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Kinematics and energetic benefits of schooling in the labriform fish, striped surfperch *Embiotoca lateralis*

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ABSTRACT: Schooling can provide fish with a number of behavioural and ecological advantages, including increased food supply and reduced predator risk. Previous work suggests that fish swimming using body and caudal fin locomotion may also experience energetic advantages when trailing behind neighbours. However, little is known about the potential energetic advantages associated with schooling in fish that swim using their pectoral fins. Using the striped surfperch *Embiotoca lateralis*, a labriform fish that swims routinely with its pectoral fins, we found that pectoral fin beat frequencies were significantly higher for schooling individuals swimming in the front of a school relative to those swimming in the back, with trailing individuals benefiting from a 14.9 ± 3.2% reduction in fin beat frequency (mean ± SE). Trailing fish were estimated to benefit from a 25.6% reduction in oxygen consumption, based on correlations between swimming speeds and pectoral fin beat frequency and between swimming speeds and oxygen consumption of solitary fish. In addition, leading individuals in a school were estimated to have higher oxygen consumption than solitary individuals swimming at the same speed, based on their higher pectoral fin frequency. We suggest that this may be explained by differences in swimming behaviour, with schooling individuals continuously correcting their position relative to their neighbours whilst solitary individuals maintained a more rigid swimming pattern. Taking into account the increased oxygen consumption in leaders vs. solitary fish, we estimated that for an energetic advantage to occur in a school of striped surfperch as a whole, more than 78% of the individuals need to be in trailing positions, which is likely to be a common occurrence based on previous observations of other schooling species.

KEY WORDS: Pectoral fin swimming · Fin beat frequency · Respirometry · Kinematics · Energics · Oxygen · Schooling · Labriform fishes

INTRODUCTION

Schooling is a common behaviour in fishes, with school sizes often varying between species, locations and seasons from a few individuals to several million fish swimming together (e.g. Coetzee 2000). In general, schooling is considered to convey ecological advantages by reducing predatory risks and increasing foraging success (Pitcher & Parrish 1993, Krause 1993, 1994). In addition, schooling is thought to reduce locomotor costs by reducing drag and increasing lift around individuals swimming within the school, depending on the swimming mode in question and structure of the school (Weihs 1973, Fish 1999).

Most fishes swim using one of 2 main modes of propulsion: body and caudal fin swimming (BCF, Webb 1984) or median and paired fin swimming (MPF, Blake 1979, Webb 1984, Westneat 1996). Whilst

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schooling is found in fishes that swim with both BCF and MPF, these are distinct swimming modes which convey very different flow structures around each individual (e.g. Müller et al. 1997, Drucker & Lauder 1999, 2000, Fish & Lauder 2006). In particular, the oscillation of the caudal fin in BCF swimming leaves alternating vortices in the wake (known as a reverse von Karman street; Müller et al. 1997), which may increase lift and reduce drag on trailing individuals positioned at some angles relative to the fish in front (Weihs 1973). A number of studies have shown that BCF swimming fishes can utilize the vortex wakes produced by stationary objects in a flow to reduce muscle activity while swimming (Liao et al. 2003a, b) and that the trailing individuals in a school of BCF swimming fish often show a reduced tail beat frequency relative to those swimming in front (Zuyev & Belyayev 1970, Fields 1990, Herskin & Steffensen 1998, Svendsen et al. 2003). Consequently, trailing fish in schools of fish swimming with BCF mode may gain energetic advantages by exploiting the vortices produced by fish in front, in a manner analogous to the exploitation of vorticity produced by stationary objects in a flow (Liao 2007).

Labriform swimming is a form of MPF locomotion (e.g. Walker & Westneat 1997) and it is the primary mode of locomotion for many substratum-associated taxa, being particularly common among the vast assemblages of reef-dwelling perciform fishes (Blake 1983, Westneat 1996). These fishes propel themselves using either ‘lift based flapping’ or ‘drag based rowing’ motions of the median and paired fins (Blake 1979, Westneat 1996). The vortices produced by labriform fishes are comparable to the vortex shedding created by birds in flight (i.e. ‘lift based flapping’, see Kokshaysky 1979, Spedding et al. 1984, Spedding 1986), and may be utilized by trailing individuals for significant energetic advantage, similar to that found for birds flying in formation (Weimerskirch et al. 2001). Akin to BCF swimming fishes, labriform fishes were found to be capable of reducing energetic demands for swimming by utilizing the flow around stationary obstacles such as substratum protuberances (Johansen et al. 2007, 2008). However, little is known about the potential hydrodynamic, and therefore energetic, advantages associated with schooling in fish that swim using their pectoral fins.

In addition to work linking hydrodynamics and schooling, a number of previous studies have attempted to estimate the energetic advantages of schooling in BCF swimming fishes by comparing the total oxygen consumption of fish schools with that of solitary swimming individuals (Parker 1973, Itazawa et al. 1978, Abrahams & Colgan 1985, Ross & Backman 1992). As argued by Herskin & Steffensen (1998) however, this approach suffers from various methodological problems, including a conflict between the low water volume necessary for accurate oxygen consumption measurements in a respirometer (Steffensen 1989), and the large working section of the respirometer necessary to minimize wall effects on a school of fish. Furthermore, this methodology does not enable the relative contributions of calming and hydrodynamic effects on the reduction in oxygen consumption found in schools to be determined (e.g. Parker 1973, Itazawa et al. 1978). An alternative approach (Herskin & Steffensen 1998) based on measuring the differences in kinematics (i.e. reduction in fin beat frequency) when comparing schooling and solitary fish allows the estimation of the reduction in oxygen consumption solely due to a hydrodynamic effect (hence a decrease in swimming effort), by using the relationships between the kinematics of locomotion (e.g. fin beat frequency and amplitude) and oxygen consumption.

Given the vast number of known MPF swimming species, many of which are gregarious (Randall et al. 1990), the possibility that schooling may provide some hydrodynamic and energetic advantages (similar to those found in BCF swimming fishes) may have significant implications for the daily movement patterns of such fishes and have direct influence on their distribution and ecology. Here, we examine the kinematics and potential energetic advantage of schooling in an MPF swimming fish, the striped surfperch *Embiotoca lateralis*, a gregarious species that swims using lift based pectoral fin locomotion, often found in schools from northern Baja California to southern Alaska (Eschmeyer et al. 1983). The oxygen consumption as well as the pectoral fin beat frequency and amplitude were evaluated for fish swimming alone and compared to the pectoral fin beat frequency and amplitude of individuals in different positions within a school, in order to test the hypothesis that schooling in a labriform fish provides energetic advantages.

MATERIALS AND METHODS

Study species. Eleven striped surfperch *Embiotoca lateralis* Agassiz, 1854 (fork length, L_F = 19.2 ± 0.9 cm, weight = 169.2 ± 24.5 g, mean ± SE) were collected with beach seines at Jackson beach, San Juan Island, Washington, USA, and transported to Friday Harbour Laboratories in June 2007. Fish were held in 60 × 130 × 125 cm tanks under a 18:6 h light:dark regime. Tanks were continuously supplied with filtered seawater (salinity 34 ppm) at a temperature of 12 °C (range 11.8 to 12.3 °C) in a flow-through system. Fishes were acclimated for a minimum of 3 d and fasted for 24 h before experimental trials to ensure a post-absorptive state that maximised the energy available for swimming (Niimi & Beamish 1974). All trials were conducted within the 18 h of the daily light regime in order to match the diurnal activities of the study species (Ebeling & Bray 1976).

Solitary swimming measurements. The oxygen consumption (MO_2) and pectoral fin movements of swimming fish were measured for 7 solitary individuals swimming in an 8.31 l clear Plexiglas respirometer with a working section of 9.0 × 26.0 × 10.0 cm (width × length × depth). Flow within the working section of the respirometer was calibrated from 0 to 80 ± 0.5 cm s^{-1} (mean ± SE) using a digital TAD W30 flow-meter. Solid blocking effects of the fish in the working section were corrected online according to Bell & Terhune (1970).

At the beginning of each trial, the respirometer was filled with temperature-controlled (12 ± 0.1°C, mean ± SE, range 11.8 to 12.3°C), filtered and fully aerated seawater. Next, a fish was placed in the respirometer and left to acclimatize for 8 to 12 h at a swimming speed of 0.5 fork lengths per second (L_F s^{-1}). Trials were started only when the oxygen consumption of the test subject reached a steady state and the fish had settled into a continuous swimming rhythm. The oxygen consumption of the test subject was then measured at 5 different swimming speeds (0.5 to 2.5 L_F s^{-1}), with 0.5 L_F s^{-1} speed increments and 3 consecutive repeats for every measure. For each oxygen measurement, a 180 s flush, 120 s wait and 300 s measurement period was applied following the intermittent flow respirometry methodology of Steffensen et al. (1984) and Steffensen (1989). This constituted a 3 × 10 min measurement cycle for every swimming speed and totaled a 2.5 h trial period for every test subject. The flushing period ensured the oxygen concentration throughout the trial did not decrease below 85% of air saturation. Oxygen levels within the swimming respirometer were measured using a fiber optic oxygen meter (Presense Fibox 3) and monitored with Oxyview v.5.31 (Presense). To reduce bacterial growth and respiration within the system, the respirometer was treated with a chlorox solution and thoroughly flushed in freshwater at the end of every second trial. This procedure ensured background respiration remained below 2% of the oxygen consumed by each fish during swimming trials (measured at the end of each trial).

School swimming measurements. Seven schools of 4 individuals were tested in a 500 l flow tunnel (working section 37.0 × 70.0 × 44.0 cm, width × length × depth). Of the 4 individuals tested in each school, 3 were used repeatedly in all 7 trials and were individuals not previously tested in the respirometer; the fourth individual was a 'test subject' previously examined in the respirometry trials. Flow within the working section of the flow tunnel was calibrated from 0 to 80 ± 0.5 cm s^{-1} (mean ± SE) using a digital TAD W30 flow-meter. Because even minor variations in body size may affect kinematic variables (Videler 1993), assessing each of the 7 'test subjects' within the same school structure (i.e. using the same 3 experimental fish) minimised variations in the flow-hydrodynamics created by the school and allowed a direct comparison of the swimming kinematics of each individual while schooling and while solitary. In the schooling experiment, a leading fish was defined as a fish in the front of the school, whilst a trailing fish was defined as a fish swimming up to 2 body lengths away from an upstream fish, ± 0.5 body depths above/below the upstream fish and up to 1 pectoral fin length to the side of the upstream fish (based on the vortex shedding patterns of similar labriform fishes; Drucker & Lauder 1999, 2000). Wall effects on the swimming performance of the school were minimized as the size of the working section was large enough to ensure that even peripheral school members had a sufficient distance to tank walls at all times ($z/B > 3$, with z = distance from pectoral fins to the nearest wall and B = length of pectoral fins, Webb 1993). All trial fish were allowed to rest for a minimum of 2 d between each solitary and schooling experiment.

In the schooling trials all schools were tested at 2.0 ± 0.1 L_F s^{-1} (mean ± SE) of 'test subject' size to facilitate direct comparison between individuals. This swimming speed was chosen as a compromise between maximising speed, since this may increase energetic advantage (Herskin & Steffensen 1998, Svendsen et al. 2003), and a speed safely below gait change ($U_{p\text{-}c}$) (i.e. around 2.2 L_F s^{-1} in *Embiotoca lateralis* of this size; based on Drucker & Jensen 1996a) as was confirmed by observations during the experimental trials. Before the trial, each school was left to acclimate in the working section of the flow tunnel for 1.5 h, consisting of 0.5 h without flow, followed by 1 h at 2.0 ± 0.1 L_F s^{-1} (speed increments were performed steadily at ~0.5 L_F s^{-1} min^{-1} until a speed of 2 L_F s^{-1} was reached after ~4 min). Following the acclimation period, an experimental period of minimum 1 h of video recording and observations was carried out.

Video recording. To measure the pectoral fin beat movements of each test subject during the trials, a mirror was placed at a 45° inclination above the working section in order to allow simultaneous video recording of the fish from above and from the side. A Sony DCR-PC100 mini DV camera was used for video recording of both solitary and schooling fish. All videos were recorded on digital video tapes and converted to video avi-files using Adobe Premiere Pro v.7.0 software. For the schooling trials, fish were recorded for a minimum of 1 h at 2.0 ± 0.1 L_F s^{-1}, until a total of 12 non-consecutive segments of 5 s each were captured of the test subject, i.e. 6 segments in a leading position and 6 segments in a trailing position within the school. Similarly, for the respirometry trials, 6 non-consecutive segments of 5 s each were captured for every test subject at every speed.

Data analysis. The fin beat frequency and fin amplitude of swimming test subjects were analysed using Logger Pro v.3.5 (Vernier software) and Microsoft Excel. In short, based on the dorsal view of the fish, fin amplitude (in degrees) was calculated as the angle between the following 3 points: Point A, on the outer most leading edge of a single pectoral fin; Point B, at the base of the pectoral fin; and Point C, on the body of the fish such that the line B–C was parallel to the body axis. Calculations of fin beat frequency and amplitude (degrees) were then based on triangulation between the 3 set points. The lateral view video sequences allowed for qualitative verification of the pectoral fin movement. This procedure was performed for every frame on each of the 5 s video sequences taken from the solitary and schooling fish trials.

Data exploration of fin movement and oxygen measures verified assumptions of normality and homogeneity of variance required for ANOVA (based on Kolmogorov-Smirnov [K-S] test on residuals and Bartlett's test for homogeneity of variance) (Fin beat frequency: K-S, $d = 0.095$, $p > 0.1$, Bartlett, $\chi^2 = 3.337$, df = 2, $p = 0.189$; Fin amplitude: K-S, $d = 0.082$, $p > 0.2$, Bartlett, $\chi^2 = 4.259$, df = 2, $p = 0.119$). Next, we tested the relationship between fin beat frequency and speed, and fin beat amplitude and speed using linear regressions. Furthermore, a non-linear regression was performed on the individual oxygen consumption rates of all 'test subjects' from each swimming speed trial. In total, this procedure used yielded 2 significant correlations, with one equation for 'fin beat frequencies versus swimming speed' and one for 'oxygen consumption versus swimming speed', while the relationship between fin beat amplitude and speed was not significant. The 2 significant correlations yielded equations that allowed the estimated oxygen consumption to be compared between leaders and trailing individuals in a school. The differences in fin beat frequencies and amplitude between leading and trailing school positions, and between solitary and grouped swimming fish, were compared within individuals using a repeated measures ANOVA with swimming positions (i.e. leading, trailing or solitary swimming at 2 L_F s^{-1}) as fixed factors and fin beat frequencies and amplitude as dependent variables. Individual differences between each fixed factor were subsequently analysed using a post-hoc Tukey's HSD test. All data analysis was conducted using Statistica v.6.1 and Sigmaplot v.9.0.

Finally, the net energetic advantage of a whole school was calculated by taking into account the advantages of being in trailing school positions and the disadvantages of being in leading positions, both compared to swimming as a solitary individual. Specifically, the net energetic consequences of forming a school (expressed as the ratio S_{EC} = energetic cost of schooling / energetic cost of solitary swimming) will depend on the relative proportion of leading and trailing individuals in a given school. S_{EC} was therefore calculated as the sum of the relative costs of being leaders (C_L, the ratio of MO_2 of leaders relative to the MO_2 of solitary fish) multiplied by the proportion of leaders (P_L), and the relative costs for trailing (C_T, the ratio of MO_2 of trailing individuals relative to that of solitary fish) multiplied by the proportion of trailing individuals ($1 - P_L$).

$$S_{EC} = C_L \, P_L + C_T \, (1 - P_L) \qquad (1)$$

For the school as a whole to have a net energetic advantage over solitary behaviour, S_{EC} should be <1 (e.g. with $S_{EC} = 0.8$ schooling is providing an energetic advantage of 20%). As a consequence energetic advantages occur when the following condition is satisfied:

$$P_L < (1 - C_T) \,/\, (C_L - C_T) \qquad (2)$$

RESULTS

Experiments on solitary individuals

Pectoral fin beat frequency increased with increasing swimming speed from 1.16 Hz at 0.5 L_F s^{-1} to 2.32 Hz at 2.5 L_F s^{-1} ($y = 0.58x + 0.86$, $R^2 = 0.79$, $p < 0.001$, Table 1, Fig. 1). Conversely, the relationship between fin beat amplitude and speed was not significant (Linear regression, $p = 0.2$, Table 1). Oxygen consumption rate was best described as a power function (see Korsmeyer et al. 2002), as it increased with increasing swimming speed from 92.9 mg O_2 kg^{-1} h^{-1} at 0.5 L_F s^{-1} to 163.2 mg O_2 kg^{-1} h^{-1} at 2.5 L_F s^{-1} ($y = 3.75x^{3.24} + 90.76$, $R^2 = 0.77$, $p < 0.001$, Table 1, Fig. 1).

Experiments on schooling individuals

Pectoral fin beat frequencies differed between swimming positions (repeated measures ANOVA, $F = 36.14$, df = 2, $p < 0.001$) with significant differences found between the following swimming positions: leaders 2.29 ± 0.11 Hz, solitary 2.05 ± 0.09 Hz, and trailing 1.95 ± 0.07 Hz (mean ± SE) (leaders vs. solitary: Tukey's HSD, df = 105, $p = 0.0001$; leaders vs. trailing: Tukey's HSD, df = 105, $p = 0.0001$; solitary vs. trailing: Tukey's HSD, df = 105, $p = 0.0372$; Table 2). No differ-

Table 1. *Embiotoca lateralis.* Pectoral fin beat frequency (Hz), fin amplitude (degrees) and oxygen consumption (MO_2, mg O_2 kg^{-1} h^{-1}) of solitary swimming striped surfperch at 0.5 to 2.5 fork lengths (L_F) s^{-1}. Values are means (± SE). Parameters from regression analyses (frequency and amplitude: $y = ax + b$, MO_2: $y = ax^b + c$) (see Fig. 1), test statistics and p-values are also given

	Swimming speed (L_F s^{-1})				
	0.5	1.0	1.5	2.0	2.5
Frequency (Hz)	1.22 (0.09)	1.39 (0.06)	1.73 (0.09)	2.05 (0.09)	2.33 (0.08)
Amplitude (degrees)	84.36 (3.87)	85.03 (1.63)	84.18 (2.55)	85.92 (4.48)	90.10 (2.65)
MO_2 (mg O_2 kg^{-1} h^{-1})	94.56 (4.03)	93.24 (2.85)	105.07 (4.36)	125.12 (4.20)	163.07 (10.15)

	Regression analysis					
	a	*b*	*c*	R^2	*F* (df)	p-value
Frequency (Hz)	0.58 (0.05)	0.86 (0.09)		0.79	117.60 (32)	<0.001
Amplitude (degrees)	2.60 (1.99)	81.95 (3.38)		0.05	1.72 (32)	0.20
MO_2 (mg O_2 kg^{-1} h^{-1})	3.75 (2.45)	3.24 (0.70)	90.76 (3.99)	0.77	54.61 (32)	<0.001

Table 2. *Embiotoca lateralis.* Pectoral fin beat frequency (Hz) and calculated oxygen consumption ($MO_{2\text{-CALC}}$, mg O_2 kg^{-1} h^{-1}) for striped surfperch swimming at 2.0 fork lengths (L_F) s^{-1} either solitary or in a leading or trailing school position. Values are mean (± SE). Thestatistical significance of fin beat frequency is marked by an asterisk: *($p < 0.05$) or **($p < 0.01$).

Position	Fin beat frequency (Hz)	Δ% Solitary	Δ% Leading	$MO_{2\text{-CALC}}$	Δ% Solitary	Δ% Leading
Solitary	2.05 (0.09)			129.25		
Leading	2.29 (0.11)	+10.58**		160.97	+24.54	
Trailing	1.95 (0.07)	−5.12*	−14.85**	119.75	−7.35	−25.61

ence was found in fin beat amplitude between swimming positions (repeated measures ANOVA, $F = 0.93$, df = 2, p = 0.41). As a result of the differences in pectoral fin beat frequencies, the same ranking was found in the estimated oxygen consumption of each experimental group (161.0 mg O_2 kg^{-1} h^{-1}; 129.3 mg O_2 kg^{-1} h^{-1} and 119.8 mg O_2 kg^{-1} h^{-1} in leaders, solitary and trailing individuals, respectively; Table 2, Fig. 1).

Energetic consequences of schooling

Based on our results (Table 2), the relative cost of leading a school (C_L) and the relative cost of trailing (C_T) correspond to 1.25 and 0.93, respectively. Therefore, the maximum proportion of leaders (P_L) for an energetic advantage of schooling to occur in striped surfperch is estimated to be 22% (based on Eq. 2).

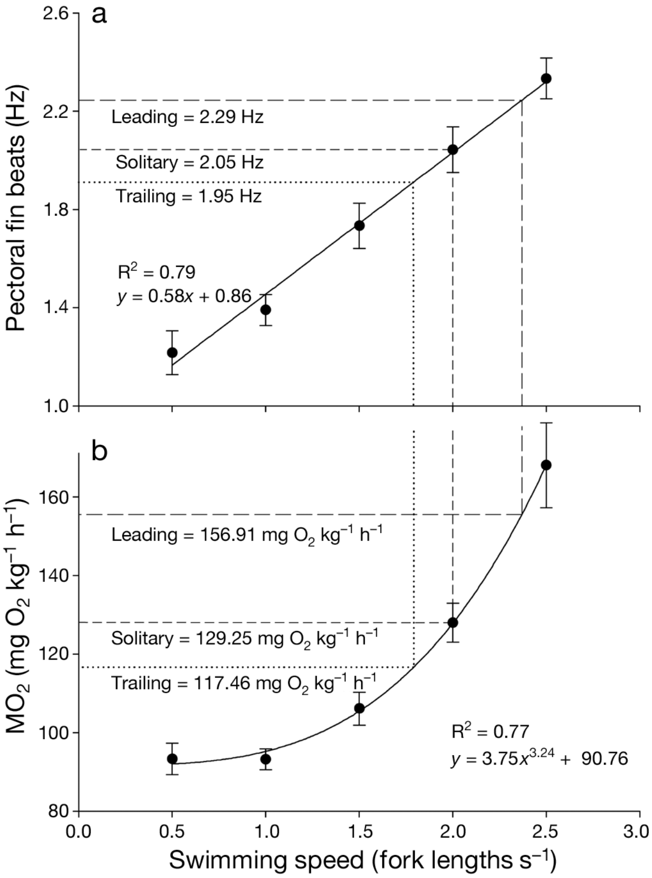

Fig. 1. *Embiotoca lateralis.* (a) Mean pectoral fin beat frequency (±SE) versus swimming speed. (b) Mean oxygen consumption (±SE) versus swimming speed. Both graphs are based on *E. lateralis* swimming solitary in a respirometer. Dotted and dashed lines show pectoral fin beat frequencies and calculated oxygen consumption for individuals swimming solitary (short dashed line) or in a leading (long dashed line) or trailing (dotted line) school position at 2.0 fork lengths (L_F) s^{-1}

DISCUSSION

Although many species of fish are known to school (e.g. Eschmeyer et al. 1983, Partridge et al. 1983, Krause et al. 2000), the energetic advantages of such behaviour are still relatively unexplored, particularly in fish that swim using MPF swimming. This study demonstrates a significant reduction in the pectoral fin beat frequency of trailing labriform fish swimming in a school, compared to solitary and leading individuals. Relative to leading fish, trailing individuals displayed a 14.9 ± 3.2% (mean ± SE) reduction in pectoral fin beat frequency at the speed used here (2.0 L_F s^{-1}), suggesting that labriform fishes swimming in a school may benefit from up to a 25% reduction in oxygen consumption over leading individuals swimming at the same speed (see Table 2). These energetic savings are comparable to the savings found for schooling in BCF swimming fishes, which show a 9 to 23% reduction in oxygen consumption for fish swimming in trailing school position vs. leaders (at a speed range of 0.6 to 1.3 total length s^{-1}, Herskin & Steffensen 1998).

Whilst several theoretical studies have speculated about the potential hydrodynamic and consequent energetic benefits of swimming in a school (e.g. Belyayev & Zuyev 1969, Weihs 1973, 1975), experimental studies have focused on BCF swimming fishes (e.g. Zuyev & Belyayev 1970, Abrahams & Colgan 1985, 1987, Fields 1990, Herskin & Steffensen 1998, Svendsen et al. 2003, Hanke & Lauder 2006). The vortex shedding created by a labriform swimming fish is different from that of a BCF swimming fish (Müller et al. 1997, Drucker & Lauder 1999, 2000), but may well be sufficient to interact with trailing individuals (based on imaging studies and force measures of vortices created by labriform swimming in fish, e.g. Drucker & Lauder 1999, 2000) Consequently, any energy saving that labriform fishes may gain by swimming in a trailing position within a school is likely to be a direct result of the hydrodynamics created by leading individuals (Drucker & Lauder 1999, 2000).

Labriform swimming fish leave vortices in their wake as a result of the up and down movement of the pectoral fins (Drucker & Lauder 1999, 2000), and these vortices may reduce the drag and increase the lift forces exerted on trailing individuals if utilized correctly. Specifically, in schools of BCF swimming fishes, trailing individuals have to place themselves at an angle to the leader to gain hydrodynamic advantage (e.g. Svendsen et al. 2003) because the vortex shedding from a beating tail fin has the structure of a reversed von Karman street (Müller et al. 1997) causing increased flow directly behind a leading individual (Müller et al. 1997, Liao 2007). Conversely, the swimming kinematics of a labriform swimmer causes vortex shedding at an angle to the body, depending on swimming speed (Drucker & Lauder 2000), whilst the rigid body reduces the flow directly behind the swimming individual. Depending on the positional angle of trailing individuals relative to the swimming speed and pectoral fin beat frequency of leading individuals (see Drucker & Lauder 2000), a trailing fish may encounter areas of both increased and decreased flow.

The ability of individuals to take advantage of the flow patterns created by leading individuals may be dependent on their sensory system (e.g. lateral line and vision), in a manner analogous to that found in fish swimming behind objects in a flow (Liao 2006). While in BCF swimmers the most advantageous positions are at an angle to the leaders (Weihs 1973, Fish 1999, Liao 2007), more work is needed to investigate the optimal positions for energetic advantages in a school of labriform swimming fish.

No use of tail beats was observed and fin amplitudes did not significantly differ among swimming speeds or fin beat frequencies, indicating that the same swimming pattern was employed in different school positions. This is in line with previous work on *Embiotoca lateralis* which found that amplitude (measured as the excursion of the tip of the pectoral fin relative to body length) is relatively constant for all but the lowest speeds (i.e. 0.5 to 1 standard length s^{-1}) for individuals maintaining a constant swimming pattern (Drucker & Jensen 1996b). Interestingly, the pectoral fin beat frequency of leading individuals in the school was higher than both trailing and solitary individuals swimming at 2.0 L_F s^{-1}. The reason for such a difference is unclear, but it could be related to schooling individuals continually correcting their position relative to the rest of the school; in this experiment schooling individuals were rarely seen swimming in a steady position, but mostly exhibited a constantly changing swimming position within the flow tunnel with trailing individuals following leaders in rapid formation. In contrast, in solitary individuals no manoeuvring was observed, although such behaviour may have been influenced by the smaller working section. The manoeuvres observed in schooling individuals may therefore have increased the pectoral fin frequencies of both leading and trailing individuals. However, despite the potential additional costs of manoeuvring, trailing individuals still showed pectoral beat frequencies that were significantly lower than those of solitary fish, most likely because of the hydrodynamic advantages experienced in trailing school positions.

Taking into account the potentially higher energetic requirements for individuals continuously correcting position within a school relative to swimming solitarily, the energetic benefit of being in a school may be more complex than previously thought. Our calculations based on Eqs. (1) & (2) suggest that schooling striped surfperch incur energetic advantages compared to solitary swimming when they are comprised of <22% leaders (i.e. >78% of the school are trailing individuals). Considering that from a hydrodynamic point of view leaders are those individuals which have no neighbours in front, it is likely that a large proportion of schools in nature contain <22% of individuals in leading positions. This is likely to be a common occurrence except for very small schools (e.g. <25 individuals), since schools of 25 individuals (in Silversides *Menidia menidia*) include approximately 5 frontal individuals (i.e. 20%) (Parrish 1989), and the proportion of leaders/total is likely to decrease with school size, assuming little variation in school shape (Parrish 1989). Notably, the present estimate of energetic saving is conservative since it is based on the energetic difference between solitary swimming and trailing or leading school positions, and would be greatly increased if, instead, the difference in energetic cost between leaders and trailing individuals were utilized.

The energetic advantages provided by schooling may help clarify the dynamics of school structure often observed in field and laboratory work. Although positional preferences have been observed in schools in relation to the physiological state of each individual (e.g. hunger level, Krause et al. 1998), schooling is a dynamic behaviour, and most fish continuously change positions from trailing to leading (Krause 1993, 1994; Domenici et al. 2002). A relatively constant reshuffling rate was found in schools of herring *Clupea harengus* which decreased when fish were exposed to hypoxia (Domenici et al. 2002). For all individuals to take advantage of schooling, sufficient shuffling should occur such that each fish can spend a relatively large proportion of the time in a trailing position (i.e. >78% of the time). The positioning of each fish in a school is the result of a number of trade-offs. For instance, leading positions may be chosen by hungry individuals, since they would react more strongly to smells or other cues from food sources, although they may also experience a higher risk of predation (Krause 1993, Bumann et al. 1997, Krause et al. 1998). Energetically, trailing individuals can enjoy energetic advantages, although in the case of relatively large schools, trailing individuals may experience a further reduction in oxygen level due to the oxygen consumption of fish in the front (McFarland & Moss 1967, Domenici et al. 2007). The energetic consequences of positioning in a school may be particularly relevant for migrating species or those routinely moving about the water column in search of food. These specific energetic advantages may be of high significance for *Embiotoca lateralis* when they migrate in schools from near-shore habitats in summer to deep offshore habitats in winter (Eschmeyer et al. 1983). Similarly, many planktivorous fishes may be benefiting from these energetic advantages when they forage in the water column in high-flow or oligotrophic habitats where even small energetic savings could constitute a significant ecological advantage (akin to the flow-refuging behaviour seen in labriform coral reef fishes; Johansen et al. 2007, 2008).

In conclusion, this study demonstrates the importance of schooling in providing an energetic advantage in fish swimming using labriform locomotion. To further demonstrate the ecological significance of schooling behaviour, additional studies of the energetic constraints and hydrodynamics challenges comparing different species of labriform fishes are needed. In particular, this study examined schools swimming at a single speed, i.e. 2.0 L_F s^{-1}, which roughly corresponds to the speed with the lowest cost of transport (U_{opt}) for *Embiotoca lateralis* (estimated from Drucker & Jensen 1996b, Cannas et al. 2006). However, many species are known to swim at speeds above U_{opt} for various reasons (e.g. Domenici et al. 2000) and such behaviour may change the relative cost of manoeuvring for leading individuals and subsequently the total energetic advantage of schooling compared to that demonstrated here. In addition, this study examined schools of 4 individuals only. We acknowledge that this corresponds to a relatively small school when compared to those found in nature. Although it is unknown whether school size has an effect on the energetic advantages of trailing in fish, a large group size has been shown to increase the energetic benefits of locomotion in other group behaviours (Fish 1999), hence our results may underestimate the energetic benefits enjoyed by followers in larger schools. Finally, as individuals inside and on the periphery of schools have different feeding rates and risk of predation (Krause 1993, 1994), the dynamics of school structure in the field under varying ecological conditions needs to be examined in greater detail, before the overall energetic consequences of schooling can be fully evaluated.

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