Tools and triggers for eel reproduction

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Chapter 2

Schooling reduces energy consumption in swimming male European eels, A*nguilla anguilla* L.

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Abstract

Swimming in schools provides fish with a number of behavioural and ecological advantages, including increased food supply and reduced predation risk. Previous work shows that carangiform and tunniform group-wise swimming result in energetic advantages for individuals using a diamond swimming formation. However, little is known about the potential energetic advantage associated with schooling for anguilliform fish, such as European eel. European eels migrate a long distance to their spawning area in the Sargasso Sea and may experience energetic advantages when swimming in schools. In this study the effect of group-wise swimming on the cost of transport was tested. In addition, the swimming pattern of eels swimming in groups was studied.

Male silver eels were individually subjected to an increased velocity test (0.4-0.9 m s^{-1}) with increments of 0.1 m s^{-1} every 2 hours. Groups comprising of seven males were swum following the same protocol. Video recordings were obtained to analyze tail beat frequency at the various water speeds.

At all swimming speeds the oxygen consumption was significantly lower in group-wise vs. individually swimming males. The cost of transport at the optimal swimming speed of group-wise swimming males was significantly lower than that of the individually swimming males (21.3 ± 3.2 vs. 32.0 ± 0.6 mg O$_2$ kg^{-1} h^{-1}, respectively). The optimal swimming speeds however, were not significantly different (0.57 ± 0.02 and 0.52 ± 0.04 m s^{-1} respectively). At speeds of 0.50 m s^{-1} and above, tail beat frequency was lower in males swimming in groups than in males swimming individually (2.6 ± 0.1 and 3.8 ± 0.1, respectively). As compared to the 'diamond' shape pattern of many group-wise swimming fish, eels tend to swim in a synchronized fashion parallel to each other. It is concluded that male eels in groups swim energetically more efficient than males swimming individually by the synchronized parallel swimming mode.

Introduction

When migrating, many fish species swim in groups, named schools, defined as a social aggregation of fish, swimming in the same direction and maintaining near-constant spacing relative to neighbouring conspecifics (Pitcher & Parrish, 1993). Schooling is a common migration behaviour in fishes, with school sizes often varying between species, locations and seasons from a few individuals to several million swimming together (e.g. Coetzee 2000). The advantages of migrating in groups are thought to be predation avoidance (Breder, 1967; Seghers, 1981; Godin & Morgan, 1985; Magurran & Higham, 1988), increase of foraging success (Pitcher et al., 1982; Wolf, 1987; Ranta & Lindstrom, 1990), or reduction of migration costs (Parker, 1973; Weihs, 1973; Webb, 1975; Ross & Backman, 1992; Herskin & Steffensen, 1998; Fish, 1999; Svendsen et al., 2003; Liao, 2007; Johansen et al, 2010; Killen et al., 2011). Also, schooling behaviour was reported to be a response to many ecological and physiological factors such as temperature (Dommasnes et al., 1994) and oxygen availability (Domenici et al., 2002).

On basis of the degree of body use for undulation during swimming, Breder (1926) divided swimming fish in four different classes: tunniform, carangiform, ostaciiform and anguilliform. In the past, schooling studies concerned only carangiform, ostraciiform or tunniform swimming fish, such as saithe, herring, tuna, salmon or mackerel, (Partridge et al., 1980; 1983, Hoar, 1953; Castonguay & Gilbert, 1995; Hansen & Jonsson, 1985). When swimming in schools during migration these fish are known to be distributed in a rhomboid or 'diamond' pattern (Weihs, 1973) induced by the hydrodynamic advantages by swimming in the wake vortices preceding school members (Breder, 1965; Weihs, 1973). By the undulatory movements of a swimming fish thrust-type vortices are generated and shed into the wake (Rosen, 1959; Müller et al., 1997). These vortices are thought to affect the swimming efficiency of a following fish depending on its position within the school (Breder, 1965). Previous studies have suggested hydrodynamic interactions of schooling fish as a possible energy conserving mechanism (Breder, 1965; Belyayev & Zuyev, 1969; Zuyev & Belyayev, 1970; Weihs, 1973; Partridge et al., 1983; Abrahams & Colgan, 1985, 1987; Pitcher & Parrish, 1993), and it has repeatedly been shown that schooling fish swimming in a rhomboid distribution have energetic advantages over fish swimming alone (Parker, 1973; Weihs, 1973; Webb, 1975; Ross & Backman, 1992; Herskin & Steffensen, 1998; Fish, 1999;

Svendsen et al., 2003; Liao, 2007; Johansen et al, 2010; Killen et al., 2011). In contrast to other swim types, vortices produced by anguilliform swimmers, as eels, are directed sideways, suggesting a different form of thrust (Tytell & Lauder, 2004). Energetic advantages of schooling in anguilliform swimmers were thus far not studied.

The swimming capacity of migrating European eels (*Anguilla anguilla* L., 1758) is subject of increasing scientific interest (van Ginneken & van den Thillart, 2000; van den Thillart et al., 2004; van Ginneken et al., 2005; Palstra et al., 2008; Sébert et al., 2009; Burgerhout et al., 2011; Methling et al., 2011). The spawning area of the European eel is assumed to be situated in the Sargasso Sea (Schmidt, 1923), which implies an average migration distance of about 6000 km from the European coast. During their spawning migration, eels do not feed and rely therefore entirely on their body reserves for energy supply (Tesch, 2003). A low cost of transport has therefore a high advantage for ecological fitness of European eels. Indeed, a very low cost of transport was observed for swimming female eels, i.e. more than 5 times lower than that of rainbow trout (van Ginneken et al., 2005). Eels swim in an anguilliform mode, i.e. they use the whole body for propulsion, with at least one wave-length present in the body (Breder, 1926, Webb, 1971). Currently, there is no information or model that predicts whether sideway vortices generated by swimming eels can be used by others to reduce their cost of transport.

Although, current knowledge on group-wise swimming of eels during the oceanic phase is lacking, there are reports that during their exodus eels tend to aggregate in large groups (Tesch, 2003). Considering the tremendous effort associated with such a long distance migration, it would be advantageous for eels to migrate in groups when this reduces swimming cost of transport. The present study examined whether European eels swimming in groups show a reduction of energy consumption compared to eels swimming individually. In addition, the swimming behaviour within a group of anguilliform swimming eels was investigated.

Methods

Animals and housing

Farmed male silver eels (n = 89; 106.6 ± 2.1 g; 38.4 ± 0.2 cm) were obtained from a commercial eel farm (Nijvis-Holding B.V., Nijmegen, The Netherlands), where they were kept in fresh water at 24°C. Prior to the swimming trials, the eels were acclimated for four weeks and housed in a ca. 8000L recirculation system, supplied with natural seawater (30 ± 1 ppt) at 18 ±1°C. The fish were kept in the dark before and during the trials, except during filming. As the eels cease feeding when silvering, they were not fed during the whole period of time.

Swimming capacity

Seven 127 L Blazka-type swimming tunnels as described by van den Thillart et al. (2004) were used. The tunnels were connected to a recirculation system with running natural seawater (28 ± 1 ppt; 18 ± 1°C) with a total volume of ca. 4000 L.

      Five days prior to the trials the eels were introduced into the swimming tunnels to acclimate. The eels were anesthetized with clove oil (1:10 dissolved in 96% ethanol, 1 mL in 1 L water); body weight (BW, g) and body length (BL, cm) were measured before placing them into the tunnels. To determine the range of swimming velocities a preliminary test was conducted at water speeds from 0.1-0.9 m s^{-1}. The eels were still able to swim steadily at 0.9 m s^{-1}, therefore 0.9 m s^{-1} (~ 2.2 BL s^{-1}) was taken as the maximum velocity in the trials.

      For the swimming trials with individuals, seven male eels (104.9 ± 6.8 g; 37.5 ± 0.6 cm) were subjected to a series of swimming speeds ranging from 0.4-0.9 m s^{-1} (0.4-0.6 m s^{-1} on the first day and 0.7-0.9 m s^{-1} on the second) with increments of 0.1 m s^{-1} at 120 minutes intervals in seven separate swimming tunnels. During the two-day trial the eels were kept in their separate tunnels. Oxygen consumption was measured during the first 90 minutes after each increase in flow speed, which was sufficient to reach a significant slope in the [O$_2$] decline (p<0.05) with an r^2 ≥ 0.80. Thereafter the tunnels were flushed for 30 minutes with well oxygenated water at 5-7 L min^{-1}. During flushing the speed was lowered to 0.05 m s^{-1}. Because of irregular swimming behaviour – i.e. changes in tail beat frequency and position within the swimming tunnel – at low swimming speeds (< 0.4 m s^{-1}), the standard metabolic rate (SMR) was determined by

extrapolating the oxygen consumption curve to zero swimming speed using the formula $\dot{M}O_2$ = SMR+aU^b; where $\dot{M}O_2$ is the weight specific oxygen consumption, U swimming speed, and a and b dimensionless constants.

For group-wise swimming trials, seven separate groups consisting of seven eels each (104.2 ± 8.0 g; 38.4 ± 0.9 cm), were placed in the seven swimming tunnels and acclimated for 5 days. The protocol was identical as the one for the swimming trials with individuals. The group size of seven individuals was estimated the largest number that could fit in the tunnels without disturbed swimming behaviour.

Swimming kinematics

A HD video camera (Panasonic, HDC-SD90, Panasonic Inc., Japan) was mounted 0.6 m above the swimming section. To compensate the spherical aberration caused by the cylindrical shape of the swimming tunnel, a Perspex adapter box with a flat surface and filled with water was placed on top of the tunnel. The eels were filmed for 10 minutes at each speed (range 0.4-0.9 m s^{-1}). Per speed, 3 movie file sequences of 20 s, randomly chosen from the beginning the middle and end of the 10 minute video recordings were used for further analysis (for details see Tudorache et al., 2009). In short: The period of ten minutes was divided in three period of 200 s. Each of these 200 s was then divided in ten periods of 20 s. One period of 20 s was chosen using mathematical randomisation (Microsoft Excel:Mac 2011, version 41.2.2, Microsoft inc., Seattle, USA). The selection criteria for a suitable video sequence were at least two individuals swimming steadily in front and one individual in the back of the tunnel during the entire period of 20 s. If the randomly chosen period did not fulfil these criteria, another period was chosen according to the same method. From each of the three sections of 20 s, tail beat frequency (*f*), and amplitude (*a*) were measured using the tracking program Vernier Logger Pro (v3.6, Vernier Software and Technology, USA), resulting in a total of 9 measurements per swimming speed. From the videos of the group-wise swimming eels, *f* and *a* values of two randomly chosen eels in the front third and of one eel in the back third of the swimming tunnel were analysed.

Statistics

First, all data were checked for normal distribution by Kolmogorov-Smirnoff tests. As the data were not normally distributed (Kolmogorov-Smirnoff; p>0.05) a Mann-Whitney U non-parametric test was used to analyze the results. Differences in oxygen consumption ($\dot{M}O_2$), standard metabolic rate, minimum cost of transport, optimal swimming speeds, tail beat frequency and tail beat amplitude between individual swimmers and group-wise swimmers were tested. Costs of transport per velocity were tested within the individual and group-wise swimming groups as well as between the two groups. Statistical difference was considered significant at p<0.05. In all cases values are expressed as average ± standard error.

Ethics Statement

The experiments complied with the Dutch law on animal experiments and were approved by the animal ethical committee of Leiden University (DEC# 09020).

Results

Behavioural observations

At low water speeds below 0.4 m s^{-1}eels, individuals as well as groups, swam irregularly and remained often motionless at the rear end of the swimming section curled up against the grid. When increasing the water speed the eels started to show regular swimming activity at water speeds of 0.30 m s^{-1}, while at 0.40 m s^{-1} all eels were swimming regularly. When swimming group-wise, a few eels swam parallel to each other in the front swimming in synchronized phase and with the same tail beat frequency, however with regular changes in and out of synchronization (Fig. 1). In contrast, eels swimming at the back of the tunnel did not show this type of synchronized swimming behaviour. The eels in the front regularly changed places with eels swimming in the rear. Thus all eels swam under similar conditions. There were no drop-outs; all fish were able to finish the trials.

Respirometry

Oxygen consumption during swimming was significantly higher (p<0.05) for males swimming individually as compared to males swimming group-wise at all swimming speeds (Figure 2a). The graph of oxygen consumption ($\dot{M}O_2$) versus swimming
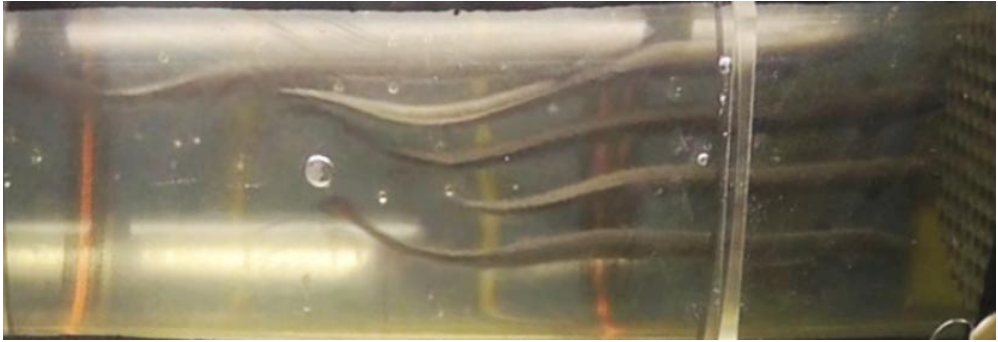
Figure 1. Anguilliform swimming motion. This photographic image shows the anguilliform swimming motion performed by group-wise swimming males in a parallel swimming formation at 0.40 m s^{-1}. For further explanation see text.

speed (U) fitted the formula $\dot{M}O_2$ = SMR+aU^b with an r^2 of 0.99 for individuals as well as for groups. The extrapolated standard metabolic rate (SMR) showed no difference between males swimming individually and those swimming group-wise, i.e. 29.7 ± 6.2 vs. 30.6 ± 4.1 mg O$_2$ kg^{-1} h^{-1} (Table 1). At all speeds, the cost of transport (COT) of males swimming individually was significantly higher than the COT of males swimming group-wise (Figure 2b). However, when comparing the COT-values within each series, no significant differences were observed between speeds 0.4 – 0.8 m s^{-1}, indicating a rather flat curve.

There was no significant difference in the optimal swimming speed (U$_{opt}$) between individuals and groups (respectively 0.52 ± 0.04 and 0.57 ± 0.02 m s^{-1}, p>0.05). The minimum cost of transport, i.e. the cost of transport at U$_{opt}$ (COT$_{min}$), was significantly higher in males swimming individually compared to males swimming group-wise; 31.99 ± 0.56 and 21.25 ± 3.24 mgO$_2$ kg^{-1} km^{-1} (p<0.05) respectively (Table 1).

Kinematics

Tail beat frequency (*f*) plotted against swimming speed (U) revealed a linear relationship; *f* = a+bU, with a being the intercept and b being the slope of the curve. At swimming speeds above 0.5 m s^{-1}, *f* was significantly higher in males swimming individually compared to males swimming group-wise at the same swimming speed (Figure 2c). There was no difference between *f* of eels swimming

at the front versus those swimming in the rear of the swimming section. The tail beat amplitude (*a*) was not affected by swimming in groups or individually and remained constant across all swimming speeds at 5.1 ± 0.1 cm (pooled data of 3 movie file sequences of 20 s, Table 1). The width of the swimming tunnel was 4 times the tail amplitude (i.e. 20 cm) and thus the eels had their full range of motion without any obstructions at all applied speeds (Steffensen, 1989).

In order to determine the cost per fin beat (CPB in mg O2 kg^{-1}), standard metabolic rate (SMR) values were subtracted from oxygen uptake ($\dot{M}O_2$) values and the resulting numbers were divided by fin beat frequency (*f*) values per speed. Data were plotted using the power function CPB=a+bU^c with a b and c being constant. The values for a are 0.0012±0.009 and 0.0016±0.003 mg O2 kg^{-1}, for b 0.0148±0.0007 and 0.0079±0.0003, and for c 2.2580±0.3783 and 2.9816±0.4324, for males swimming individually and for males swimming group wise, respectively (Figure 2d). Only values for b were significantly different from each other. The ratio of CPB values per swimming speed of group wise and individually swimming males did not differ with speed and resulted in the pooled value of 0.59±0.02.

Discussion

In order to establish the advantages of group-wise anguilliform swimming, male silver eels were swum over a range of 0.4 to 0.9 m s^{-1} individually and in groups of seven in swim tunnels. This study shows for the first time that group-wise anguilliform swimming, measured in terms of cost of transport (COT), is energetically more advantageous than swimming individually by ca. 30% (31.99 ± 0.56 vs. 21.25 ± 3.24 mg O$_2$ kg^{-1} km^{-1}, respectively). These results for anguilliform swimmers agree with observations on other fish species representing carangiform, ostaciiform and tunniform swimming modes (Parker, 1973; Webb, 1975; Ross & Backman, 1992; Herskin & Steffensen, 1998; Fish, 1999; Svendsen et al., 2003; Liao, 2007; Johansen et al, 2010; Killen et al., 2011).

Video analysis of swimming eels revealed that when swimming group-wise eels have a lower tail beat frequency (*f*) than when swimming individually. As *f* is almost linearly related to swimming speed (Figure 1c), this suggests that eels in a group take advantage of the wake of their neighbours. In addition, the amplitude of the tail beat (*a*) was not significantly different between individual and group-wise swimming. So, the amount of thrust force is only dependent on *f*.
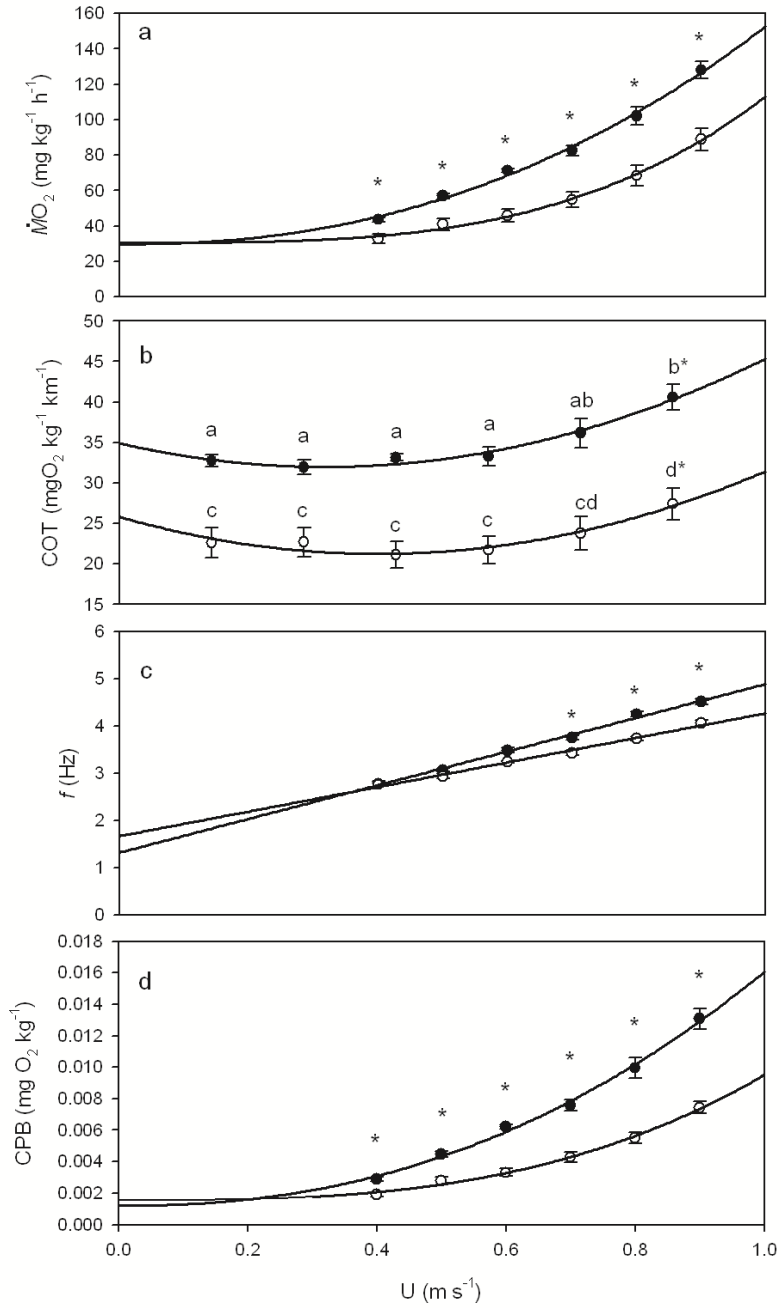
Figure 2 (opposite page). Energetics and kinematics of male silver eels swimming individually and group-wise. Swimming energetics and kinematics of male silver eels swimming individually (closed circles, n=7) and male silver eels swimming group-wise (n=7, 7 males per group, open circles). a. Oxygen consumption ($\dot{M}O_2$, mg kg^{-1} h^{-1}) as a function of swimming speed (U; m s^{-1}) with the formula $\dot{M}O_2$ = SMR+aU^b. Significant differences are indicated by an asterisk (*); Mann-Whitney U test, n=7, p<0.05). b. Cost of transport (COT, mgO$_2$ kg^{-1} km^{-1}) as a function of U (m s^{-1}) with the formula COT = $\dot{M}O_2$ U^{-1}. Letters indicate significant differences between data points; an asterisk indicates significant difference between X and COT$_{min}$ (see Table 1; Mann-Whitney U test, n=7, p<0.05). c. Tail beat frequency (*f*, Hz) as a function of U (m s^{-1}) with the formula f= a+ bU. Significant differences are indicated by an asterisk (*); Mann-Whitney U test, n=7, p<0.05). All lines (a, b and c) are regression lines (refer to Table 1 for regression values). Abbreviations: SMR: standard metabolic rate. d. Costs per fin beat (CPB, mg kg^{-1}) as a function of swimming speed (U; m s-1) with the formula CPB = a+bUc. Significant differences are indicated by an asterisk (*); Mann-Whitney U test, n=7, p<0.05).

Additionally, group-wise swimming suggests a lower mean cost per fin beat (CPB) at the same speed (Figure 1d) and thus should reduce the COT (Table 1). Indeed, a lower CPB was observed in group-wise swimming eels.

Also, the present study shows that male silver eels were able to swim steadily at 0.9 m s^{-1} (corresponding to ca. 2.3 BL s^{-1}). A preliminarily conducted velocity test showed that they also swim steadily at speeds even above 0.9 m s^{-1} (E. Burgerhout et al., unpublished). Quintella et al. (2010) observed a critical swimming speed (U$_{crit}$) of 0.66 m s^{-1} for wild male silver eels. Our results indicate that male eels can have sustained swimming speeds above 0.9 m s^{-1}, with a calculated optimal swimming speed (U$_{opt}$) of above 0.50 m s^{-1} (Table 1). The differences in results between the two studies might be due a difference in e.g. origin (wild versus farmed), conditioning or handling protocol. Stress may be an important factor as farmed eels are less sensitive to handling stress than wild eels. Furthermore, the present study used swimming tunnels with a longer swimming section; it has been shown that fish can obtain higher speeds in longer swimming tunnels (Tudorache et al., 2007) As shown in this study male silver eels can reach endurance speeds, even above 0.9 m s^{-1} (~2 BL s^{-1}).

Table 1. Energetics and kinematics of male silver eels swimming individually and group-wise. Oxygen consumption (mgO_2 kg^{-1} h^{-1}) was expressed as a function of swimming speed (U, m s^{-1}) with the formula $\dot{M}O_2$ = SMR+aU^b. SMR, standard metabolic rate; U_{opt}, optimal swimming speed (speed at the lowest cost of transport); COT_{min}, minimum cost of transport. Tail beat frequency (*f*, Hz) was expressed as a function of swimming speed (U, m s^{-1}) with the formula f = a + bU. Values are mean ± s.e.. P-values <0.05 are considered significantly different, and are expressed in bold.

Energetics	Individual	Group-wise	Mann-Whitney U
SMR (mgO_2 kg^{-1} h^{-1})	29.72±6.16	30.62±4.05	p=0.91
constant a	122.88±5.54	82.39±3.61	**p<0.01**
constant b	2.25±0.37	3.38±0.43	**p<0.01**
U_{opt} (m s^{-1})	0.52±0.04	0.57±0.02	p=0.28
COT_{min} (mgO_2 kg^{-1} km^{-1})	31.99±0.56	21.25±3.24	**p<0.01**
Kinematics			
frequency slope (b)	3.8±0.1	2.6±0.1	**p<0.05**
frequency intercept (a)	1.31±0.02	1.66±0.31	p=0.27
amplitude (cm)	5.1±0.1	5.6±0.6	p=0.43

In addition, we observed the behaviour of eels swimming group-wise, i.e. the swimming pattern in group-wise swimming eels, as many carangiform, ostraciiform or tunniform swimming species tend to swim in a rhomboid or 'diamond' shape pattern when swimming group-wise (Breder, 1965; Weihs, 1973; Partridge et al., 1980; 1983, Hoar, 1953; Castonguay & Gilbert, 1995; Hansen & Jonsson, 1985). Remarkably, instead of this rhomboid or 'diamond' schooling pattern, eels swam rather close to each other in a temporarily synchronized anguilliform swimming motion (Fig. 1). In studies on the hydrodynamics of eel

swimming, it was shown that the jet forces are directed laterally to the swimming direction (Tytell & Lauder, 2004; Kern & Koumoutsakos, 2006; Lauder & Tytell, 2006). Therefore, it is assumed that the lower energy consumption of the group-wise swimmers was at least in part due to this type of synchronized swimming motion where the individuals in the group use the lateral forces of the neighbours. This mechanism can be compared to the so called Karman gait, where thrust can be generated entirely passively by a foil when placed in an oscillating flow (reviewed in Liao, 2007). The actual mechanism of how eels use the water flow in group-wise swimming still needs to be studied in further detail using kinematic techniques.

In conclusion, the present study shows for the first time that group-wise swimming in eels is energetically more advantageous than swimming individually by the significant reduction of cost of transport. The synchronized swimming mode observed in group-wise swimming eels is expected to contribute to the lower energy consumption per capita.

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