

## The swimming endurance of threespine sticklebacks, *Gasterosteus aculeatus* L., from the Afon Rheidol, Wales

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The endurance of threespine sticklebacks, *Gasterosteus aculeatus*, swimming with pectoral fin locomotion at 20°C in a laboratory flume was measured. Each trial lasted a maximum of 480 min. At a speed of 4 body lengths per sec ( $L s^{-1}$ ) all fish were still swimming at the end of the trial, but endurance decreased at higher speeds. At speeds of 5 or 6  $L s^{-1}$  (20–30  $cm s^{-1}$ ) a few fish still maintained labriform locomotion for the 480 min. However, at a speed of 7  $L s^{-1}$  all fish furled their pectoral fins and used body and caudal fin propulsion but fatigued rapidly. During sustained swimming, fish could cover distances of 6 km or more. No significant differences between males and females were found.

### I. INTRODUCTION

Sticklebacks (Gasterosteidae) are one of a small number of fish families which use their pectoral fins for normal locomotion (Lindsey, 1978), by 'rowing' (Taylor & McPhail, 1986). Analyses of pectoral fin 'rowing' suggest that this labriform mode of locomotion provides high manoeuvrability and propulsive efficiency at low swimming speeds, but at the cost of adaptations that would favour sustained swimming at moderate speeds (Lindsey, 1978; Blake, 1983; Webb, 1984). However, many stickleback populations undertake anadromous breeding migrations (Wootton, 1976, 1984). Whoriskey *et al.* (1986) reported apparent tidal stream transport (Greer Walker *et al.*, 1978; McCleave & Kleckner, 1982) of anadromous threespine sticklebacks over their breeding grounds in a Quebec salt marsh. This suggests that sticklebacks may overcome a limited capacity for prolonged swimming by harnessing favourable currents for migratory movements. Recently, Taylor & McPhail (1986) found that threespine sticklebacks from an anadromous population in British Columbia had long swimming endurances at relatively high speeds of 5 body lengths per second ( $L s^{-1}$ ).

This study examined, experimentally, the swimming endurance of threespine sticklebacks taken from a population permanently resident in freshwater on the west coast of the U.K.

### II. MATERIALS AND METHODS

Threespine sticklebacks were collected from a backwater of the Afon Rheidol near Aberystwyth, mid-Wales. The population is permanently resident in freshwater and contains only the low-plated morph of *G. aculeatus* (Wootton, 1976, 1984, 1985).

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After capture, the fish were held in a 37 × 95 × 30 cm aquarium containing filtered and aged tap water. They were fed chopped liver, occasionally supplemented with live enchytraeid worms. Fish were tested 1 month after collection.

Swimming trials were conducted in an artificial stream. This was constructed of plexiglass and divided longitudinally into three flumes each 150 cm long × 16 cm wide × 15 cm deep. The water supply to each flume came from a common, 182-l, head tank which generated similar flow regimes in each flume. A wire mesh screen was placed between the head tank and the entrance of the flumes to control turbulence and help maintain a rectilinear flow pattern. Water leaving the flumes dropped 0.7 m into a 182-l basin. This fall saturated the water with oxygen. From the lower basin, water was returned to the head tank by a Turner Turbines industry pump. The pump was powered by a belt from an electric motor to minimize heat exchange between the pumping system and the water flowing through it (Gee, in prep).

Water temperature was usually controlled by controlling the air temperature of the room. Occasionally, cool water was added to the head tank if water temperature started to rise during a trial. During all experiments, water temperature was maintained at  $20 \pm 1^\circ \text{C}$ . The temperature in the holding aquarium was  $20 \pm 2^\circ \text{C}$ . This temperature is reached in the backwater from which the fish were collected during the breeding season.

One fish was swum in each of the flumes during each trial. Because current velocity varied between different parts of each flume, each fish was confined to the interior of a clear, plexiglass cylinder, 30 cm long × 11 cm diameter. The cross-sectional area of a cylinder ( $95 \text{ cm}^2$ ) was much greater than that of the fish ( $2.26 \text{ cm}^2$ , assuming fish shape is an ellipse). Thus, the body cross-section of the fish did not cause a significant solid blocking of the water channel. Each end of a cylinder was covered with a wire mesh, and the cylinder placed in a region of homogeneous flow of the desired speed. Current flow in the flume and at the entrance and exit of the cylinder was measured with a Nixon Streamflo model 401 flowmeter. The 2-cm diameter impeller of the flowmeter measured current speeds on a fine scale. Current velocities at the entrance and exit of the cylinder were identical. Dyes passed through the cylinder at all the current speeds used in the trials showed that current flow was homogeneous.

Swimming endurance was determined separately for males and females selected at random from the holding aquarium. Males were identified by their breeding colouration of red throats and blue irises. None of the females was distended with eggs. There was no external evidence that parasites were present in the fish selected. Three hours after a meal, each fish was transferred rapidly from the aquarium to the cylinder in the flume and given a warm-up period of 20 min swimming at a current speed of  $8 \text{ cm s}^{-1}$  ( $1.5\text{--}2 \text{ L s}^{-1}$ ). (Fish were fed before the trial because sticklebacks normally have food in their stomachs when moving to the breeding grounds.) The fish swam readily into the current without previous training. After the warm-up, current speed was increased in increments of  $1 \text{ L s}^{-1}$  (about  $5 \text{ cm s}^{-1}$ ). Fish were given 5 min to adjust to the new velocity before it was increased. When the desired swimming speed was reached, timing of the endurance of the test fish began. A trial lasted a maximum of 480 min from the time the test speed was initiated. Each of the 69 fish was used in only one trial at one speed.

If a fish fatigued before the end of a trial, the current was stopped and the fish removed from the cylinder. A fish was defined as fatigued when it could not keep itself from being pushed against the downstream screen by the current, despite repeated rapping of this screen with a glass rod. Typically, fish swam in the centre of the cylinder and drifted downstream only when exhausted, so that raps of the glass rod were rarely needed.

The distance travelled by each fish was calculated as the product of the time swum and current velocity ( $\text{cm s}^{-1}$ ).

The total length of each fish was determined before a trial in order to set the velocity in the flume. Each fish was weighed after a test.

Data were analysed using the 'Survival' routine in SPSS-X (1983).

### III. RESULTS AND DISCUSSION

Neither sex nor length of fish had a significant effect on endurance at any of the velocities tested. At current speeds of  $4 \text{ L s}^{-1}$ , none of the fish fatigued within the

480-min trial (Table I). At a speed of  $5 \text{ L s}^{-1}$ , some fish fatigued within the 480 min, but more than half the fish swam for the full trial (Fig. 1). At speeds greater than  $5 \text{ L s}^{-1}$ , all except one of the fish fatigued within the first 40 min of a trial (Fig. 1).

At the two highest speeds, fish could not usually maintain position using pectoral 'rowing' and switched to body and caudal fin propulsion, but fatigued rapidly (Table I). This latter mode of propulsion is usually seen when a stickleback is escaping from a source of disturbance or swimming rapidly towards a source of food (Wootton, 1984).

Sustained swimming speeds have been defined as speeds which a fish can maintain for longer than 200 min without suffering muscular fatigue, while prolonged speeds have been defined as velocities which are maintained from 20 s to 200 min but end with fatigue (Beamish, 1978). The transition from sustained to prolonged swimming for the Rheidol sticklebacks occurred at speeds of about  $5 \text{ L s}^{-1}$  (Fig. 1). Taylor & McPhail (1986) found that for a resident freshwater population of threespine sticklebacks the time at which 50% of the test fish fatigued ( $FT_{50}$ ) ranged from 12 to 24 min at a speed of  $5 \text{ L s}^{-1}$ . For an anadromous population the  $FT_{50}$  ranged from 116 to 150 min. These endurance are shorter than those of the Rheidol sticklebacks (Table I). The fish used by Taylor & McPhail were about 1 cm longer than the Rheidol fish, the water temperature was  $9.5^\circ \text{C}$  and the fish had been deprived of food for 24 h, so the conditions for the two studies were not comparable (our studies were completed before their results were available).

Fish which did not fatigue during a trial swam the equivalent of 5–7 km in the 480 min (Table I). Three fish weighed before and after their trials at  $5 \text{ L s}^{-1}$  showed no detectable weight loss at the end of 480 min. Two other fish were swum for 600 min at the same speed without fatiguing. None of the fish used in the experiment died in the two weeks following its swimming trial. These results suggest that a trial of 480 min had not stressed the fish and was not long enough to test for the maximum endurance of sticklebacks swimming at sustained speeds.

A speed of  $5 \text{ L s}^{-1}$  corresponds to a low absolute velocity of 20–30  $\text{cm s}^{-1}$ . Sticklebacks are typically found in slow-moving or sheltered waters (Wootton, 1976), but they may encounter fast currents. Whoriskey *et al.* (1986) reported apparent tidal stream transport of sticklebacks between tide pools in a salt marsh where surface water currents were highly directional and exceeded  $30 \text{ cm s}^{-1}$ . The Afon Rheidol is a mountainous stream, prone to spate, so that even in the backwaters, periods of flow exceeding  $30 \text{ cm s}^{-1}$  may occur. A combination of active swimming and passive drift may allow significant movement of sticklebacks both within and between habitats.

An assessment of the swimming ability of threespine sticklebacks is relevant to an understanding of their evolution and present geographical distribution. The origin of populations that are permanently resident in fresh waters is controversial. One possibility is that resident populations within a watershed are derived from an anadromous population that utilizes that watershed for its reproduction: this model assumes that most freshwater populations have evolved independently (Bell, 1984; Reimchen, 1985). An alternative hypothesis assumes that most of the freshwater populations are derived from a small number of ancestral populations by colonization through the sea (Wootton, 1984). The euryhalinity of the stickleback, together with its swimming capacity demonstrated by Taylor & McPhail (1986) for two Canadian populations and for the Rheidol population, makes short

TABLE I. Results of the 480-min swimming endurance tests. Current velocity is given in body lengths per second ( $L s^{-1}$ ). Length and weight values are means  $\pm$  S.D. Ranges in parentheses

$L s^{-1}$	Total length (cm)	Weight (g)	Endurance median (min)	Distance swum by median fish (m)	No. fish swimming 480 min	<i>n</i>
<b>Females</b>						
4	5.0 $\pm$ 0.1 (4.8–5.1)	1.076 $\pm$ 0.140 (0.826–1.326)	480+	5760+ (5760–6134)	9	9
5	4.9 $\pm$ 0.3 (4.6–5.3)	1.045 $\pm$ 0.145 (0.844–1.309)	403 (60–480)	5920 (867–6940)	4	9
6	5.0 $\pm$ 0.6 (4.1–5.9)	1.096 $\pm$ 0.413 (0.567–1.762)	1.5 (0–14)	27 (0–210)	0	9
7	5.0 $\pm$ 0.1 (4.8–5.3)	1.129 $\pm$ 0.184 (0.837–1.461)	1 (0–4)	21 (0–88)	0	9
<b>Males</b>						
4	4.7 $\pm$ 0.2 (4.5–5.0)	0.913 $\pm$ 0.121 (0.722–1.061)	480+	5410+ (5184–5472)	9	9
5	4.6 $\pm$ 0.3 (4.3–5.0)	0.784 $\pm$ 0.171 (0.600–1.029)	480+ (5–480)	6620+ (75–7200)	4	6
6	4.4 $\pm$ 0.1 (4.3–4.7)	0.790 $\pm$ 0.138 (0.553–1.060)	5 (0–480)	80 (0–7600)	1	9
7	4.8 $\pm$ 0.2 (4.6–5.2)	0.94 $\pm$ 0.102 (0.831–1.155)	0 (0–3)	0 (0–65)	0	9

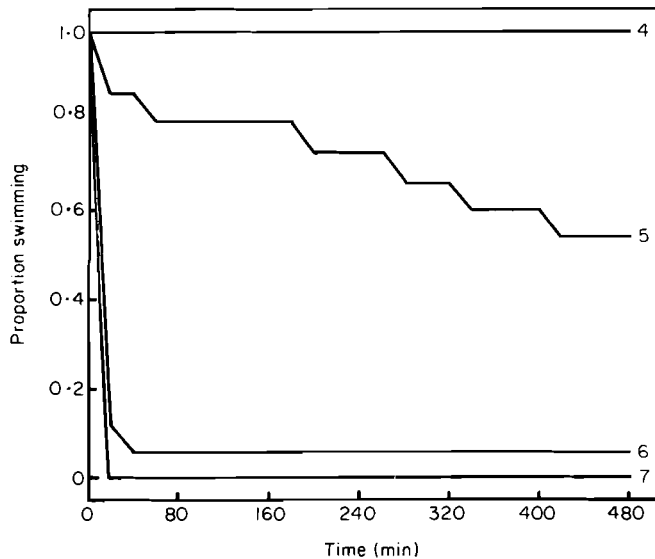


FIG. 1. Proportion of fish swimming at the beginning of successive 20-min intervals during a 480-min endurance trial. Current speeds (in  $L s^{-1}$ ) are on right of figure.

movements along the coast between adjacent watersheds a plausible mechanism for the expansion of ranges of populations normally resident in fresh water.

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