

Constraints on starting and stopping: behavior compensates for reduced pectoral fin area during braking of the bluegill sunfish *Lepomis macrochirus*

Timothy E. Higham^{1,*}, Brett Malas², Bruce C. Jayne³ and George V. Lauder⁴

¹Section of Evolution and Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA,

²Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92717, USA, ³Department of Biological Sciences, University of Cincinnati, PO Box 210006, Cincinnati, OH 45221-0006, USA and ⁴Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

*Author for correspondence (e-mail: tehigham@ucdavis.edu)

Accepted 1 November 2005

Summary

Many natural animal movements involve accelerating from a standstill and then stopping. Obstacles in natural environments often limit the straight-line distance available for movement, and decreased braking ability theoretically can limit speed for short distances. Consequently, braking ability can be important for avoiding collisions with obstacles and exploiting resources effectively in complex environments. A presumed morphological correlate of improved braking performance in fish is increased pectoral fin area, because most fish protract these structures as they decelerate. However, the kinematics and modulation of velocity during starting and stopping are poorly understood for most species of fish as well as most species of animals. Thus, for bluegill sunfish *Lepomis macrochirus* with complete and partially ablated pectoral fins (35% original fin area), we analyzed high speed video recordings (200 images s⁻¹) of predatory attacks with a start and stop in a short, standardized distance (40 cm). We quantified body displacement, velocity, acceleration, deceleration and

several fin angle variables during each feeding. Unexpectedly, several variables including maximum velocity and maximum deceleration (grand means 72 cm s⁻¹ and -512 cm s⁻², respectively) did not change significantly with reduced pectoral fin area. The average values of braking movements of the median and caudal fins did increase with decreased pectoral fin area but lacked statistically significant differences. The primary mechanism of attaining similar braking performance with decreased area of the pectoral fins was that they were protracted significantly more (mean difference=42°) and with a significantly faster average velocity of protraction. Thus, pectoral fin area appears unlikely to be the primary constraint on braking performance for this particular task.

Key words: intermittent locomotion, kinematics, braking, deceleration, Centrarchidae, *Lepomis macrochirus*, pectoral fin, morphology, acceleration, swimming, stopping, starting, predation, feeding.

Introduction

Much of the locomotion of animals in nature involves starts and stops, which are often associated either with physical obstacles in the environment or the use of resources. However, laboratory investigations of animal locomotion commonly go to great lengths to elicit steady locomotion of animals in areas devoid of obstacles that might impede the forward progress. Consequently, even for groups of animals such as fishes, for which locomotion has been studied intensively (reviewed in Webb and Weihs, 1983; Videler, 1993; Blake, 2004; Lauder, 2005), data on unsteady locomotion are rare compared to those for steady locomotion, and most of what is known about unsteady locomotion is for accelerating rather than decelerating (e.g. Tytell, 2004). Furthermore, no previous study of fish has quantified the accelerations involved in both starting and stopping. Despite the scarcity of literature on the

mechanisms and performance of stopping, stopping is a pervasive phenomenon since it always occurs prior to the stationary period. Furthermore, stopping ability is important so that animals do not collide with obstacles and can arrive predictably at a particular location. Although it may seem counterintuitive, stopping ability theoretically could constrain maximal and average speed over short travel distances (Fig. 1), which may arise either from physical barriers in the environment or from the behavior of the animal.

When most fish stop, the fins extend away from the body as it is held in an S-shape posture. Thus, the fins of most fishes are involved in stopping, and several features of fins make them well-suited for studying the interrelationships between structure, behavior and locomotor function. The fins of ray-finned fishes are versatile control surfaces for actively

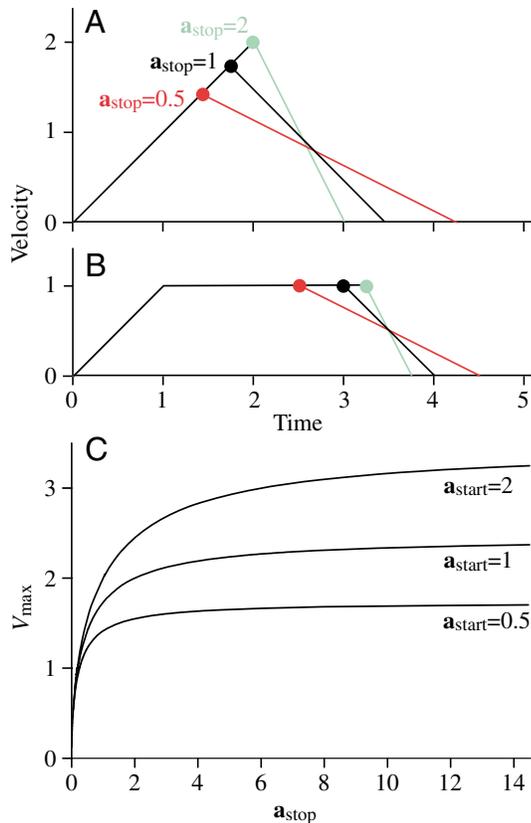


Fig. 1. A model of how stopping ability and total travel distance could constrain modulation of velocity during a start and stop. The hypothetical movements in A and B have identical starting accelerations ($a_{\text{start}}=\text{slope}=1$) and total displacements ($S_{\text{total}}=\text{areas under the triangles or trapezoids with a vertex indicated by a circle}=3$ units), but the stopping acceleration (a_{stop}) varies among the cases indicated by the different colors within each panel. (A) Starting acceleration continues up to the instant when stopping begins (indicated by circles). Compared to $a_{\text{stop}}=1$, increased stopping ability (green) allows more distance to accelerate to a greater maximal velocity (V_{max}), which decreases total travel time. Decreased stopping ability (red) has detrimental effects on V_{max} and total travel time. Consequently, the average velocities (S_{total} divided by total time) for $a_{\text{stop}}=2$ and 0.5 are 115% and 81% of the value when $a_{\text{stop}}=1$, respectively. (B) When the total distance provides sufficient time so that a physiologically maximum speed is attained and momentarily sustained, stopping ability will not affect V_{max} . However, increased stopping ability decreases total time and hence the average velocities for $a_{\text{stop}}=2$ and 0.5 are 107% and 89% of the value when $a_{\text{stop}}=1$, respectively. Maintaining a constant velocity in between the starting and stopping accelerations (B) increases total travel time and hence decreases average velocity compared to beginning a stop immediately after the cessation of a starting acceleration (compare A vs B for equal values of a_{start} and a_{stop}). If the only objective of starting and stopping is to minimize total travel time (and maximize average speed) for a given distance, then maximal accelerating and decelerating capacities should be used. (C) For a linear increase in velocity followed immediately by a linear decrease in velocity as in A, $V_{\text{max}}=a_{\text{start}}[(2S_{\text{total}})/(a_{\text{start}}+1/a_{\text{stop}})]^{0.5}$ and hence the upper limit of V_{max} is $a_{\text{start}}^{0.5}(2S_{\text{total}})^{0.5}$. Axes show arbitrary units.

modulating drag during stopping since their size, posture and movement can all be modulated. Within fishes, much interspecific variation in fin sizes and body shapes is consistent with the biomechanical expectations for optimizing different locomotor tasks (Webb, 1984). For example, fish with large fins and deep bodies are often assumed to be the more adept at stopping and maneuvering than sustaining high speeds (Webb and Fairchild, 2001). The fins of ray-finned fishes are also amenable to experimental manipulation of morphology, which facilitates isolating the functional consequences of morphological variation while minimizing confounding sources of morphological variation that are common among different species (Harris, 1937b; Webb, 1973, 1977; Reimchen and Temple, 2004). The hypothesis that morphology is the limiting factor to performance can be rejected if altering morphology does not affect performance.

The prominent role played by the pectoral fins for increasing drag during stopping has long been recognized (Breder, 1926; Harris, 1937a,b; Bainbridge, 1963), and the size and shape of pectoral fin morphology varies widely among different species of ray-finned fishes (Drucker and Lauder, 2002; Lauder and Drucker, 2004; Thorsen and Westneat, 2005; Wainwright et al., 2002; Westneat, 1996). The drag of pectoral fins increases with both increased area and increased fluid speed. Thus, accounting for both fin morphology and kinematics is important for understanding variation in stopping performance. However, no previous study has quantified the kinematics of the pectoral fins during the stopping of ray-finned fishes.

We studied the bluegill sunfish *Lepomis macrochirus*, which has the large pectoral fins and deep body that characterize maneuvering specialists. Similar to many other predatory species of fish (Webb, 1984; Webb and Gerstner, 2000), our study species stops during prey capture by actively braking rather than gliding (Drucker and Lauder, 2002; Higham et al., 2005). This behavior facilitated quantifying the kinematics, velocity and accelerations of ecologically relevant start-stop episodes over a standard distance. To gain further insights into roles of morphology and behavior during braking, we experimentally reduced the area of the pectoral fins. We addressed the following two primary questions. (1) What are the magnitudes of starting and stopping accelerations, and are they similar within a single predatory strike? (2) Does reduced pectoral fin area affect stopping performance and attack speeds? We expected reduced fin area to decrease the maximal deceleration or at least alter the movements and postures used by fish during stopping. With a reduced ability to stop, fish also might use slower attack speeds to avoid overshooting the location of prey.

Materials and methods

Experimental subjects

We studied the bluegill sunfish *Lepomis macrochirus* Rafinesque, a member of the freshwater family Centrarchidae. The fish were collected in California, USA and were maintained in separate 38 liter aquaria containing water at a

temperature of 18–20°C. We analyzed data from four fish with similar mass (mean \pm S.E.M.=73.9 \pm 7.2 g) and standard length (average=14.9 \pm 0.8 cm). Experiments complied with all guidelines for the use and care of animals in research at the University of California, Irvine, USA, where all experiments were conducted.

Experimental protocol

All tests were performed at water temperatures of 18–20°C. The test arena was a 114 liter tank divided into three sections, which facilitated obtaining start–stop episodes with a standardized predator–prey distance (Fig. 2). We used a suture line with a small weight to suspend the prey item (earthworm, *Lumbricus*) 10 cm past the second divider, 40 cm from the trap door holding the fish in the starting compartment and centered in the opening of the second partition (Fig. 2). The openings in the two opaque partitions were 14 cm \times 14 cm. The investigator hid behind an opaque partition and raised the trap door *via* a string to prevent the fish from having extraneous visual stimuli.

We videotaped the fish with two synchronized high-speed cameras (NAC HSV-400) operating at 200 images s⁻¹ to obtain ventral views of the fish *via* a mirror (Fig. 2). The overlapping camera views (Fig. 2) enabled us to digitize a common stationary reference point that was used to standardize the *x*-coordinates to a common axis, which was parallel to the length of the tank and the overall direction of fish movement. A 2 cm \times 2 cm grid on the bottom of the filming tank provided a distance scale. Two floodlights spaced evenly above the test arena provided silhouettes suitable for digitizing.

We tested each individual both with unaltered pectoral fins and when the fins had been trimmed to reduce their area.

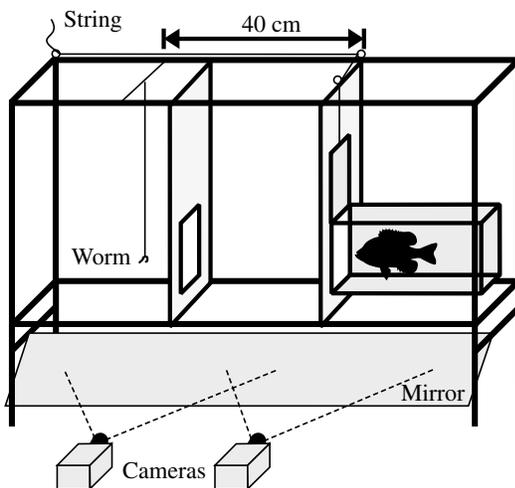


Fig. 2. Schematic diagram of our test arena and equipment. A mirror below the tank provided ventral views of the fish for two cameras. The right portion of the tank is the starting chamber, and the stopping chamber at the left contains a worm attached to a weighted line. Note the two openings in the vertical partitions, which required the sunfish to travel in a straight line to reach the worm and execute the braking action.

Following the trials with intact fins, we anesthetized the fish using MS-222 and cut the fin nearly parallel to the distal edge all the way from the most ventral to the most dorsal fin ray. The average ($N=4$ individuals; $N=8$ fins) area of an intact pectoral fin (5.01 \pm 0.3 cm²) was reduced to approximately 35% (1.76 \pm 0.1 cm²) of its original size. After 1 night of recovery, we tested the individuals with partially ablated fins.

The fish were not fed for 1 week prior to the day of testing, and the time between the tests conducted on a single individual with intact and partially ablated fins was 1 week. The time between successive trials of a single individual within a single day was 10 min. With only one exception (one individual tested twice, 1 week apart, after partial ablation), fewer than 10 trials per individual per treatment within a single day were sufficient to obtain 4 or 5 sequences conforming to the criteria below as suitable for detailed kinematic analysis. Preliminary analyses did not reveal any significant correlations between any measures of velocity or acceleration with trial number of an individual within a day. Furthermore, the within-day trial numbers for the subset of 4 or 5 trials used for detailed analysis differed among different individuals. Consequently, our analyses of variance did not include a factor encoding trial number since we were using multiple trials within an individual and day primarily to increase our statistical power for detecting the effects of partial fin ablation, and we had no evidence of any systematic variation in motivation associated with trial number within a day.

Kinematic measurements

For our frame-by-frame analysis of our videotape, we chose only those trials where the trajectory of the fish was straight, parallel to the long axis of the tank, beginning from a standstill (velocity=0), lacking pauses (velocity=0), and coming to a complete stop at the end. For each combination of individual and fin reduction we analyzed between 4 and 5 trials (total of 37 trials) that met these criteria.

From play-back of the videotapes we determined the durations (\pm 10 ms) of four broad categories of locomotion to provide an overview of the behaviors used by the fish. Propulsion only (P) indicated that all of the movements of axial structures and the pectoral fins appeared to be contributing to forward thrust. Glide (G) indicated forward movement of the fish without any movement or postures that would appear to contribute either to thrust or to actively decelerating the fish. Braking only (B) indicated that any movements or postures of the axial structures or pectoral fins were being used only to decelerate the fish. Propulsion plus braking (PB) indicated that some movements were contributing to forward thrust, while others were simultaneously retarding forward progression. For example, during PB the pectoral fins were often held bilaterally slightly away from the body (creating drag) while the axial structures, body and caudal fins simultaneously undulated in a manner (posteriorly propagated wave) so as to contribute to the forward speed of the fish. We converted all event durations to percentages of the total time from start to stop to facilitate pooling data from different sequences.

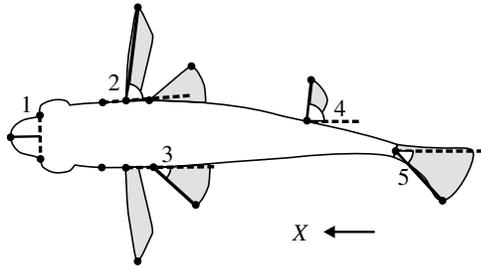


Fig. 3. Landmarks digitized in each mirror ventral view of fish. Kinematic variables calculated included jaw protrusion (1), angles of the pectoral (2) and pelvic fins (3) relative to the body, and angles of the median (4) and caudal fins (5) relative to the overall trajectory of the fish (x axis). Although only illustrated for one side, the angles of the paired fins were determined for both sides of the fish.

We digitized the two-dimensional coordinates of up to 17 anatomical locations, including the left and right paired fins (depending on visibility) in ventral view (Fig. 3). To provide a minimum of 65 time intervals for each of the attack sequences of variable duration, we digitized points at 10 or 20 ms intervals from when the fish initiated movement until the fish came to a complete stop and consumed the food item.

For each frame, we calculated the forward displacement of the fish using the average of the x coordinates of the anterior edges of the left and right eyes (Fig. 3). We then used the Quicksand algorithm of Walker (1998) to smooth the x -displacement data with a quintic spline and used the first and second derivatives to determine velocities and accelerations, respectively.

Three variables described attributes of entire movement bouts, including total duration and total forward displacement. We also divided the total displacement per movement by total duration of movement to calculate average forward velocity (V_{avg}).

From the ventral view coordinates we calculated four fin angles during the final portion of each feeding event, when at least some portion of the pectoral fins was visible (Fig. 3). The pectoral and pelvic fin angles were each a two-dimensional angle calculated between lines from the anterior margin of the base of the fin to the distal tip of the fin and a point on the body anterior to the fin (Fig. 3). We also determined the angles between the x -axis and lines from the base to the most lateral point of the median fins and to the most lateral point of the trailing edge of the caudal fin (Fig. 3). The median fins (dorsal and anal fin) of sunfish are located above each other, and hence often overlapped in ventral view, and are often moved synchronously to the same side of the fish during braking (Breder, 1926; Drucker and Lauder, 2002). Thus we refer to 'median fin' as the greatest excursion of either of these two fins. To facilitate pooling values indicating bending to either the left or the right in different trials, we used the absolute value of the median and caudal fin angles in the statistical analysis.

We calculated the distance between the anterior tip of the lower jaw and a reference line connecting the anterior margins

of the eyes (Fig. 3). Maximum jaw protrusion (MJP) occurred when this distance was maximal. MJP of bluegill sunfish corresponds closely with the time of prey capture (Day et al., 2005; Higham et al., 2005).

We calculated six variables describing the timing of kinematic events as percentages of the total duration of movement (Table 1). The time of the initial V_{max} was defined as the time of the earliest local maximum velocity. The time of V_{max} was the time at which the greatest speed was observed for the entire movement (global maximum). All of the remaining values of maximal magnitudes (MJP, and angles of pectoral, pelvic, median and caudal fins) were determined over the time interval from when the tips of the pectoral fins first became clearly visible after V_{max} during the final rapid deceleration until the fish came to a complete stop.

Statistical analyses

We used SYSTAT version 10 for all statistical analyses, and $P < 0.05$ was the criterion for statistical significance. To determine the effects of reducing the area of the pectoral fins, we performed two-way analyses of variance (ANOVAs) with fin area (fixed and crossed factor with 2 levels) and individual (random and crossed factor with 4 levels) as the independent categorical variables and values of kinematic variables as the dependent variables. In order to properly account for our replication of observations within individuals, the denominator in the F -test for the main effect of the fin area reduction effect was the two-way interaction term between fin area and individual (Zar, 1996).

Results are presented as means \pm S.E.M., unless stated otherwise.

Results

General description of starting and stopping

For the total of 37 trials and the four behaviors of propulsion only (P, $N=40$), propulsion plus braking (PB, $N=19$), gliding (G, $N=7$) and braking only (B, $N=38$), the transitions of P followed by PB ($N=19$) and PB followed by B ($N=19$) occurred most often, and P followed by B ($N=14$) was also very common. Gliding never occurred after either PB or B. All but 3 of the total of 37 sequences had just one occurrence of P, and the grand mean of these initial episodes of P was $61.1 \pm 1.5\%$ of the total sequence duration. When present, G always followed the initial P episode. The grand means of G duration without and with values of 0 (indicating absent) were $13.0 \pm 2.5\%$ and $2.4 \pm 0.9\%$, respectively. Approximately one-half of the sequences had PB, and when PB was present it always followed P and preceded B. The grand means of PB duration without and with values of 0 were $11.4 \pm 2.5\%$ and $5.7 \pm 1.2\%$, respectively. With only one exception B occurred just once per sequence and was the last behavior in each sequence, with a grand mean for the duration of the terminal episode of $29.4 \pm 1.8\%$. Most commonly B followed PB or P. The variation in the behaviors used by different individuals was substantial as indicated by the complete absence of G in

Table 1. Variables calculated for all individuals with intact or reduced pectoral fin area

Variable	Intact fin	Reduced fin	F value (d.f.=1,3)	P value
Distance traveled (cm)	40.3±1.4	40.5±0.9	0	0.98
Duration of trial (s)	0.91±0.05	0.93±0.08	0.1	0.93
Duration of initial P (%)	61.8±1.5	60.4±2.6	0.9	0.41
Duration of final B (%)	29.1±2.5	29.3±2.7	0	0.85
V_{avg} (cm s ⁻¹)	45.1±2.0	46.1±2.3	0.2	0.72
V_{max} (cm s ⁻¹)	70.9±3.5	73.7±3.2	0.2	0.66
Initial V_{max} (cm s ⁻¹)	46.3±3.9	51.8±4.9	1.0	0.39
Accel _{max} (cm s ⁻²)	721±77	625±72	0.6	0.51
Decel _{max} (cm s ⁻²)	-479±44	-546±82	0.7	0.46
Decel _{MJP} (cm s ⁻²)	-295±48	-310±53	0.2	0.72
V_{MJP} (cm s ⁻¹)	21.9±1.7	23.0±1.8	0.6	0.51
Time of initial V_{max} (%)	17.2±1.6	23.4±3.6	1.6	0.29
Time of V_{max} (%)	44.6±2.7	47.3±3.6	0.1	0.73
Time of MJP (%)	93.5±1.0	95.3±0.6	4.2	0.13
Time of min pect. angle (%)	98.1±1.0	99.7±0.1	1.5	0.31
Time of min pelv. angle (%)	92.6±1.6	93.3±1.1	0.2	0.66
Time of max med. angle (%)	92.9±2.0	93.1±1.8	0	0.99

Values are means ± S.E.M.; $N=19$ for intact and $N=18$ for reduced pectoral fin area. The F values from two-way ANOVAs, which were performed separately on each variable.

P, propulsion only; B, braking only; V_{max} , maximum velocity; V_{avg} , average velocity; V_{MJP} , velocity at max jaw protrusion; MJP, maximum jaw protrusion; Accel_{max}, maximum acceleration; Decel_{max}, maximum deceleration; Decel_{MJP}, deceleration at maximum jaw protrusion; pect., pectoral fin; pelv., pelvic fin; med., median fin.

all sequences from one individual and the complete absence of PB in another individual.

Rather than accelerating continuously up to a maximal forward speed, every sequence had an early local maximum in forward velocity that preceded the global maximum velocity by approximately 0.2 s (Fig. 4B,F). The maximum accelerations uniformly occurred prior to the first local maximum of forward velocity. Fish always used caudal fin undulation during the initial episode of propulsion, but use of the pectoral fins over the same time interval was variable. In less than one-third (9 of 37) of the sequences, the pectoral fins remained against the body until after V_{max} was attained. More commonly (28 of 37) the fish simultaneously used caudal undulations with propulsive movements of the pectoral fins, which could be either bilateral or alternating and unilateral (Fig. 5). Approximately one-third (13 of 37) of the trials had more than one local maximum in forward velocity before V_{max} was obtained. Thus, modulation of speed from the start until V_{max} resulted mainly from modulating propulsive forces rather than employing braking behaviors.

The initial decline in velocity immediately after V_{max} was usually slight (Fig. 4B, 0.36–0.43 s; Fig. 4F, 0.24–0.31 s) and a result of less vigorous propulsive movements (30 of 37) or a cessation of propulsive movements (7 of 37). Often (19 of 37 trials), after minimal changes in forward velocity, a prolonged moderate deceleration occurred (Fig. 4B, 0.48–0.74 s; Fig. 4F, 0.36–0.64 s), during which the pectoral fins were slightly protracted with little conspicuous change in angle (Fig. 5A,

middle). The median fins were often not visible during moderate deceleration (Fig. 5A, 600 ms). A rapid decline in forward velocity usually occurred for the final 100–120 ms during which rapid changes in position were evident for paired and unpaired fins (Figs 4, 5). The caudal and median fins consistently angled towards opposite sides of the body, which was flexed laterally to create an S-shape, and at the same time, the pectoral fins were protracted bilaterally (Figs 4, 5). Hence, frontal area increased rapidly during the final rapid decline in velocity. Maximal deceleration usually occurred substantially (80–100 ms) before stopping and was usually coincident with maximum jaw protrusion and maximum displacement of the median fin (Fig. 4). The time of maximal pectoral fin protraction consistently occurred after the time of maximal jaw protrusion (Figs 4, 5; Table 1).

When fish performed gliding after V_{max} , the duration of the glide was usually so short that the decrease in forward velocity was modest (Fig. 6A). When the pectoral fins remained slightly protracted as the axial structures continued to undulate (PB) after V_{max} , the decreases in forward velocity were also usually small (Fig. 6B).

Effects of reducing pectoral fin area

None of the attributes of entire movement bouts differed significantly for the trials with intact pectoral fins compared to those with reduced fin areas (Table 1). The entire distance traveled during the attack was similar and the grand mean of all observations was 40.4±0.8 cm. Similarly, the total duration of movement and average velocity for each entire bout of

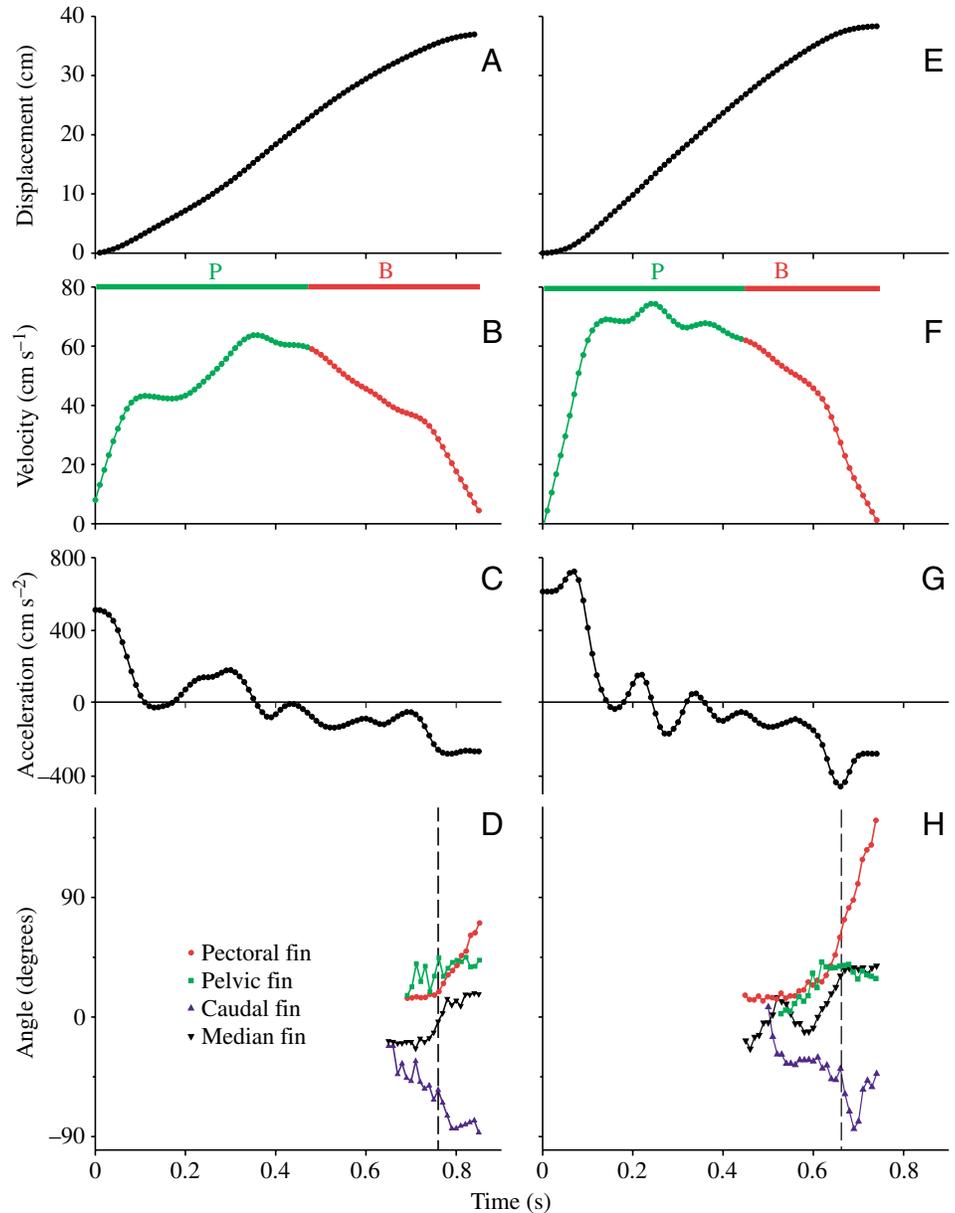


Fig. 4. Representative kinematics for sequences before (A–D) and after (E–H) pectoral fin reduction from the same individual, including displacement (A,E), forward velocity (B,F), acceleration (C,G) and angles of the median and paired fins during the final rapid deceleration (D,H). The broken vertical line indicates the time of maximal jaw protrusion, which is nearly coincident with prey capture. P (green) and B (red) indicate the behaviors of propulsion only and braking only, respectively.

locomotion were statistically indistinguishable (grand means = 0.92 ± 0.04 s and 45.9 ± 2.2 cm s⁻¹, respectively). The relative durations of the initial episode of P and the final episode of B were also not affected significantly by the reduction in pectoral fin area (Table 1).

Contrary to our expectation, reduction of pectoral fin area did not significantly affect any of the major descriptors of modulating velocity including maximum forward velocity (V_{\max}), maximum acceleration, and maximum deceleration (Table 1). Furthermore, none of the times of landmark kinematic events, such as maximum fin angles or maximum velocities, were affected significantly by reduction of pectoral fin area (Table 1). V_{\max} occurred slightly before the halfway point (grand mean = $45.9 \pm 2.2\%$) of the total movement duration, and the average velocity profiles for both intact fins and trimmed fins were nearly symmetric about the midpoint (Fig. 7).

For all of the angular variables describing fin positions, the only statistically significant effects of reducing pectoral fin area were for pectoral fin angles at the global maximum (most protracted), maximum jaw protrusion and stopping, all of which had a more protracted position for the reduced fin treatment (Table 2). At the time of stopping the average position of the tip of the intact pectoral fin was approximately 20° less than the perpendicular position (Table 2), and hence the tip of the intact fin was usually posterior to its base. The tip of the reduced pectoral fin was approximately 20° beyond the perpendicular position (Table 2), and hence the tip of the reduced fin was usually anterior to its base at the time of stopping (Fig. 5). The lack of a position perpendicular to the body indicates that the pectoral fins are not simply maintaining a posture during stopping that would maximize the frontal area (area of the fin projected onto a plane perpendicular to the

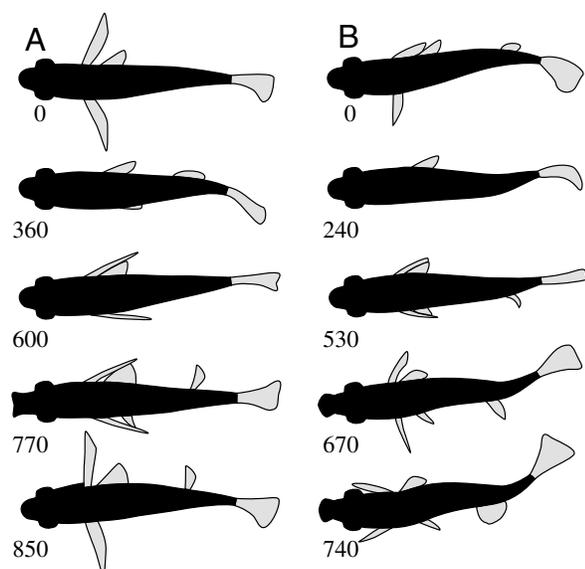


Fig. 5. Outline figures drawn directly from bitmaps of the mirror ventral view videotapes of representative start–stop episodes before (A) and after (B) pectoral fin reduction of the same individual. Elapsed times (ms) from the initiation of movement are indicated at the lower left of each figure. From top to bottom, the images within each sequence represent the following events: start, maximum velocity, moderate deceleration, maximum jaw protrusion (during rapid deceleration), and stop.

Table 2. *Fin angles for all individuals with intact and reduced pectoral fins at different times during the trial*

Variable	Intact fin	Reduced fin	<i>F</i> value	
			(d.f.=1,3)	<i>P</i> value
Pectoral angle _{max}	70±3.2	112±5.0	27.6	0.01
Pelvic angle _{max}	52±6.5	44±1.5	1.8	0.27
Median angle _{max}	74±3.2	83±1.1	3.3	0.17
Pectoral angle _{MJP}	38±2.0	69±5.2	12.9	0.04
Caudal angle _{MJP}	18±2.6	28±2.9	3.6	0.15
Median angle _{MJP}	55±4.7	63±3.0	1.3	0.34
Pectoral angle _{stop}	68±3.7	111±5.1	22.6	0.02
Caudal angle _{stop}	25±3.9	39±3.9	5.6	0.10
Pelvic angle _{stop}	38±3.4	31±3.1	0.8	0.43
Median angle _{stop}	65±3.8	70±4.1	0.5	0.52
Pectoral fin prot. (degrees s ⁻¹)	490±56	957±82	6.3	0.09

Values are means ± S.E.M.; *N*=19 for intact and *N*=18 for reduced pectoral fins. The *F* values are from the two-way ANOVAs performed separately on each variable.

MJP, maximum jaw protrusion; pectoral fin prot., pectoral fin protraction velocity for 50 ms prior to stopping.

Unless stated otherwise, all values are in degrees.

overall direction of travel) and presumed drag. However, the reduced pectoral fins usually did briefly pass through a position perpendicular to the body. A large amount (>30°) of pectoral fin protraction occurred over the very short time interval

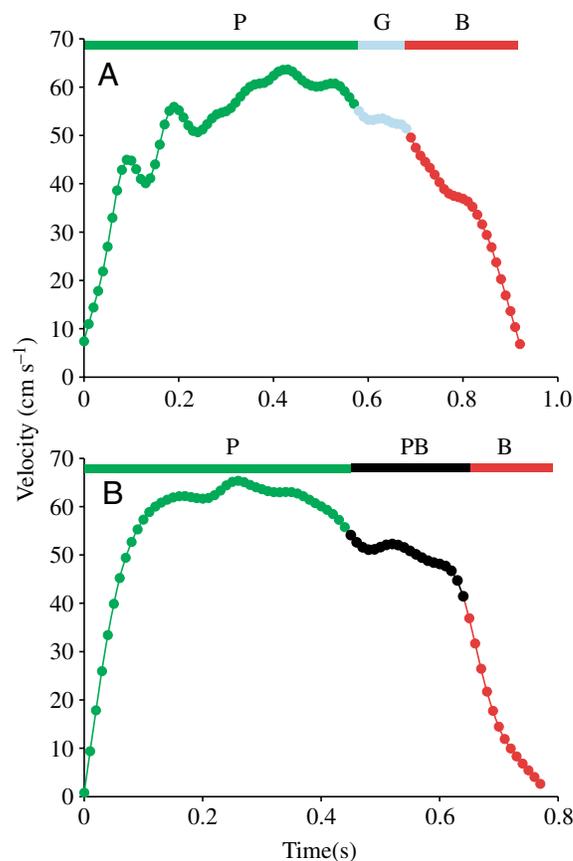


Fig. 6. Variation in modulation of velocity and locomotor behaviours, including (A) a sequence with a glide (G) and (B) one with propulsion plus braking (PB). Note that V_{max} is attained substantially before the cessation of propulsion.

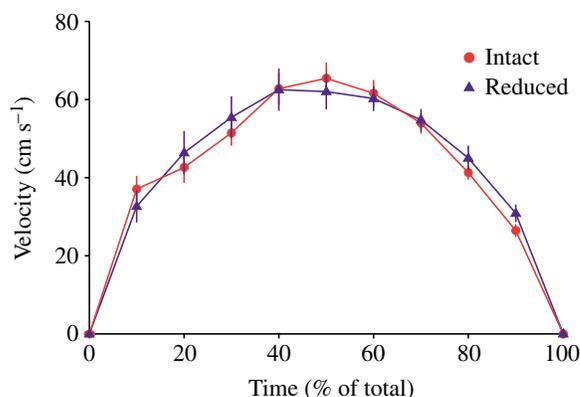


Fig. 7. Forward velocity vs time (percentage of total) for both intact (*N*=19, red circles) and reduced (*N*=18, blue triangles) pectoral fin treatments. Values are mean ± S.E.M.

between maximum jaw protrusion and stopping (Table 2). Thus, the average speeds of pectoral fin protraction over the final 50 ms of movement were very high and values of the reduced fin treatment were nearly twice those of the intact fin treatment (Fig. 8; Table 2).

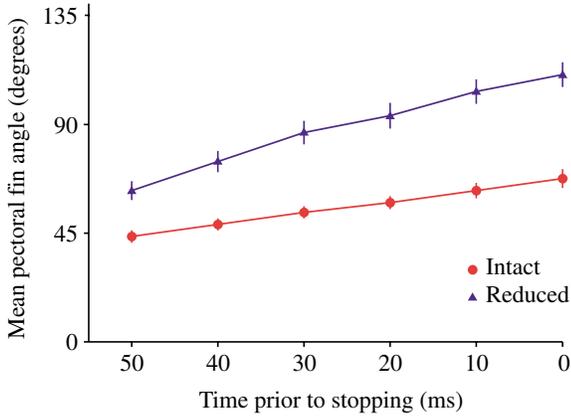


Fig. 8. Pectoral fin angles for the final 50 ms of each trial before ($N=19$, circles) and after ($N=18$, triangles) pectoral fin reduction. Values are mean \pm S.E.M.

Discussion

In this study we quantified both the acceleration and deceleration involved in a continuous movement of a given distance beginning from a standstill and continuing until a complete stop. We observed diverse mechanisms for modulating speed in bluegill sunfish including varying propulsive effort, gliding (absence of both propulsive and braking movements and postures), braking in the absence of propulsive movements, and simultaneous use of propulsive movements and braking postures. This last mechanism was unexpected, previously unreported for fish and akin to the driver of a motor vehicle 'riding the brakes' while stepping on the accelerator. An unexpected and particularly interesting result was how our fish with decreased pectoral fin area used similar maximal attack speeds to intact fish and were able to attain similar braking performance by modifying braking behavior. Two broad categories of braking behavior used by the fish in our experiments were static postures and movements of fins that could generate reverse thrust.

Stopping vs starting

Unlike starting, where fluid drag is an impediment, fluid resistance facilitates stopping. Indeed, the forces retarding forward progression were sufficiently large that we commonly observed decreases in forward velocity both before and after the global maximum in velocity within a sequence as fish continually undulated their caudal fins with variable intensity. Before V_{\max} , decreases in speed resulted only from variable propulsive effort, but after V_{\max} all mechanisms for decreasing speed occurred. For fish with intact and reduced fin areas, a sizable period after V_{\max} [15% = average cessation of initial P (61%) – average time of V_{\max} (46%)] often involved only decreased propulsive effort. Thereafter, some fish glided or combined propulsion with braking before performing only braking behaviors, and these differences in behavior contributed to considerable variation in accelerations. However, the greatest magnitude acceleration and deceleration

were consistently near the beginning and end of the start–stop episode, respectively.

Disparities in starting and stopping capacities are interesting because of the manner in which they can theoretically constrain the tactics available for modulating speed within a confined space (Fig. 1). The paucity of data on both starting and stopping accelerations leaves open the question of whether or not these capacities are usually matched within individual fish. However, several indirect lines of evidence suggest that many fish have a greater capacity to start than to stop.

The amount of axial vs appendicular musculature and the manner in which axial structures are used suggest more power can be generated during starting than in stopping. The mass of axial muscles of most fish species, which commonly exceeds 40% body mass (Bone, 1978), is huge compared to that of the pectoral fins, which may be less than 1% body mass (Geerlink, 1983). During the rapid starting accelerations of escapes, large amounts of lateral axial bending occur along nearly the entire length of the fish, as all the red and white musculature is activated along one side and then along the contralateral side (Jayne and Lauder, 1993). We never observed a substantial amount of lateral bending in the anterior region of bluegill sunfish braking in this study (Fig. 5), nor during our previous studies of escape locomotion in this species. Figures of other species of fish stopping also show little axial bending anteriorly (Geerlink, 1987). Thus, many fish probably have a greater muscle mass that is useful to recruit during starting compared to stopping.

The limited empirical data for accelerations during starting are much greater than those for stopping. For diverse species of fishes, maximal starting accelerations during escape responses determined from kinematic analysis range from 40–50 m s^{-2} (reviewed in Blake, 2004), whereas the scanty data available for stopping accelerations are all less than 9 m s^{-2} (Table 3). The values of maximum acceleration that we observed for sunfish are low compared to values in the literature for escape responses of similar size fish, and by definition all but one of our multiple observations per individual per experimental treatment were submaximal. Furthermore, the variability in both stopping and starting accelerations that we observed among trials within an individual and experimental treatment was high. Thus, most of the rapid initial accelerations and final decelerations in our study appear much less than physiological maximums, which could be attained either in different experimental conditions or in our particular experimental conditions.

Although many accelerations that we observed are probably less than those sunfish can attain physiologically, maximal accelerations and decelerations within a sequence had some trends that paralleled expectations for a greater ability to accelerate than decelerate. For example, our data had a mean value of maximal acceleration nearly 50% greater than that of maximal deceleration within a sequence (Table 1). Maximal acceleration exceeded maximal deceleration in most sequences (17 of 19 intact trials; 10 of 18 reduced area trials) (Fig. 9). Furthermore, with increased maximal acceleration the

Table 3. Values of braking performance from the literature

Species	Fish length (cm)	Fish mass (g)	Speed before braking (cm s ⁻¹)	Maximum braking (cm s ⁻²)	Study
<i>Scomber scombrus</i> (mackerel)	34	335	110	-370	Geerlink, 1987
<i>Gadus virens</i> (saithe)	35	571	190	-870	Geerlink, 1987
<i>Gadus morhua</i> (cod)	26	182	55	-170	Geerlink, 1987
<i>Gadus morhua</i> (cod)	46	676	126	-230	Videler, 1981
<i>Carassius auratus</i> (goldfish)	6.6	3.05	46.7	-356	Webb and Fairchild, 2001
<i>Metynnus hypsanchen</i> (silver dollar)	6.1	4.65	51.3	-354	Webb and Fairchild, 2001
<i>Pterophyllum scalare</i> (angelfish)	5.9	2.98	16.1	-13.0	Webb and Fairchild, 2001
<i>Lepomis macrochirus</i> (bluegill)	14.9	73.9	72.3	-479	This study

probability of a lesser corresponding maximal deceleration increased (Fig. 9). An unresolved but interesting issue is whether speeds closer to a physiological maximum would exaggerate apparent differences in acceleration and braking capacities. However, the sunfish studied here still showed relatively high braking decelerations relative to literature values (Table 3). Diverse stimuli reliably elicit escape responses, which involve a specialized neural circuit and a high degree of stereotypy (Eaton et al., 2001), but predictably eliciting a volitional stop poses a significant technical challenge. If one could establish the maximal accelerating and stopping capacities, then one could determine whether the acceleration and deceleration within a single start–stop episode were similar proportions of different maximal capacities.

Behavioral compensation for reduced fin area

To compensate for the detrimental effects of reduced pectoral fin area, behaviors that could preserve the ability to stop at a particular location include the following: (1) decrease the acceleration or maximal speed prior to braking (Fig. 1), (2)

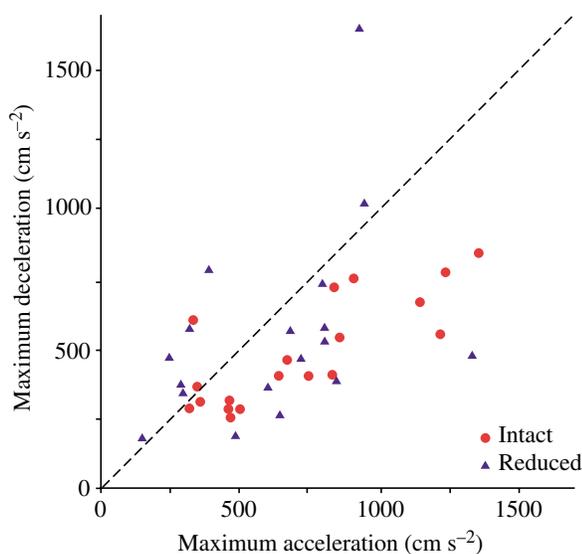


Fig. 9. The magnitudes of maximum acceleration vs maximum deceleration within each of 37 trials of fish with intact ($N=19$, red circles) or partially ablated ($N=18$, blue triangles) pectoral fins. The broken reference line indicates a 1:1 ratio of these two quantities.

increase the duration of braking behavior (Fig. 1), (3) increase the displacement of surfaces during braking postures, (4) increase the movement speed of the braking surfaces, and (5) increase the reliance on intact braking surfaces. The fish in our study did not use either of the first two types of compensation. Values of V_{max} in our study occurred at nearly 50% of the total start–stop duration and were not affected significantly by a reduction in fin area. Furthermore, neither the duration of the final rapid deceleration nor any of the trends in the durations in the different locomotor behaviors suggested that the duration of behaviors was altered significantly as a means of compensation. To varying extents the fish in our study did use the remaining types of compensation for reduced pectoral fin area.

The most conspicuous mechanisms for compensating for the reduced pectoral fin area in our study were greater displacement and faster protraction speeds of the pectoral fins (Table 2). Previous work on the stopping of fishes has focused on how a pectoral fin angle of 90° relative to the body is likely to maximize drag and hence set an upper limit to braking performance. When the sunfish in our study had intact fins, they rarely attained angles of 90°. Similarly, other fish often do not attain pectoral fins angles of 90° during braking, and Geerlink (1987) suggested that this may be a result of having pectoral fin abductor muscles that are too small to generate sufficient force to hold a 90° angle for the pectoral fins over a wide range of swimming speeds. Since the force of the fluid acting on the fin is proportional to its area, one reason for the greater pectoral fin angles we observed in fish with reduced fin area might be that force production of the abductor muscles is no longer a limiting factor to fin displacement.

Even if the fin abductors were sufficiently strong to position the base of the fin perpendicular to the body, the mechanical stiffness of pectoral fin rays may not be sufficient to maintain a perpendicular position along the entire length of the fin. Long-axis curvature of the pectoral fins was conspicuous during braking for the fish in our study with intact fins, whereas little long-axis bending was apparent for the shortened pectoral fins. Three factors suggest that much of the decrease in bending of the shortened pectoral fins results primarily from the properties of the fin rays rather than differences in the external loads. First, for two cylinders with identical diameter made of the same material, less force is required to bend the longer rod

a given amount (Wainwright et al., 1976). Second, the diameter of the rays decreases from proximal to distal. Finally, the elastic modulus of the fin rays decreases from proximal to distal (G. V. Lauder, unpublished data; also see Lauder, 2005).

Although the partially ablated pectoral fins of our sunfish transiently had angles of 90°, their ultimate position was well beyond this angle and resulted in a sub-maximal frontal area. The substantial amount of forward movement of the pectoral fins of both the intact and reduced area treatments in the final stages of braking also suggests that the generation of reverse thrust contributes to braking forces in addition to static postures, which increase frontal area and drag. The behavior of increasing protraction speed of partially ablated fins is consistent with the expectation for a compensatory mechanism to maintain braking performance because thrust decreases with decreased surface area and increases with increased fluid speed.

In addition to drag, a swimming animal will experience the acceleration reaction, which resists changes in velocity and thus inhibits deceleration (Daniel, 1984). The acceleration reaction is dependent on the shape, size and acceleration of a body, and thus abducted pectoral fins will increase drag but also increase the acceleration reaction. By protracting their fins to a greater extent, and thus achieving a sub-maximal frontal area, the sunfish with reduced pectoral fins will actually reduce the acceleration reaction and thereby increase braking performance.

Additional compensation for reduced pectoral fin area was the trend for fish in our study to have greater excursions of the median and caudal fins even though these were not statistically significant. A key feature of locomotor functional design in fishes is the extent to which different structures have redundant function or can function in a decoupled fashion from each other (Blake, 2004; Lauder and Drucker, 2004; Webb, 2004). The redundancy for braking of median and paired fins was clearly one factor that can ameliorate the anticipated negative effects of reduced pectoral fin area on braking performance. Furthermore, sunfish displayed a remarkable capacity to decouple function of the paired fins and axial structures as they simultaneously held the pectoral fins in a static braking posture while the axial structures continued to have propulsive movements. However, we did not observe any movement of the median fins that suggested they could be used as braking structures while the caudal fin was generating propulsive forces (as indicated by a posterior propagation of maximum lateral displacement and bending).

Although the combined function of the median structures and paired fins in braking is widely recognized (Breder, 1926; Harris, 1937a; Jayne et al., 1996; Webb and Fairchild, 2001), the relative contributions of each are not well understood. Geerlink (1987) estimated that the pectoral fins and the body of the fish he studied could contribute no more than 30% and 15%, respectively, of the total braking force, but he did not account for either curvature of the median and caudal fins or generation of reverse thrust by the pectoral fins. Drucker and Lauder (2003) found that for a trout braking from a slow

swimming speed ($0.5 \text{ lengths s}^{-1}$), the braking force of the pectoral fins was nearly twice that of the dorsal fin, but the contribution of whole body drag to braking was not determined. The sunfish in our study have larger pectoral fins than those of both trout and the species studied by Geerlink (1987). Consequently, the relative contributions of different structures to braking at similar speed probably vary widely among species. Furthermore, the role of different structures during braking for a single species probably varies with swimming speed. For example, we (B. C. Jayne and G. V. Lauder, unpublished) have observed braking of sunfish after eliciting a rapid escape response (Jayne and Lauder, 1993), and high forward velocity of the fish appeared to bend the tips of the pectoral fins near the body, which had an extreme displacement of the caudal fin that probably indicated its increased importance for braking. Consequently, if the axial structures are better than the pectoral fins at resisting passive bending that occurs as a result of the resistive forces of the water, then the axial structures may assume greater importance for braking as speed increases.

Ecological relevance of stopping

Feeding and avoidance of collisions are two ecological contexts for which we consider the benefits of an enhanced ability to stop. A related issue is whether or not the ecological context in which a behavior is performed affects the extent to which a maximal capacity is used ('ecological performance' of Irschick and Garland, 2001).

Braking potentially has two key benefits for aquatic suction feeding. First, generating suction can pull the predator forward and increase the chances of colliding with the substrate (Muller et al., 1982), unless the predator actively brakes to avoid this. Second, swimming fast during feeding could decrease the fluid speeds generated by suction due to the hydrodynamic interactions between swimming (ram) and mouth expansion (Higham et al., 2005). Braking immediately before prey capture could alleviate this negative interaction and thus preserve suction performance. The extent to which fish stop completely when feeding varies considerably among different species as they use varying combinations of swimming towards prey (ram) and suction to move the prey towards the fish (Norton and Brainerd, 1993; Wainwright et al., 2001; Higham et al., 2005). Experimentally exploiting these rich sources of behavioral and morphological variation among fishes in integrated studies of feeding and locomotion holds great promise for gaining further insights into how animals modulate speed.

Braking seems likely to be important for preventing collisions for a wide variety of predators besides fish that attack prey close by or attached to solid objects. Avoiding collisions could have consequences for both the attack trajectories of predators and the anti-predator tactics of prey. For example, prey might obtain some protection from predators simply by being very close to a solid object rather than hiding behind it. Predators could compensate for this prey tactic or for their poor braking ability by using an attack trajectory oblique rather than

normal to the surface behind the prey in order to increase the distance between the prey and the background along the attack trajectory. A general understanding of the importance of braking behavior could be enhanced by future comparisons of limbed and limbless animals. Limbless animals such as fish risk cranial injury if they collide with an object while traveling forward. Limbed animals theoretically could use their forelimbs to absorb the shock collision for some range of forward speeds, but the extent to which this strategy is used or facilitates prey capture is unknown.

An increasing number of studies of locomotor performance are finding that animals often move with less than their maximal capacity, even when evading a predator or capturing prey (Jayne and Ellis, 1998; reviewed in Irschick and Garland, 2001; Bolnick and Ferry-Graham, 2002). The maximal speeds that we observed during the 40 cm predatory attacks of sunfish were substantially lower than the speeds attained by species under different conditions (Jayne and Lauder, 1993), but starting and stopping ability seem unlikely to be limiting V_{\max} . Some of the following alternatives regarding energetic and environmental influences may help to explain why the values we observed for attack speeds and accelerations are so low.

Modeling by Bolnick and Ferry-Graham (2002) suggests that energetic considerations may cause the effort expended by a predator to capture prey to vary with the potential benefit of the prey rather than being an all or none maximal effort. The prey items we used were not elusive, and the elusiveness of prey affects the attack speeds of some fish (Nemeth, 1997). If attack speed is not significantly correlated with predatory success, then swimming quickly would have no benefit, but it would incur an extra energetic cost because of how drag forces increase with swimming speed. Perhaps processing and integrating sensory information regarding prey location constrains speed and acceleration to a greater extent than locomotor capacity. Moving submaximally during a predatory attack might also facilitate changing the attack trajectory in response to prey movements and thus maintain strike accuracy (Higham et al., 2005). If predatory attack behaviors evolved in cluttered habitats with such short unobstructed distances that physiologically maximum capacities could not be used, then animals may not have sufficient behavioral plasticity to increase their attack speeds when placed in less cluttered surroundings. Further experimental manipulations of prey type, predator-prey distances, and distance from the prey to background object could provide many additional insights into these issues regarding seemingly low attack speeds.

Although the ecological relevance and pervasiveness of intermittent locomotion of animals have been increasingly recognized (Higham et al., 2001; Kramer and McLaughlin, 2001; Weinstein, 2001), most work on intermittent locomotion has concentrated on how the pauses affect recovery, rather than on the functional basis of stopping, which results in a pause. Despite the current lack of comparative data on modulating velocity between a start and stop, systems such as the predatory attacks of suction-feeding fishes and fiddler crabs returning to their home burrows (Layne et al., 2003) may prove to be useful

model systems for future investigation of starts and stops in which experimenters can manipulate distance and have animals come to a stop at a predictable location.

This research was supported by NSF BNS 8919497 (to B.C.J. and G.V.L.) and grants from NSF (IBN 0316675) and ONR to G.V.L. M. Higham provided valuable comments on earlier drafts of the manuscript and S. Day provided valuable discussion. J. Layne provided insightful feedback regarding the model of constraints on starting and stopping over a fixed distance.

References

- Bainbridge, R.** (1963). Caudal fin and body movement in the propulsion of some fish. *J. Exp. Biol.* **40**, 23-56.
- Blake, R. W.** (2004). Fish functional design and swimming performance. *J. Fish Biol.* **65**, 1193-1222.
- Bolnick, D. I. and Ferry-Graham, L. A.** (2002). Optimizing prey-capture behavior to maximize expected net benefit. *Evol. Ecol. Res.* **4**, 843-855.
- Bone, Q.** (1978). Locomotor muscle. In *Fish Physiology*, Vol. 7 (ed W. S. H. Randall and D. J. Randall), pp. 361-424. New York: Academic Press.
- Breder, C. M.** (1926). The locomotion of fishes. *Zoologica* **4**, 159-296.
- Daniel, T. L.** (1984). Unsteady aspects of aquatic locomotion. *Am. Zool.* **24**, 121-134.
- Day, S. W., Higham, T. E., Cheer, A. Y. and Wainwright, P. C.** (2005). Spatial and temporal patterns of water flow generated by suction feeding bluegill sunfish (*Lepomis macrochirus*) resolved by Particle Image Velocimetry. *J. Exp. Biol.* **208**, 2661-2671.
- Drucker, E. G. and Lauder, G. V.** (2002). Wake dynamics and locomotor function in fishes: interpreting evolutionary patterns in pectoral fin design. *Integr. Comp. Biol.* **42**, 997-1008.
- Drucker, E. G. and Lauder, G. V.** (2003). Function of pectoral fins in rainbow trout: behavioral repertoire and hydrodynamic forces. *J. Exp. Biol.* **206**, 813-826.
- Eaton, R. C., Lee, R. K. K. and Foreman, M. B.** (2001). The Mauthner cell and other identified neurons of the brainstem escape network of fish. *Prog. Neurobiol.* **63**, 467-485.
- Geerlink, P. J.** (1983). Pectoral fin kinematics of *Coris formosa* (Teleostei, Labridae). *Neth. J. Zool.* **33**, 515-531.
- Geerlink, P. J.** (1987). The role of the pectoral fins in braking of mackerel, cod and saithe. *Neth. J. Zool.* **37**, 81-104.
- Harris, J. E.** (1937a). The mechanical significance of the position and movements of the paired fins in the Teleostei. *Pap. Tortug. Lab.* **31**, 173-189.
- Harris, J. E.** (1937b). The role of the fins in the equilibrium of the swimming fish II. The role of the pelvic fins. *J. Exp. Biol.* **14**, 32-47.
- Higham, T. E., Davenport, M. S. and Jayne, B. C.** (2001). Maneuvering in an arboreal habitat: the effects of turning angle on the locomotion of three sympatric ecomorphs of *Anolis* lizards. *J. Exp. Biol.* **204**, 4141-4155.
- Higham, T. E., Day, S. W. and Wainwright, P. C.** (2005). Sucking while swimming: evaluating the effects of ram speed on suction generation in bluegill sunfish *Lepomis macrochirus* using digital particle image velocimetry. *J. Exp. Biol.* **208**, 2653-2660.
- Irschick, D. J. and Garland, T., Jr** (2001). Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annu. Rev. Ecol. Syst.* **32**, 367-396.
- Jayne, B. C. and Ellis, R. V.** (1998). How inclines affect the escape behaviour of a dune dwelling lizard, *Uma scoparia*. *Anim. Behav.* **55**, 1115-1130.
- Jayne, B. C. and Lauder, G. V.** (1993). Red and white muscle-activity and kinematics of the escape response of the bluegill sunfish during swimming. *J. Comp. Physiol. A* **173**, 495-508.
- Jayne, B. C., Lozada, A. F. and Lauder, G. V.** (1996). Function of the dorsal fin in bluegill sunfish: Motor patterns during four distinct locomotor behaviors. *J. Morphol.* **228**, 307-326.
- Kramer, D. L. and McLaughlin, R. L.** (2001). The behavioral ecology of intermittent locomotion. *Am. Zool.* **41**, 137-153.
- Lauder, G. V.** (2005). Locomotion. In *The Physiology of Fishes*. 3rd edn (ed. D. H. Evans and J. B. Claiborne), pp. 3-46. Boca Raton: CRC Press (in press).
- Lauder, G. V. and Drucker, E. G.** (2004). Morphology and experimental

- hydrodynamics of fish fin control surfaces. *IEEE J. Ocean. Eng.* **29**, 556-571.
- Layne, J. E., Barnes, W., Jon, P. and Duncan, L. M. J.** (2003). Mechanisms of homing in the fiddler crab *Uca rapax* 2. Information sources and frame of reference for path integration system. *J. Exp. Biol.* **206**, 4425-4442.
- Muller, M., Osse, J. W. M. and Verhagen, J. H. G.** (1982). A quantitative hydrodynamical model of suction feeding in fish. *J. Theor. Biol.* **95**, 49-79.
- Nemeth, D. H.** (1997). Modulation of attack behavior and its effect on feeding performance in a trophic generalist fish, *Hexagrammos decagrammus*. *J. Exp. Biol.* **200**, 2155-2164.
- Norton, S. F. and Brainerd, E. L.** (1993). Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J. Exp. Biol.* **176**, 11-29.
- Reimchen, T. E. and Temple, N. F.** (2004). Hydrodynamic and phylogenetic aspects of the adipose fin in fishes. *Can. J. Zool.* **82**, 910-916.
- Thorsen, D. H. and Westneat, M. W.** (2005). Diversity of pectoral fin structure and function in fishes with labriform propulsion. *J. Morphol.* **263**, 133-150.
- Tytell, E. D.** (2004). Kinematics and hydrodynamics of linear acceleration in eels, *Anguilla rostrata*. *Proc. R. Soc. Lond. B* **271**, 2535-2540.
- Videler, J. J.** (1981). Swimming movements, body structure and propulsion in cod *Gadus morhua*. *Symp. Zool. Soc. Lond.* **48**, 1-27.
- Videler, J. J.** (1993). *Fish Swimming*. London: Chapman and Hall.
- Wainwright, P. C., Ferry-Graham, L. A., Waltzek, T. B., Carrol, A. M., Hulsey, C. D. and Grubich, J. R.** (2001). Evaluating the use of ram and suction during prey capture by cichlid fishes. *J. Exp. Biol.* **204**, 3039-3051.
- Wainwright, P. C., Bellwood, D. R. and Westneat, M. W.** (2002). Ecomorphology of locomotion in labrid fishes. *Environ. Biol. Fish.* **65**, 47-62.
- Wainwright, S. A., Biggs, W. D., Currey, J. D. and Gosline, J. M.** (1976). *Mechanical Design in Organisms*. London: Edward Arnold Limited.
- Walker, J. A.** (1998). Estimating velocities and accelerations of animal locomotion: a simulation experiment comparing numerical differentiation algorithms. *J. Exp. Biol.* **201**, 981-995.
- Webb, P. W.** (1973). Effects of partial caudal-fin amputation on the kinematics and metabolic rate of underyearling sockeye salmon (*Oncorhynchus nerka*) at steady swimming speeds. *J. Exp. Biol.* **59**, 565-581.
- Webb, P. W.** (1977). Effects of median-fin amputation on fast-start performance of rainbow trout (*Salmo gairdneri*). *J. Exp. Biol.* **68**, 123-135.
- Webb, P. W.** (1984). Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.* **24**, 107-120.
- Webb, P. W.** (2004). Maneuverability – general issues. *IEEE J. Ocean. Eng.* **29**, 547-555.
- Webb, P. W. and Fairchild, A. G.** (2001). Performance and maneuverability of three species of teleostean fishes. *Can. J. Zool.* **79**, 1866-1877.
- Webb, P. W. and Gerstner, C. L.** (2000). Fish swimming behaviour: predictions from physical principles. In *Biomechanics in Animal Behaviour* (ed. P. Domenici and R. W. Blake), pp. 59-77. Oxford: BIOS Scientific.
- Webb, P. W. and Weihs, D.** (1983). *Fish Biomechanics*. New York: Praeger.
- Weinstein, R. B.** (2001). Terrestrial intermittent exercise: common issues for human athletics and comparative animal locomotion. *Am. Zool.* **41**, 219-228.
- Westneat, M. W.** (1996). Functional morphology of aquatic flight in fishes: kinematics, electromyography, and mechanical modeling of labriform locomotion. *Am. Zool.* **36**, 582-598.
- Zar, J. H.** (1996). *Biostatistical Analysis*. Upper Saddle River (NJ): Prentice Hall.