



Cost of transport and optimal swimming speed in farmed and wild European silver eels (*Anguilla anguilla*)

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ABSTRACT

A swimming speed of 0.4 meters per second (m s^{-1}) is the minimal speed for European female silver eels to reach the spawning sites in the Sargasso Sea in time. As silver eels cease feeding when they start their oceanic migration, the cost of transport (COT) should be minimised and the swimming speed optimised to attain the highest energetic efficiency. In this study, we have investigated the optimal swimming speed (U_{opt}) of silver eels since U_{opt} may be higher than the minimal swimming speed and is more likely to resemble the actual cruise speed. A variety of swimming tests were performed to compare endurance swimming between farmed eels and wild eels, both in freshwater and in seawater. The swimming tests were run with 101 silver female eels (60–96 cm, 400–1500 g) in 22 Blazka-type swim tunnels in a climatized room at 18 °C with running freshwater or seawater. Tests were run at 0.5–1.0 m s^{-1} with increments of 0.1 m s^{-1} , and either 2 h or 12 h intervals. Remarkably, both tests revealed no changes in oxygen consumption (MO_2) and COT over time. U_{opt} values ranged between 0.61 and 0.68 m s^{-1} (0.74–1.02 BL s^{-1}) for the different groups and were thus 53–70% higher than the minimal speed. At U_{opt} , the COT was 37–50 $\text{mg O}_2 \text{kg}^{-1} \text{km}^{-1}$. These relatively very low values confirm our earlier observations. COT values in seawater were about 20% higher than in freshwater. Assuming that migrating female silver eels cruise at their U_{opt} , they will be able to cover the distance to the Sargasso Sea in 3–4 months, leaving ample time for final maturation and finding mates.

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1. Introduction

The 5500-km migration to the spawning grounds in the Sargasso (Schmidt, 1923) is crucial for the reproduction of European eel. Most certainly the effective genitors contributing to the future generation must therefore be characterized by an excellent swimming performance. Female eels leave the continent in October–November and spawning is believed to occur primarily in the following March and April (McCleave, 2003). Migration in the field is thus generally assumed to last for 6 months. Since distance and duration are known, a minimal swimming speed of about 0.4 m s^{-1} can be calculated (or 0.5 BL s^{-1} for average female eels of 80 cm) which is generally assumed to be the cruising speed.

Recently, we subjected large female eels to long term swimming trials at this speed in order to estimate the energy costs of transport (van Ginneken and van den Thillart, 2000; van den Thillart et al., 2004; van Ginneken et al., 2005a). The results showed that eels swam four to six times more efficiently than non eel-like fish, utilizing ca. 60 g fat/kg during sustained swimming. Other experimental data available on swimming performance of *anguillids* are limited and were obtained

from small yellow eels (<15 cm) (Langdon and Collins, 2000) or intermediate sized yellow eels (Schmidt-Nielsen, 1972; Webb, 1975; van Ginneken et al., 2002). However, the onset of migration is preceded by a change of ‘continental’ yellow eels into ‘oceanic’ silver eels. This so called ‘silvering’ process is a metamorphic event; a physiological and morphological preparation for their journey to the Sargasso Sea (Tesch, 2003; Lokman et al., 2003; Durif et al., 2005) or rather a pubertal event; an expression of sexual maturation (Pankhurst, 1982; Aroua et al., 2005). Drastic changes occur during silvering; most apparent is the enlargement of the eyes which is widely used to discriminate between the yellow and silver phase (Pankhurst, 1982). The silver phase is characterized by the impressive swimming performance.

As silver eels, they cease feeding and rely primarily on their fat stores for swimming and reproduction. Because of this, the COT should be minimised and the swimming speed optimised. Like with salmonids that cease feeding, energy management is the key to successful migration and maturation. Besides the costs for swimming of about 40% of the energy stores, an additional 28% is required for deposition in the oocytes of European silver eels (Palstra et al., 2006). With the total costs of 68% of the energy stores eel's lifestyle is most likely a semelparous one. Starting migration with the maximum fuel reserve can be viewed as an optimum strategy (Lucas and Baras, 2001) and the same accounts for optimal swimming. For salmonids, it is suggested that intraspecific migration energetics and abilities are

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correlated to migration distance (Bernatchez and Dodson, 1985; Lee et al., 2003a). When comparing the migration distances between salmonids (up to 1500 km) and European silver eels (5500 km), the need for optimal swimming in eels is very clear. It may well be that U_{opt} is higher than the generally assumed cruising speeds and it is likely that silver eels would cruise at U_{opt} .

In this study, we have investigated U_{opt} of silver eels and the minimal COT. A variety of swimming tests were performed to compare critical swimming speeds (U_{crit}), U_{opt} and COT between farmed eels and wild eels, both in freshwater as in seawater.

2. Materials and methods

2.1. Experimental eels

Eels were collected at three locations:

1. Farmed eels were obtained from a commercial freshwater eel farm (Royaal BV, Helmond, The Netherlands) in October 2001 and in September 2004. They originated as glass eels from France. The October 2001 batch was immediately transferred to SW (32 ppt), acclimated during a 2-week period and used in SW experiments in November and December 2001. The September 2004 group was used in FW experiments within a week after arrival.
2. Wild migratory eels in the FW River Loire (France) were caught by local fishermen at Saint-Florent le Vieil between Angers and Nantes in November 2003. They were used in experiments in December 2003.
3. Wild migratory eels were caught during their seaward migration in the brackish Lake Grevelingen (The Netherlands). Fish were caught at the North Sea sluice at 32 ppt (Bout, Bruinisse, The Netherlands) in November 2001. They were used in experiments in January 2002.

2.2. Swim tunnel set-up and oxygen consumption

A set of 22 Blazka-type 127-L swim tunnels as described by van den Thillart et al. (2004) was used for the swimming trials. The swim tunnels were placed in the direction of the Sargasso Sea (WSW) in a climatized room of about 100 m². The total water content of about 7000 L was recirculated continuously over a bio-filter. The illumination in the climatized room was switched to 670-nm light (bandwidth 20 nm). Based on eye pigment changes during silvering, it was assumed that this far-red light is invisible for eels (Pankhurst and Lythgoe, 1983). Indeed the eels did not respond to the movement of the experimenter during red light illumination. The oxygen level in each swim tunnel was measured continuously by an oxygen electrode (Mettler Toledo, Tiel, The Netherlands). The oxygen level in the tunnels was controlled as described before (van den Thillart et al., 2004). If oxygen levels dropped below 75% air saturation, rinsing occurred automatically, raising the level to 85%. The oxygen consumption rate was calculated from the oxygen decline after automatic closure of the water-inlet by a magnetic valve. From the decline of the O₂ concentration, the O₂ consumption rate was calculated following the formula:

$$\dot{M}O_2 = (127 \Delta [O_2] \Delta t^{-1})(BW)^{-1}; \text{ in mg } O_2 \text{ kg}^{-1} \text{ h}^{-1}$$

where $\Delta[O_2] \Delta t^{-1}$ is the decrease of the O₂ content in mg h⁻¹.

2.3. Pre-swimming measurements

Experiments complied with the current laws of the Netherlands and were approved by the animal experimental commission. Before introduction into the swim tunnels, eels were anaesthetized (250 ppm MS222, benzocaine 80 ppm, or clove oil 1:10 dissolved in 100% ethanol 1–1.5 mL L⁻¹ water) and tagged with small passive transponders for

individual identification (TROVAN, Aalten, The Netherlands). Morphometric parameters were measured including: body length (BL, cm), body mass (BW, g), eye diameter horizontal (EDh, mm) and eye diameter vertical (EDv, mm).

The following indices were calculated:

$$\text{Condition factor: } K = 100 \text{ BW BL}^{-3}$$

$$\text{Eye index: EI} = 100 \left[((\text{EDh} + \text{EDv})0.25)^2 \pi (10 \text{ BL})^{-1} \right]$$

Blood samples were taken from the caudal vessels with heparin flushed (10,000 IU mL⁻¹) 1 mL syringes, which were immediately replaced on ice. Hematocrit (Hct) values were measured in 9 μ L whole blood samples in triplicate using a micro-centrifuge (Bayer, Mijdrecht, The Netherlands). Haemoglobin (Hb) content in 10 μ L was determined in duplicate by a spectrophotometer (LS50B, Perkin Elmer, Wellesley, Massachusetts, USA) measuring the absorbance at 550 nm using the MPR 3 kit (1 mL, Roche Diagnostics, Almere, The Netherlands).

2.4. Experimental protocols

Eels were introduced into the swim tunnels at least two days before the experiment. Trials were performed in either freshwater (FW) or artificial salt water (SW) depending on the origin of the eels: the FW River Loire eels were subjected to FW trials while the SW Lake Grevelingen eels were subjected to SW trials. Farmed eels served as reference groups and were subjected to either FW or SW swimming trials. Salinity and water temperature were measured just before every trial. Salinity values of SW during experiments were 32 ± 1 ppt. Water temperature values during experiments were 18 ± 1 °C. Oxygen electrodes were calibrated with sodium sulphite (0% air saturation, AS) and air (100% AS).

The oxygen consumption during resting state was measured for a period of 3–4 h before the onset of the swimming trials. The swimming protocol consisted of seven experimental trials: on day 1, eels were subjected to the first speed test (= speed test 1). Eels swam initially at $U = 0.5 \text{ m s}^{-1}$ for 2 h during which the oxygen decline in the tunnel was measured over the first 1.5 h, thereafter the tunnel was flushed for 0.5 h while eels continued swimming. Hereafter the U was raised with 0.1 m s^{-1} to 0.6 m s^{-1} for 2 h, using the first 1.5 h for oxygen consumption measurements and the last 0.5 h for flushing. Subsequently, this procedure was repeated with increments of 0.1 m s^{-1} up to 1.0 m s^{-1} .

From day 2 to day 6, eels were subjected to endurance tests which lasted 12 h for each speed. During endurance tests, the oxygen consumption was measured continuously. As flushing occurred automatically eels swam at levels between 75 and 85% air saturation (AS). On day 2, eels swam at 0.5 m s^{-1} for 12 h, followed by an overnight rest. On day 3, swimming started with 1 h at 0.5 m s^{-1} followed by 11 h at 0.6 m s^{-1} . On subsequent days the speed was raised with increments of 0.1 m s^{-1} up to 8 h at 0.9 m s^{-1} . On day 7 the same speed test as on day 1 was carried out (= speed test 2). When fish fatigued at high swimming speeds; they stopped swimming and rolled up against the back screen, the flow was lowered to 0.1 m s^{-1} . The oxygen consumption at this speed was considered as standard metabolic rate as the eels were resting on the bottom. The low water flow was maintained to ensure sufficient mixing of the water in the tunnel.

2.5. Background on the quantification of endurance swimming

In the 1960s and 1970s intensive research has been performed on the fundamentals of salmonid swimming. Jones and Randall (1978) reviewed the pioneer work of especially Brett (1964, 1965a,b) and Glass (Brett and Glass, 1973), providing the parameters for quantification of sustained exercise. When measuring sustained exercise, it is generally assumed that respiratory and circulatory adjustments are

Table 1
Biometric parameters

		Farm, small (SW)	Farm, large (SW)	Farm, large (FW)	Lake Grevelingen (SW)	Loire River (FW)
		(n=20)	(n=22)	(n=20)	(n=19)	(n=20)
BL (cm)	Mean	64	71	71	79	82
	SE	1	1	1	1	1
BW(g)	Mean	536	799	824	949	1018
	SE	18	27	30	36	56
K	Mean	0.199	0.227	0.234	0.194	0.179
	SE	0.004	0.005	0.005	0.004	0.004
EI	Mean			11.0	11.7 ^a	11.2
	SE			0.2	0.4	0.3
Hct (%)	Mean	29.10	31.20	29.82	24.35	39.60
	SE	1.47	0.79	1.45	1.67	1.27
Hb (mM)	Mean			7.49	4.52	5.52
	SE			0.28	0.37	0.16

Parameters (means \pm SE) were measured on experimental eels of 5 groups of silver eels before the start of swimming trials. (For abbreviations see Glossary.)

^a data taken from similar eels ($n=10$) from the same batch for comparison.

adequate to meet increased energy demands aerobically. During sustained swimming, it is assumed that the anaerobic energy contributions are negligible and that there are no changes in the mode of propulsion. An exponential relation exists between oxygen uptake and swimming speed (U), as described by Brett (1964) for sockeye salmon *Oncorhynchus nerka*. This relationship further depends on water temperature (Brett, 1964) and body size (Brett, 1965a,b; Brett and Glass, 1973). The maximum oxygen uptake is achieved just before fatigue in an incremental velocity test. Since the drag on fish increases in the squared proportion to swimming speed, the same applies for the cost of transport (COT) (Fry, 1971). Because oxygen is also consumed at rest, there is a U-shaped relationship between the COT and swimming speed, U_{opt} is obtained when COT is minimal. Only recently, such experiments have been resumed, again mainly with salmonids.

2.6. Endurance swimming parameters

Three parameters were used to characterize swimming endurance:

- 1) U_{crit} : The critical aerobic swimming speed ($m\ s^{-1}$ and $BL\ s^{-1}$) calculated according to Brett (1964), see also Farrell (2008) for recent review
- 2) U_{opt} : The optimum swimming speed ($m\ s^{-1}$ and $BL\ s^{-1}$) where the cost of transport (COT, $mg\ O_2\ kg^{-1}km^{-1}$) reaches a minimum (Tucker, 1970)
- 3) COT_{min} : The cost of transport ($mg\ O_2\ kg^{-1}km^{-1}$) at U_{opt}

The U_{opt} was determined by plotting a polynomial trend line through COT values vs. swimming speeds per individual eel. The point

on this trend line with the lowest COT (COT_{min}) was calculated by equalling the first derivative to zero.

2.7. Statistics

Comparisons were performed between groups for the biometric parameters and for the parameters describing the swimming performance. Normality of the data and homogeneity of variances were checked by Kolmogorov–Smirnov tests. For comparison of biometric parameters between groups (Table 1) and of swimming parameters between speed and endurance trials, t -tests were used either paired for values of the same eels or unpaired for values of different eels. With a univariate general linear model (GLM), analysis of covariance (ANCOVA) was performed on log transformed data in search for group effects in swimming parameters with BL and BW as cofactors. In case of significant group effects, ANCOVA was followed by ANOVA with a post-hoc Bonferroni test to specify the effects between particular groups. P -values ≤ 0.05 were considered to indicate statistically significant differences. Results were calculated and plotted as means \pm standard error (SE). All statistical analyses were performed with SPSS 12.0 for Windows.

3. Results

3.1. Biometric comparisons between experimental groups of eels

All biometric data are presented in Table 1. Farmed eels had eye indices ≥ 9.6 and were therefore considered as silver according to Pankhurst (1982). The 2001 batch was split on the basis of their mass into a group of small ($BW=409\text{--}648\ g$, $n=20$) and a group of large eels ($BW=659\text{--}1191\ g$, $n=22$). The characteristics of the FW group ($n=20$) were comparable with those of the large eels of the SW group.

The wild eels from the SW Lake Grevelingen ($n=19$) were longer ($P\leq 0.01$), and heavier ($P\leq 0.05$) than the SW group of large farmed eels. The condition factor of the Grevelingen eels was significantly lower than that of the farmed eels (Table 1). All Grevelingen eels were silver. The Hct of Lake Grevelingen eels was 22% lower than the SW group of large farmed eels ($P\leq 0.05$). The wild eels from the FW River Loire ($n=20$) were silver. The Hct of River Loire eels was 33% higher than in FW farmed eels ($P\leq 0.01$). However, the Hb was 26% lower ($P\leq 0.01$).

In general, the wild migratory silver eels from both Lake Grevelingen and River Loire were 8 to 11 cm longer and about 150 g heavier. However, their condition factor was lower.

3.2. Individual swimming performance

All experimental eels were females, thus excluding sex related differences. All eels appeared to be in good health, none died during the trials. A few eels did not swim at the beginning of an experiment,

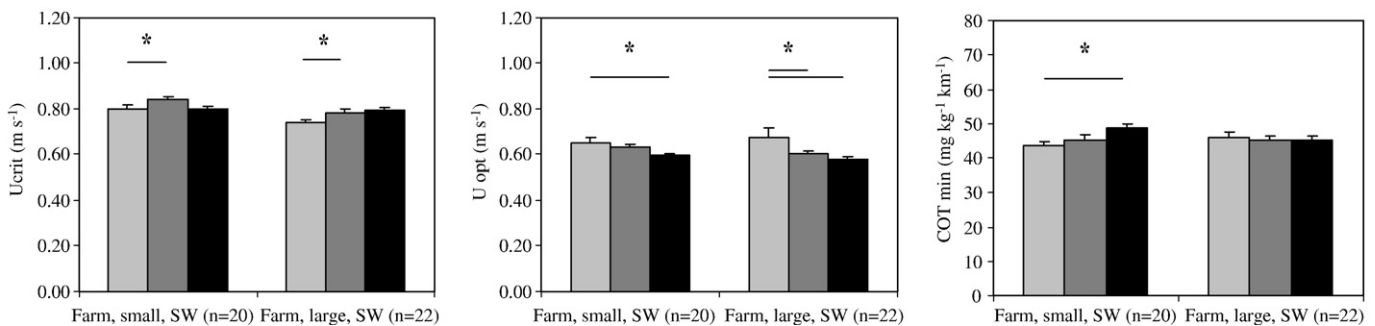


Fig. 1. Swimming parameters. Parameters (means \pm SE) of a group of small ($\sim 500\ g$) and a group of large ($\sim 800\ g$) farmed eels in SW during speed test 1 (light-grey), speed test 2 (dark-grey) and endurance tests (black). Indicated are statistical significant differences ($P\leq 0.05$) between speed test 2 and endurance tests with speed test 1. (For abbreviations see Glossary.)

Table 2
Oxygen consumption and cost of transport

		Swim speed (m s ⁻¹)						
		0.5	0.6	0.7	0.8	0.9	1.0	
$\dot{M}O_2$ (mg kg ⁻¹ h ⁻¹)	Speed test 1	Mean	89	101	125	140	147	161
		SE	2	2	3	4	9	10
		n	35	36	30	17	8	3
	Speed test 2	Mean	87	100	126	150	167	173
		SE	2	3	3	3	4	7
		n	40	41	41	39	31	7
	Endurance tests	Mean	85	104	129	153	161	
		SE	2	2	2	3	7	
		n	39	42	39	32	11	
COT (mg kg ⁻¹ km ⁻¹)	Speed test 1	Mean	49	47	50	49	45	58
		SE	1	1	1	1	3	4
		n	35	36	30	17	8	3
	Speed test 2	Mean	49	46	50	52	52	62
		SE	1	1	1	1	1	2
		n	40	41	41	39	31	7
	Endurance tests	Mean	47	48	50	53	50	
		SE	1	1	2	1	2	
		n	39	42	40	32	11	

$\dot{M}O_2$ and COT data of farmed eels (SW) were pooled to obtain a higher *n* per speed and per test (speed test 1, 2 and the endurance tests). Although increase in $\dot{M}O_2$ level per speed increment shows a linear relation in the range 0.5–0.9 m s⁻¹, fewer eels were able to swim at each higher speed. Comparison between means of the pooled group for the different tests shows that $\dot{M}O_2$ data of the first speed test and endurance tests are similar. In bold is indicated a significant ($P < 0.05$) difference between the first speed test and the endurance test at 0.8 m s⁻¹. (For abbreviations see Glossary.)

but could be stimulated by shining a flashlight or by knocking on the swim tunnel. Some eels were “brushing the wall” (Brett, 1964), i.e. swimming close to the wall of the swim tunnel in search for a lower flow in the first 2 cm from the wall (van den Thillart et al., 2004). This occurred with a few small eels (~60 cm) at high speeds (0.9–1.0 m s⁻¹). Data of those eels were rejected. Most eels swam a few cm below the centre in the front part of the tunnel near the grid. We did not observe any other irregularities in swimming behaviour.

3.3. Groupwise comparisons of swimming performance

3.3.1. Comparison between the first and second speed test: training effects on swimming performance

The mean U_{crit} of the SW group of small farmed eels during the first speed test was lower than the mean U_{crit} during the second speed test (Fig. 1). This difference was significant ($P \leq 0.05$) and expressed a mean training effect of 5.6%. Also, among the SW group of large farmed eels this difference was significant ($P \leq 0.05$) and expressed a training effect of 5.7%, similar to the training effect for the smaller eels.

The mean U_{opt} during the second speed test of large farmed eels was lower than during the first speed test ($P \leq 0.05$). This indicates the training effect: eels with lower performance during the first speed test fatigued later during the second speed test. These extra data-points at higher speeds made it possible to calculate U_{opt} and COT_{min} values for these eels that respectively decreased and increased average values.

3.3.2. Comparison between speed and endurance tests: time effects on swimming performance

Swimming performances between speed test 1 and endurance tests were similar (Fig. 1). For small farmed eels of the SW batch, the mean U_{opt} for endurance trials was slightly lower ($P \leq 0.05$). COT values at U_{opt} were slightly higher for endurance trials. For large farmed eels of the SW batch, the mean U_{opt} for endurance trials was also lower than the mean U_{opt} during the first speed test ($P \leq 0.05$). Again this indicated the described training effect causing lower U_{opt} and higher COT_{min} values.

To investigate the relation between the first speed test and endurance trials, we investigated the $\dot{M}O_2$ and COT values per speed, pooled for the two groups of farmed eels swimming in SW to obtain a higher

number of values. For the mean $\dot{M}O_2$ values, we found that the increase per speed increment in the range 0.5–0.9 m s⁻¹ for each of the tests was similar (Table 2). The mean $\dot{M}O_2$ values increased about two-fold when the speed was increased two-fold. However, with every speed increment fewer eels were able to continue swimming. Some eels stopped swimming soon after $\dot{M}O_2$ levels started to rise as a result of the induced speed increment. In contrast to individual values, group averages of $\dot{M}O_2$ levels therefore showed a linear relation with swimming speed while group averages of COT values showed similar values at each swimming speed rather constant between 45 and 53 mg O₂ kg⁻¹ km⁻¹ at swimming speeds of 0.5 up to 0.9 m s⁻¹. Only at a U of 1.0 m s⁻¹ the COT values were higher at 58 and 62 mg O₂ kg⁻¹ km⁻¹ but only 7 out of the total 42 farmed eels were able to swim at 1.0 m s⁻¹ for longer periods (> 10 min) during the speed tests.

The pooled $\dot{M}O_2$ and COT values found for speed test 1; swimming for 2 h at each speed, and the endurance tests; swimming for 12 h at each speed, were very similar (Table 2). No significant differences were found except for slightly higher $\dot{M}O_2$ values ($P \leq 0.05$) during the endurance tests at a swimming speed of 0.8 m s⁻¹. O_2 and COT values found for speed test 1 were therefore highly representative for results obtained at

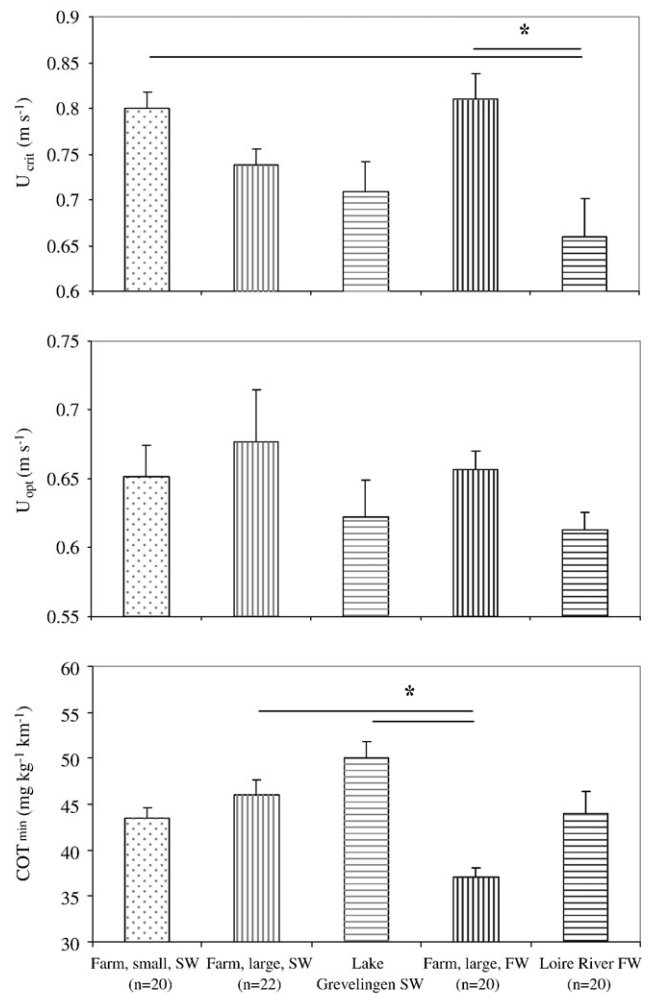


Fig. 2. Swimming endurance tests. Swimming parameters (means \pm SE) of experimental eels of all groups from speed test 1: farmed small eels in SW (light-grey dots), farmed large eels in SW (light-grey vertical stripes), Lake Grevelingen eels in SW (light-grey horizontal stripes), farmed large eels in FW (dark-grey vertical stripes), Loire eels in FW (dark-grey horizontal stripes). Indicated are statistical significant differences ($P \leq 0.05$; Table 3) between groups. For U_{crit} and U_{opt} were the absolute values in m s⁻¹ compared because ANCOVA showed no effects of BL and BW (Table 4). For COT_{min} were the relative values in mg kg⁻¹ km⁻¹ because ANCOVA showed an effect of BW (Table 3). (For abbreviations see Glossary.)

Table 3
Statistical tests comparing swimming parameters between the experimental groups

ANCOVA		Group	BL	BW		
U_{crit}^a		0.001	ns	ns		
U_{opt}^a		ns	ns	ns		
COT_{min}^b		<0.001	ns	<0.001		
		ANOVA	Farm, large (SW)	Farm, large (FW)	Lake Grev. (SW)	Loire (FW)
Farm, small (SW)	U_{crit}^a	ns	ns	ns	ns	0.005
	U_{opt}^a	ns	ns	ns	ns	ns
	COT_{min}^b	ns	ns	ns	ns	ns
Farm, large (SW)	U_{crit}^a	ns	ns	ns	ns	ns
	U_{opt}^a	ns	ns	ns	ns	ns
	COT_{min}^b		0.008	ns	ns	ns
Farm, large (FW)	U_{crit}^a			ns	ns	0.004
	U_{opt}^a			ns	ns	ns
	COT_{min}^b			< 0.001	ns	ns
Lake Grev. (SW)	U_{crit}^a				ns	ns
	U_{opt}^a				ns	ns
	COT_{min}^b				ns	ns

Panel A: ANCOVA showing overall group effects and effects of BL and BW. Panel B: ANOVA showing the significant effects between particular groups. In bold are indicated the P values at ≤ 0.05 . (For abbreviations see Glossary.)

^a absolute values compared because there were no effects of length and weight (U_{crit} : $m s^{-1}$, U_{opt} : $m s^{-1}$).

^b relative values compared because of an effect of weight (COT_{min} : $mg kg^{-1} km^{-1}$).

the endurance tests. Therefore, for the remaining comparisons we subjected the different groups of eels to a single speed test.

3.3.3. Comparison between eels of the SW group and the FW group: salinity effects on swimming performance

Farmed eels of the SW group and farmed eels of the FW group were of the same origin and similar in size and Hct, and therefore considered as completely comparable (Table 1). The U_{opt} for both groups was similar, but the COT_{min} at these speeds was significantly lower for swimming in FW vs. SW ($P \leq 0.01$; Fig. 2; Table 3).

3.3.4. Comparison between farmed eels and wild eels: environmental effects on swimming performance

Results of the swimming speed tests between the large farmed eels and the wild migratory eels were compared (Fig. 2; Table 3). For SW and FW identical differences were observed: the wild migratory eels had lower U_{crit} , lower U_{opt} and higher COT_{min} . However, ANCOVA showed effects of BW on COT_{min} . By eliminating effects of BW and effects of swimming in SW or FW, only U_{crit} was significantly different between farmed and wild eels. Differences between farmed and wild eels were more pronounced in freshwater.

4. Discussion

This study has been the first to test the swimming endurance of large female silver eels on a large scale. Earlier swimming experiments were performed only on small eels (<60 cm) and often in low numbers. Our set-up of 22 Blazka swim tunnels allows large scale investigations. Recent long term simulated migration trials of large female eels swimming at a fixed speed of $0.5 BL s^{-1}$ (on average $0.4 m s^{-1}$) revealed that large silver eels have a very low COT (van Ginneken and van den Thillart, 2000; van den Thillart et al., 2004; van Ginneken et al., 2005a). With this study, we aimed to determine the unknown U_{opt} that was assumed to be faster than the minimal swimming speed of $0.4 m s^{-1}$ that is necessary to reach the Sargasso.

4.1. Critical swimming speeds and oxygen consumption

The majority of eels in this study were able to swim at the low subjected speeds of 0.5 and $0.6 m s^{-1}$ during both periods of 2 h and

12 h swimming. Most individual eels fatigued starting at speeds of $0.7 m s^{-1}$, just after reaching their U_{opt} and before the steep increase of the $\dot{M}O_2$ as related to swimming speed. At higher swimming speeds, the measured $\dot{M}O_2$ values were lower than expected on the basis of an exponential relation. Measurements of oxygen uptake during swimming can considerably underestimate the true COT near U_{crit} (Farrell, 2007) thereby challenging the exponential relation between $\dot{M}O_2$ and U . Measuring excess post-exercise oxygen costs (EPOC) shows that the non-aerobic cost of swimming to U_{crit} in adult sockeye (*O. nerka*) and coho salmon (*Oncorhynchus kisutch*) adds an additional 21.4–50.5% to the oxygen consumption measured at U_{crit} (Lee et al., 2003b). Adjusting for EPOC approaches the difference between the measured $\dot{M}O_2$ and the fitted exponential relation between $\dot{M}O_2$ and U .

Forced swimming trials in a swim tunnel respirometer may underestimate U_{crit} , possibly because fish in a swim tunnel respirometer are unable to sustain a ground speed (Farrell, 2007). Peake and Farrell (2006) suggested that fatigue in a swim tunnel respirometer is a behavioural decision made near gait transition in smallmouth bass *Micropterus dolomieu*. Tudorache et al. (2007) reported that U_{crit} in carp *Cyprinus carpio* increased by using longer swim tunnels because the duration of their burst and glide swimming increased. Despite these potential limitations, comparison of U_{crit} between the different groups of silver eels in this study is possible since all eels swam in the same swim tunnels. U_{crit} values ranged between 0.66 and $0.81 m s^{-1}$ (or 0.81 – $1.24 BL s^{-1}$) for the various groups of experimental eels (range 60–80 cm). Blaxter and Dickson (1959) reported burst speeds of $1.14 m s^{-1}$ ($1.9 BL s^{-1}$) for a 60-cm eel swimming for 2–5 s in a swim tunnel, thus not much higher than the U_{crit} of eels in our study. For small eel elvers, McCleave (1980) reported burst speeds of $0.53 m s^{-1}$ or $7.5 BL s^{-1}$. The values in this study are comparable to other migrating species with an elongated body. The sea lamprey *Petromyzon marinus* (90 cm) for example has U_{crit} values of 0.82 – $1.19 m s^{-1}$ (1.01 to $1.34 BL s^{-1}$) (Almeida et al., 2005). Values of eels are low in comparison to cyprinid and salmonid species which have prolonged swimming speeds above $3 BL s^{-1}$ and mean burst speeds of $10 BL s^{-1}$ (reviewed by Videler, 1993).

4.2 Training effects

About half of the eels of each group fatigued during swimming at $0.8 m s^{-1}$ during the first speed test. More eels were able to swim at this speed during the second speed test indicating a significant training effect. At the second speed test, the farmed eels showed about 5% higher U_{crit} (Fig. 1). Effects of training have been reviewed by Davison (1997) and Kieffer (2000) who showed that training increases aerobic and anaerobic capacities, and speed of recovery making trained fish prepared for additional bouts of exercise. Training effects for eels swimming for either 2 h or 12 h as found in this study are difficult to compare with data on other fish species since most training studies have focused on either long term endurance exercise training (weeks up to months), short-term sprint training (minutes) or repeated swimming tests with relatively short recovery times, thus without significant training effects. Gallaughier et al. (2001) exposed chinook salmon (*O. tshawytscha*) to either continuous swimming at low speeds or a high-intensity training regime with continuous swimming at low speeds but U_{crit} swimming challenges on alternate days. No change in U_{crit} between both groups was observed. In contrast, trained rainbow trout *Oncorhynchus mykiss*, sockeye salmon *O. nerka* and coho salmon *O. kisutch* fatigued later than unexercised individuals (reviewed by Beamish, 1978). When trained over a 1–2 month swimming period, *O. mykiss* improved their U_{crit} with 12% (Farrell et al., 1990) up to 25% (Holk and Lykkeboe, 1998). The 5% increase in U_{crit} of silver eels in this study achieved over 7 experimental days of swimming trials thus seems high in comparison with these results for salmonids.

4.3. Cost of transport and optimal swimming speed

This study showed no difference between swimming for 2 h and 12 h with respect to $\dot{M}O_2$ and COT (Table 2). Hence the results of the speed test have a highly predictive value for these parameters, and allow the estimation of the COT and U_{opt} of eels in a one day speed test.

Silver eels swam at optimum swimming speeds of 0.61–0.68 m s⁻¹ (0.74–1.02 BL s⁻¹), thus 53–70% higher than the minimal speed. The corresponding COT_{min} values were 37–50 mg O₂ kg⁻¹ km⁻¹. The lowest COT values were found for the large farmed eels swimming in FW, the highest for Lake Grevelingen eels in SW. These COT values that were determined by one day swimming trials were perfectly confirmed by long term migration trials (Palstra et al., 2006); Large farmed eels (n=6) swimming 27 days at 0.8 BL s⁻¹ in FW had an average COT of 34±2 mg O₂ kg⁻¹ km⁻¹ and Lake Grevelingen eels (n=6) swimming 22 days at 0.8 BL s⁻¹ in SW had an average COT of 52±5 mg O₂ kg⁻¹ km⁻¹. In comparison, Videler (1993) reviewed results for 12 undulatory swimming fish species and reported U_{opt} values of 0.18–0.51 m s⁻¹ (0.8–2.8 BL s⁻¹). At those swimming speeds, which were in the same range as in this study, much higher energy consumption rates were observed with corresponding COT values of 113–475 mg O₂ kg⁻¹ km⁻¹. In contrast to their high swimming endurance, we found that silver eels cannot swim fast relatively to other species. However, from the relatively low COT levels we can conclude that silver eels are highly efficient cruisers.

4.4. Cost of transport in SW and FW

Energy expenditure during exercise was higher in SW than in FW. The COT_{min} of two identical groups of farmed eels (same farm, same holding conditions at the farm, same length of stay at the farm, same glass eel source) was 20% higher when swimming in SW vs. FW. Also wild silver eels showed a higher COT_{min} in SW although this effect could also be due to differences in origin (River Loire vs. Lake Grevelingen). Literature data are scarce on this topic and do not provide a clear picture. Morgan and Iwama (1998) did not find significantly different oxygen consumption rates in juvenile coho salmon *O. kisutch* swimming at a speed of 1 BL s⁻¹ after an increase in salinity. Energy expended for swimming by rainbow trout *O. mykiss* and tilapia *Oreochromis niloticus* was independent of salinity. However, changes in metabolic rate did occur, suggesting that overall performance would still be reduced (reviewed in Beamish, 1978). Adult migrating wild sockeye salmon (*O. nerka*) had higher routine $\dot{M}O_2$ and active $\dot{M}O_2$ in SW compared with fish in FW (Wagner et al., 2006). Higher $\dot{M}O_2$ was associated with higher viscosity of SW and ionoregulatory costs, and four additional potential costs; non-steady state ionoregulation, nutritional energetic status, reproduction, and restlessness. All these may also account for the higher $\dot{M}O_2$ of silver eels in SW. The osmoregulatory capacity may be specific to life-history stage as suggested for salmonids by Morgan and Iwama (1991). Recently, Rankin et al. (2006) found that marine osmoregulation in eels improves during silvering, as shown by a positive correlation between eye index and plasma osmolality at 36 h after transfer to seawater.

4.5. Environmental constraints on swimming performance

Although we expected that the wild eels would be better cruisers than the farmed eels, we found higher COT_{min} values and lower U_{crit} values for wild silver eels than that of farmed eels. The wild silver eels in this study thus seem to have lower swimming performance than farmed eels. Their lower swimming performance may correspond to a lower physical condition as illustrated by their Hct and Hb values. In general, yellow eels have Hct values between 20 and 30% (Larsson and Fänge, 1969; Johansson et al., 1974) and Hb values of 6–7 mM (van

Ginneken et al., 2007). Silver eels have Hct values between 30 and 40% and Hb values of 8–9 mM. Values of the farmed eels in this study fell well within these ranges. The silver eels from River Loire also had normal Hct values but low Hb values. For Lake Grevelingen silver eels, both Hct and Hb were low.

Firstly, silver eels from the Loire River, which scored the lowest U_{crit} and U_{opt} values, suffered from severe infection with the swim-bladder parasite *Anguillicola crassus*. Out of the twenty experimental eels, only one had a healthy large, thin-walled swim-bladder without any parasites. Thirteen eels had normal swim-bladders with 1 to 13 parasites; the remaining six eels had empty but severely damaged swim-bladders. Recently, we have found that eels with a high parasite load or with a damaged swim-bladder have a reduced swimming performance (Palstra et al., 2007a). Such eels had a 20% higher COT_{min} at U_{opt} that was 20% lower than eels with healthy swim-bladders. Almost half of the eels with severely damaged swim-bladders (43%) stopped swimming already at low maximum aerobic swimming speeds (<0.7 m s⁻¹). So, the reduced swimming performance of the silver eels from the Loire River seems, at least partly, associated with swim-bladder dysfunction caused by infection with the swim-bladder parasite. The low Hb can be explained by the capacity of adult parasites to degrade Hb (Polzer and Taraschewski, 1993). We found that especially silver eels have much higher infection levels than yellow eels, suggesting that migrating silver eels with severely infected or damaged swim-bladders are unable to reach the spawning grounds.

Secondly, silver eels from Lake Grevelingen showed low Hb and low Hct. They may have suffered from infection with the rhabdovirus EVEX. In a recent study by van Ginneken et al. (2005b) where similar silver eels from Lake Grevelingen from a year before were subjected to simulated migration, the eels developed hemorrhage and anemia and died after 1000–1500-km swimming in contrast to virus-negative animals that swam the full 5500 km. Virus-positive eels showed a decline in Hct, which was related to the swimming distance while virus-negative eels showed increased Hct. Also the Lake Grevelingen eels in this study had lower Hct values than normal for Lake Grevelingen silver eels (van Ginneken et al., 2007) suggesting that they may have suffered from EVEX.

Infection with the swim-bladder parasite (Palstra et al., 2007a,b) and the EVEX virus (van Ginneken et al., 2005b) may prevent silver eels from their reproductive migration and may in this way contribute to the collapse of eel populations world-wide (Stone, 2003).

4.6. Potential implications for reproductive migration to the Sargasso

The average U_{opt} found in this study for wild silver eels in SW was 0.62 m s⁻¹ (or 0.77 BL s⁻¹). Assuming that those silver eels cruise at U_{opt} , cruise speeds are about 50% higher than the generally assumed cruise speed of 0.4 m s⁻¹ or 0.5 BL s⁻¹. This U_{opt} agrees well with the sustained cruise speeds found for 11 silver eels (69 to 96 cm) tracked in the North Sea by Tesch (1974; reviewed by Beamish, 1978) which ranged between 0.6 and 0.9 BL s⁻¹. As for other tracking studies on migrating silver eels, the optimum swimming speeds found in this study correspond only to the fastest migration speeds found in the wild (Tesch, 1978, 1989, 2003; Tesch et al., 1991; McCleave and Arnold, 1999; Jellyman and Tsukamoto, 2002).

In the wild, eels most probably swim deep at daytime (500–1000 m; reviewed by Tesch and Rohlf, 2003) at lower temperatures (5–10 °C) than those applied of 18 °C in this study. However, during a 1000-km simulated migration of Lake Grevelingen silver eels at daily decreasing temperatures from 18 back to 10 °C, we found that $\dot{M}O_2$ was independent from these water temperatures (Palstra et al., 2006).

When cruising at an optimum swimming speed of 0.62 m s⁻¹ European female silver eels would reach the spawning grounds in ~3.5 months instead of the generally assumed 6 months. The ground speeds in the field may however be even higher than the optimal

swimming speed as measured in this study because migrating eels may use the North Equatorial Current, at least initially. This would leave them with ample time for final maturation and finding mates.

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EDh eye diameter horizontal
EDv eye diameter vertical
EI eye index
FW freshwater
Hb hemoglobin
Hct hematocrit
K condition factor
MO₂ oxygen consumption
SW sea water
U swimming speed
U_{crit} critical aerobic swimming speed
U_{opt} optimum swimming speed

Glossary

AS air saturation
BL body length
BW body weight
COT cost of transport
COT_{min} minimum cost of transport at optimal swim speed