

## Pectoral fin coordination and gait transitions in steadily swimming juvenile reef fishes

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### Summary

A common feature of animal locomotion is its organization into gaits with distinct patterns of movement and propulsor use for specific speeds. In terrestrial vertebrates, limb gaits have been extensively studied in diverse taxa and gait transitions have been shown to provide efficient locomotion across a wide range of speeds. In contrast, examination of gaits in fishes has focused on axial gaits and the transition between synchronous paired fin locomotion and axial propulsion. Because many fishes use their pectoral fins as their primary propulsors, we aimed to examine more broadly the use of pectoral fin gaits in locomotion. We used juvenile reef fishes in these experiments because their swimming could be recorded readily across a wide range of Reynolds numbers, which we thought would promote gait diversity. Based on previous work in larval fishes, we hypothesized that juveniles have alternating pectoral fin movements rather than the synchronous, or in-phase, coordination pattern of adults. In flow tank swim studies, we found that juvenile sapphire damselfish *Pomacentrus pavo* used two fin gaits during steady swimming. Below approximately  $3 \text{ BL s}^{-1}$ , *P. pavo* primarily swam with alternating fin strokes  $180^\circ$  out of phase with one another. At speeds in the range of

$3\text{--}4 \text{ BL s}^{-1}$ , they performed a gait transition to synchronous fin coordination. Between approximately 4 and  $8 \text{ BL s}^{-1}$ , *P. pavo* primarily beat their fins synchronously. At around  $8 \text{ BL s}^{-1}$  there was another gait transition to body-caudal fin swimming, in which the pectoral fins were tucked against the body. We suggest that the transition from alternating to synchronous fin coordination occurs due to mechanical limits of gait performance rather than to energy efficiency, stability or transitions in hydrodynamic regime. To determine whether this gait transition was species-specific, we surveyed pectoral fin locomotion in juveniles from 11 species in three reef fish families (Pomacentridae, Labridae and Scaridae). We found that this gait transition occurred in every species examined, suggesting that it may be a common behavior of juvenile reef fishes. Greater inclusion of early life history stages in the study of fin-based locomotion should significantly enhance and inform the growing body of work on these behaviors.

Key words: gait, pectoral fin, development, functional morphology, locomotion, biomechanics.

### Introduction

Locomotion is classified into gaits based on discontinuous transitions in characteristics of movement (reviewed by Alexander, 1989). Most often these characteristics are patterns of movement such as the order of limb support during terrestrial locomotion (reviewed by Biewener, 2004), although discrete differences in control of locomotion, such as use of red muscle or white muscle to generate movement (e.g. Webb, 1994; Alexander, 1989), can also define gaits even without distinct changes in movement pattern. Animals often make transitions through several gaits before reaching their peak speed. They

are thought to change gaits in order “to minimize the energy cost of traveling at their chosen speed” (Alexander, 2003) or due to biomechanical and physiological limitations on movement patterns (Drucker and Jensen, 1996b; Korsmeyer et al., 2002).

In terrestrial vertebrates, common gaits include walking, running/trotting and galloping. Limbed gaits can be classified as symmetrical and asymmetrical. During symmetrical gaits, paired limbs are either actuated synchronously, in phase with one another, or alternate  $180^\circ$  out of phase. Asymmetrical gaits encompass all other limb relationships. The speeds at which

gait transitions occur are related to aspects of body size. For terrestrial limb-based locomotion, the body dimension used is hip height, which is expressed as a component of the Froude number, a dimensionless number which “normalizes the forward velocity of a moving animal to its limb length and gravitational acceleration” (Biewener, 2004). Gait transitions tend to occur at about the same Froude number across species (Alexander and Jayes, 1983; Alexander, 1989; Griffin et al., 2004).

In contrast to terrestrial locomotion, in which multiple gaits have been well studied, the research on gaits during swimming has largely focused on axial propulsion. During swimming, fishes often go through the following series of gaits with increasing swimming speed (reviewed by Alexander, 1989; Alexander, 2003; Webb, 1994): (1) fin propulsion, (2) burst and coast axial locomotion powered by red muscle, (3) steady swimming with red muscle, (4) burst and coast axial locomotion powered by white muscle, (5) steady swimming with white muscle. However, the studied fish from which these gait transitions were proposed, including carp (Rome et al., 1990), milkfish (Katz et al., 1999), cod and saithe (Videler and Weihs, 1982), tend to rely heavily on the axis and caudal fin as their primary propulsors, rather than the pectoral fins.

Many fish species use the pectoral fins as the primary propulsors, using axial propulsion only near peak speeds (Westneat, 1996). Pectoral fin, or labriform, locomotion is particularly common among reef fishes. In this form of swimming the pectoral fins are generally actuated synchronously with one another in forward swimming (Webb, 1973; Archer and Johnston, 1989; Gibb et al., 1994; Drucker and Jensen, 1996a; Westneat, 1996; Walker and Westneat, 1997; Mussi et al., 2002). Speed can be increased gradually by increasing fin beat amplitude and/or frequency. Labriform swimmers change to body–caudal fin swimming near their peak speed. Recent work (Korsmeyer et al., 2002) suggested that at least some of these species are not able to swim steadily at low speeds, below approximately  $1.5 L s^{-1}$ , due to decreased stability.

While synchronous pectoral fin actuation is the most common fin coordination pattern, symmetrical alternating fin movements have also been described. Alternating pectoral fin movements have been shown to function during station holding, maneuvering and other nonlinear swimming events (Drucker and Lauder, 2003; Hove et al., 2001), and several studies have described alternating fin movements associated with steady forward locomotion. Burrfish (*Chilomycterus shoepfi*) maintain pectoral fin strokes that are approximately  $180^\circ$  out of phase through a wide range of speeds (Arreola and Westneat, 1996). As with synchronous fin movement, burrfish fin beat frequency increased with increasing swimming speed. Larval plaice (Batty, 1981) and zebrafish (Müller and van Leeuwen, 2004; Thorsen et al., 2004) have been shown to alternate their pectoral fins during slow locomotion. In the zebrafish, this behavior is generally lost during the juvenile stage of development (Thorsen et al., 2004). In several cases, fishes have been shown to perform a gait transition from

alternating pectoral fin locomotion to axial/caudal locomotion with an increase in swimming speed (Müller and van Leeuwen, 2004; Thorsen et al., 2004) or type of movement (Drucker and Lauder, 2003). Sub-adult fish swimming has received little attention compared to that of adults but data from larval fishes indicate that, in at least some species such as zebrafish (Thorsen et al., 2004), fin movement patterns are distinct from ones observed in adults and that these patterns change markedly through ontogeny.

In this study, we investigated pectoral fin gait transitions of fishes by examining swimming through a range of speeds in juveniles of the sapphire damselfish *Pomacentrus pavo* and an additional 11 reef species from three families. By examining a range of juveniles from species that are pectoral fin specialists, we aimed to explore the patterns and performance of fin swimming in sub-adult fishes and to examine the use of synchronous and alternating pectoral fin coordination in swimming. We found a discrete transition from alternating to synchronous fin beats at intermediate speeds, prior to the pectoral fin to body–caudal fin transition. Informed by studies of the synchronous fin coordination to body–caudal fin gait transition, we investigated the alternating to synchronous gait transition and hypotheses for the cause of the transition, including energy efficiency across speeds, stability within specific speed ranges (Korsmeyer et al., 2002; Arreola and Westneat, 1996) and mechanical or physiological limits of the observed gait (Drucker and Jensen, 1996b; Korsmeyer et al., 2002). We propose that alternating pectoral fin beats may be a common swim propulsion mechanism early in development and that the transition from alternating to synchronous pectoral fin gaits is a common feature of juvenile fish locomotion in coral reef species that use their pectoral fins as a primary mode of propulsion as adults.

## Materials and methods

Fishes were collected on shallow coral reefs in the Tuvalu and Kiribati islands of the South Pacific with small hand nets, according to IACUC approved protocols (FMNH99-03) and with local collecting permits. We focused our analysis on *Pomacentrus pavo* Bloch 1787; however, we opportunistically filmed all species for which we could collect appropriately sized specimens. This resulted in data from a total of 33 individuals from 11 species in three families. Fishes were maintained and kinematics recorded on board the research vessel *Turmoil* within 48 h of capture.

To record kinematics at a range of steady swimming speeds, we filmed the animals in a small flow tank (working section  $3.5 \text{ cm} \times 3.5 \text{ cm} \times 12.5 \text{ cm}$ ) in flow that ranged from  $1.12$ – $11.13 \text{ cm s}^{-1}$ . Ventral views provided the clearest images of bilateral fin movement. Because filming directly from ventral view was not possible due to the flow tank structure, a first surface mirror was positioned at a  $45^\circ$  angle under the tank to reflect ventral views so that images could be collected by a camera positioned to the side of the tank. We monitored each fish visually to determine its dorsoventral position in the tank.

We used small fish (<4 cm) in our experiments and only analyzed video in which the fishes swam in the center of the tank, in order to minimize wall effects. Fishes were filmed using a Sony digital video camera de-interlacing frames to achieve a frame rate of 60 Hz. This frame rate is too low to capture fine details of fin movements at most of the fin beat frequencies recorded and we focused instead on describing patterns of pectoral fin coordination. After we recorded locomotor kinematics, fish were euthanized and preserved for subsequent morphological analysis and to confirm species identifications.

Video clips were viewed with an Apple Macintosh G4 using Adobe Premiere 6.5. The videos of *Pomacentrus pavo* were analyzed and cut into clips featuring the fish performing steady swimming for approximately 5 fin beats against a steady current. Clips were then de-interlaced for field-by-field analysis with QuickImage, a NIH Image based program written by Dr Jeff Walker, University of Southern Maine, ME, USA. Coordinate points were digitized on physical landmarks along the central midline of the fish, the base and tip of both pectoral fins, the caudal peduncle, and the tip of the caudal fin, and for each frame of a sequence. Based on the movement of these landmarks, kinematic variables were calculated using a series of algorithms in a custom-written kinematics program (CodeWarrior Pascal, Metrowerks Corporation, Austin, TX, USA) on an Apple Macintosh G5. Variables included pectoral fin frequency, fin angle to the body (amplitude), pectoral fin chord length in ventral projection, axial bending angle at midbody and at the tail base, change in fore-aft (thrust) and left-right (yaw) position of the nose tip, phase lag, advance ratio and reduced frequency.

#### *Kinematic analysis for Pomacentrus pavo*

We analyzed trials from three fish at 5–6 swimming speeds per fish. The number of trials varied among animals: 15, 25 and 19, respectively for fish 1–3 for a total of 59 trials. Of these trials, 21 were of alternate pectoral fin swimming, 27 of synchronous and 11 included the transition between gaits. Phase lag between fins during swimming was calculated to identify left-right oscillation patterns. If two oscillatory waves have the same frequency, then their phase relations can range from 0° (synchrony) to 180° out of phase (asynchrony) up to 360° (back to synchrony) (Denny, 1988). The relative position of the right and left fins during each fin beat was used to calculate phase lag by determining the position of the left fin at the time of maximum right pectoral fin abduction (maximum angle away from the body). Phase lag thus ranged from 0° (perfectly in phase, with both fins reaching maximum abducted position synchronously) to 180° (perfectly out of phase, indicating alternate fin beats, with left fin maximally adducted at the time of peak right fin abduction). Intermediate values of phase lag ( $0 < \text{phase} < 180$ ) were computed by the equation  $(\text{abs}(T_{r_{\max}} - T_{l_{\max}}) / T_{\text{cycle}}) \times 360$ , where  $T_{r_{\max}}$  = time of peak right angle,  $T_{l_{\max}}$  = time of peak left angle, and  $T_{\text{cycle}}$  = total fin cycle time. Taking the absolute (abs) value of timing between right and left peaks ensured that phase lag ranged from 0 to 180°.

We examined fin beat amplitude and frequency to determine whether, as in adult fishes, these parameters vary with swimming speed and whether there is a discontinuity in either parameter at the transition from asynchronous to synchronous fin beats. The angle of each pectoral fin leading edge to the body was computed and used to determine angular displacement of each fin for each video frame and the time of maximum and minimum fin position. Fin beat frequency (Hz) was computed for each video clip by dividing the number of fin beats by total time of the video sequence. In addition, we determined the speed of the transition from pectoral fin swimming to body and caudal fin swimming ( $U_{pc}$ ). Caudal fin amplitude was calculated as the angular movement of the tip of the caudal fin relative to the axis of the body rostral to the caudal peduncle.

To examine the efficiency of fin propulsion during alternating and synchronous forms of pectoral fin locomotion we calculated the advance ratio ( $J$ ). The advance ratio is a dimensionless number that relates the velocity of the body to the velocity of the fin. Thus, higher advance ratios indicate higher fin beat efficiency. Advance ratio is calculated as:

$$J = U / 2L_p\phi F_p, \quad (1)$$

where  $\phi$  = fin angle/180°,  $U$  = forward speed (m s),  $L_p$  = pectoral fin length (m), and  $F_p$  = pectoral fin beat frequency (Hz) (Drucker and Jensen, 1996a).

Oscillating fins accelerate water, particularly at the start and end of a stroke. A force called the acceleration reaction resists these changes in velocity of the fluid surrounding the fin. Daniel summarized the importance of acceleration reaction nicely: “while drag is the resistance to motion through a fluid, the acceleration reaction is resistance to changes in velocity of that motion” (Daniel, 1984). The reduced frequency parameter is a dimensionless number that characterizes the importance of acceleration reaction in the thrust obtained from an oscillating appendage (Daniel, 1988; Vogel, 1994). Reduced frequencies were calculated for each fin by the following equation:

$$f_a = 2\pi F_p c / U, \quad (2)$$

where  $n$  = fin beat frequency (Hz),  $c$  = maximum chord of the fin perpendicular to the fin rays (in cm), and  $U$  = forward velocity (in  $\text{cm s}^{-1}$ ) (Vogel, 1994). Typically acceleration reaction forces dominate at reduced frequency numbers above 0.5.

We calculated Reynolds number (Re) to examine whether the change in pectoral fin gait is associated with changes in the fluid regime experienced by the fish. Reynolds number is a dimensionless number calculated as:

$$\text{Re} = \rho UL / \mu, \quad (3)$$

where  $\rho$  = water density ( $\text{kg m}^{-3}$ ),  $U$  = swimming speed ( $\text{m s}^{-1}$ ),  $L$  = characteristic length (m), and  $\mu$  = dynamic viscosity ( $\text{kg ms}$ ). We used fish body length ( $BL$ ) as the characteristic length in our calculations. Although studies differ, frequently locomotion at Re values <100 is considered to be dominated by viscous (resistive) forces and >1000 to be dominated by inertial (reactive) forces.

We assessed the pattern of thrust by tracking the oscillatory motion of the tip of the snout, our most reliable single point that served as a proxy for the center of mass of the fish. Increased snout tip oscillation from left to right (increased yaw) was predicted for alternate fin strokes. In order to estimate thrust oscillations, we calculated the mean excursion of the point digitized at the tip of the snout in the direction flow through each trial. To determine yaw, we calculated the mean excursion of the tip of the snout perpendicular to the direction of flow through each trial.

#### Comparative data

For our survey of pectoral fin gaits, we found that all species followed the same general pattern as *P. pavo*: the pectoral fins alternated at low speeds and moved synchronously at high speeds. We scored the observations for whether the fins were alternating or synchronous and examined that transition relative to swimming speed and Reynolds number.

#### Statistics

We used regression analysis to test the significance of the relationship between swimming velocity and kinematic variables. To test whether variables such as frequency, amplitude, advance ratio, phase lag, Reynolds number and thrust oscillation were significantly different when the fish were performing synchronous *versus* alternating gaits, we performed simple two-way analyses of variance (ANOVA) with gait and individual as main effects. All variables were tested for homogeneity of variance, and for two variables in which the variance was significantly different between gaits, we report Welch ANOVA values corrected for unequal variance. Sequential Bonferroni correction (Rice, 1989) was used to

determine significance of *F* ratios due to the use of eight ANOVAs on the data set. For those variables that had a significant overall regression with swimming speed (such as frequency, amplitude and advance ratio), we asked whether the relationship with speed was significantly different during use of the two pectoral fin gaits. For this we applied analyses of covariance (ANCOVA) to determine whether the slopes or intercept of the velocity regression were significantly different, using synchronous *versus* asynchronous gait as the main effect. All analyses were performed using the JMP version 3.16 statistical package (SAS Institute, Cary, NC, USA).

## Results

### Patterns of locomotor gaits and gait transition in *Pomacentrus pavo*

We observed three distinct gaits performed by *Pomacentrus pavo* during steady swimming: alternating pectoral fin (Fig. 1A), synchronous pectoral fin (Fig. 1B), and axial-caudal fin propulsion. At most swimming speeds, propulsion was driven by pectoral fin beats while the caudal fin remained relatively stable. Alternating fin strokes occurred from the lowest steady swimming speeds up to the gait transition to synchronous pectoral fin coordination at 3–4  $BL s^{-1}$  (Figs 2, 3). The pectoral fins retained a consistent phase relationship while alternating (Fig. 4) of nearly 180° out of phase. From speeds of about 4  $BL s^{-1}$  to about 8  $BL s^{-1}$ , *P. pavo* generally swam with a synchronous pattern of fin movement, adducting and abducting right and left fins together during the fin cycle (Fig. 1B, Fig. 3C). The transition between alternating and synchronous fin beat patterns occurred rapidly, usually in 1–2 fin strokes (Fig. 2, Fig. 3B), and no intermediate sustained patterns were observed. The fish often switched between these gaits several times during a trial at a constant flow tank speed (Fig. 3). For example, Fig. 3B illustrates a sequence in which the early coordination pattern was synchronous fin strokes. The fish switched to alternating strokes between 0.15 and 0.25 s and then back to synchronous fin movements between 0.34 and 0.40 s.

The gait transition from alternate to synchronous pectoral fin motion is most evident when viewing the phase lag between the oscillating fins (Fig. 4). At low speeds, the fins were alternating and phase lag values were high,

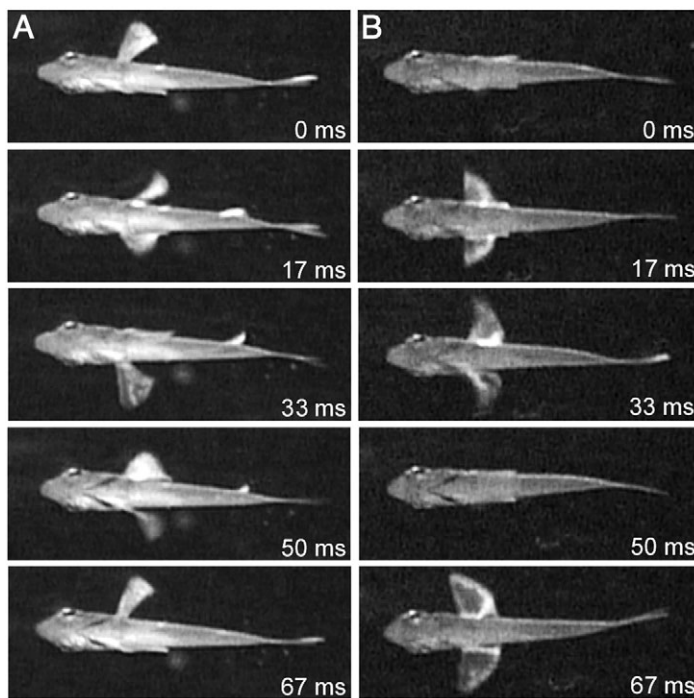


Fig. 1. Kinematics of (A) alternating and (B) synchronous pectoral fin propulsion in ventral view during steady swimming in the blue damselfish *Pomacentrus pavo*. (A) At 2  $BL s^{-1}$ , the fish swims by alternating its pectoral fins at approximately 180° out of phase from one another. At 0 ms the left (upper) pectoral fin is protracted (abducted) and at 17 ms the left is retracted (adducted) while the right (lower) fin begins protraction. At 50 ms the left fin is seen during protraction and right during retraction. (B) At higher speeds (7  $BL s^{-1}$ ), damselfish switch gaits to an in phase fin beat pattern with simultaneous protraction (frame 17 ms and 67 ms) and retraction (0 and 50 ms). At 33 ms the fins are shown in mid-retraction phase.

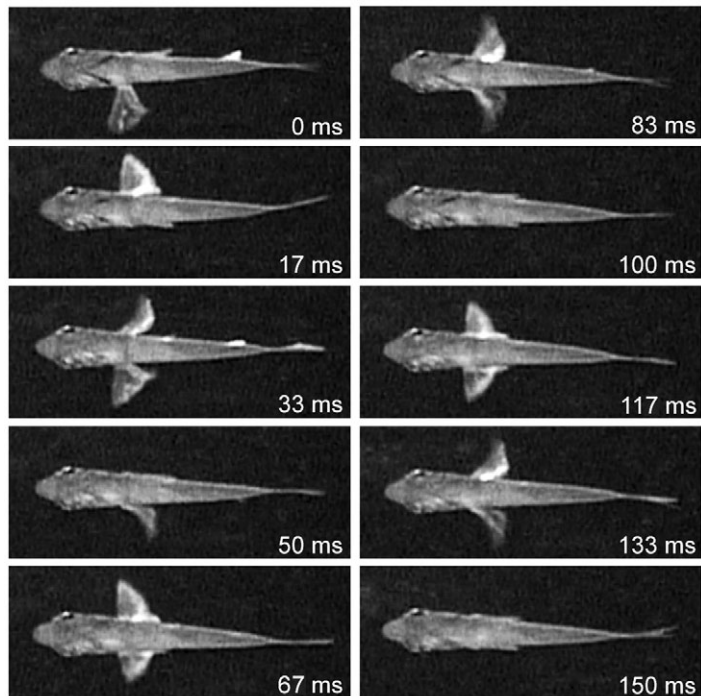


Fig. 2. The transition between alternating and synchronous pectoral fin coordination during steady swimming in the blue damselfish *Pomacentrus pavo* at a critical swimming speed of approximately  $4 BL s^{-1}$ . This gait transition occurs rapidly, within 1–2 fin strokes. Asynchronous swimming (left panels) is seen from 0–33 ms, then is partially out of phase during the transition (33–67 ms). Mostly synchronous locomotion is seen from 83–150 ms (right panels).

generally at or near  $180^\circ$  (perfect asynchrony). At  $3\text{--}4 BL s^{-1}$ , the phase lag dropped to near zero and remained at this level until speeds were reached that required caudal fin propulsion.

The pectoral fin to axial–caudal fin transition occurred at approximately  $8 BL s^{-1}$  (Fig. 5). As at the alternating to synchronous pectoral fin transition, fish often switched back and forth between these locomotor gaits at the transition speed. Fig. 5B illustrates a transition from pectoral fin swimming before 0.17 s to axial locomotion and then back to pectoral fin locomotion at approximately 0.25 s. We did not record sustained axial steady swimming in any species examined due to constraints on the maximum flow speeds produced in our tank and rapid fatigue of the fish at the highest speeds recorded.

#### *Swimming performance and locomotor gaits in P. pavo*

Amplitude and frequency of the fin beats both increased with increasing swimming speed (Fig. 6). There was no significant difference in regressions of frequency by speed through alternating and synchronous gaits so data were combined for analysis. The overall linear regression had a slope of 1.3, different from zero ( $P < 0.0001$ ,  $R^2 = 0.44$ ), and an intercept of 12.9. Frequency ranged from  $10.9\text{--}25.0$  beats  $s^{-1}$  (mean  $\pm$  s.e.m.:  $17.9 \pm 0.5$  Hz) (Fig. 6A). Frequency was significantly higher for the synchronous than for the alternating gait ( $P < 0.0001$ ,  $F = 40.05$ ), with synchronous beats ranging from  $12.5\text{--}25$  Hz (mean:  $20.1 \pm 0.55$  Hz) and alternating beats from  $10.9\text{--}20.0$  Hz (mean:  $15.0 \pm 0.59$  Hz). There were no significant differences in either slope or intercept between the regressions fitted to data for alternating and synchronous fin coordination (ANCOVA; Table 1).

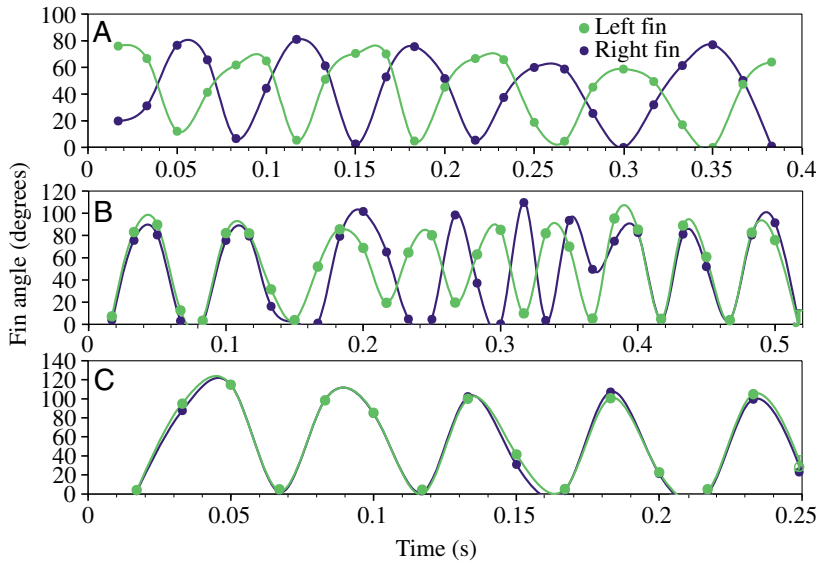
Amplitude (Fig. 6B) ranged from  $50^\circ$  to  $142^\circ$  across gaits (mean  $98 \pm 3.0^\circ$ ),  $50\text{--}113^\circ$  (mean:  $79.7 \pm 3.2^\circ$ ) for alternating fin

beats,  $87\text{--}142^\circ$  (mean:  $112.3 \pm 2.9^\circ$ ) for synchronous and was significantly different ( $P < 0.0001$ ,  $F = 56.7$ ) between the two gaits. Across alternating and synchronous gaits there was an overall increase in amplitude with length-specific swimming speed ( $R^2 = 0.70$ ) with a slope significantly different from zero ( $P < 0.0001$ ) (Table 1). There was a significant difference in the slopes of amplitude with swimming speed for the two gaits (ANCOVA;  $P < 0.038$ ,  $F = 4.52$ ) with amplitude increasing more rapidly with increasing swimming speed during the alternating fin gait (Table 1).

The reduced frequency parameter showed that acceleration reaction was a dominant force at all speeds for the juvenile fishes (Fig. 7A). Acceleration reaction forces dominate at reduced frequencies of greater than 0.5 (Webb, 1988), and all values for *P. pavo* were greater than 1.0. Reduced frequency was particularly high at low swimming velocities where, despite low speeds, the fins were oscillating rapidly. Values dropped off quickly to below 10 as swimming speed increases to  $2 BL s^{-1}$ . There was no apparent discontinuity in reduced frequency at the gait transition speeds (Fig. 7A).

Across all swimming trials, advance ratio varied from 0.23 to 1.72 (mean:  $1.08 \pm 0.04$ ) (Fig. 7B). The advance ratio for the two fin gaits overlapped considerably. For alternating fin swimming trials it ranged from 0.23 to 1.63 (mean:  $0.93 \pm 0.06$ ) and for synchronous fin swimming trials it ranged from 0.80 to 1.72 (mean:  $1.19 \pm 0.05$ ); however, overall, the advance ratio was significantly greater for the synchronous fin gait ( $P < 0.005$ ). The advance ratio increased with swimming speed through both alternating and synchronous gaits. For alternating fins, the  $R^2$  value for linear regression was 0.51 and for the synchronous fin beats  $R^2$  was 0.57 (Table 1). The slopes of the regressions differed significantly (ANCOVA;  $P < 0.01$ ). At the transition between alternating and synchronous fin coordination gaits (Fig. 7B), the advance ratio decreased with the initiation of synchronous fin beats and then it rose again as swimming speed increased to reach nearly the same peak levels.

Oscillation of the position of the head in the direction of forward movement provided an indicator of thrust oscillations during the fin stroke cycles (Fig. 8). Head oscillation increased linearly with swimming speed ( $R^2 = 0.64$ ) from a minimum of 0.017 cm to a maximum of 0.076 cm (Fig. 8, Table 1). Overall, oscillations were lower during the alternating fin gait (range:  $0.017\text{--}0.056$  cm, mean:  $0.028 \pm 0.002$  cm) than during the synchronous fin gait (range:  $0.031\text{--}0.076$  cm, mean:  $0.0528 \pm 0.002$  cm) and there was no discrete transition in forward oscillation between the two gaits.



Yaw, or the amount of side-to-side oscillation (Fig. 8B), showed no trend with increasing swimming speed for each gait independently (for alternating:  $R^2=0.027$ ,  $P<0.43$ ; for synchronous:  $R^2=0.072$ ,  $P<0.14$ ), and  $R^2$  is very low for the combined data ( $R^2=0.096$ ), although significantly different from zero ( $P<0.024$ ) with a positive slope (Fig. 8, Table 1). There was no overall difference in yaw between gaits ( $t$ -test,  $P=0.088$ ,  $F=3.032$ ). Yaw during alternating fin coordination ranged from 0.0089–0.041 cm (mean:  $0.0192\pm 0.00014$  cm) and yaw during synchronous fin coordination ranged from 0.012–0.038 cm (mean:  $0.022\pm 0.00123$  cm).

Reynolds number ranged from 118–3543 (mean:  $1243\pm 101$ ), an interval in which fluid conditions are shifting from being dominated by viscous forces to being dominated by inertial forces. Individual fishes showed clear (by definition) trends of increasing Re with increasing speed, but there was no significant correlation between Reynolds number and the

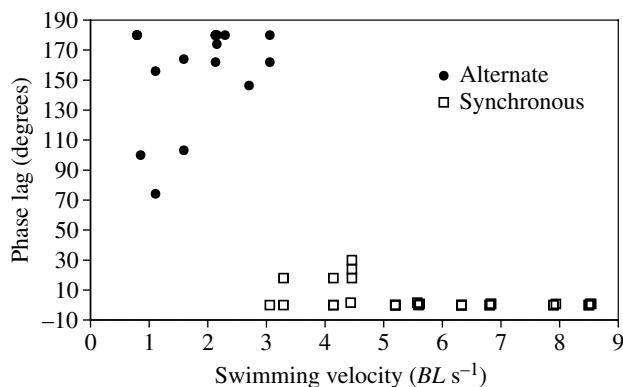


Fig. 4. Phase lag of left and right pectoral fins with increasing swimming velocity. Points are the mean of 5–8 fin beats in a swimming sequence. Note the sharp gait transition from alternate to synchronous fin motions between 3 and 4  $BL s^{-1}$ .

Fig. 3. Representative kinematic data for angular rotation of left and right pectoral fins of juvenile *Pomacentrus pavo* during (A) slow, alternating fin strokes, (B) a transition from synchronous to alternating fin coordination and back again, and (C) synchronous fin strokes at higher speed.

transition point between alternating and synchronous fin gaits across individuals (Table 1).

#### Pectoral fin gaits in juveniles of multiple species

In order to determine whether the alternating to synchronous fin gait transition observed in *P. pavo* is a more general phenomenon, we surveyed gaits in 33 individuals from 10 other coral reef species (Table 2). Because of the difficulties in collection and performance of these experiments on small subadult fishes under

field conditions, we had to be opportunistic when collecting and the numbers of specimens per species varies. In these species we saw the same pattern of alternating fin beats at low speeds switching to synchronous fin beats at higher speeds that we observed in *P. pavo*.

Across all species and trials recorded, synchronous fin coordination occurred at a significantly higher length-specific speed than alternating fin coordination [alternating:  $2.57\pm 0.12$ ; synchronous:  $3.43\pm 0.18$  ( $P<0.0001$ )]. However, the transition did not occur at a particular length-specific speed. That point is demonstrated by the range of swimming speeds recorded for each gait, which show considerable overlap. Alternating fin coordination occurred at  $0.79$ – $7.52 BL s^{-1}$  and synchronous fin coordination was observed at  $0.89$ – $8.50 BL s^{-1}$ .

#### Discussion

We found that pectoral fin gaits of juvenile reef fishes are more complex than previously thought. Our central result is that many labriform swimmers use both alternating and synchronous pectoral fin gaits to swim steadily through a range of speeds. Alternating fin beats are used at lower speeds; synchronous fin beats at higher speeds. Unlike previous pectoral fin gait transitions recorded (Hove et al., 2001), these two gaits were distinct with a rapid transition between fin coordination patterns.

The gait pattern reported here in fishes is similar to that observed in tetrapod taxa. For example, frogs and toads have been shown to use alternating hindlimb movements for slow walking but transition to synchronous hindlimb movement with increasing speed (Nauwelaerts and Aerts, 2002). A similar transition has been demonstrated for frog swimming, a switch from alternating to synchronous hindlimb movement with increasing speed (Nauwelaerts and Aerts, 2002).

Steady pectoral fin swimming in fishes has generally been

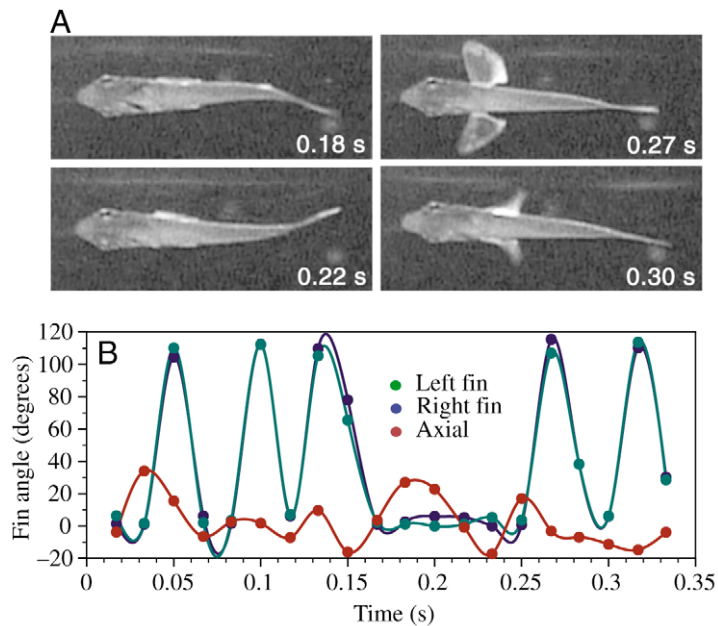


Fig. 5. Transitions between synchronous pectoral propulsion and axial propulsion. (A) Video images showing axial propulsion (0.167–0.217 s) followed by synchronous pectoral swimming with body held straight (0.267–0.3 s). (B) Kinematics of synchronous pectoral rotation (blue and green), ceasing at about 0.15 s accompanied by two strokes of the caudal fin (red) and then pectoral propulsion resuming at 0.25 s.

described as either synchronous (e.g. Drucker and Jensen, 1996a; Walker and Westneat, 1997; Mussi et al., 2002) or alternating (Arreola and Westneat, 1996). Fin beat amplitude and frequency increase with increasing swimming speeds until the fish either switch to an axial gait or reach peak swimming speed. In the unusual case of the boxfish, alternating and synchronous pectoral fin coordination patterns are both used (Hove et al., 2001). The use of these gaits by boxfish differed strikingly from the patterns we describe in *P. pavo*, the other juvenile fishes studied here and terrestrial vertebrates. First, the use of synchronous fin beats by boxfish occurred at slow speeds and transitioned to alternating at higher speeds of 1.3–4.5  $BL s^{-1}$  (Hove et al., 2001). Second, the transition was not discrete, as observed here or in other vertebrates. Instead, boxfish appear to combine the movement of the two pectoral fins asymmetrically and smoothly transition between synchronous and alternating patterns. Due to this gradual transition, alternating and synchronous pectoral fin patterns do not fall into typical definitions of gaits that specify a discontinuity in movement during transition. Because of the unusual swimming pattern and the extensive use of unpaired fins during boxfish locomotion, it is not surprising that these animals may use the pectoral fins in uncommon coordination patterns.

#### Why a pectoral fin gait transition?

The presence of two distinct pectoral fin gaits raises questions of why fish use multiple pectoral fin gaits and what

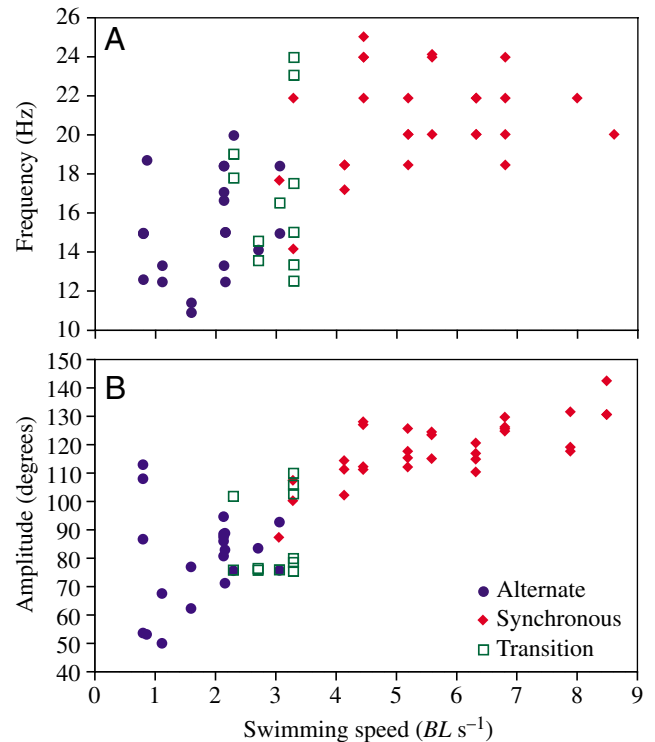


Fig. 6. Frequency (A) and amplitude (B) of pectoral fin beats during increasing swimming velocity trials in *Pomacentrus pavo*. Both frequency and amplitude increase with speed, smoothly across the transition to synchronous fin beats at 3–4  $BL s^{-1}$ . Transition points include a range of behaviors in which switching between modes was observed.

determines the transition between them. More broadly, the diverse representation of taxa that use alternating fin/limb movement at slow speeds and transition to synchronous coordination at higher speeds suggests there may be common constraints or benefits of the use of these fin movement patterns. Based on previous studies, we raise several possibilities for why fish may use multiple gait transitions. First, above a given speed, synchronous fin beats may be more efficient than alternating propulsive strokes. Studies on oxygen consumption of terrestrial vertebrates, particularly horses, show that animals use the locomotor gait that is most energy efficient for a particular speed range (e.g. Hoyt and Taylor, 1981; Griffin et al., 2004). Second, particular gaits may be more or less stable at a given speed and fish may transition between gaits to maintain stability (Arreola and Westneat, 1996; Hove et al., 2001). Energy efficiency and stability of a gait at specific speeds are related to the hydrodynamics of movement at those speeds, thus we might expect changes in indicators of locomotor hydrodynamics such as reduced frequency or Reynolds number at gait transitions. Third, there may be mechanical constraints on the speed range in which a particular gait can operate (Drucker and Jensen, 1996b).

Work on the median and paired fin (MPF) to body and caudal fin (BCF) transition may provide insight into these issues.

Table 1. Results of analysis of variance and covariance on kinematic parameters of juvenile pectoral fin locomotion of *Pomacentrus pavo*, comparing synchronous and alternating gaits

	Synchronous	Alternating	F ratio	
			ANOVA	ANCOVA
Frequency (Hz)	20.0±0.5	15.0±0.6	40.0**	0.5
Amplitude (degrees)	112.3±2.9	79.7±3.2	56.7**	4.5*
Phase lag (degrees)	16.2±6.1	150.0±6.9	208.4**	a
Reduced frequency (Hz)	5.0±1.0	10.3±1.1	12.4*	a
Advance ratio	1.2±0.06	0.93±0.06	9.3*	7.5*
Reynolds number	1368±134	1084±152	2.0	a
Forward displacement (cm)	0.05±0.002	0.03±0.002	57.4**	0.5
Yaw (cm)	0.02±0.001	0.02±0.001	2.4	a

Values are means ± s.e.m.,  $N=3$  fish, 48 trials (11 trials that included the gait transition were excluded from these comparisons).

\*Significant  $P$  value by sequential Bonferroni criterion. Significant ANCOVA results were significant differences in slope of regression against speed.

\*\* $P<0.0001$ .

<sup>a</sup>An ANCOVA was not computed because regression analysis is not valid for the distribution of the data or regression was not significant.

Examination of oxygen consumption at the transition between slow MPF swimming and fast BCF swimming (Korsmeyer et al., 2002) found that transitioning to the faster gait did not decrease energy costs. In fact, energy expenditure was greater for BCF swimming than was predicted for MPF swimming at the same speed. Instead, they believe that the MPF to BCF transition appears to be due to physical constraints, so that the switch to axial propulsion occurs when the fin-based mode of

locomotion has reached the limit of thrust production (Korsmeyer et al., 2002).

The transition from alternating to synchronous fin movement in the juvenile fish we examined differs from the MPF to BCF transition in that the same propulsors are used but in a different pattern of coordination. The most comparable previous study of gait transitions in vertebrates is the switch from alternating to synchronous limb movement in swimming frogs

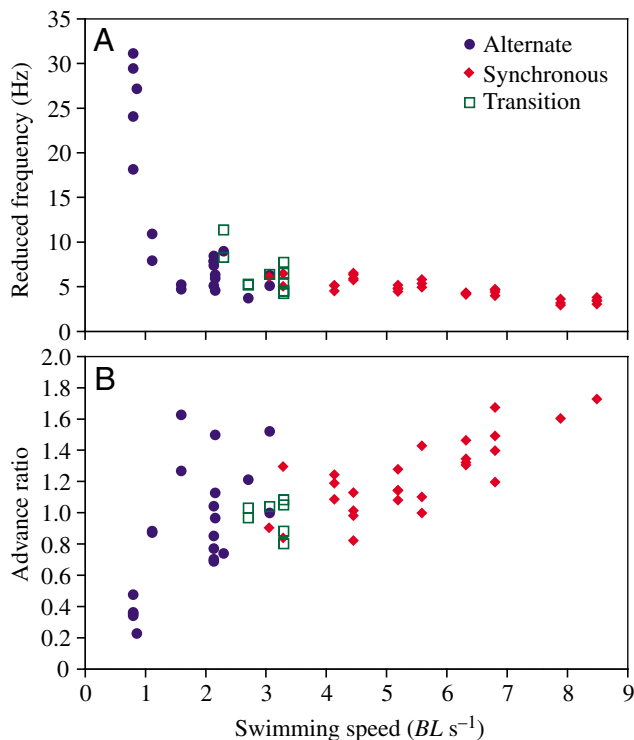


Fig. 7. Reduced frequency (A) and advance ratio (B) of juvenile pectoral fin locomotion in *Pomacentrus pavo*.

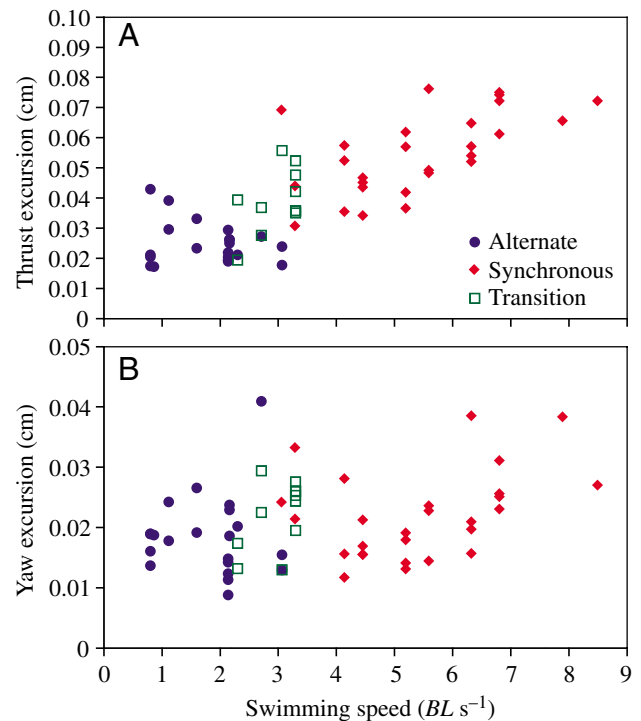


Fig. 8. Distance traveled by the tip of the snout each frame illustrating (A) fore–aft excursion due to forward thrust and (B) lateral motion (yaw) during pectoral fin locomotion in *Pomacentrus pavo*.



Table 2. Morphometrics and results of pectoral fin gait survey (alternating to synchronous transition speed and Reynolds number range) for 12 juvenile coral reef fish species swimming steadily in a flow tank

Species	N	Body length (cm)	Fin length (cm)	A-S transition ( $BL s^{-1}$ )	Re range
<i>Chromis weberi</i>	3	1.82±0.05	0.35±0.04	4.50	618–2498
<i>Cirrhilabrus punctatus</i>	4	1.97±0.32	0.33±0.05	2.16	569–3845
<i>Dascyllus aruanus</i>	3	2.75±0.28	0.55±0.06	3.73	805–4263
<i>Halichoeres biocellatus</i>	3	2.82±0.33	0.53±0.06	3.51	865–3204
<i>Halichoeres chrysus</i>	3	1.83±0.29	0.29±0.06	4.95	523–2092
<i>Halichoeres trimaculatus</i>	3	2.58±0.36	0.42±0.06	4.48	703–4237
<i>Labroides dimidiatus</i>	3	3.04±0.21	0.49±0.32	1.87	929–4394
<i>Pseudochelinus hexataenia</i>	1	2.6	0.28	4.28	918–3400
<i>Pomacentrus pavo</i>	3	1.81±0.45	0.37±0.12	4.14	118–3544
<i>Scarus</i> sp.	3	2.76±0.56	0.42±0.11	3.20	900–4995
<i>Thalassoma amblycephalum</i>	2	1.78±0.02	0.28±0.01	4.07	523–2354

A–S, alternating to synchronous; Re, Reynolds number.

Values are means ± s.e.m.

(Nauwelaerts and Aerts, 2002). At slow swimming speeds the frog *Rana esculenta* used alternating left and right limb strokes for propulsion. At faster swimming speeds, frogs switched to a simultaneous hindlimb movement while tucking the forelimbs against the body. Nauwelaerts and Aerts calculated the work required for these two gaits and found that the energy requirements for swimming out of phase are lower than those for in-phase swimming. Thus, as with the MPF to BCF transition in fishes, the gait transition is likely due to mechanical constraints on thrust generation.

The difference in efficiency may be due to the relative steadiness of these locomotor modes (Nauwelaerts and Aerts, 2002). Simultaneous limb movements result in greater accelerations during a swim bout and thus greater loss of inertial energy at slow speeds (Nauwelaerts and Aerts, 2002). At higher swimming speeds, the simultaneous strokes of the hindlimbs may generate jetting that does not occur at lower speeds and this overcomes the energy disadvantage of using the in-phase locomotor mode at lower speeds. Similarly, it has been suggested that the alternating fins of burrfish may allow more steady thrust and efficient locomotion than synchronous fin beats (Arreola and Westneat, 1996). In our study of *P. pavo*, forward oscillation was considerably lower for alternating pectoral fin locomotion than for synchronous, supporting the steadiness hypothesis (Fig. 8). However, we would expect that if alternating movements reduced these oscillations at low speeds then the oscillations during synchronous fin coordination would be highest immediately following the gait transition and either decrease or remain level with increasing speed. This was not the case and suggests that, if steadiness is a factor in the gait transition, it is not the only one or, possibly, that gait transitions are coupled with fine fin control to prevent fluctuations in thrust excursion after the transition.

Related to the issue of steadiness is that of stability. Reduced stability has also been suggested as a disadvantage of synchronous pectoral fin beats of MPF swimmers at low speeds

for parrotfish (Korsmeyer et al., 2002) and wrasses (Walker and Westneat, 1997). These species would not swim steadily at speeds below approximately  $1.5 BL s^{-1}$  and  $1.2 BL s^{-1}$ , respectively. Flow visualization studies find that fish swimming steadily with synchronous fin beats at low speeds ( $0.5$  and  $1.0 BL s^{-1}$ ) generate unusually high laterally oriented forces (Drucker and Lauder, 2000) and suggest that orientation of force may provide increased stability at low speeds.

There was no significant trend in yaw magnitude with swimming speed (Fig. 8), indicating that either yaw is not a factor in asynchronous fin propulsion or that the fishes are able to compensate for yaw with other fins. As the symmetrical in-phase movements of synchronous fin activity would not be expected to generate yaw, this control would be more important during asymmetric movements. Observation of dorsal, anal and caudal fin coordination during the two pectoral fin gaits may provide insight into this issue, and flow visualization studies to determine the forces generated by these gaits and through the pectoral fin gait transition would help to address some of these issues.

Both energy efficiency and steadiness/stability might be linked closely to changes in the hydrodynamic environment, in particular, reduced frequency and Reynolds number. Reduced frequency values were high at low speeds (Fig. 7) and, although they decreased with speed, did not shift below about 3.0, indicating that acceleration reaction forces dominate throughout the trials examined. Reynolds number ranged from about 200 up to about 2000 for the *P. pavo* swimming trials we analyzed (Table 2). We found no significant relationship between gait and Re across the individuals examined. Additional testing of fish larvae and juveniles across a broader size range and Re span may clarify the effect of hydrodynamic regime on fin gait.

Mechanical and physiological limits of fin muscle believed to explain the MPF to BCF transition in fishes may also explain the alternating to synchronous fin coordination gait transition. We predicted that amplitude and/or frequency of the fins during

alternating strokes would peak immediately before the transition to synchronous fin coordination and be lower for synchronous strokes. While this was not the case in our data, the advance ratio, which reflects both amplitude and frequency (Fig. 7) exhibits the predicted trend. Advance ratio increases with swimming speed through both gaits with the highest ratios calculated for each speed being relatively similar. We suggest that *P. pavo* reaches a peak in advance ratio for alternating fin swimming then transitions to synchronous swimming, with which the same speed can be achieved with a lower advance ratio, possibly at lower energetic costs. Advance ratio of synchronous fin swimming increases with speed again until it reaches a peak, at which point the fish transitions to BCF swimming. Because fin length does not change across speeds, frequency and amplitude variability determine the denominator of the advance ratio. This suggests that it is a peak in combined amplitude and frequency that provides the upper speed limits of pectoral fin gait use for an individual animal.

#### Ontogenetic differences in gait use

It is interesting to consider why the gait transition pattern we observed only seems to occur in young fish. None of the labriform swimmers previously studied, including several from the same families that we examined (e.g. Walker and Westneat, 1997; Walker and Westneat, 2000), have been shown to use alternating fin beats for steady swimming at adult life history stages. Our original hypothesis was that the use of alternating fin strokes was an effect of size and that at low Reynolds numbers or at low reduced frequency, alternating fin strokes may be advantageous for steady locomotion. Indeed, the Reynolds numbers for the fish we examined were low relative to those of adults, suggesting that flow regime is a critical factor in the fin gaits used by developing fishes. However, the limited range of our analysis of Reynolds number and reduced frequency across juvenile swimming emerged with no significant trends with locomotor gait transitions within juveniles, indicating that other factors may be important.

Comparisons of the swimming speed ranges we recorded to those reported for adults of other species suggest that younger fish can swim with paired fins at a considerably greater range of length-specific body speeds than adults. In fact, the transition between pectoral fin gaits in juveniles of *P. pavo* and other species occurs at the same length-specific speed or a higher speed than the MPF to BCF transition in adults (e.g. Drucker and Jensen, 1996b; Mussi et al., 2002). Juvenile fishes appear to have a high performance capability for sustained swimming. This has been shown previously for fish larvae (Stobutzki and Bellwood, 1994) and with small sized adults as compared to larger ones (Mussi et al., 2002) and may be due to changes in size and shape of body and fins or changes in locomotor physiology.

In this study we have demonstrated that juvenile fishes from a number of species across several major clades exhibit an alternating to synchronous gait transition in pectoral locomotion. This dramatic phase shift in the pattern of propulsive appendages has not been documented widely in

aquatic locomotion, but has been observed in a number of tetrapods. It is possible that the low reported occurrence of this transition in fishes is due to the fact that the locomotion of sub-adult fishes has been largely overlooked due to technical issues of acquiring, maintaining and recording these sensitive animals. We suggest that, through the dynamic transition from larval to adult, much locomotor complexity will be evident that is not observed in adults since, during this period, fish often move between environments and alter diets, change in shape, size and physiology, and face new demands of reproduction.

#### List of symbols

$\phi$	fin angle
$BL$	body length
$c$	maximum chord of the fin perpendicular to the fin rays
$F_p$	pectoral fin beat frequency
$J$	advance ratio
$L$	characteristic length
$L_p$	pectoral fin length
$Re$	Reynolds number
$T_{cycle}$	total fin cycle time
$T_{lmax}$	time of peak left angle
$T_{rmax}$	time of peak right angle
$U$	forward speed
$U_{pc}$	speed of the transition from pectoral fin swimming to body and caudal fin swimming
$\mu$	dynamic viscosity
$\rho$	water density

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