

Endurance swimming of European eel

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A long-term swim trial was performed with five female silver eels *Anguilla anguilla* of 0.8–1.0 kg (c. 80 cm total length, L_T) swimming at 0.5 body lengths (BL) s^{-1} , corresponding to the mean swimming speed during spawning migration. The design of the Blazka-type swim tunnel was significantly improved, and for the first time the flow pattern of a swim tunnel for fish was evaluated with the Laser-Doppler method. The velocity profile over three different cross-sections was determined. It was observed that 80% of the water velocity drop-off occurred over a boundary layer of 20 mm. Therefore, swim velocity errors were negligible as the eels always swam outside this layer. The fish were able to swim continuously day and night during a period of 3 months in the swim tunnel through which fresh water at 19°C was passed. The oxygen consumption rates remained stable at $36.9 \pm 2.9 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ over the 3 months swimming period for all tested eels. The mean cost of transportation was $28.2 \text{ mg O}_2 \text{ kg}^{-1} \text{ km}^{-1}$. From the total energy consumption the calculated decline in fat content was 30%. When extrapolating to 6000 km this would have been 60%, leaving only 40% of the total energy reserves for reproduction after arriving at the spawning site. Therefore low cost of transport combined with high fat content are crucial for the capacity of the eel to cross the Atlantic Ocean and reproduce.

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Key words: efficiency; endurance; migration; reproduction; respirometry; swim tunnel.

INTRODUCTION

In the 1960s and 1970s swimming experiments were performed mainly with salmonids in a stream gutter or swim tunnel (Webb, 1971; Brett, 1973). Other studies were also carried out in swim tunnels with goldfish *Carassius auratus* (L.) (Bainbridge, 1963; Smit *et al.*, 1971), rainbow trout *Oncorhynchus mykiss* (Walbaum) (Wood *et al.*, 1983) and carp *Cyprinus carpio* L. (Van Dijk *et al.*, 1993). Thus far little information is available about the construction of swim tunnels even in studies which describe the experimental set-up (Blazka *et al.*, 1960; Brett, 1964; Bell & Terhune, 1970; Smith & Newcomb, 1970). The hydrodynamic aspects of water flow in swim tunnels are rather complex and have never been evaluated in experiments with fishes. Brett (1964) optimized the flow pattern in his swim tunnels by inserting small buttons in the flow grids. This was done by

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trial and error (J.R. Brett, pers. comm.). The water flow in a tunnel easily becomes turbulent. Laminar flow, which can be reached in long flow tubes, has a wide velocity drop-off zone at the wall in contrast to semi-turbulent flow, which has a short drop-off zone. The width of this zone should be smaller than that of the fish. The double cylinder design of Blazka *et al.* (1960) enables the construction of large flow tubes requiring much less space (Van Dijk *et al.*, 1993).

Eels *Anguilla anguilla* L. migrate great distances to reach their spawning sites. As silver eels they leave the west coast of Europe in the autumn and reach the Sargasso Sea in *c.* 6 months (Tesch, 1977). The distance they have to cover is *c.* 6000 km, which means for a 80 cm total length (L_T) female eel (1.5 kg) an average swimming speed of *c.* 0.5 body lengths (BL) s^{-1} . A characteristic for silver eels is that they stop feeding when they start migrating down the rivers (August to October in the Netherlands). At the start of their journey they are still immature, and their gonads must therefore develop during or after their migration. Eels have considerable quantities of fat as energy stores. As they have to swim a long distance, it is important to know how much of this energy store is needed for swimming and how much for maturation. In order to be able to study the energetics of long-term swimming 22 swim tunnels were constructed. The flow in the swim tunnel was validated by a Laser-Doppler system.

MATERIAL AND METHODS

SWIM-TUNNEL

The Blazka-type swim-tunnel used is shown in Fig. 1. The perspex tube has a length of 2000 mm and a diameter of 288 mm. The inner diameter of the swim-tunnel is 190 mm.

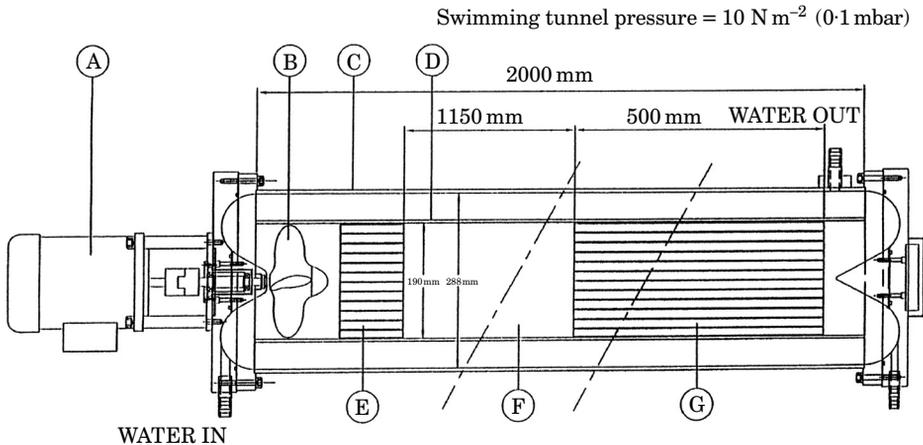


FIG. 1. Schematic drawing of a 2.0 m swim tunnel. The tunnel consists of two concentric perspex tubes of 2 m and two PVC endcaps. A, electromotor; B, propeller; C, perspex outer swim-tunnel tube; D, perspex inner swim-tunnel tube; E, PVC end-streamer; F, animal compartment; G, PVC front streamer. The propeller pushes water into the outer ring and 'sucks it' out from the inner tube. The cross-section area of the inner tube and of the outer ring have the same surface area. This results in equal flow rates at both sides. The turbulent water is pushed through streamers that have internal diameters of *c.* 10 mm.

The mean \pm s.d. volume is $127.1 \pm 0.9 > 1$ ($n = 5$). The surface area of the inner tube is equal to the surface area of the outer ring (after correction for wall thickness), such that the water velocity is the same in both compartments. The power of the three-phase electromotors is 400 W and drives a propeller consisting of three blades of 190.5 mm with a pitch of 177.8 mm. The power is controlled by a Siemens Micro Master (Basic 370) digital power and frequency controller. The motor is equipped with an additional tachometer on the axis for independent (on-line) frequency measurement. The maximal flow is *c.* 1 m s^{-1} . At the front end of the swim tunnel a PVC flow streamer is placed with a length of 500 mm, while at the propeller end the flow streamer is 120 mm and the spacing of the streamers is 10 mm. The free space for swimming is 1300 mm. At the end of the animal compartment, just before the flow streamer, a screen is placed covered with silver wire of 1 mm for electrical stimulation of the fish. The electrical AC current is a sinusoid with a peak of 6.5 V, a frequency of 1 s and duration of *c.* 20 ms.

A magnetic valve controlled the water inlet. When the valve was open the waterflow through each tunnel was set at $5\text{--}71 \text{ min}^{-1}$. After introducing the fish, the waterflow in the inner compartment was corrected for the diameter of the fish according to the formulae described by Smit *et al.* (1971). The cross sectional area (A) of the fish was calculated according to: $A = \pi \cdot 0.5h \cdot 0.5w$, where h is maximum height and w is maximum width. The corrected speed is $V_c = V_m (1 + A_{\text{fish}} \cdot A_{\text{cylinder}}^{-1})$, where V_m is measured speed. From the maximal dimensions of the eels ($h = 5 \text{ cm}$, $w = 4 \text{ cm}$) the maximal cross-section is 16 cm^2 , resulting in a speed correction of *c.* +5.5%.

FLOW MEASUREMENTS

The measurements with the Laser Doppler technique were performed at the Delft Hydraulics Laboratory, Technical University Delft, The Netherlands. The principle of the Laser Doppler technique is described elsewhere (Drain, 1980; Durst *et al.*, 1981). A two-dimensional Laser Doppler anemometer (type LDVS02) with a mean value meter (MVM + UCC) was used. The measuring signal of the signal processor (Counter-Tracker) was connected with the mean value meter, which integrates and calculates the mean value of the measured analogue signal over a period of 30 s.

The relation between the revolutions per min (rpm) of the motor and the water velocity was determined in the centre of the swim tunnel at 10 cm downstream of the front streamer. The rpm values of the motor were tested in the range of 285–720 rpm. The relation between the measured flow and the rpm value appeared to be linear in this range: $y = 0.0013x - 0.0748 \text{ ms}^{-1}$ ($r^2 = 0.997$), where x is rpm. At three positions in the swim-tunnel, at 110, 610 and 1100 mm downstream of the front streamer, the velocity profile was determined over the cross-section of the inner tube. The flow was measured from the wall of the swim-tunnel tube towards the centre at 5, 10, 20, 40 and 95 mm from the wall. The distance of 95 mm from the wall corresponds to the centre of the inner swim-tunnel tube (Fig. 2). The velocity profile was measured at a water velocity of 0.5 ms^{-1} . At 110 mm from the inlet, the water velocity at 40 mm from the wall was still equal to the velocity at the centre. From there the drop-off was steeper than at the other two positions (610 and 1100 mm). The most ideal profile was clearly at 110 mm from the inlet (at the opposite site of the propeller). At the 610 and 1100 mm position the profile at 40 mm from the wall was 15 and 20% respectively below central velocity. So, over the whole length of the animal compartment the velocity at 40 mm from the wall was still close to the set point. This means that animals with a width of $>40 \text{ mm}$ swim outside the boundary layer and were thus swimming at the set speed.

SET-UP

The 22 swim tunnels were placed in the direction of the Sargasso Sea (WNW) in a climatized room of *c.* 100 m^2 . The total water content of *c.* 7000 l was re-circulated continuously over a bio-filter. A high capacity protein defoamer, sandfilter, UV-irradiation and ozonizer were included to improve the water quality. The ozone level was kept low by a feedback control *via* a redox electrode. The NH_3 and NO value of the water was

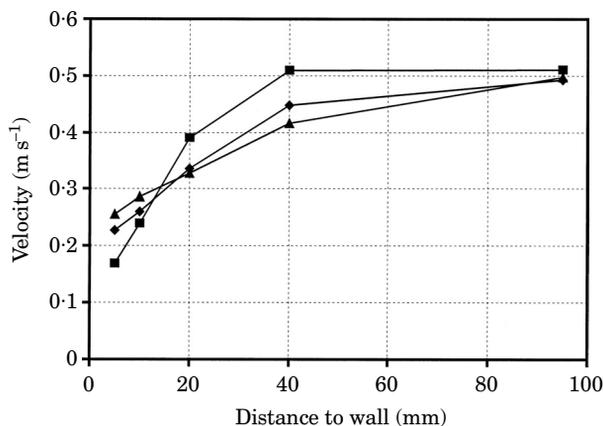


FIG. 2. The velocity profile from the wall towards the centre of the inner tube of the swim tunnel. The flow was measured by a Laser-Doppler system at three cross-sections from the inflow site (■ 110, ◆ 10 and ▲ 1100 mm). At each cross-section the flow was measured at five distances from the wall (5, 10, 20, 40 and 95 mm). The water velocity at the centre of the inner tube was 0.5 m s^{-1} .

measured daily. At values $>0.1 \text{ ppm NH}_3$ the water was refreshed from a 30001 tank. The water temperature was controlled by a separate cooling system. Important variables such as temperature, salinity, water level, oxygen level and motor frequency were monitored constantly, logged on a computer, and connected to a telephone alarm system. The data logger was a HP 34970A multichannel logger and controller, equipped with two 40-channel multiplexers (34907A and 34901A). The oxygen electrodes (type Inpro 6415) and the preamplifier (OPA) were from Mettler Toledo (The Netherlands). The illumination in the climatized room was switched to 670 nm light (bandwidth 20 nm) during experiments. Based on pigment changes during silvering, it is assumed that this far-red light is invisible for eels (Pankhorst & Lythgoe, 1983). The temperature was kept at 19°C , range $\pm 0.5^\circ \text{C}$, and the oxygen level between 90 and 75% air saturation.

OXYGEN CONSUMPTION

The oxygen level in the tunnel was measured continuously by an oxygen electrode (Mettler Toledo). The oxygen consumption rate was calculated from the oxygen decline after automatic closure of the water-inlet by a magnetic valve. The oxygen levels changed between 85 and 75% air saturation. The valve was normally open allowing a refreshment rate of $5\text{--}71 \text{ min}^{-1}$ and automatically operated between 1400 and 1700 hours to measure oxygen consumption. From the decline of the O_2 -concentration, the oxygen consumption rate ($V\text{O}_2$) was calculated following the formula: $V\text{O}_2 = 127 \Delta[\text{O}_2] \Delta t^{-1} f$ ($\text{mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$), where: $\Delta[\text{O}_2] \Delta t^{-1}$ is the decrease of the oxygen content per hour, $f = (0.001M)^{0.8}$, and M is the mass of the fish (van den Thillart & Kesbeke, 1978).

ANIMALS

Eels were obtained from a commercial eel farm, Royaal BV, Helmond, The Netherlands. Before transfer into the swim tunnels seven eels were anaesthetized with 200 ppm MS222 (tricaine methanesulphonate, Sandoz). Immediately after losing equilibrium they were placed in the swim tunnels, where they recovered quickly. The flow in the swim tunnels was set at low speed to let the animals habituate to the new environment. The next day the speed was increased stepwise by 0.1 m s^{-1} per hour to 0.5 BL s^{-1} . Most eels were willing to follow the water current, two were taken out because of poor swimming performance, the others appeared to be good sustained swimmers. The swim tunnels were positioned in the direction of the Sargasso Sea to have a corresponding earth magnetic

field direction. For every individual eel the water velocity was set at 0.5 BL s^{-1} . So, the smallest animal of $69.5 \text{ cm } L_T$ swam 30.0 km day^{-1} and the largest animal 32.4 km day^{-1} .

RESULTS

The five eels in this study did not show any disturbance or fatigue during the swim trial of 3 months. The length, body mass and oxygen consumption rates of the individual swimmers are presented in Table I. The animals swam day and night from March until July for a period of 95 days. The distance covered by the eels was $95 \times 30 = 2850 \text{ km}$. The oxygen consumption rates remained constant throughout the 3 months period between 30 and $50 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$. The oxygen consumption pattern over a period of 3 months is shown in Fig. 3. The individual lines in Fig. 3 show the variability in oxygen consumption of the animals, which differed sometimes by $15 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ on a day to day basis. The behaviour of the animals was, however, rather quiet. The differences in oxygen consumption rates could not be related to visual differences in swimming pattern. At a mean swimming speed of 1.4 km h^{-1} and an oxygen consumption rate of $36.9 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$, the mean cost of transportation over 2850 km was 36.9 divided by $1.4 = 26.4 \text{ mg O}_2 \text{ kg}^{-1} \text{ m}^{-1}$.

DISCUSSION

The principle of the Blazka swim-tunnel has been given in earlier publications (Blazka *et al.*, 1960; Smith & Newcomb, 1970; Van Dijk *et al.*, 1993) but flow characteristics of a Blazka-type swim-tunnel as far as is known, has never been described before. In this study the very accurate Laser-Doppler system was used to demonstrate the homogeneity of the flow in the swim tunnels. The actual flow was measured at different cross-sections and at different distances from the wall. A linear relationship was observed between the number of rpm and the measured water velocity. The linearity existed up to 0.9 m s^{-1} . The flow between 40 mm from the wall to the centre stayed within a few per cent of the setpoint. So, fish with a width of $>40 \text{ mm}$ cannot swim in the boundary layer. The eels used in this study needed an even wider space because of the large amplitude of

TABLE I. Total length, mass and mean \pm s.d. oxygen consumption of five individual silver eels that swam continuously at a speed of 0.5 BL s^{-1} for 95 days in 2.0 m swim tunnels

Fish number	L_T (cm)	Body mass (g)	Oxygen consumption ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$)
1	69.5	854	34.1 ± 5.5
2	74.0	857	36.6 ± 4.8
3	75.0	953	40.3 ± 3.1
4	74.0	907	34.1 ± 5.2
5	71.0	1025	39.4 ± 6.8
Mean \pm s.d.	72.7 ± 2.1	919 ± 64	36.9 ± 2.9 ($n = 5$)

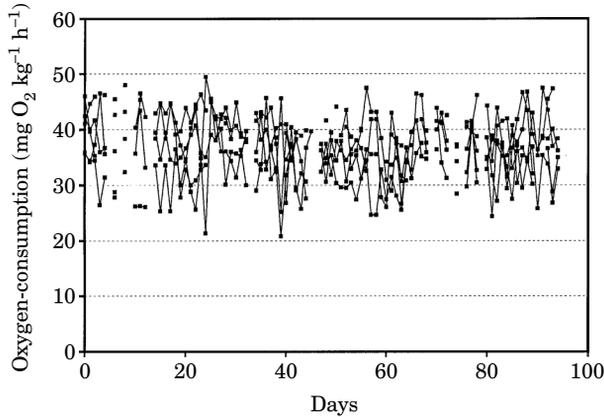


FIG. 3. The oxygen consumption rates of five adult eels of *c.* 1 kg. The eels were swimming continuously at 0.5 BL s^{-1} and at 19° C during a period of 95 days. Details of individual animals used in this experiment are given in Table I.

their tail beat. Furthermore, the head of swimming eels remained between 50 and 100 mm from the wall.

The long-term swim experiments with five eels of *c.* 0.9 kg indicated that eels can be forced to swim under laboratory conditions for a very long period without resting. Five out of seven eels were able to swim for 3 months at 0.5 BL s^{-1} , covering a distance of 2850 km. The applied swimming speed was deduced from the scarce data on spawning migration of *A. anguilla*. If the female eels leave the European coasts in September to October and the smallest leptocephali larvae are observed in the Sargasso Sea in the period February to June (Schmidt, 1923; Fricke & Kaese, 1995), the migrating silver eels have to cover a distance of 6000 km in <6 months. This is 33 km day^{-1} or a mean swimming speed of 0.39 m s^{-1} , corresponding to 0.5 BL s^{-1} for 80 cm eels.

There are limited data available on swimming performance of other anguillids (Webb, 1975; McCleave, 1980). The swimming movement of eels is less efficient than that of for example salmonids (Videler, 1993; Bone *et al.*, 1995). Biomechanical efficiency is, however, different from overall efficiency. The latter is expressed in $\text{J kg}^{-1} \text{ km s}^{-1}$, which is for the energy budget of the animal the most relevant measure. Based on a 10 day swim trial with *A. anguilla* silver eels the energy costs of swimming of those eels was found to be extremely low, $0.58 \text{ J g}^{-1} \text{ km}^{-1}$ (Van Ginneken & van den Thillart, 2000). This is 2.4–3.0 times lower than values reported in literature for other fish species (Schmidt-Nielsen, 1972). Eels have a fat content of 10–28% with a mean of 20% (Svedäng & Wickström, 1997), which is obviously the predominant energy store. From the oxygen consumption rate (Table I) the total energy consumption was 2367 kJ kg^{-1} for a 3 months period, and the equivalent fat loss was 60.0 g kg^{-1} . Extrapolating from 2850 to 6000 km, the fat consumption for a complete run would have been 126.5 g kg^{-1} . This amount is 60% of the total fat reserve of most silver eels, assuming $200 \text{ g fat kg}^{-1}$. Thus animals with <13% fat would not be able to reach their spawning site. Obviously a low cost of swimming combined with a fat content of >13% is crucial for the capacity of the eel to swim across the ocean.

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