Bluegill *Lepomis macrochirus* synchronize pectoral fin motion and opercular pumping

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The relative timing between operculum and pectoral fin motion was examined in swimming bluegill *Lepomis macrochirus* to determine if respiratory fluid flows from the operculum might have an effect on flow over the pectoral fin. Five bluegill were filmed swimming at speeds from 0·5 to 1·5 body (total) lengths s^{-1}. The timing of opercular pumping and pectoral fin beating was noted and analysed using circular statistics. Fish tended to ventilate their gills every second or third pectoral fin beat. While locomotion and ventilation had different frequencies, however, they were synchronized: fish maintained a consistent phase relationship between them. Thus, within pectoral fin beats when the operculum pumps, the jet consistently occurred during pectoral fin abduction, ending just after the fin was fully abducted and beginning adduction. Based on the distance between the opercular slit and the pectoral fin base, the jet was estimated to reach the fin during maximum abduction. Dye flow visualization confirmed this estimate, revealing that the opercular flow wraps around the base of the fin during peak abduction, when it is likely to have little hydrodynamic effect.   © 2007 The Authors

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Key words: bluegill; *Lepomis macrochirus*; locomotor-respiratory coupling; operculum; pectoral fin; ventilation.

INTRODUCTION

In most fishes, and particularly in percomorphs, the pectoral fin is located just posterior to the opercular valve. During respiration, fishes push fluid over the gills and out through the opercular valve, producing a jet aimed towards the pectoral fin. This jet has the potential to alter the forces produced by the pectoral fin dramatically. Engineers have found that small changes in the flow encountered by a flapping propulsor can substantially change its thrust or drag (Gopalkrishnan *et al.*, 1994; Triantafyllou *et al.*, 2004; Akhtar & Mittal, 2005). Thus, to exploit either beneficial hydrodynamic interactions or to avoid detrimental ones, it seems possible that fishes may synchronize opercular jetting and pectoral fin motion.

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Such locomotor-respiratory synchronization is well known in running and flying animals. Many birds and running quadrupeds breathe in synchrony with their wingbeats or footfalls, co-opting the mechanical forces of locomotion to aid in respiration (Bramble & Carrier, 1983; Alexander, 1989; Lafortuna *et al.*, 1996; Boggs, 1997; Funk *et al.*, 1997). In running lizards, in contrast, locomotory forces may decrease respiratory efficiency (Carrier, 1987). Beneficial or not, the effect acts in one direction: the forces from locomotion affect respiration.

Webb (1975) found an effect in the same direction in shiner perch *Cymatogaster aggregata* Gibbons. He observed that they flap their pectoral fins in synchrony with mouth opening. Pectoral fin adduction accelerates the body, reducing the energy required to inspire fluid into the buccal cavity (Webb, 1975). As is in tetrapods, locomotion in *C. aggregata* thus affects respiration.

In this study, the opposite relationship is examined. Does respiration in fishes affect their locomotion? More specifically, does the jet from the operculum alter the flow over the pectoral fin? A simple test of this question is to look for a specific phase relationship between opercular pumping and pectoral fin beating. Consistent timing between the two would indicate one of two possibilities. If the opercular jet, which is known to remain close to the body's surface (Aleyev, 1977), consistently encounters the pectoral fin when the fin itself is close to the body, then hydrodynamic interaction could be influential. Among many possible effects, for example, respiratory flow could aid in fin abduction through the Bernoulli effect (Vogel, 1994), or could reduce the thrust by decreasing the relative difference in velocity between the pectoral fin and the surrounding flow (Vogel, 1994). In contrast, if the relative timing consistently results in the jet reaching the fin when the fin is substantially abducted, then the potential for significant hydrodynamic interaction is small.

The relative timing of opercular pumping and pectoral fin motion is currently undocumented in any fish. Although Aleyev (1977) used dye to observe the opercular jet, he did not measure the timing of pumping with respect to pectoral fin motion or the tail beat cycle. Webb (1975) examined the relative timing of mouth opening and pectoral fin motion, but did not consider the opercular jet. Additionally, he did not provide a quantitative description of the phase differences between ventilation and pectoral fin motion, which is important for establishing the mechanical consequences of synchronization.

This study therefore examines relative timing between opercular pumping and pectoral fin motion in the bluegill *Lepomis macrochirus* Rafinesque, a generalized percomorph fish that swims steadily using its pectoral fins at low speeds. This species was chosen to allow comparison with existing data on the hydrodynamics of pectoral fin swimming (Drucker & Lauder, 1999, 2000) which helps to evaluate the effects of interaction between the locomotory and respiratory flow. Phase differences between locomotion and ventilation are documented using ventral video, and the interaction between the opercular jet and the flow over the pectoral fin is examined using dye flow visualization.

MATERIAL AND METHODS

Bluegill were collected with nets in ponds near Concord, MA, U.S.A., and housed individually in 40 l aquaria at room temperature. Experiments were conducted in

a 600 l closed-circuit flow tank with a $26 \times 26 \times 80$ cm working section. Animals were confined to the working section using plastic grids. During experiments, water was maintained at $20°$ C and kept fully oxygenated by the use of air stones. Data were collected from five bluegill 19.7 ± 0.9 cm (mean $\pm$ S.E.) in total length (L_T) (range 18–22 cm).

Before the experimental procedure, a bluegill was allowed to acclimate in the flow tank at a slow swimming velocity for at least an hour. During the procedure, the animal was gently manoeuvred into position using a wooden probe. Pectoral fin and opercular motion were filmed from below using a Photron FastCam high-speed digital camera (Photron, San Diego, CA, U.S.A.) at 125 frames s^{-1}. Video data were captured during swimming at speeds ranging from 0.5 to 1.5 L_T s^{-1} in increments of 0.25 L_T s^{-1}.

The video was analysed using Photron Motion Tools Player (Photron), manually noting the times of maximum opercular dilation and contraction (Fig. 1), and pectoral fin abduction and adduction for both the left and right fins. Opercular dilation is defined as the time when the opercula have reached their maximum width, visible from below [Fig. 1(a)]. The opercular valve, a muscular flap on the caudal edge, keeps the cavity closed until maximum dilation, after which the valve opens and water jets out (Hughes & Shelton, 1958). Maximum contraction is when the opercula are the narrowest, viewed from below [Fig. 1(b)]. These two events were easily identified in moving videos, although the differences shown in still images in Fig. 1 are subtle. Pectoral fin abduction is when the fin is moving away from the body, and adduction is when it is coming in against the body.

The null hypothesis of this study was that locomotion and respiration have different, unrelated frequencies. The alternative hypothesis is that the two processes are correlated in some way. This hypothesis was tested in two ways. First, the time durations between fin beats and those between breaths were examined. If the durations of periods between breaths and between fin beats are integer multiples of one another, then the two are tending toward synchrony, providing support to reject the null hypothesis. Second, if locomotion and respiration are coupled, then they should have a consistent phase relationship. Significance of phase relationships can be tested using circular statistics, described below. If a significant relationship is established, then the timing of the jet must be examined to determine its functional consequences, if any.

Phase values (from 0 to 1) for locomotory and respiratory events were calculated by subtracting the time of the previous pectoral fin adduction and dividing by the instantaneous fin beat period (the time between the current fin beat and the next). Analysis was conducted with custom Matlab 6.5 (Mathworks, Natick, MA, U.S.A.) functions. First, phase values ϕ_i were converted into unit vectors ($\cos 2\pi\phi_i$,
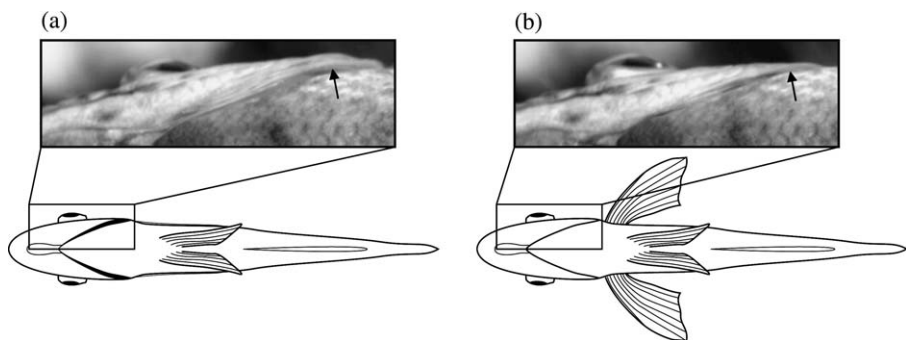

FIG. 1. Definitions of respiratory events, based on ventral view. Schematics and example images are shown for each event: (a) opercular dilation and (b) opercular contraction. Images are from swimming at 1.0 total length s^{-1}. →, the edge of the opercular slit, where the differences between dilation and contraction are most visible.

$\sin 2\pi\phi_i$). Mean phase is thus the angle of the mean vector (Fisher, 1995), $\phi_{mean} = (2\pi)^{-1}\tan^{-1}[(\sum\sin 2\pi\phi_i)(\sum\cos 2\pi\phi_i)^{-1}]$ and the angular S.E. according to Fisher (1995) is $(2\pi\sqrt{nR\kappa})^{-1}$, where n is the number of data points, R is the mean vector's length, $R = n^{-1}[(\sum\sin 2\pi\phi_i)^2 + (\sum\cos 2\pi\phi_i)^2]^{0.5}$, and κ is the estimated concentration parameter, analogous to the S.D. in linear statistics. All phase values are presented using the angular mean and the angular S.E. To determine if opercular pumping had a non-random phase with respect to the pectoral fin motion, the phase value was tested for a significant mean using a Rayleigh test (Fisher, 1995).

To examine the functional consequences of synchronization, the position of the fin when it encountered the opercular jet was estimated. The phase of maximum opercular dilation, when the jet starts, was advanced by a 'travel phase offset' proportional to the length of time it would take the jet to move from the operculum to the fin. As an approximation for this phase offset, the jet from the operculum was assumed to travel the distance d between operculum and the pectoral fin base at the swimming speed U. The validity of this assumption is tested later. The time of travel, $d\ U^{-1}$, was used to produce the travel phase offset $\delta\phi$: $\delta\phi = fd\ U^{-1}$, where f is the fin beat frequency. The distance d was defined as the distance from the dorso-ventral centre of the fin base along the fish's long axis to the opercular slit. It was measured from still images of three bluegill of the same approximate size as the experimental animals.

To verify the timing predicted by the travel phase offset and to examine the pattern of opercular flow around the pectoral fin, the fluid pumped out of the opercular cavity was traced using dye in one individual. The fish was anaesthetized using a buffered 0·03% solution of tricaine methanosulphate (MS222). A small (c. 2 mm) hole was drilled through the pectoral girdle using a Dremel drill (Dremel, Racine, WI, U.S.A.) into the dorsal portion of the left opercular cavity. A 1·2 mm outer diameter polyethylene cannula was threaded through the hole and blue food dye was pumped in using gravity feed. The fish was allowed to recover for an hour before beginning the experiment. The surgical procedure is detailed more thoroughly in Lauder (1984).

All experimental animal procedures were approved by the Harvard University Institutional Animal Care and Use Committee (license number 20-03 to G. V. Lauder).

Finally, the changes in the observed patterns at different swimming speeds and among different individuals were examined in two ways. First, differences in phasing among swimming speeds and among individuals were tested separately using a non-parametric test that determines significant differences in mean phase, but not concentration (Watson, 1983; Fisher, 1995). *Post hoc* pair-wise comparisons were made using a two-sample version of the same test with a Bonferroni correction on the significance level (Quinn & Keough, 2002). Second, the number of fin beats per breath was compared at different speeds and among individuals using ordinal logistic regression (Quinn & Keough, 2002) performed with JMP 5.1 (SAS Institute, Cary, NC, U.S.A.).

RESULTS

The timing of pectoral fin beating and opercular pumping was analysed in fin beats during which the fish pumped their opercula. The motion of the left and right fins was usually synchronous, although the fish occasionally (<12% of fin beats in the videos) adopted an alternating pattern, particularly at high speed. For this study, analysis was restricted to 367 synchronous fin beats (defined as those in which the fins reached maximum abduction within 10% of the fin beat cycle of each other).

The mean $\pm$ S.E. period between maximal fin abductions decreased from 0.63 ± 0.02 s at $0.5\ L_T\ s^{-1}$ to 0.426 ± 0.007 s at $1\ L_T\ s^{-1}$ (corresponding to frequencies of 1.71 ± 0.08 and 2.40 ± 0.03 Hz, respectively), after which the fish began caudal fin swimming and used their pectoral fins more irregularly.

Nonetheless, the fin beat period continued to decrease slowly to 0.40 ± 0.01 s (2.58 ± 0.07 Hz) at 1.5 L_T s^{-1}.

Initial inspection of the video indicated that opercular motion had a clear relationship to fin motion. Typical motions and measured times are shown schematically in Fig. 2. Examining the time periods between breaths in detail, however, revealed a more complex pattern, with a multimodal distribution at all speeds. Fig. 3 shows a sample histogram from swimming 1 L_T s^{-1}. Here, the median fin beat period was 0.4 s. The time between breaths showed peaks near twice and three times the fin beat period. Although no peak is visible at one times the fin beat period, fish occasionally breathed on successive fin beats for some of the longer fin beat periods (where the black and white bars overlap in Fig. 3). Similar patterns were seen at all speeds. Thus, the frequency of opercular pumping appears not to be independent of the fin beat frequency.

To determine whether this relationship was statistically significant, the phase of opercular pumping within the fin beat cycle was examined. A histogram of the timing of maximum opercular dilation and contraction, and of left fin abduction, relative to left fin adduction is shown in Fig. 4(a). Both distributions for the operculum had clear peaks, which were significantly different from random (Rayleigh test; $P < 0.001$ in both cases). Thus, ventilation and locomotion are synchronized.

The mean phase relationship between locomotion and respiration, averaged over all swimming speeds, is summarized in Fig. 4(b). The operculum typically reached maximum dilation at $28 \pm 2\%$ (angular mean $\pm$ angular s.e.) of the fin beat cycle, keeping the valve closed. The opercular valve then opened and the operculum itself started closing, jetting fluid until it reached maximum contraction at a phase of $64 \pm 1\%$, shortly after the fin reached maximum abduction at $55.2 \pm 0.4\%$. These phase relationships were significant for all animals as a group and for each animal separately (Rayleigh test, $P < 0.001$ in all cases), but varied significantly among individuals (Watson test, d.f. $= 4$,
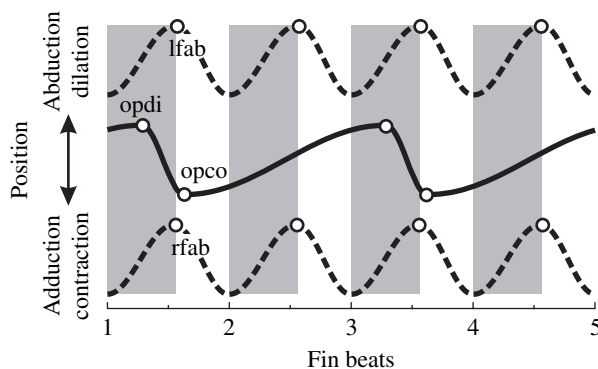

FIG. 2. Schematic of typical fin and operculum motion (——, operculum motion; ---, fin motion). Upper trace is the left fin and the lower trace is the right fin. ▪, left fin abduction and ▫, adduction. ○, the timing of the events that were analysed (lfab, left fin maximum abduction; rfab, right fin maximum abduction; opdi, operculum dilation; opco, operculum contraction). Phases were constructed relative to the maximum left fin adduction (left side of the grey bar). Typically, the operculum pumped every other fin beat, as is indicated here, although other patterns also occurred.
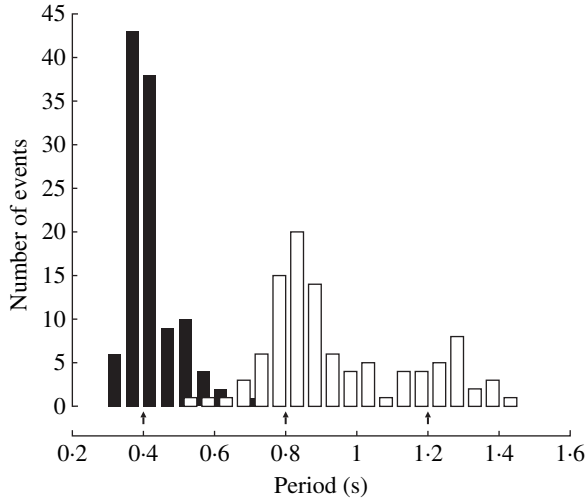
FIG. 3. Histogram of periods between fin beats (■) and between breaths (□) during swimming at 1 total length s^{-1}. ↑, one, two and three times the median fin beat period.

$P < 0.001$). For example, median opercular contraction phase ranged from 51 to 70% of the fin beat cycle among individuals.

The jet must traverse the distance between the operculum and the fin before it can have any effect on flow around the fin. Measurements from three fish of the same size as those in this study showed that the mean distance from the centre of the fin base to the opercular slit was $0.043\ L_T$ (range 0.041 to $0.045\ L_T$). Based on the swimming speed, this distance corresponds to a travel phase offset of 15% of the cycle at $0.5\ L_T\ s^{-1}$, decreasing to 10% at $1\ L_T\ s^{-1}$ and 7% at $1.5\ L_T\ s^{-1}$. Adding these offsets to the maximum opercular dilation and contraction phases resulted in an estimate of when the opercular jet should encounter the fin, shown at the bottom of Fig. 4(b). On average, the jet was estimated to reach the fin at $39 \pm 2\%$ of the fin beat cycle, continuing to interact with the fin until $74 \pm 1\%$, a time window that straddles maximum fin abduction. Although both the time of jetting and fin abduction varied across speeds, in 72% of cases peak fin abduction occurred during the estimated time in which the jet encountered the fin.

To verify this estimate, the flow from the operculum was visualized using dye in one fish, swimming at speeds from 0.6 to $1.0\ L_T\ s^{-1}$. Dye injected through a cannula into the opercular cavity completely filled the cavity; all fluid jetted out appeared to contain dye. As predicted, dyed fluid reached the fin while it was abducted away from the body. Opercular flow wrapped around the fin base, interacting only with the most proximal portions of the fin (Fig. 5).

Finally, the effect of swimming speed on the synchronization between locomotion and ventilation was investigated in two ways. First, Fig. 6 shows that the phase of breaths within the fin beat cycle (measured by maximum opercular contraction phase) stayed fairly constant. Although there is a significant difference among speeds (Watson test, d.f. $= 4$, $P < 0.001$), pair-wise *post hoc*
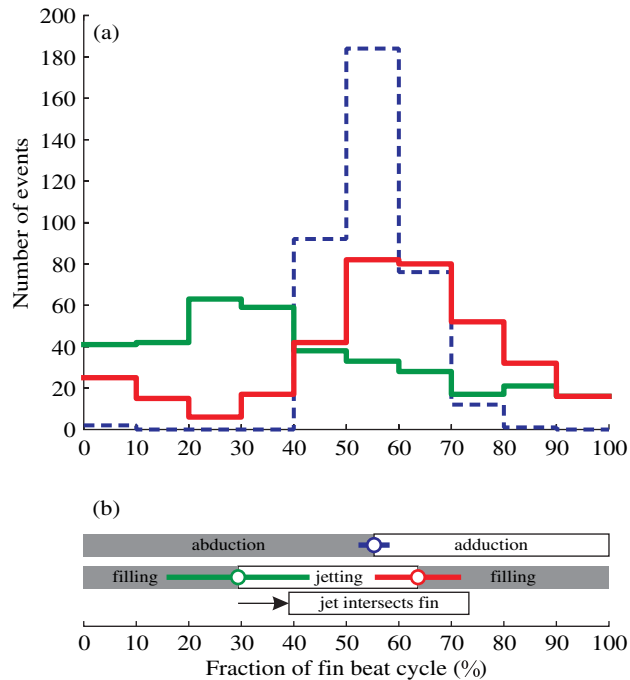
FIG. 4. Phase relationship between locomotion and ventilation over all swimming speeds. (a) Histogram showing the number of locomotory and ventilatory events that occurred at particular phases within the fin beat cycle (---, left fin maximum abduction; —, maximum operculum dilation; —, maximum operculum contraction). (b) Mean timing of fin beating and opercular pumping from the histogram (⬤, left red fin maximum abduction; ○, maximum opercular dilation; ○, maximum opercular contraction; ▮, pectoral fin abduction and opercular cavity filling; □, fin adduction and opercular jetting). Coloured error bars are angular s.e. The bottom box shows the jetting phase shifted later in the cycle by the travel phase offset (→), to account for the time it takes the jet to reach the fin.

Watson tests showed that all speeds were statistically indistinguishable except for $1.25 \, L_T \, s^{-1}$, in which fish breathed significantly later in the cycle. Additionally, within each speed, breathing maintained a phase that was significantly different from random (Rayleigh test, $P < 0.05$ in all cases).

Second, although fish maintained synchronized breathing and pectoral fin motion at all speeds, they showed a trend to breathe slightly faster at high speeds. Across all speeds, breaths occurred most often on every second fin beat (72% of cases; Fig. 7, grey bars). As speed increased, however, fish more often took breaths on every fin beat (Fig. 7, white bars), while at 0.75 and $1 \, L_T \, s^{-1}$ they more often skipped two or more fin beats before breathing (Fig. 7, black bars). At $0.5 \, L_T \, s^{-1}$ the data were less clear, possibly because swimming became somewhat irregular at such a low speed. Logistic regression showed that the trend towards faster breathing at higher speeds is marginally significant (likelihood ratio, $P = 0.086$). Individuals also showed significant variability (likelihood ratio, $P < 0.001$).
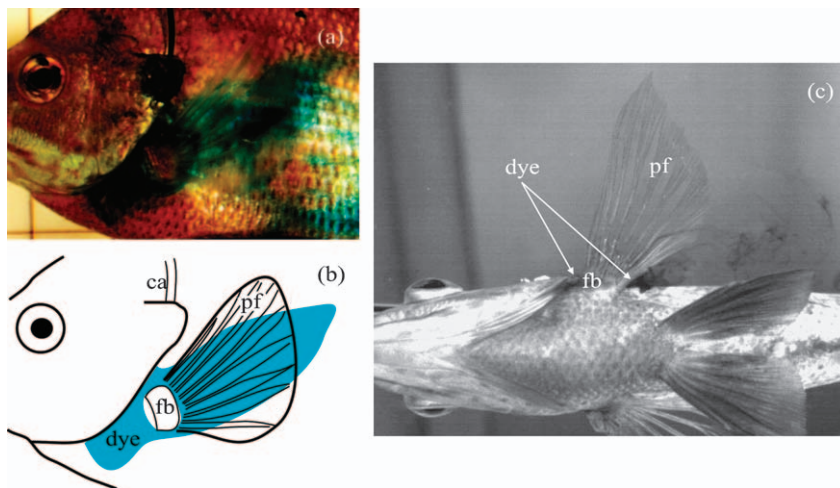
FIG. 5. Dye visualization of flow from the operculum confirmed that the opercular jet reached the pectoral fin during maximal fin abduction. Representative images from swimming at 0.75 total length s^{-1} are shown: (a) lateral image, (b) lateral schematic and (c) ventral image. The jet of fluid from the operculum wraps around the base of the pectoral fin when the fin is fully abducted, minimizing interaction between the flow from the operculum and flow over the pectoral fins. ca, cannula; pf, pectoral fin; fb, fin base.

DISCUSSION

This study demonstrates that bluegill synchronize opercular pumping and pectoral fin beating, though in a complex manner. This is the first time the interaction between the opercular jet and pectoral fin motion has been examined in any fish. Although the two occur at different rates, with the fins beating approximately twice for every breath, they are correlated: the opercular jet occurs primarily during pectoral fin abduction, as the fins are moving away from the body, and finishes shortly after maximum fin abduction [shown schematically in Fig. 2 and quantitatively in Fig. 4(b)].

The bluegill does not stick to a constant ratio between breathing and fin beating, although it usually breathes every second fin beat in the range of
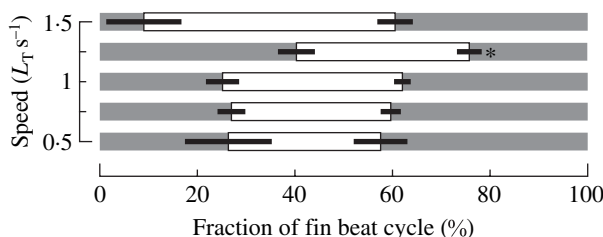

FIG. 6. Opercular pumping maintained a consistent phase within the fin beat cycle at speeds <1.25 total length (L_T) s^{-1}. At each speed, the mean timing of opercular filling (dilation; ■) and opercular jetting (contraction; □) are indicated. Angular S.E. around the mean dilation and contraction times is shown with solid lines (*, significant difference; $P < 0.001$). Note that the operculum may continue filling for several fin beats after it jets.
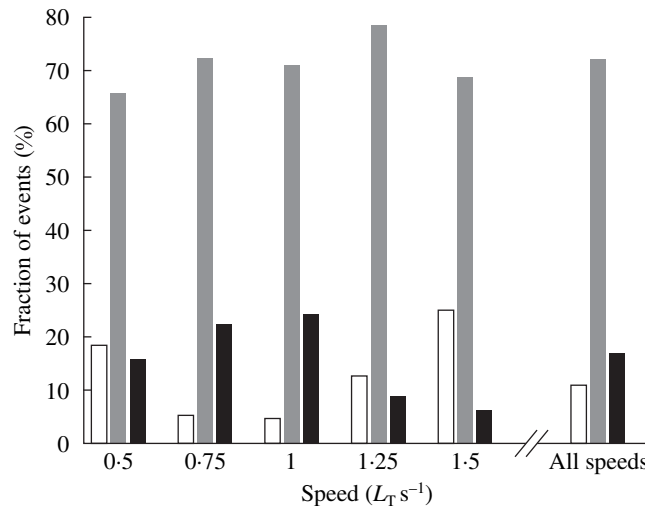
FIG. 7. Histogram of the number of fin beats per breath at a range of swimming speeds. The fraction of breaths for each swimming speed that occurred with periods that were different multiples of the fin beat period (□, one beat per breath; ▨, two beats per breath; ■, three or more beats per breath). Numbers of fin beats per breath averaged over all speeds are also shown.

speeds studied (Fig. 7). Inspection of the timing between breaths suggests that opercular pumping is timed in integer multiples of the fin beat period (Fig. 3). Circular statistical analysis of the phase relationship between locomotion and ventilation shows that breaths are not distributed randomly with respect to the fin beat (Fig. 4). Thus, the null hypothesis that locomotion and ventilation have separate, independent rhythms can be rejected.

Circular statistics are necessary to analyse such phase relationships, because the range of possible phase values is bounded. Phase values range from 0 to 100%; after that they repeat. Thus, a set of phase measurements does not necessarily have a mean. For example, if two periodic events are uncorrelated, then their phase differences would be evenly distributed between 0 and 100% and no mean phase could be defined. Other standard statistical tests, such as ANOVA, have to be modified for phase data. For example, the Watson test is the equivalent of a non-parametric one-way ANOVA used to test for differences among multiple groups.

Having rejected the null hypothesis, the two proposed alternative hypotheses must be examined: that the opercular jet might consistently be timed, (1) to reach the fin when the fin is close to the body, allowing scope for hydrodynamic interaction, or (2) to reach it when it is substantially abducted, minimizing the potential for interaction. Both estimated timing [Fig. 4(b)] and dye flow visualization (Fig. 5) support the second proposal: that hydrodynamic interaction between the opercular jet and the flow around the pectoral fin is small.

This timing has three potential functional interpretations. First, the two may both be tied to some other cyclical process, such as the heartbeat (Taylor *et al.*, 1999), which was unobserved in this study. In this interpretation, the

synchronization of ventilation and locomotion is an artefact, having no functional relevance. While this possibility cannot be excluded, other explanations seem more likely. Specifically, while there is some controversy on the mechanism for generating cardiorespiratory synchrony in fishes, it appears that the ventilatory rhythm entrains the heartbeat (Taylor *et al.*, 1999), but not the other way around. Additionally, other, non-periodic factors may also affect the rhythms. For example, the bluegill changes ventilation rate depending on both the dissolved oxygen levels and the water temperature (Spitzer *et al.*, 1969). Such changes may reduce the average number of fin beats per breath, but may not alter the synchronization. The multimodal distribution of times between breaths suggests that the synchronization is not simply a coincidence due to the water temperature, but rather an active process.

A second functional interpretation is thus that the phase relationship may be actively tuned to take advantage of an interaction between locomotion and respiration, but not the hydrodynamic relationship proposed in this study. In particular, the bluegill may behave like *C. aggregata*, using the body acceleration during pectoral fin adduction to help inspire fluid into the buccal cavity, as Webb (1975) proposed. A ventral video does not allow this relationship to be examined directly. Hughes & Shelton (1958), however, found that the mouth is open at approximately the same time as opercular filling in three teleost fish species [brown trout *Salmo trutta* L., tench *Tinca tinca* (L.) and roach *Rutilus rutilus* (L.)]. Therefore, the bluegill probably also open its mouth while the operculum fills, an event that starts just after the pectoral fin begins adduction [Fig. 4(b)]. Thus, the bluegill probably maintains a timing that is consistent with Webb's (1975) proposal. Unlike the shiner perch, the bluegill probably does not derive much advantage from this effect, because it continues inspiring fluid through several pectoral fin beats (shown schematically in Fig. 2). During this period, the body both accelerates, helping inspiration, and also decelerates, hindering inspiration. The net energy savings for respiration is probably small, particularly at low swimming speeds.

Finally, although the observed timing minimizes hydrodynamic interaction between the opercular jet and pectoral fin flow, such an interaction could nevertheless be the root cause of the observed synchronization. If the interaction was detrimental, perhaps reducing thrust, bluegill might actively avoid it by timing breaths to minimize the scope for hydrodynamic interaction. Unlike Webb's (1975) hypothesis, avoiding negative interaction is beneficial even with multiple fin beats per breath. Although the assumption of detrimental hydrodynamic interaction is plausible based on engineering data (Gopalkrishnan *et al.*, 1994; Akhtar & Mittal, 2005), it has not been tested directly.

More detailed flow visualization, probably using particle image velocimetry (Drucker & Lauder, 2000), will be necessary to determine the effect of such interactions, and whether they are indeed detrimental. Taking advantage of the fact that breathing and locomotion are not perfectly phase locked, flow around the pectoral fin could be examined when the phasing is 'wrong,' such that the opercular jet encounters the fin during adduction, when the fin is close to the body. Comparing this flow to flow during the 'right' timing could elucidate the hydrodynamic effects and help to distinguish between this mechanism and that proposed by Webb (1975).

This study was performed in fully oxygenated water, at a controlled moderate temperature, and at low swimming speeds. Neither the locomotor nor the respiratory capabilities of the fish were challenged, a condition in which optimization of ventilation or locomotion is not very important. If the benefits of synchronization were small, then it might be expected to disappear entirely under these non-challenging conditions, because the control seems to be complex (Fig. 3). The fact that it remains could be a sign of its generality: its benefits, whatever they might be, remain higher than the costs, even at low swimming speeds. It may also explain why the synchronization is complex; at high speeds or low oxygen levels, it may become more regular.

Lepomis macrochirus, however, stops using its pectoral fins at high speeds, preventing synchronization from being examined during energetically challenging tasks, in which the potential benefits might become more important. Indeed, no substantial change in the synchronization was observed with changing speed (Fig. 6). The phase relationship at $1.25 \, L_T \, s^{-1}$ was significantly different from that at other speeds, but this may be an effect of the gait transition at *c.* $1.1 \, L_T \, s^{-1}$ (Drucker, 1996). Other species, particularly consistently labriform swimmers such as wrasses, continue using their pectoral fins at high speeds and may be more optimized for efficient pectoral fin locomotion. If these fishes synchronize breathing and locomotion, they may do it in a way that makes its function more obvious.

Additional functional implications may become clearer by studying this phenomenon in many species. If synchronization patterns are common across different fishes, then that provides a stronger argument for their adaptive significance. Indeed, inspection of videos from one yellow perch *Perca flavescens* (Mitchill) indicates that they also synchronize breathing and pectoral fin beating. This species was examined because it seemed unlikely to synchronize: it uses its caudal fin together with its pectoral fins at low swimming speeds, and tends to alternate left and right pectoral fin beats. Despite the alternating gait, the video indicates that yellow perch, like the bluegill, tends to breathe around the time that one of the two pectoral fins is maximally abducted, suggesting that the pattern described here is not specific to bluegill. Further comparative studies will determine if synchronization of ventilation and locomotion, whether beneficial or not, is a common feature of pectoral fin swimming.

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