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Eel migration to the Sargasso: remarkably high swimming efficiency and low energy costs

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Summary

One of the mysteries of the animal kingdom is the long-distance migration (5000–6000 km) of the European eel *Anguilla anguilla* L. from the coasts of Europe to its spawning grounds in the Sargasso Sea. The only evidence for the location of the spawning site of the European eel in the Sargasso Sea is the discovery by Johannes Schmidt at the beginning of the previous century of the smallest eel larvae (leptocephali) near the Sargasso Sea. For years it has been questioned whether the fasting eels have sufficient energy reserves to cover this enormous distance. We have tested Schmidt's theory by placing eels in swim tunnels in the laboratory and allowing them to make a simulated migration of 5500 km. We find that eels swim 4–6 times more efficiently than non-eel-like fish. Our findings are an important advance in this field because they remove a central objection to Schmidt's theory by showing that their energy reserves are, in principle, sufficient for the migration. Conclusive proof of the Sargasso Sea theory is likely to come from satellite tracking technology.

Key words: eel, *Anguilla anguilla*, trout, swimming efficiency, metabolic costs, muscle performance, swimtunnel, cost of transport.

Introduction

At the beginning of the previous century Johannes Schmidt found the smallest eel larvae (leptocephali) of the European eel *Anguilla anguilla* L. near the Sargasso Sea (Schmidt, 1923) and the bigger leptocephali nearer to the European coast. This is the only evidence to date that places the spawning grounds in the Sargasso Sea (neither eggs nor mature adults have ever been found in this area). For Schmidt's theory to be substantiated, the following three conditions must be met. (1) Adult European eels must be able cover a distance of 6000 km in a fasting state, implying that they have sufficient energy reserves to cover this enormous distance (Tucker, 1959). (2) Mature European eels and fertilized eggs must be found in the Sargasso Sea. (3) Eel larvae must be shown to migrate towards the European coasts. Concerning condition (3), the most recent observations on larval migration patterns were published by McCleave et al. (1987). Several questions concerning the large variation in age (Antunes and Tesch, 1997) and genetic make up (Wirth and Bernatchez, 2001) of glass eels collected at different places and times (suggesting the existence of more than one spawning site) have not yet been resolved, however. To test condition (2), Tesch's group (Post and Tesch, 1982) have tried, so far without success, to catch adult eels in the Sargasso. Until now there have only been two reports of silver eels *A. anguilla* caught incidentally in the open Atlantic (Ernst, 1977; Bast and Klinkhardt, 1988). Concerning condition (1), Tucker (1959) expressed severe doubts as to whether the European eel would be able to swim across the ocean and suggested that all European eels are the offspring of the American eel. Tucker's '*new solution to the Atlantic eel problem*' provoked a long debate (D'Ancona and Tucker, 1959; Deelder and Tucker, 1960) and was finally rejected when a distinction was made between the two Atlantic eel species based on allozymes (Williams and Koehn, 1984), enzymes (Comparini and Rodino, 1980), mitochondrial DNA (Avise et al., 1986, 1990; Tagliavini et al., 1995) and genomic DNA (Nieddu et al., 1988). Hence, if we assume a long-distance spawning migration to the Sargasso Sea, energy reserves may easily be critical (Svedäng and Wickström, 1997). An estimation of the energy required to cover the distance was presented in a recent paper. Based on the oxygen consumption rates during a 10-day swim trial, the equivalent fat consumption extrapolated to 6000 km was 120 g kg^{-1} or 40% of the initial fat reserves (van Ginneken and van den Thillart, 2000). Female silver eels of 0.8 m body length (*BL*) swimming at 0.5 *BL* s^{-1} would cover a distance of 6000 km in about 180 days. However, direct proof that European eels are able to

swim the long distances between Europe and the Sargasso Sea is still missing, and the question remains as to whether eels can continue swimming for up to 180 days at the same low energetic cost. The objective of this study was to determine the energy costs of swimming over a complete 5500 km swim trial in the laboratory.

Materials and methods

We conducted two sets of experiments, one over the entire distance of 5500 km, which lasted 173 days, and another set over the duration of 1 week. The second set served as confirmation of the results obtained during the first set by comparing our measurements on eel with the performance of another well-studied fish species, trout. In experiment 1, we performed respirometry in combination with bomb-calorimetry on the eel carcasses. In experiment 2, using trout and eel, we performed respirometry only in the swim tunnels.

Animals

For experiment 1, 3 year old hatchery eels *Anguilla anguilla* L. (*N*=30, 860±81.9 g, 73.1±3.8 cm *BL*) were used. In experiment 2, we used eels *A. anguilla* (*N*=5, 155.0±18.3 g, 43.2±3.2 cm) and trout *Oncorhynchus mykiss* Walbaum (*N*=5, 161.5±21.5 g, 24.6±1.0 cm) of the same body mass. The eels used in both experiments 1 and 2 were in the non-migratory yellow stage. Eels were obtained from Royal B.V., Helmond, The Netherlands, and trout were obtained from the Dutch Organization of Fisheries, O.V.B. Geertruidenberg, The Netherlands.

Flow tank experiments

In experiment 1, the oxygen consumption rates of eels (*N*=9) swimming at 0.5 *BL* s^{-1} were measured over a period of 173 days in 2 m Blazka-type flow tanks with a volume of 127.1±0.9 l. In addition, to establish the routine metabolic rate (RMR), we measured the oxygen consumption, over the same period of 173 days, of six eels resting in Blazka-type flow tanks with continuous water refreshment. The cross section of the flow tanks is circular with an inner diameter of 190 mm. Outside the boundary layer the flow speed is constant over the cross section of the inner tube. The flow tanks were calibrated using a Laser Doppler method. Thus the eels swam at a constant known speed with negligible wall effects (van den Thillart et al., 2004). Swimming experiments were performed over 173 days under a 12 h:12 h day:night light cycle at a temperature of 19.0±0.3°C at 0.5 *BL* s^{-1}. 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 (Pankhurst and Lythgoe, 1983). The time lapse between the start of migration and the first leptocephali in the Sargasso Sea is about 6 months. Thus to cover a distance of 5000–6000 km in 6 months requires a mean swimming speed of 0.4 m s^{-1} (Ellerby et al., 2001).

For experiment 2, five eels and five trout were placed in the same 127 l flow tanks at a constant temperature of 18±0.3°C under the same illumination protocol. Eels swam at 0.5 *BL* s^{-1} (21.5±1.6 cm s^{-1}), whereas the trout swam at a slightly higher speed of 0.7 *BL* s^{-1} (17.2±0.7 cm s^{-1}). We ensured that both species swam at their maximum range or optimal swimming speed, which is the relevant speed for migration, to facilitate the comparison between costs of transport of eel and trout. The optimal swimming speed of trout is available in the literature (Webb, 1971), whereas the value for eel is based on a study of eel muscle efficiency (Ellerby et al., 2001; for a more detailed explanation, see Discussion).

Swimming behavior was recorded at regular intervals during the entire period using an infrared video camera (frame rate 25 Hz) during the dark period to document the position of the animal in the flow tank as well as to detect possible long-term changes in swimming behavior.

Before sampling, the animals were quickly anaesthetized with 300 p.p.m. MS222 (3-aminobenzoic-acid-ethyl-ester methane sulfonate salt; Sigma, St Louis, MO, USA). All experiments were approved by the local committee on animal experimentation.

Oxygen consumption

The oxygen level in the tunnel was measured continuously using an oxygen electrode (Mettler Toledo, Tiel, The Netherlands). 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 5–7 l min^{-1} and automatically operated between 14:00 h and 17:00 h to measure oxygen consumption. The oxygen value was not allowed to fall below 75% in order to prevent the animals from becoming hypoxic (van den Thillart and van Waarde, 1985).

From the decrease in O_2 concentration, the rate of oxygen consumption $\dot{V}_{O_2}$ (mg O_2 h^{-1} kg^{-1}) was calculated from the formula: $\dot{V}_{O_2}=127\delta[O_2]\delta t^{-1}$, where $\delta[O_2]\delta t^{-1}$ is the decrease in oxygen content per hour. Oxygen consumption data were corrected for the decline in mass of the animals.

Carcass analyses

To quantify the energy cost of transportation by a second method, independently from our respiratory measurements, we analyzed the changes in body composition. Carcass analyses were performed according to ISO-standards (International Organization for Standardization, Animal feeding stuffs; ISO 5983 and ISO/DIS 6492, Geneva, Switzerland). After weighing, fish samples were cut into pieces of about 3 cm and nearly submerged in water in a glass beaker. The samples were autoclaved at 2 atm (2.013×10^5 Pa) at 120°C for 4 h. They were then homogenized and subsequently sampled in triplicate for dry matter, protein and fat analyses. Dry matter content was measured by freeze drying of the sub-samples to constant mass. Protein was measured according to procedures described in ISO 5983 (1979). For fat determination, freeze dried sub-samples were extracted as described in ISO/DIS 6492 (1996).

Table 1. *Energy consumption parameters of female yellow eels after 6 months of rest and after 6 months of swimming at 0.5* BL s^{-1}

	Method used			
	Oxygen consumption		Bomb-calorimetry	
	Swim (*N*=9)	Rest (*N*=6)	Swim (*N*=9)	Rest (*N*=15)
Animal length (cm)	74.7±3.4	70.6±3.6	74.7±3.4	71.7±3.3
Wet mass at beginning (g)			914.7±58.4	795.0±71.9***
Wet mass at end (g)			734.3±44.9	691.1±70.7
Wet mass loss (g)			180.3±38.2	103.9±26.3***
Dry matter loss (g kg^{-1} fish)			84.3±12.6	42.7±22.2***
Rate of oxygen consumption (ml O_2 kg^{-1} fish h^{-1})	29.55±4.2***	14.26±1.8***		
Total energy consumption (kJ kg^{-1} fish)	2316.58±221.31	1122.86±107.72***	3450.6±723.9	1941.0±1172.0***
COT (kJ kg^{-1} km^{-1})	0.42	–	0.62	–

The eels swam 5533±354 km over a period of 173 days. For details of the methods used, see text.
COT, mean gross Energy Costs of Transportation (Schmidt-Nielsen, 1972).

Calculations and statistics

In order to calculate the cost of transportation (COT: mean gross energy costs of transportation; Schmidt-Nielsen, 1972), total energy consumption was first calculated from oxygen consumption by multiplying the mean measured rate of oxygen consumption (Table 1, in ml O_2 kg^{-1} fish h^{-1}) with the number of swimming hours (4152 h = 173 days) and the applied energy conversion factor for respirometry of 18.89 kJ ml^{-1} O_2 (Elliot and Davison, 1975). This gives a total energy consumption of 2316.58 kJ kg^{-1} fish over 5533.2 km or a COT of 0.42 kJ kg^{-1} km^{-1}. Alternatively the energy used during the 5533 km run was calculated by bomb-calorimetry. Bomb-calorimetry could be only used once on eels at the start of the experiment, so a control group of 15 animals was also measured for comparison with the swim- and the rest-groups (Table 2).

The calculations for the bomb-calorimetry were as follows:
(1) Initial wet body mass (g) × initial dry matter fraction (%) = initial dry matter content (g dry mass $fish^{-1}$).
(2) End wet body mass (g) × end dry matter fraction (%) = end dry matter content (g dry mass $fish^{-1}$).
(3) Initial energy content (kJ g^{-1} dry mass) × initial dry matter content (g dry mass $fish^{-1}$) = total energy content begin (kJ $fish^{-1}$).
(4) End energy content (kJ g^{-1} dry mass) × end dry matter content (g dry mass $fish^{-1}$) = total energy content end (kJ $fish^{-1}$).
(5) Total energy content begin (kJ $fish^{-1}$) – total energy content end (kJ $fish^{-1}$) = total energy difference (kJ $fish^{-1}$).
(6) Total energy difference (kJ $fish^{-1}$) / geometric body mass (g) × 1000 = total energy usage (kJ kg^{-1}),
with:

$$\text{geometric body mass} = \exp[\ln(\text{start wet body mass}) + \ln(\text{end wet body mass})]/2 .$$

The COT was total energy usage (= total energy consumption in kJ kg^{-1} fish; Table 1) multiplied by the applied energy conversion factor for bomb-calorimetry of 33.73 kJ g^{-1} dry mass (Brafield and Llewellyn, 1982). Values are means ± S.D. Statistics were performed using a two-way independent sample *t*-test using SPSS 10.0. (***$P \leqslant 0.001$, **$P \leqslant 0.05$, *$P \leqslant 0.01$).

Results

The 'swimming' eels in experiment 1 used 2.1 times more oxygen than the 'resting' eels (29.55 *vs* 14.26 ml O_2 kg^{-1} h^{-1}; Table 1). The regression lines show that the oxygen consumption of the swimming eels increased by 2.56% over nearly 6 months, that of the resting group increased by 2.66% (Fig. 1). There was a significant difference in mass loss: 13.1% in the resting group and 19.7% in the swimmers. Analysis of body constituents of the eels at the start and end of the experiment revealed that the ratio of all three substrates (lipid, carbohydrate, and protein) remained constant despite significant mass losses (Table 2). This means that body composition did not change during the six months and that fat, protein and carbohydrate were metabolized in the same proportion. A similar result was also found in reef fish migrating over much smaller distances (Stobutzki, 1997).

We obtained two independent estimates for cost of transport. From the first method, oxygen uptake (using the oxycaloric value of the three substrates; Elliot and Davison, 1975), we

Table 2. *Body constitution as % of dry mass of female yellow eels at the start and after 6 months swimming or resting*

	Start (*N*=15)	5500 km swim (*N*=9)	6 months rest (*N*=15)
Fat	67.92 (1.91)	68.16 (2.47)	68.09 (2.20)
Protein	28.17 (1.79)	28.28 (2.16)	27.99 (1.90)
Carbohydrate	0.9 (0.43)	0.57 (0.49)	0.87 (0.53)
Ash	2.97	2.99	3.05
Dry matter	49.57 (2.41)	50.25 (2.86)	50.77 (2.18)

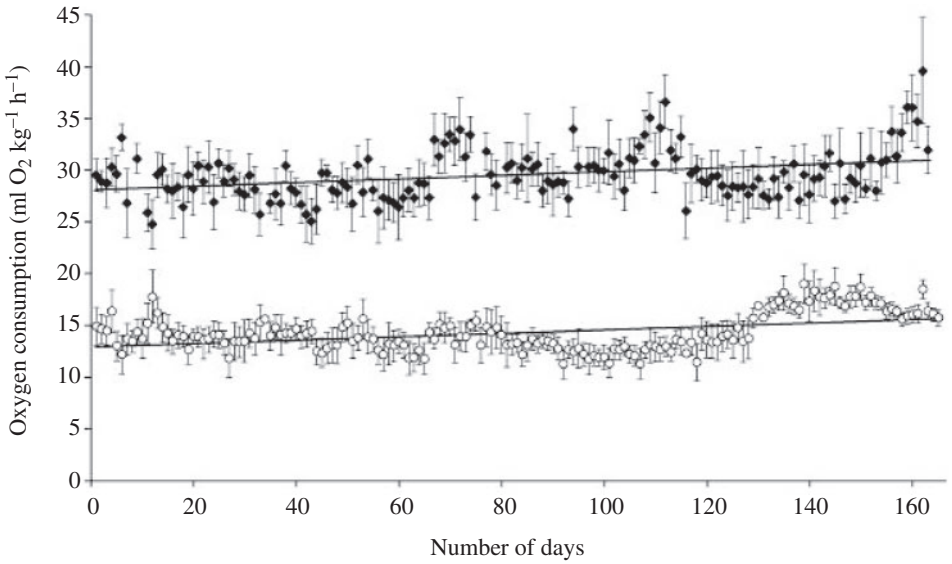

Fig. 1. Oxygen consumption of fasting yellow eels from a hatchery (860±81.9 g, 73.1±3.8 cm *BL*) during a 6 month period of rest (circles) or 6 months of continuously swimming at 0.5 *BL* s^{-1} (diamonds) at 19°C. Regression lines: Rest-group: y=0.0326x+25.294; Swim-group: y=0.0394x+54.86.

obtained a value of 2317 kJ kg^{-1} fish for the energy cost of 6 months swimming covering a distance of 5500 km. This corresponds to a COT value of 0.42 kJ kg^{-1} km^{-1}. The swimming group lost more total body mass than the resting group (180.3 g compared with 103.9 g; Table 1). Hence, based on the second method, which uses mass loss, body composition and energy conversion factors (Brafield and Llewellyn, 1982), we calculated that energy used for swimming was 3450 kJ kg^{-1} fish, corresponding to a COT value of 0.62 kJ kg^{-1} km^{-1}. The two COT estimates obtained independently (Table 1) are of the same order of magnitude.

In experiment 2, where eels and trout swam in identical experimental set-ups, we measured an oxygen consumption of 43.9±8.42 mg O_2 kg^{-1} h^{-1} and 130.4±9.49 mg O_2 kg^{-1} h^{-1}, respectively. During 7 days the eels and trout covered a mean distance of 132.5±12.1 km and 102.8±2.3 km, respectively. From these data we calculated COT values for eel and trout of 0.68 and 2.73 kJ kg^{-1} km^{-1}, respectively. Our video recordings of the fish swimming in the flow tank show that the fish were swimming in the free-stream and did not benefit from wall effects: the fish swam mostly in the centre of the flow tank and therefore are more than 2 (eel) up to 3 (trout) tail heights removed from the wall (results not shown).

Discussion

Efficiency, commonly defined as the rate of useful energy expenditure divided by the total rate of energy consumption, is a crucial parameter for animals migrating over long distances. During long-distance migration, animals are likely to maximize the distance covered per given fuel unit, which corresponds to maximizing efficiency. Amongst the various eel species, the European eel needs to migrate the farthest to reach its spawning grounds: European eel *A. anguilla*, 5500 km (Schmidt, 1923), American eel *A. rostrata*, 4000 km (Tucker, 1959; McCleave et al., 1987), Australian eel *A. australis*, 5000 km (Jellyman, 1987) and Japanese eel *A. japonica*, 4000 km (Tsukamoto, 1992). So European eels need to be very efficient swimmers.

There are various levels of energy conversion in a swimming animal. The overall metabolic efficiency (how much heat is generated at a given swimming speed) comprises the efficiencies of various processes, e.g. propeller efficiency (how much momentum is gained by the animal and wasted in the wake) and the muscle efficiency (how many ATP molecules are used per myosin-head cycle). The concept of efficiency used here corresponds to overall metabolic efficiency and encompasses propeller and muscle efficiency, for example. During locomotion, propeller and muscle efficiency are likely to contribute significantly to overall metabolic efficiency, so it is interesting to compare the hydrodynamic and muscle performance of eel to those of other undulatory swimmers.

To reduce costs of transport and increase overall metabolic efficiency, all or some of the processes that determine the costs of transport can be optimized. Efficiency can be improved most effectively by improving those processes in which efficiency increases nonlinearly and progressively with a given performance parameter. Performance parameters that only weakly or linearly affect efficiency are less likely to bring about a drastic increase in efficiency.

In order to explain the remarkable difference in cost of transport between eel and trout, it is important to identify the processes that cause it. To this end, we have studied the literature on propeller efficiency and muscle efficiency in undulatory swimmers.

Hydrodynamic performance and propeller efficiency

A fish can alter its propeller efficiency by changing its structural design and its motion pattern. Both carangiform and anguilliform swimmers undulate their body, the former with a narrower amplitude envelope than the latter. How the shape of the body undulations affect locomotory efficiency has been estimated using analytical approximations. Lighthill's elongated body theory (EBT) concludes that efficient swimmers should undulate only the most posterior section of their body – in the ideal case only their trailing edge – to maximise propeller efficiency (Lighthill, 1971; Tytell and Lauder, 2004). Daniel's predictions (Daniel, 1991) differ in

part: the propeller efficiency of undulatory swimming decreases linearly as the rearward speed of the body wave increases relative to the swimming speed, and it is independent of the frequency and the amplitude of the body wave. Given that the swimming kinematics of trout and eel mainly differ in the amplitude envelope of their body wave, but have a similar range of body wave speeds (for a review, see Videler, 1993), it is unlikely that kinematic differences between trout and eel can explain the difference in their overall metabolic efficiency.

The combined effect of propeller shape and motion on performance can be studied by visualising the flow generated by anguilliform and carangiform swimmers. The ratio of forward to total momentum of the entire wake provides the mean propeller efficiency over a complete tail beat. This approach, whether using experimental or computational flow fields, requires the quantification of the three-dimensional flow in the complete wake, which so far has not been done. The currently available two-dimensional slices through the wake suggest that eels generate considerable lateral momentum, which do not contribute to the forward motion and therefore reduce efficiency (Müller et al., 2001; Tytell and Lauder, 2004). Tytell estimated a hydrodynamic efficiency of 0.5 to possibly up to 0.87 (Tytell and Lauder, 2004). Equivalent estimates for carangiform fish are reported in the range 0.74–0.97 (Drucker and Lauder, 2001; Müller et al., 2001; Nauen and Lauder, 2002a,b). These values suggest that trout has a higher propeller efficiency than eel, which does not explain the higher overall metabolic efficiency of eels.

Efficiency is also inversely related to thrust (Lighthill, 1971; Daniel, 1991). However, a 25% difference in swimming speed is insufficient to explain a fourfold difference in efficiency. So, the currently existing evidence on the hydrodynamics of undulatory swimming contradicts rather than explains the high swimming efficiency of eels.

Muscle performance and efficiency

The efficiency with which a muscle converts chemical energy into mechanical work is important in prolonged aerobic locomotion, such as migration. Cruising is characterized by cyclic contractions at a well-defined frequency. Swimming speed depends linearly on tail-beat frequency, and tail-beat frequency corresponds to contraction frequency. The mechanical efficiency of muscle contractions depends on contraction speed in a non-linear fashion. This relationship can be predicted from Hill's model of muscle contractions (McMahon, 1984) and has also been documented in fish swimming muscles (Curtin and Woledge, 1993). There is a narrow range of contraction frequencies over which efficiency remains high. At contraction frequencies above and below this range, efficiency drops off progressively (McMahon, 1984; Curtin and Woledge, 1993). McMahon's calculations (McMahon, 1984) show that maximum efficiency occurs at a contraction speed at 13% of the maximum contraction speed of the muscle, which is a slightly lower speed than the speed at maximum power. To swim at maximum muscle efficiency, the fish should maintain a tail-beat frequency that allows the muscle to contract at this optimal speed.

If we take the contraction frequency that maximizes power as a first approximation of the contraction speed that maximizes efficiency, we can compare eel aerobic swimming muscles to those of trout. Eel muscles deliver peak power at much lower contraction frequencies (0.5–0.8 Hz in silver eel, measured at 14°C; Ellerby et al., 2001) than the muscles of trout (2–3 Hz, measured at 11°C; Hammond et al., 1998). The swimming speeds that correspond to these contraction frequencies are $0.5\,l\,s^{-1}$ for eel and $0.4–1.0\,l\,s^{-1}$ for trout (Webb, 1971). These values confirm that in our experiments both eel and trout were swimming at close to their optimal swimming speed, and hence the much higher COT of trout is probably not due to the trout having been forced to swim under considerably suboptimal conditions for its swimming muscles.

Muscle fibre type recruitment and swimming speed

At the low speeds used in this study, the eels will recruit only the posterior red muscle to swim continuously. As demonstrated in the work of Gillis (1998), muscle fiber type recruitment was clearly dependent upon swimming speed. A pattern of 'posterior-to-anterior' recruitment within a fiber type was observed as eels increased their swimming speed (figs 2, 3A,F in Gillis, 1998). For example, eels typically used mainly posteriorly located red muscle (at 0.75 and 0.6 *BL*) to power slow-speed swimming, but would then additionally recruit more anteriorly located red muscle (at 0.45 and 0.3 *BL*) to swim at the higher speeds (figs 2, 3A in Gillis, 1998). These unusual muscle activation pattern and kinematics may explain the low COT in eels compared with trout, in which most of the red muscle on each side of the body is stimulated during a tail-beat cycle – assuming that the European and American eels are similar in this regard.

In contradiction to this theory/hypothesis of Gillis (1998) to explain the low swimming efficiency of eel by recruitment patterns of muscle, Wardle et al. (1995) showed that the muscle activity pattern (% time active during one tail-beat cycle) does not differ substantially between different undulatory swimmers. Wardle's values for eel (based on Williams et al., 1989) agree with those mentioned by Gillis (1998). Compared with trout and other fish, recruitment in eel is certainly not less by a factor of 2–4. Hence it is not likely that more posterior muscle recruitment in eel can explain the many-fold difference in efficiency between eel and trout.

Metabolism and non-locomotory influences on costs of transport

Overall metabolic efficiency is also influenced by the efficiency of the respiration and energy-conversion processes themselves. The whole-organism locomotory performance is determined by its metabolic machinery, bringing us to the whole-body oxygen consumption (routine metabolic rate, RMR) of the animal. In this study, we found a RMR for eel of $29.55±4.2\,ml\,O_2\,kg^{-1}\,h^{-1}$, which corresponds to $42.21±6.0\,mg\,O_2\,kg^{-1}\,h^{-1}$. This value is similar to values

reported in literature: 35 mg kg^{-1} h^{-1} (for the similar sized animals at 18°C; Degani et al., 1989; McKenzie et al., 2000) for eel and also the RMR measurements of other fish species (Winberg, 1956). Hence, we may conclude that, based on metabolic rate comparisons with other fish species, the mitochondrial capacity remains the same. However, in the wild, eel do not migrate at the surface but in the deep sea: a migrating eel has been photographed in the Bahamas at a depth of 2000 m (Robins et al., 1979). There, they experience considerably larger pressures, which might further increase metabolic efficiency at the mitochondrial level by increasing the efficiency of their oxidative phosphorylation (Theron et al., 2000). In a laboratory study in which eels were exposed for 21 days to 10.1 MPa hydrostatic pressure, Theron et al. (2000) demonstrated that the ADP/O ratios, calculated from mitochondrial respiration measurements, were significantly increased.

Eels actually performing the migration will not only experience higher pressures, but also lower temperatures, which will also affect their efficiency. Furthermore, eels might adapt their migratory route to take advantage of favorable sea currents, which would further reduce the energy requirements. However, with the migratory routes unknown, nothing can be said about the possible energy savings from pressure, temperature and sea-current effects.

Metabolic costs and efficiency compared

Our respiratory measurements and the carcass analyses suggest that eels have a much higher metabolic efficiency than trout. In eel, the COT values obtained from oxygen consumption data and carcass analyses are 0.42 and 0.62 kJ kg^{-1} km^{-1}, respectively, whereas trout has much higher COT values (respirometry only) of 2.73 kJ kg^{-1} km^{-1}, respectively. The COT in trout matches the value measured by Webb (1971), and is similar to other salmonids (Brett, 1973) and many adult fish species (for a review, see Videler, 1993). This means that eel swim 4–6 times more efficiently than many other fish species, even across swimming styles.

In conclusion, we demonstrate in this study that fasting European eels are able to swim 5500 km, a distance corresponding to their supposed spawning area in the Sargasso Sea, with a remarkably high swimming efficiency and at low energy costs. At this moment, this high efficiency can be explained neither by propeller nor muscle efficiency. How the extremely low optimal contraction frequency of eel aerobic muscle affects muscle efficiency has not yet been studied. So far, the only evidence that eels have a remarkably high swimming efficiency comes from metabolic energy costs. The source of the eel's remarkably high efficiency remains at present unknown, providing ample stimulation for biomechanists and physiologists alike to investigate eel migratory swimming performance.

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