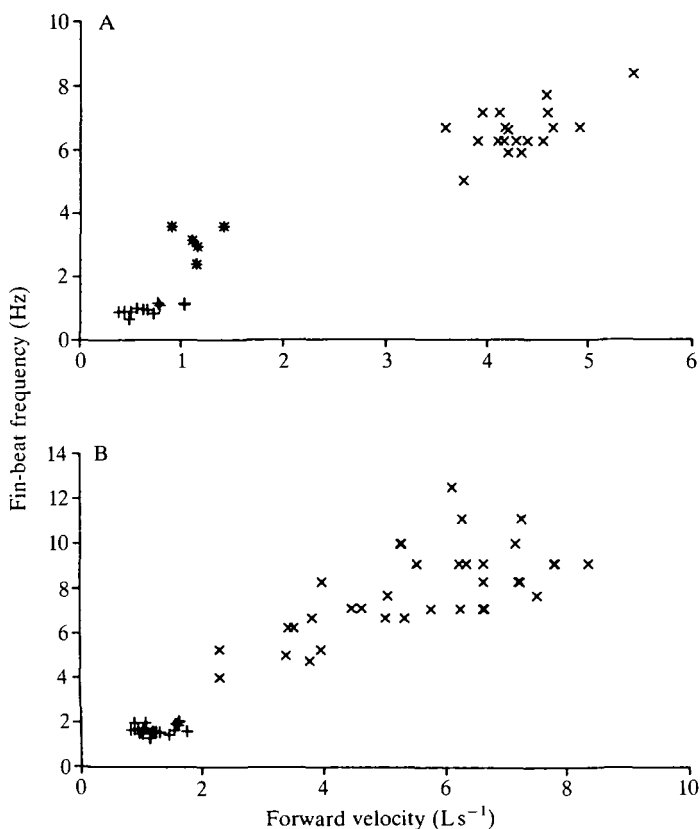


Fig. 4. Swimming behaviour in adult (A) and juvenile (B) *Notothenia neglecta*, illustrating the length-specific speeds at which different swimming modes are utilized. Points are single steady swimming sequences. +, labriform; ×, subcarangiform; *, mixed motion.

pectoral fins (0.22 s) was considerably quicker than that observed during steady labriform motion.

Range of swimming mode

A comparison of range of swimming speeds at which different steady swimming modes are employed in juvenile and adult fish is shown in Fig. 4. The juvenile fish exhibit a greater range of steady subcarangiform speeds (2.3–8.4 Ls⁻¹), and tail-beat frequencies (4.0–12.5 Hz). Although no overlap between steady labriform and steady subcarangiform motion was observed, the gap between maximum pectoral and minimum caudal fin-powered motion in the juvenile fish was small. In comparison, the adult fish have a distinct two-gear system, with steady pectoral powered motion reaching speeds of less than 1 Ls⁻¹ and the lowest steady subcarangiform motion being 3.6 Ls⁻¹. Occasionally, adult fish used both swimming modes, consisting of several tail flicks of low amplitude, during normal labriform motion. This type of swimming behaviour was not

observed in the juvenile fish, although at low subcarangiform speeds the pectoral fins were abducted.

Discussion

Developmental changes

Following an inshore migration, the pelagic blue fingerling stage of *Notothenia neglecta* undergoes a gradual transition *via* brown fingerling and juvenile stages to the demersal adult form with associated changes in pigmentation and body morphology (Norman, 1938). Adults are ambush feeders and can be observed perching amongst rocks or partially burying themselves in soft mud in wait for a prey organism to approach (Daniels, 1982). In contrast, juvenile *N. neglecta* spend long periods in the water column. Juveniles are not recruited into the demersal population until they are between 1 and 2 years of age and over 10 cm in standard length (Everson, 1970). The transition from a pelagic fingerling to a demersal adult stage is also associated with a major structural remodelling of the skeletal muscle of the myotomes. For example, slow fibres constitute up to 24% of the cross-sectional area of myotomes in fingerlings compared with only 3% in adults (Johnston & Camm, 1987). The consequences of these changes in life-style and locomotory musculature on the swimming performance and behaviour of *N. neglecta* are discussed.

Locomotion of adult fish

Adult *N. neglecta* use the labriform mode of swimming almost exclusively at slow sustained speeds. Low-amplitude beats of the tail are occasionally used to increase the forward velocity slightly, during labriform motion (Fig. 4). Harrison *et al.* (1987) have made a detailed study of the anatomy and histochemical characteristics of the pectoral fin muscles, which together constitute 2.5% of the total body weight. The main propulsive phase, the adduction stroke (Fig. 2), is powered by the m. adductor profundis, the largest of the pectoral muscles. All six pectoral muscles play a part in articulating the complex dorsal and ventral movements of the fin during adduction and abduction, respectively (Harrison *et al.* 1987). It is clear that there must be a phase difference in activation and contraction of different parts of the m. adductor profundis of the same duration as that between the leading and trailing fin rays during a pectoral fin beat. The muscles of the pectoral fins in both adult and juvenile fish are composed mainly of slow fibres of small diameter (24.2–42.5 μm) and relatively high capillary numerical (500–1730 mm^{-2}) and mitochondrial volume (34–37%) densities (Johnston & Camm, 1987). The rapid adduction of the fins during the transition from labriform to subcarangiform motion involves a power stroke (Fig. 3) and may be associated with recruitment of the large-diameter, fast fibres found on the periphery of the adductor muscles (Harrison *et al.* 1987).

Fastest swimming speeds during labriform motion are not necessarily maximum

sustainable speeds. Two species that use labriform motion at low speeds, *Cymatogaster aggregata* (Webb, 1973) and *Lepomis gibbosus* (Brett & Sutherland, 1965), achieve higher critical swimming speeds by the use of subcarangiform motion. However, the cryopelagic antarctic fish *Pagothenia borchgrevinki*, 23 cm total length, have 15 min critical swimming speeds (Foster *et al.* 1987) of the same value (1.8 L s^{-1}) as the maximum pectoral fin-powered speeds observed in static water (Montgomery & Macdonald, 1985). This suggests that there is only a limited contribution to aerobic powered swimming by the trunk muscles in *P. borchgrevinki*.

Some notothenioids have adopted a secondarily pelagic mode of life as adults (Andriashev, 1987). Studies of the swimming behaviour of *P. borchgrevinki* (Montgomery & Macdonald, 1985) and of muscle fibre distribution in *Pseudochacnicthyis georgianus* and *Chamsocephalus gunnari* (Dunn *et al.* 1988) suggest that these secondarily pelagic species also rely on labriform swimming at sustained speeds. It has been suggested that pectoral drag-based mechanisms of propulsion are an adaptation to slow swimming, where the efficiency of the subcarangiform mode is low (Blake, 1979).

The almost total reliance by adult *N. neglecta* upon labriform motion for sustained swimming observed in this study (Fig. 4) questions the role of the myotomal slow muscle. These slow muscle fibres are of larger diameter ($92.0 \mu\text{m}$) and lower mitochondrial content (13.1%) than those found in the pectoral fin muscles (Johnston & Camm, 1987). Histochemical studies of other demersal notothenioids also suggest that the myotomal slow muscle has a lower aerobic capacity than the pectoral fin muscles (Davison & Macdonald, 1985; Dunn *et al.* 1988). Turning movements during labriform motion involve using the tail as a rudder and the slow muscle of the myotomes may play a part in bending the trunk. The low-amplitude tail flicks occasionally observed during labriform motion may also involve recruitment of the myotomal slow muscle.

The very small proportion and relatively low aerobic capacity of slow muscle in the trunk of adult *N. neglecta* result in a swimming behaviour in which the trunk muscle is utilized almost solely for anaerobic power output. Anaerobic energy production is supplied largely *via* an enhanced creatine phosphate hydrolysis pathway, the glycolytic capacity of the trunk muscle of adult *N. neglecta* being relatively reduced (Dunn & Johnston, 1986). This metabolic organization is geared to rapid, short-term rates of ATP production, but limits the burst endurance capacity of adult *N. neglecta*.

Accelerations attained and the duration of the kinematic stages during transitions from labriform to subcarangiform motion in *N. neglecta* (Fig. 3) are not comparable to the 'Mauthner-initiated' startle responses which are involved in avoidance reactions (Eaton *et al.* 1977; Webb, 1976). The acceleration produced by the large-amplitude, rapid tail beats during fast starts is obviously important to prey capture during ambush feeding of adult *N. neglecta*; these feeding bursts are probably of short duration. Constraints on burst endurance imposed by utilizing the phosphocreatine pathway of anaerobic energy supply would be expected to

affect predator avoidance to a greater extent than prey capture in adult *N. neglecta*.

Locomotion of juvenile fish

The cross-sectional area of slow muscle in the trunk of juvenile *N. neglecta* is of similar proportion (Johnston & Camm, 1987) to that found in small pelagic species from warmer waters (Greer-Walker & Pull, 1975). In contrast, the myotomes of adult stages contain very little slow muscle ($\geq 3\%$) (Johnston & Camm, 1987). The higher proportion of slow myotomal muscle in juvenile *N. neglecta* allows them to use subcarangiform swimming at speeds around 2 L s^{-1} (Fig. 4), much slower than observed in adults. Slow fibres of the myotomes in juveniles have a similar fine structure to those of the pectoral fin muscles, with high capillary numerical densities (1225 mm^{-2}) and high volume densities of mitochondria (37.0%) (Johnston & Camm, 1987).

Smaller fish are capable of higher length-specific swimming speeds owing, in part, to faster tail-beat frequencies (Bainbridge, 1958; Hunter & Zweifel, 1971). Size-related variations in body wavelength, tail-beat amplitude and depth of the trailing edge of the tail also determine the thrust produced by fish of different sizes (Webb *et al.* 1984). Highest tail-beat frequencies of juvenile *N. neglecta* appear to be particularly slow; the variation between adult and juveniles is not significant at the 0.05 probability level (Table 2), despite significantly different fastest swimming speeds (body lengths per second) ($P \leq 0.02$).

Temperature adaptation of swimming performance

It has been suggested that isotonic twitch contraction times can be used to predict maximum swimming speeds (Wardle, 1975). Twitch contraction times of myotomal muscle of *P. borchgrevinki* at -1.9°C are only slightly shorter than for various temperate species extrapolated to the same low temperature (McVean & Montgomery, 1987). This has led some authors to predict that the burst swimming speeds of antarctic fish do not show capacity adaptations to low temperature (Macdonald *et al.* 1987). However, such analyses do not take into account many dynamic properties of muscle relevant to locomotion: for example, the number of cycles of stimulation and the effects of stretch on subsequent contractions (Altringham & Johnston, 1988). Although tail-beat frequency may place an upper boundary on the maximum swimming speed, it is only one of a number of parameters involved; others include muscle force, power and endurance (Johnsrude & Webb, 1985; Webb & Johnsrude, 1988). It is clear that some of these parameters exhibit more substantial adaptations to low temperature. For example, studies with demembranated fibres have shown that the power output of fast muscle is 6–10 times higher for antarctic than for tropical species at 0°C (Johnston & Altringham, 1985). This largely reflects the higher maximum tensions that fibres from antarctic fish generate at low temperatures (Johnston & Brill, 1984; Johnston & Altringham, 1985).

Comparisons of the maximum observed burst swimming speeds of antarctic,

Table 3. Comparative data on the maximum swimming speeds and tail-beat frequencies of antarctic and temperate-water fish

Species	Total length (cm)	Maximum velocity ($L s^{-1}$)	Tail-beat frequency (Hz)	Environmental temperature ($^{\circ}C$)	Source
(A) Adult fish					
<i>Notothenia neglecta</i>	26.9	5.4	8.3	Antarctic ($2^{\circ}C$)	This study
<i>Pagothenia borchgrevinki</i>	23	4.9	5.7	Antarctic ($-1.8^{\circ}C$)	(1)
<i>Leuciscus leuciscus</i> (dace)	24	9.2	13	Temperate	(2)
<i>Salmo gairdneri</i> (trout)	29.3	10.8	17	Temperate	(2)
<i>Carassius auratus</i> (goldfish)	22.5	3.6	5	Temperate	(2)
<i>Salmo salar</i> (salmon)	25–28	10	16.7	Temperate ($12^{\circ}C$)	(3)
<i>Pollachius virens</i> (saithe)	40	6.2	6.7	Temperate	(4)
<i>Scomber scombrus</i> (mackerel)	34	18	18	Temperate ($12-14^{\circ}C$)	(5)
<i>Sebastes mystinus</i> (blue rockfish)	15.1	7.0		Warm temperate	(6)
(B) Juvenile fish					
<i>Notothenia neglecta</i>	7.2	8.7	11.1	Antarctic ($2^{\circ}C$)	This study
<i>Leuciscus leuciscus</i> (dace)	9.0	17.8	25	Temperate	(2)
<i>Carassius auratus</i> (goldfish)	7.0	9.5	16	Temperate	(2)
<i>Melanogrammus aeglefinus</i> (haddock)	10	26	25	Temperate ($12^{\circ}C$)	(3)
<i>Cymatogaster aggregata</i> (surf perch)	9.3	10.9		Warm temperate ($15-20^{\circ}C$)	(6)
<i>Chromis punctipinus</i> (blackfish)	8.5	11.1		Warm temperate	(6)
<i>Trachurus symmetricus</i> (jack mackerel)	6.4	21.7	17	Warm temperate ($17-19^{\circ}C$)	(7)

(1) Montgomery & Macdonald (1984). (2) Bainbridge (1958). (3) Wardle (1975). (4) Videler & Hess (1984). (5) Wardle & He (1988). (6) Dorn *et al.* (1979). (7) Hunter & Zweifel (1971).

temperate and tropical fish are complicated by the variety of methods of analysis used and the limited data available. Values shown in Table 3 were measured over a similar duration to those in this study, in essentially static water, and they are from fish of comparable size. However, none of the data is directly comparable to that of *N. neglecta*. Values of maximum swimming speeds of tropical species are limited to measurements on large pelagic scombrid species (Walters & Fierstein, 1962; Yuen, 1966). Body form is an important determinant of maximum swimming speed; the lateral profile (Fig. 1) of *N. neglecta* is of a design maximizing thrust, with large dorsal and anal fins that give the fish a deep silhouette along the length of the body (Webb, 1984). Typical of many demersal species, *N. neglecta* has a large head and relatively small trunk, and myotomal muscle constitutes only 30% of the total body weight (Harrison *et al.* 1987). In comparison, the myotomal muscle of trout, *Salmo gairdneri*, 30 cm in total length, makes up 58% of the total body weight (Webb, 1976).

In spite of the limitations of the data on the maximum swimming speeds of fish of similar body shape and behaviour, it is clear that there is some overlap between antarctic and temperate fish more than 20 cm long. It seems likely that adult *N. neglecta* are able to swim as fast as similar bottom-living fish from temperate environments. However, the higher length-specific swimming speeds and tail-beat frequencies observed in smaller temperate fish (Table 3) are not matched by juvenile *N. neglecta*. The relatively low tail-beat frequencies in juvenile *N. neglecta* may, in part, be compensated for by significantly greater specific tail-beat amplitudes (Table 2). However, it seems likely that the poor burst swimming performance of juveniles reflects incomplete adaptation of the myotomal muscle to low temperature.

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