

## LOCOMOTOR MECHANICS DURING EARLY LIFE HISTORY: EFFECTS OF SIZE AND ONTOGENY ON FAST-START PERFORMANCE OF SALMONID FISHES

MELINA E. HALE\*

Department of Organismal Biology and Anatomy, University of Chicago, 1027 East 57th Street, Chicago, IL 60637, USA and Field Museum of Natural History, Roosevelt Road at Lakeshore Drive, Chicago, IL 60605, USA

\*Address for correspondence: Department of Neurobiology and Behavior, Life Sciences Building, State University of New York at Stony Brook, Stony Brook, NY 11794-5230, USA (e-mail: mhale@neurobio.sunysb.edu)

Accepted 8 March; published on WWW 6 May 1999

### Summary

Fast-start locomotor behavior is important for escaping from predators and for capturing prey. To examine the effects of size and other aspects of developmental morphology on fast-start performance, the kinematics of the fast-start escape behavior were studied through early post-hatching development in three salmonid species: chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*) and brown trout (*Salmo trutta*). These three species, while morphologically and developmentally similar, hatch and mature at different sizes (total length). Comparison of these species shows that some fast-start performance variables, including stage duration, maximum velocity and maximum acceleration, are highly dependent on ontogenetic state, while another, the overall distance traveled during stage 2, scales with total body length. Brown trout were studied from hatching

into the juvenile development period. Aspects of fast-start performance peak at the end of yolk-sac absorption (the end of the eleutheroembryo phase) when the fish reaches the juvenile period. At this time, the durations of the fast-start stages are at their minima, and maximum velocity and maximum acceleration are at their highest levels relative to body length. Thus, escape behavior reaches its maximum size-specific performance at a relatively small size, just as the fish absorbs its yolk sac and begins to search for food. This peak in fast-start performance occurs during a life history period in which fast-start ability is likely to be particularly important for survival.

Key words: fast-start, ontogeny, life history, locomotion, swimming, fish, *Salmo trutta*, *Oncorhynchus tshawytscha*, *Oncorhynchus kisutch*, Salmonidae, functional morphology.

### Introduction

Fast-starts are high-acceleration locomotor behaviors used by fishes to escape predators, during feeding events and during social interactions (for a discussion, see Domenici and Blake, 1997). The C-start type of fast-start is commonly used as an escape response. It can initiate burst swimming away from a potential predator and/or towards a refuge. C-starts can also function without subsequent burst swimming to move the threatened fish quickly out of a predator's path or suction feeding forces. In the present study, the term fast-start refers specifically to C-start escape responses.

The kinematics of the fast-start escape response are, at a broad level, stereotypical. The behavior may be defined by three distinct stages (Weihs, 1973). During stage 1, the fish bends rapidly and tightly to one side of the body around its center of mass, forming an overall C-shape. Stage 1 is called the preparatory stage because body bending during stage 1 prepares the fish for the stage 2 tail stroke. During stage 2, the propulsive stage, the fish moves away from its initial position during its first propulsive tail stroke, bending its body in the opposite direction to the stage 1 bend. Stage 2 ends when the tail stroke reaches its maximum excursion on the opposite side

of the body. Stage 3 is a more variable fast-start stage encompassing continued locomotion after stage 2. Because of the importance of the C-start to surviving a predatory attack, the behavior is believed to be performed at a fish's maximal locomotor ability.

Body size affects the fast-start performance of fishes. Several studies (Webb, 1976, 1978; Domenici and Blake, 1993b) have examined the relationship between performance and total length in adult fishes. The durations of the fast-start stages 1 and 2 and the distance traveled during the fast-start increase with increasing body length in adults (Webb, 1976, 1978; Domenici and Blake, 1993b). Maximum velocity is more variable. Domenici and Blake (1993b) found maximum velocity in the angelfish (*Pterophyllum eimekei*) to be length-independent, while Webb's studies of rainbow trout (*Oncorhynchus mykiss*) (Webb, 1976) and seven teleost species (Webb, 1978) showed that maximum velocity scales with body length. Domenici and Blake (1993b) suggest that the difference in scaling of maximum velocity between their study and those of Webb (1976, 1978) is due to the inclusion of lower-performance angelfish fast-starts in their data. In all

three studies, maximum acceleration is length-independent (Webb, 1976, 1978; Domenici and Blake, 1993b).

Several studies have examined the C-start behavior of fishes during early post-hatching development, encompassing changes both in length and in other aspects of developmental morphology and physiology. An identifiable fast-start develops by the time of hatching (e.g. Kimmel et al., 1974; Eaton et al., 1977; Eaton and Nissanov, 1985; Taylor and McPhail, 1985; Hale, 1996). Although the overall behavior pattern does not change dramatically during post-hatching development, pronounced changes in fast-start performance occur during the pre-hatching (Eaton et al., 1977; Eaton and Nissanov, 1985) and post-hatching (Kimmel et al., 1974; Taylor and McPhail, 1985; Hale, 1996) developmental periods.

The fast-start performance of larval fishes improves as a fish grows older and larger. The durations of fast-start stages decrease during early development (Eaton and Nissanov, 1985; Hale, 1996), as does the time to peak head speed (Kimmel et al., 1974; Hale, 1996). The distance traveled, either within a given period (Eaton and Nissanov, 1985) or during stage 2 (Hale, 1996), and absolute maximum head speed (Eaton et al., 1977; Eaton and Nissanov, 1985; Taylor and McPhail, 1985; Hale, 1996) increase through development. Comparisons of larval and adult zebrafish (*Danio rerio*) show that head speed relative to body length is much greater in larval zebrafish than in adults (Kimmel et al., 1974).

Most previous studies of fast-start behavior in larval fishes have compared two developmental stages or size classes (e.g. Eaton et al., 1977; Eaton and Nissanov, 1985; Taylor and McPhail, 1985) or have looked at overall escape performance combining stage 1 and stage 2 performance with subsequent burst swimming (e.g. Williams and Brown, 1992; Williams et al., 1996). A study of length-specific scaling of fast-start kinematics (Hale, 1996) found that aspects of C-start performance changed disproportionately with total length increase during the post-hatching period of yolk-sac absorption (the eleutheroembryo phase; Balon, 1975) of chinook salmon (*Oncorhynchus tshawytscha*). The durations of stages 1 and 2 decreased disproportionately with increase in total body length (scaling exponents less than  $-1$ ), and distance traveled and head velocity increased disproportionately (scaling exponents greater than  $1$ ). Several variables describing the overall form of the behavior did not change through early post-hatching development (Hale, 1996). Maximum bending at the center of mass at the end of stage 1 relative to body length remained constant, as did the relative timing of the fast-start movements. Hale (1996) showed that, although the behavior pattern did not change, escape performance resulting from the behavior improved markedly during early post-hatching development.

More work has been done on the scaling of overall escape performance, including C-start stages 1–3 (e.g. Webb, 1981; Webb and Corolla, 1981; Yin and Blaxter, 1987; Williams and Brown, 1992; Fuiman, 1993; Williams et al., 1996). As with C-start behavior, overall escape performance generally improves with increasing larval length. In general, distance

traveled during the escape or burst of activity was found to increase linearly with larval length (e.g. Webb and Corolla, 1981; Williams and Brown, 1992; Fuiman, 1993), as were mean and maximum velocities (Webb, 1981; Webb and Corolla, 1981; Williams and Brown, 1992; Fuiman, 1993). Ontogenetic changes are thought to affect larval locomotion (Fuiman and Webb, 1988) and predator escape success (Fuiman, 1994). Fuiman (1994) found that ontogenetic state (which reflects developmental morphology other than length) was a critical factor when examining a larval fish's ability to respond to and escape from a predator. However, developmental changes other than length have not been examined with respect to the development of the C-start performance variables.

Comparison of C-start size scaling between adult and larval fishes shows discontinuities in the trends of performance with increasing total length. The durations of the fast-start stages decrease with body length through early post-hatching development but increase with length in adults. The differences in scaling trends of fast-start performance variables imply that there is a point during development at which the scaling of fast-start variables with length changes dramatically. This point at which this occurs has not been previously documented.

The present study examines development of the C-start behavior in three salmonid species: chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*) and brown trout (*Salmo trutta*). In particular, it addresses two main questions. First, what are the relative influences of body length and other aspects of morphological development on the fast-start ability of larval fishes? I hypothesize that developmental change in performance will not be due primarily to length increase, but that other morphological and physiological changes occurring through ontogeny will drive changes in fast-start performance. Second, how does escape ability change through the end of the period of yolk-sac absorption and into the juvenile period? I hypothesize that, when examined through the development of one species, the trends observed in larval performance will make a smooth transition into the adult performance trends.

## Materials and methods

### *Fishes and fish care*

Fertilized eggs of chinook salmon (*Oncorhynchus tshawytscha* Walbaum), coho salmon (*Oncorhynchus kisutch* Walbaum) and brown trout (*Salmo trutta* L.) were acquired from the Jake Wolf Fish Hatchery, Illinois Department of Natural Resources, USA. The eggs were initially obtained by the hatchery from populations in the North Central United States. In total, 100 chinook salmon, 91 coho salmon and 97 brown trout were studied during the developmental periods from hatching through and beyond the end of yolk-sac absorption into the juvenile period (in which I include the alevin or fry phase). These species have very similar developmental morphologies, but brown trout hatch and mature at a smaller size than the two salmon species (Figs 1,

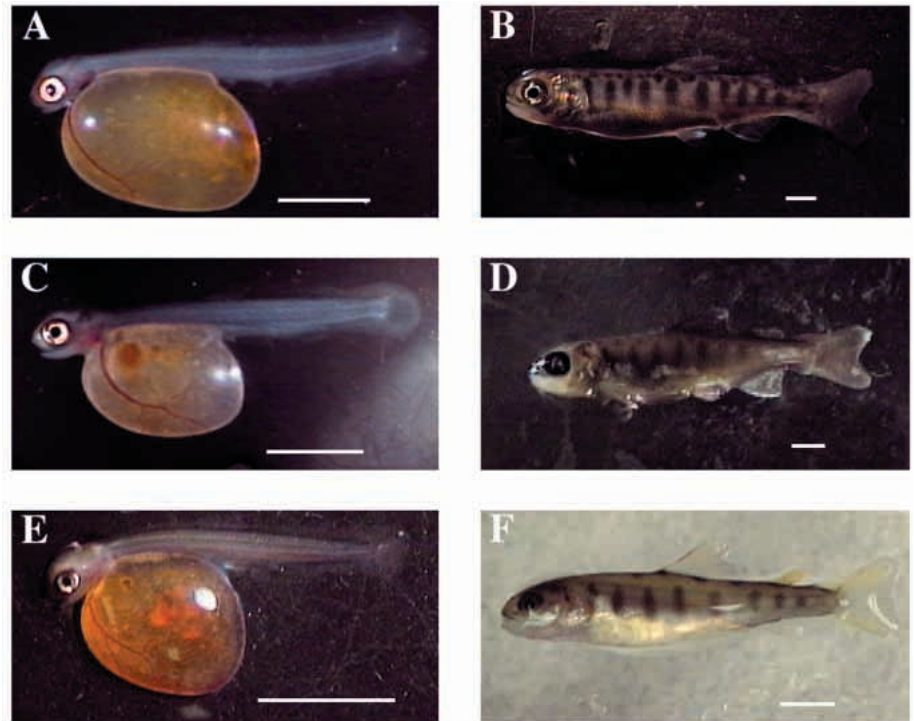


Fig. 1. External morphology of the three species used in this study several days after hatching (A,C,E) and after yolk-sac absorption (B,D,F). (A,B) Chinook salmon (*Oncorhynchus tshawytscha*). (C,D) Coho salmon (*Oncorhynchus kisutch*). (E,F) Brown trout (*Salmo trutta*). Scale bars, 5 mm.

2). Across the three species, the fishes studied ranged in length from 13 mm to 72 mm (Table 1).

Care of eggs and fish was the same for all three species. Eggs and fish were held in 351 aquaria with aerators. Because the eggs and hatchlings are delicate, the water was changed manually. During hatching and once the fish were feeding, the

water was changed at least once daily to prevent excess food, egg membranes and waste from fouling the aquaria. At other times, the water was replaced every 2–3 days or as necessary. The aquaria were kept at a constant temperature by partially immersing them in a large tank (approximately 2 m × 1 m × 0.5 m) equipped with a pump (Little Giant pump; model 3-MD-SC) and Aquanetics chiller (model AFC-3). The temperature in the fish tanks was maintained at 12 °C, which is the temperature preferred by the hatchery for rearing to maximize the health and survival of these species. Light was kept at low levels on a 12 h:12 h light:dark cycle. Once old enough to feed, automatic feeders (Sweeney Enterprises Inc. fish feeder; model AF6) dispensed small amounts of finely ground Kyowa salmon chow every few hours throughout the day. Fish were not fed for several hours before filming. Because frequent feeding is very important to young fishes, starving for longer periods, as is common in preparation for kinematic studies of adult fishes, was not possible.

#### Recording fast-start behavior

Fish were filmed individually in a glass tank (0.2 m × 0.2 m × 0.1 m) holding water at 12 °C. A 0.65 cm grid was placed at the bottom of the tank. A high-speed video camera (Kodak Ektapro EM Motion Analyzer; model AG-1012) was positioned over the tank with the lens directed downwards to film the dorsal view of the fish. Fast-start behavior was recorded at 1000 images s<sup>-1</sup>. Captured images were recorded onto SVHS tape on a Panasonic AG-1970 video recorder.

Fishes were stimulated to fast-start by touching the head dorsolaterally with a fine wire (31 gauge or finer). Although other methods of stimulating the fishes to fast-start were

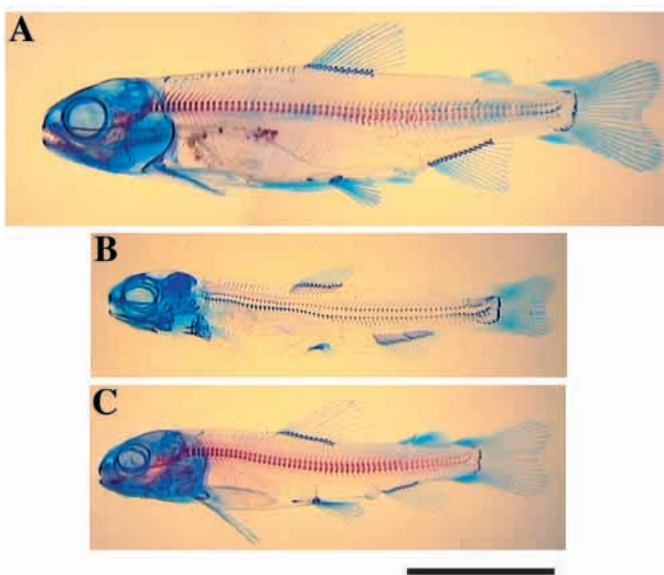


Fig. 2. Cleared and stained specimens of chinook salmon (*Oncorhynchus tshawytscha*) (A,B) and brown trout (*Salmo trutta*) (C) showing bone in red and cartilage in blue. The brown trout, while the same size as the smaller and younger of the two chinook salmon (B), is more similar in its bone development to the larger chinook salmon. Scale bar, 10 mm.

Table 1. *Numbers of Oncorhynchus tshawytscha, Oncorhynchus kisutch and Salmo trutta specimens studied during eleuthroembryo and juvenile developmental stages*

Species	Length range (mm)	Ontogenetic state range	N
Chinook salmon ( <i>O. tshawytscha</i> )			100
Eleuthroembryo	21–33	88.1–101.2	72
Juvenile	39–65	106.1–120.8	28
Coho salmon ( <i>O. kisutch</i> )			91
Eleuthroembryo	19–32	87.4–102.8	69
Juvenile	32–72	102.8–126.9	22
Brown trout ( <i>S. trutta</i> )			97
Eleuthroembryo	13–22	84.5–101.8	57
Juvenile	22–66	101.8–138.0	40

Ontogenetic state ranges correspond to length ranges (mm) for each species and developmental stage.  
Ontogenetic state was calculated using equation 1.

attempted, this was the only method that worked consistently throughout the developmental periods examined and with which I could apply a directional stimulus.

After filming, fish were killed with a dilute solution of 3-aminobenzoic acid ethyl ester (MS-222; Sigma Chemical Company). Lateral and dorsal views of body morphology were videotaped using a CCD color video camera (Sony CCD-IRIS DXC-107A with camera adapter model CMA-D7) and microscope (Leica; model MZ6) equipped with a video adapter. Specimens were weighed (Perkin-Elmer AD-4 autobalance) after discrete droplets of water on the surface of the fish had been removed. Complete drying was not feasible because of the delicate nature of the yolk sac in the very young specimens. The center of mass in the anterior–posterior orientation was determined using a small balance (a small version of that described by Westneat et al., 1998).

#### Data acquisition

One fast-start by each experimental animal was used in this study. In a few trials, fish swam upwards in the tank, rather than performing the fast-start in one plane of focus, or rolled to one side during the start. These trials were eliminated from the data set. Additionally, any trial in which the fish swam within 3 body lengths of the side of the tank was not used because of potential wall effects on hydrodynamics. There were no differences in performance between fast-starts with stage 1 bending to the right side of the body and those with stage 1 bending to the left, so the trials were combined for analysis. Although fast-starts without a stage 2 bend have been observed in other studies (e.g. Domenici and Blake, 1991; Kasapi et al., 1993), only fast-starts with distinct stages 1 and 2 are examined in the present study.

In the fast-starts of some fishes, the end of the tail is bent back at the end of stage 1 so that the body does not form a true C-shape (Jayne and Lauder, 1996). The data presented here are from fast-starts without a backward bend of the tail during stage 1 (see Fig. 3). However, when referring to other papers, I use the more inclusive definition of the term ‘C-start’, irrespective of curvature at the end of the tail, so as not to misrepresent previous studies that do not specifically address tail bending or that may not have been filmed at sufficiently high frame rates to assess such movement.

The durations of fast-start stages 1 and 2 were determined directly from the time-coded video recordings. The first movement of the head after applying the stimulus marks the beginning of stage 1. There are discrepancies in the fast-start literature on how to define the end of stage 1 (Domenici and Blake, 1997). In the present study, the end of stage 1 was determined by the change in direction of the head after the fish had formed the C-shaped bend of stage 1 (as in Kasapi et al., 1993).

Kinematic variables were determined by digitizing the dorsal view of the fish at 11 equally spaced points along the body (at one-tenth body length intervals including the tip of the snout and tail) as described by Hale (1996). Although approximating curved sections of the body with straight-line segments may lead to a point being estimated as being farther along the body than it actually is, because of the number of segments used and the amount of body bending, points were not noticeably skewed in the present study. The procedure was implemented in the digitizing program JAW image (by J. A. Walker, Field Museum). Every second frame of the video was digitized (effective frame rate of 500 frames s<sup>-1</sup>) from the beginning of stage 1 to the end of stage 2 using a Panasonic AG-1970 video recorder, a Sony trinitron monitor (model PVM-13510) and TelevEyes/Pro by Digital Vision Inc. The screen lengths of the fishes were 0.25–0.5 of the monitor screen size on which the images were digitized. The center of mass determined directly from the specimens was approximated with the closest digitized point. Although during the fast-start behavior the center of mass moves off the fish’s midline as the fish bends, the center of mass position for the fish in the straight position is generally used as an approximation for the true center of mass (Domenici and Blake, 1997). I have followed this convention in the data analyses presented in the present study.

The distance traveled by the center of mass during stage 2 was determined by calculating the straight-line distance between the position of the center of mass at the beginning and the end of stage 2. Velocity and acceleration at the center of mass were determined through both stage 1 and stage 2 of the fast-start. Because of the impracticability of using accelerometers on such small fishes, velocity and acceleration were calculated by differentiation and double differentiation of distance *versus* time data. Although previous studies have found digitized data to be problematic for such calculations (Harper and Blake, 1989a,b) when fitted by a quadratic moving regression (Lanczos, 1956), Walker’s (1998) simulation

studies have shown excellent recovery of velocity and acceleration information from distance/time data. One of the methods found to be particularly stable and useful at high frame rates and low magnification (as is the video system used this study), was a quintic spline applied with a previously determined mean square error (Walker, 1998). The mean square error was determined by digitizing the same image 20 times non-consecutively. Walker's (1998) equation for error variance was used to calculate variance.

Turning angles during stage 1 and 2 and the overall turning angles for the fast-starts were determined from the digitized points. Similar to previous studies (Foreman and Eaton, 1993; Eaton and Emberley, 1991; Domenici and Blake, 1991), angles of movement were calculated for the fast-start stages. Following the procedure and the nomenclature of Foreman and Eaton (1993), three angles were measured: the angles moved by the anterior body midline during stage 1 (angle 1) and during stage 2 (angle 2), and the overall escape trajectory angle (ETA) during the fast-start (from the beginning of the fast-start to the end of stage 2). The line between the center of mass and the tip of the snout used by Foreman and Eaton (1993) did not accurately reflect the movement of the anterior part of the body during stage 1, because of the curvature of the body in some of the fishes examined, so I recalculated the angles using the line from the tip of the snout to point 2 (one-tenth of the body length posterior to the snout tip).

Fuiman (1994) presents an equation that aligns ontogenies based on an identified stage:

$$O_L = (\log_{10}L / \log_{10}L_{juv})100, \quad (1)$$

where  $L$  is the total length of the fish,  $L_{juv}$  is the total length of the fish at a known developmental state and  $O_L$  is the ontogenetic state of the fish. This equation was used to assign ontogenetic states for comparison of fast-start performance variables among the three species examined in the present study. The equation is sensitive to the units used. Data were input in millimeters, as in the paper that originally presented the equation (Fuiman, 1994). The value of  $L_{juv}$  was the mean length of each species at the end of yolk-sac absorption as determined by the specimens in the present study. The reference lengths used for  $L_{juv}$  were  $32 \pm 1$  mm ( $N=12$ ) for chinook salmon,  $29 \pm 1$  mm ( $N=10$ ) for coho salmon and  $21 \pm 1$  mm ( $N=15$ ) for brown trout (means  $\pm$  S.D.).

#### Data analysis

Data taken during the eleutheroembryo phase were examined separately from data collected from juvenile fishes (Table 1). The time at which skin fuses over the remnant of the yolk sac (referred to in the present study as the end of yolk-sac absorption) was used as the cut-off point because it was easily discernible in the specimens and because it approximates the time of an important change in the life of a fish, the transition from using the yolk for nutrition to exogenous feeding.

Changes in kinematics with changes in length and ontogenetic state within each species were examined by log-

transforming the data and fitting them with ordinary least squares (OLS) and reduced major axis (RMA) regressions (implemented with Systat 5, JMP 3.1.5 and programs custom-written by M. LaBarbera and P. Magwene, University of Chicago). OLS regressions were calculated and are presented in the present study for comparison with OLS regressions from other studies. RMA regression results are discussed since they are preferable for studies in which error in measurement must be taken into account for both variables (Rayner, 1985; McArdle, 1988; LaBarbera, 1989). 95 % confidence intervals for the slopes and intercepts were established by calculating the RMA regression 2000 times from resampled data with 100 % replacement and determining the 97.5 % and 2.5 % quartiles. Differences between resampled means and intercepts were tested using Student's  $t$ -test as specified by Efron and Tibshirani (1993). Analysis of variance (ANOVA) was used to test for differences in means among species and classes. When examining the significant differences in the data among the species or between size classes of an individual species, the sequential Bonferroni test was used to adjust  $P$ -values (Rice, 1989), and these adjusted table-wide  $P$ -values ( $\alpha=0.05$ ) were used to determine significance.

The angles of movement of the fish during kinematic stages 1 and 2 and the overall escape trajectory angle (Foreman and Eaton, 1993) were also examined through development. Because the data were not treated as if from a circular distribution (positive and negative angles were considered, and angles greater than  $360^\circ$  were treated as such), circular statistics are not presented. As with other kinematic variables, angular data were examined using OLS and RMA regressions. Data were compared among the three species using ANOVA.

## Results

### Fast-start behavioral pattern

The fast-start escape response was easily recognizable throughout the eleutheroembryo and juvenile periods (Fig. 3). Fishes always performed the initial C-bend away from the side of the body to which the stimulus was applied. The kinematics followed the general behavior pattern described previously for the C-start, with characteristic stage 1 and stage 2 movements. Often there was no stage 3 swimming subsequent to stage 1 and stage 2.

The angles of movement varied considerably within the species examined, with standard deviations of over  $20^\circ$  for each of the variables (Fig. 4). There are no significant differences in the angles of movement of chinook and coho salmon; however, the angles of movement made by brown trout tended to be larger. Angle 1 of brown trout (mean  $153 \pm 29^\circ$ ) was significantly larger ( $P < 0.05$ ) than angle 1 of the other two species (chinook,  $128 \pm 35^\circ$ ; coho,  $118 \pm 36^\circ$ ). Mean angle A2 of brown trout ( $44 \pm 25^\circ$ ) was significantly larger ( $P < 0.05$ ) than angle A2 of chinook salmon ( $31 \pm 21^\circ$ ) but not of coho salmon ( $37 \pm 24^\circ$ ). ETA of brown trout ( $116 \pm 40^\circ$ ) was significantly larger ( $P < 0.05$ ) than that of coho salmon ( $98 \pm 48^\circ$ ) but not of chinook salmon ( $106 \pm 37^\circ$ ) (means  $\pm$  S.D.).

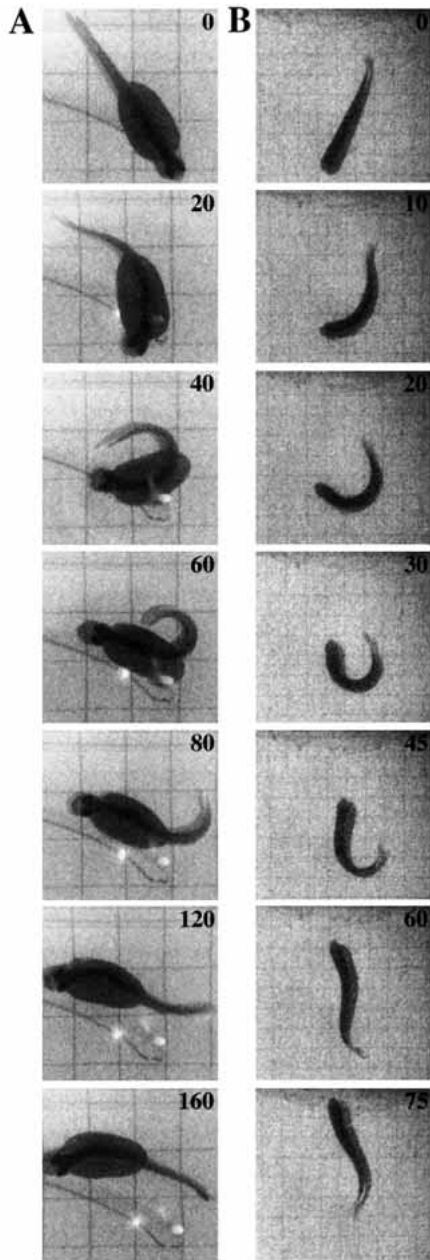


Fig. 3. The C-start behavior of chinook salmon (*Oncorhynchus tshawytscha*) (A) 4 days after hatching and (B) as a juvenile. The overall pattern of the fast-start is similar in these two specimens, while the timing of the fast-start movements differs considerably, with the combined stage 1 and stage 2 lasting over twice as long in the younger fish. Time (ms) is given in the top right corner of each panel.

There were significant relationships between both the angle 1 and the escape trajectory angle and fish body length, although  $r^2$  values were consistently low. For chinook and brown eleutheroembryos, there was a significant decrease in angle A1 with increasing total length (for each;  $P < 0.01$ ,  $r^2 = 0.23$ ). For all three species, there was a significant decrease in ETA with increasing total length (chinook,  $P < 0.01$ ,  $r^2 = 0.29$ ; coho,

$P < 0.01$ ,  $r^2 = 0.14$ ; brown,  $P < 0.01$ ,  $r^2 = 0.16$ ). Angle A2 had no significant relationship with total length nor did angles A1, A2 or ETA for juveniles. The consistently low  $r^2$  values preclude detailed scaling analysis of these variables.

#### Duration of the fast-start stages

All three species showed a significant decrease in durations of stages 1 and 2 during eleutheroembryo development (Table 2; Figs 5, 6). For example, at hatching, brown trout stage 1 duration could be up to 50 ms in length, while at the end of eleutheroembryo development, stage 1 lasted less than 20 ms. During eleutheroembryo development, means of stage 1 and stage 2 durations were not significantly different among the three species (ANOVA;  $F = 2.7565$ ,  $P = 0.066$ ), and the overall range of the data was similar for all three species. The data ranges are, for the duration of stage 1, 18–46 ms (chinook), 17–44 ms (coho) and 15–50 ms (brown), and for the duration of stage 2, 30–168 ms (chinook), 28–190 ms (coho) and 24–198 ms (brown). The slopes of log-transformed duration on log-transformed body length (the scaling exponents) were not significantly different among the three species ( $P > 0.05$ ). For stage 1 duration, the y-intercepts were significantly different in comparisons between brown trout and the two salmon species ( $P < 0.05$ ), but not between the chinook and coho salmon ( $P > 0.05$ ). Brown trout stage 2 data were not log-normally distributed and so were not compared statistically with data for chinook and coho salmon. Chinook and coho salmon slopes were not significantly different for stage 2 duration; however, the y-intercepts were significantly different ( $P < 0.05$ ).

In contrast to the species-specific patterns seen in plots of stage 1 duration versus length (Figs 5A,B, 6A,B), the stage 1 duration data for the three species are nearly superimposed when plotted against ontogenetic state (Figs 5C,D, 6C,D). Because slopes of the regressions on ontogenetic state were generally significantly different from one another, instead of comparing intercepts, the ontogenetic state values were divided into four classes representing the range of ontogenetic states that overlapped among the species (80–90, 90–100, 100–110 and 110–120). For stage 1 duration, there were no significant differences among species in duration at a given ontogenetic state ( $P > 0.05$ ). Stage 2 duration curves were also closer after ontogenetic state transformation, although several comparisons of ontogenetic state classes still showed differences in mean duration values.

In all three species, the decrease in duration of the fast-start stages stopped at the end of larval development. Brown trout were the only species for which there were enough data through juvenile development to evaluate the trend of duration through this period. Even though this study only examined the beginning of the juvenile period, the duration of stage 1 had already increased by over 30% to 40–50 ms in the largest (and oldest) specimens compared with a mean duration of less than 30 ms at the end of the period of yolk-sac absorption. The slope of stage 1 duration versus length for juveniles was significantly different from the slope of eleutheroembryo stage 1 duration ( $P < 0.0001$ ) and from a slope of zero ( $P < 0.0001$ ) (Table 2);

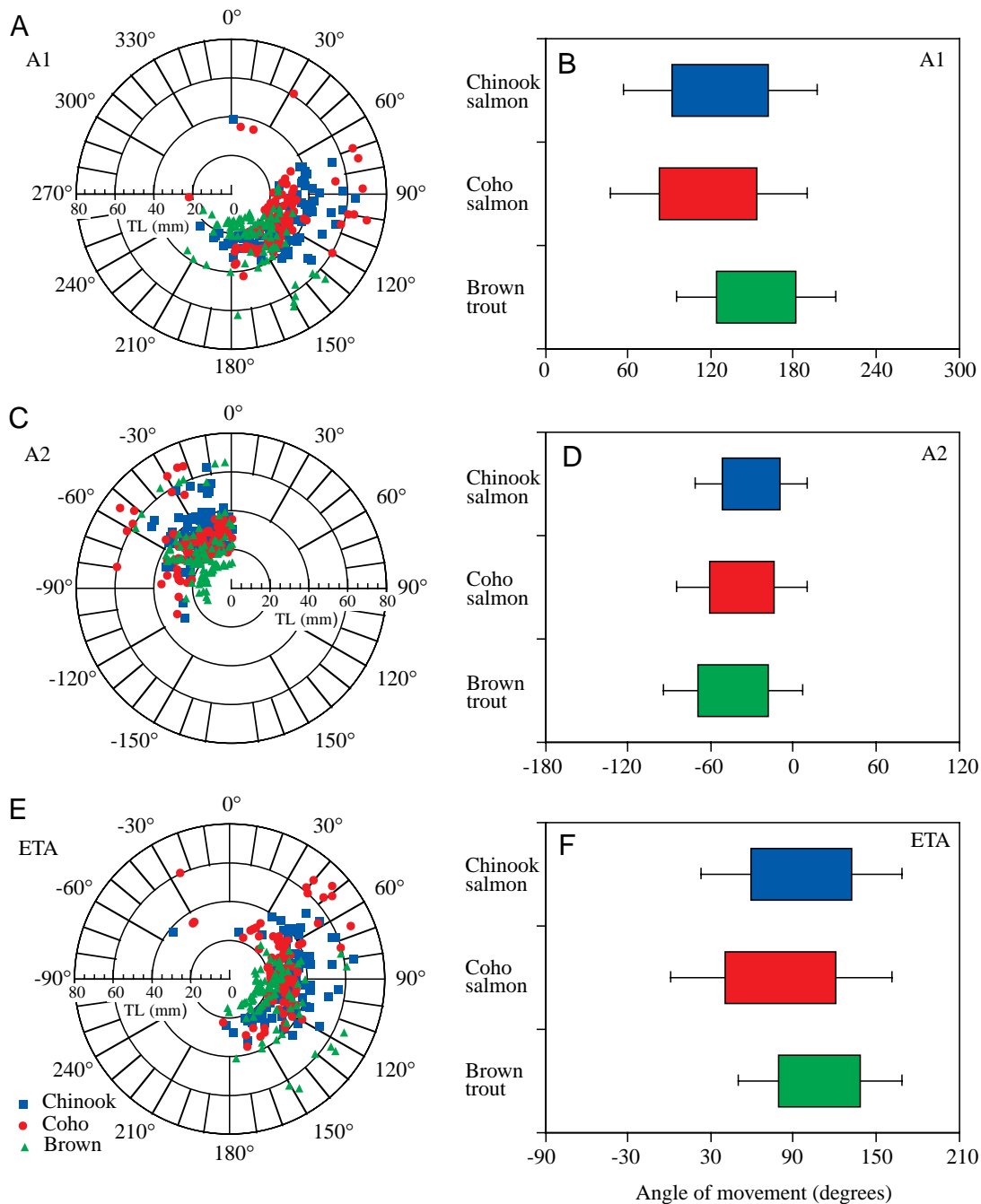


Fig. 4. Angles of movement during stage 1 (A1) and during stage 2 (A2) and the escape trajectory angle (ETA) for the chinook salmon (*Oncorhynchus tshawytscha*), the coho salmon (*Oncorhynchus kisutch*) and the brown trout (*Salmo trutta*). (A,C,E) The angular data for each fish in this study. 0° indicates the starting position at the beginning of the fast-start in A and E and at the beginning of stage 2 in C. (B,D,F) The angles of movement for the chinook and coho salmon and the brown trout. Boxes represent the mean ± 1 s.d. and the error bars indicate 2 s.d. For *O. tshawytscha*,  $N=100$ ; for *O. kisutch*,  $N=91$ ; for *S. trutta*,  $N=97$ . TL, total length.

however, the slope was not significantly different from a value of 1.0 ( $P=0.671$ ).

#### Distance, velocity and acceleration

The distance traveled during stage 2 by all three species increased with total length through eleutheroembryo development with a slope significantly greater than 1.0

( $P<0.01$ ) (Fig. 7A; Table 3) for log-transformed data. At hatching, fish generally traveled less than 10 mm from their initial position during stage 2. By the end of yolk-sac absorption, the distance traveled had more than doubled. This increase in distance traveled during stage 2 occurred despite the fact that stage 2 duration decreased considerably through this period.

Table 2. Results of ordinary least squares and reduced major axis regressions of log(stage 1) and log(stage 2) durations against log(total length) for chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*) and brown trout (*Salmo trutta*)

	Species	N	OLS slope	OLS y-intercept	RMA slope	RMA slope 95% C.I.		RMA y-intercept	RMA intercept 95% C.I.		r <sup>2</sup>	F-ratio	P-value
						Low	High		Low	High			
Duration of stage 1	Chinook <sup>1</sup>	72	-1.219	3.280	-1.431	-1.586	-1.287	3.589	3.383	3.807	0.729	184.780	<0.0001
	Coho <sup>1</sup>	69	-1.253	3.257	-1.513	-1.669	-1.358	3.636	3.415	3.858	0.679	139.385	<0.0001
	Brown <sup>1</sup>	57	-1.255	3.051	-1.433	-1.596	-1.277	3.273	3.074	3.480	0.761	175.386	<0.0001
	Brown <sup>2</sup>	40	0.724	0.294	0.894	0.766	1.042	0.029	-0.211	0.239	0.663	74.582	<0.0001
Duration of stage 2	Chinook <sup>1</sup>	72	-1.336	3.869	-1.990	-2.243	-1.707	4.828	4.416	5.194	0.436	51.939	<0.0001
	Coho <sup>1</sup>	69	-1.988	4.768	-2.536	-2.846	-2.238	5.561	5.137	6.010	0.612	103.946	<0.0001
	Brown <sup>1</sup>	57	-1.458	3.532	-2.338	-2.721	-1.951	4.631	4.130	5.125	0.386	34.453	<0.0001
	Brown <sup>2</sup>	40	0.804	0.440	1.303	1.101	1.546	-0.340	-0.695	-0.034	0.371	24.033	<0.0001

OLS, ordinary least squares; RMA, reduced major axis; C.I., confidence interval. Eleutheroembryo and juvenile data were separated for analysis. <sup>1</sup> indicates only eleutheroembryo data; <sup>2</sup> indicates only juvenile data.

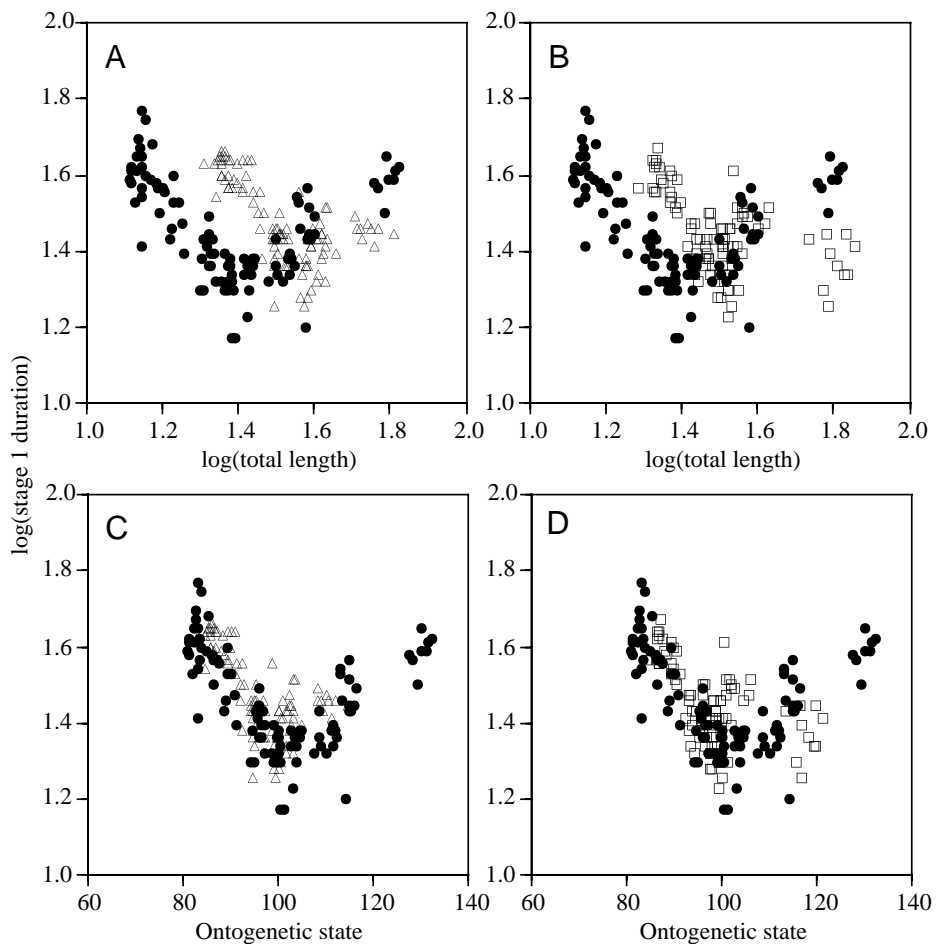


Fig. 5. Plots of stage 1 duration (ms) against total length (mm) and ontogenetic state (calculated using equation 1). Log-transformed durations of fast-start stage 1 in chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*) and brown trout (*Salmo trutta*) plotted against (A,B) log-transformed total length and (C,D) ontogenetic state. Data for chinook and coho salmon are plotted independently, with brown trout data, because the overlap between chinook and coho data makes it difficult to distinguish points.  $\Delta$ , chinook salmon;  $\square$ , coho salmon;  $\bullet$ , brown trout. For *O. tshawytscha*, N=100; for *O. kisutch*, N=91; for *S. trutta*, N=97.

Distance traveled during stage 2 continued to increase with length throughout the juvenile period. The largest brown trout studied traveled approximately 40 mm during stage 2, more than quadrupling the distance traveled at hatching. The slope

of distance traveled against body length is significantly greater through the eleutheroembryo phase than through the juvenile period ( $P<0.01$ ), being 2.125 ( $r^2=0.689$ ) in eleutheroembryos and 1.419 ( $r^2=0.662$ ) in juveniles.

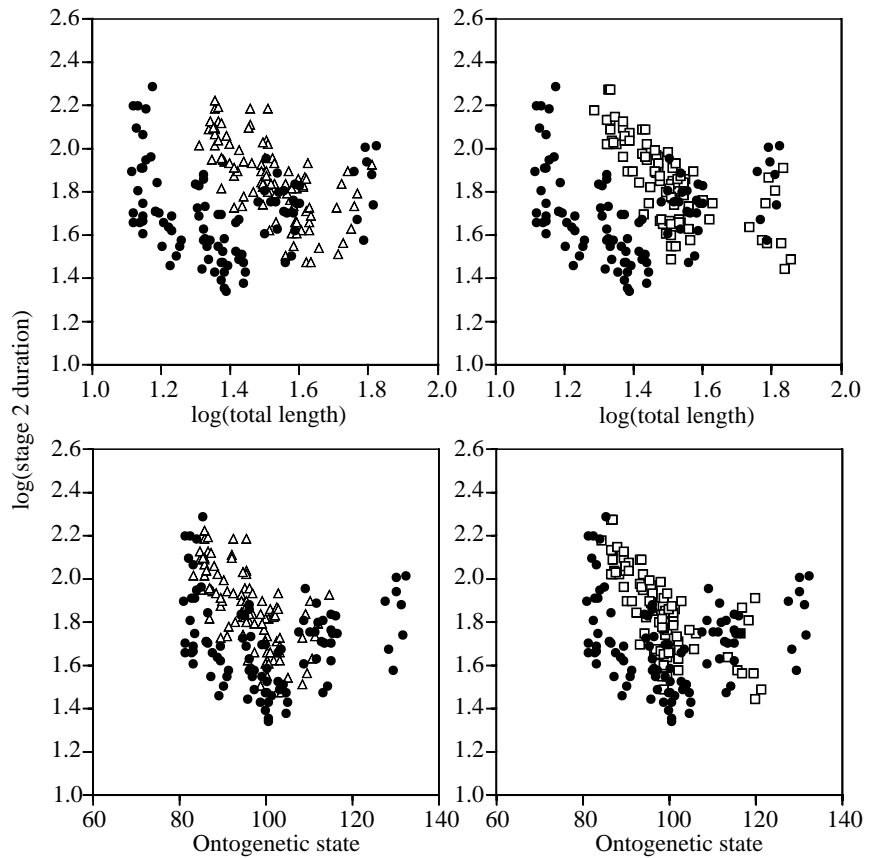


Fig. 6. Plots of stage 2 duration (ms) against total length (mm) and ontogenetic state (calculated using equation 1). Log-transformed durations of fast-start stage 2 in chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*) and brown trout (*Salmo trutta*) plotted against (A,B) log-transformed total length and (C,D) ontogenetic state. Data for chinook and coho salmon are plotted independently, with brown trout data, because the overlap between chinook and coho data makes it difficult to distinguish points.  $\Delta$ , chinook salmon;  $\square$ , coho salmon;  $\bullet$ , brown trout. For *O. tshawytscha*,  $N=100$ ; for *O. kisutch*,  $N=91$ ; for *S. trutta*,  $N=97$ .

Distance traveled tracked body length more closely than it did ontogenetic state (Fig. 7B). Distances traveled in stage 2 were compared among the size classes (20–24 mm, 25–29 mm, 30–34 mm, 35–39 mm) between brown trout and the two other species. Chinook salmon and brown trout were not significantly different ( $P>0.05$ ) in three of four of the comparable size classes, and coho and brown trout were not

significantly different in any of the comparable classes ( $P>0.05$ ). After ontogenetic state transformation, the data were divided into the four categories described for the stage duration data. Chinook salmon and brown trout were significantly different ( $P<0.05$ ) in three of the four classes, and coho salmon and brown trout differed significantly in all four classes ( $P<0.05$ ).

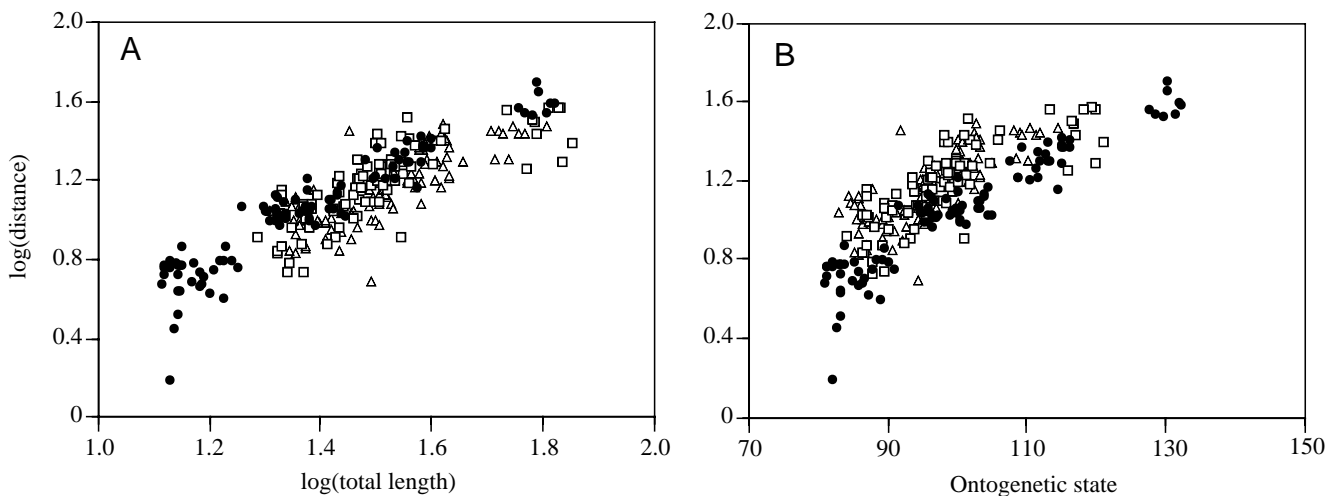


Fig. 7. Plots of distance traveled in stage 2 (mm) against (A) log-transformed total length (mm) and (B) ontogenetic state (calculated using equation 1) for chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) salmon and brown trout (*Salmo trutta*). Distance varies more among the species at a given ontogenetic state than it does at a given total length.  $\Delta$ , chinook salmon;  $\square$ , coho salmon;  $\bullet$ , brown trout. For *O. tshawytscha*,  $N=100$ ; for *O. kisutch*,  $N=91$ ; for *S. trutta*,  $N=97$ .

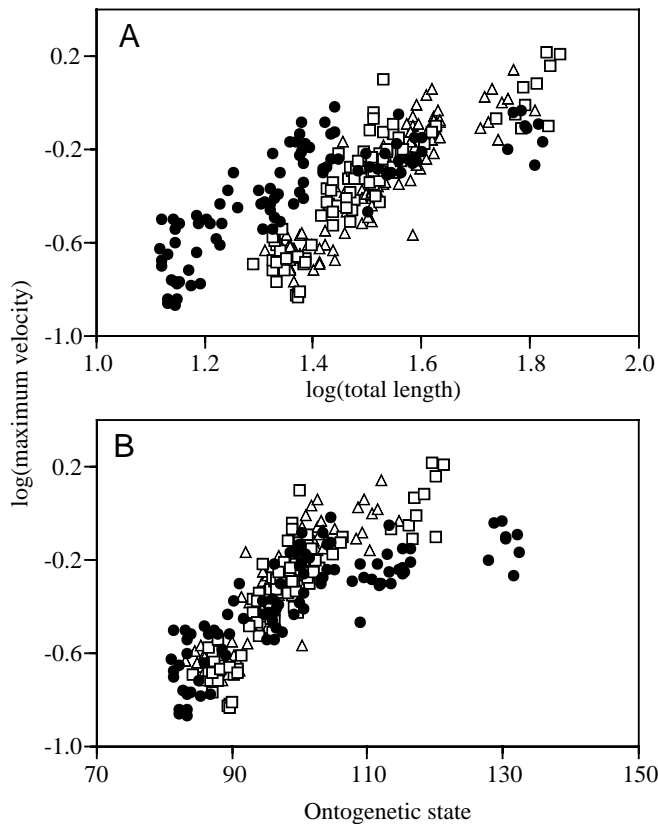


Fig. 8. Maximum velocity of the center of mass. Log-transformed maximum velocity ( $\text{mm ms}^{-1}$ ) of chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) salmon and brown trout (*Salmo trutta*) plotted against (A) log-transformed total length (mm) and (B) ontogenetic state (calculated using equation 1).  $\Delta$ , chinook salmon;  $\square$ , coho salmon;  $\bullet$ , brown trout. For *O. tshawytscha*,  $N=100$ ; for *O. kisutch*,  $N=91$ ; for *S. trutta*,  $N=97$ .

Maximum velocity also increased through post-hatching development in all species. At hatching, maximum velocity was as low as  $0.15 \text{ m s}^{-1}$ , and by the end of the developmental period studied reached maximum values of well over  $1.0 \text{ m s}^{-1}$ . The slopes of velocity against body length were greater than 1 for log-transformed data in all three species ( $P < 0.01$ ) (Fig. 8A; Table 3). As with the duration data, the maximum velocity data for brown trout were offset on the length axis from the data for chinook and coho salmon. There was a significant difference in velocity between brown trout and the two salmon species compared at the point during eleutheroembryo development at which the two species overlap in size (body lengths of approximately 20–35 mm,  $P < 0.05$ ). There was no significant difference among the species after ontogenetic state transformation (compared at the 80–90 and 90–100 ontogenetic states ranges, which represent eleutheroembryo development) ( $P > 0.05$ ) (Fig. 8B).

The slope of maximum velocity against total length differed significantly ( $P < 0.01$ ) between eleutheroembryo and juvenile brown trout. It increased steeply through early post-hatching development, then leveled off during juvenile development.

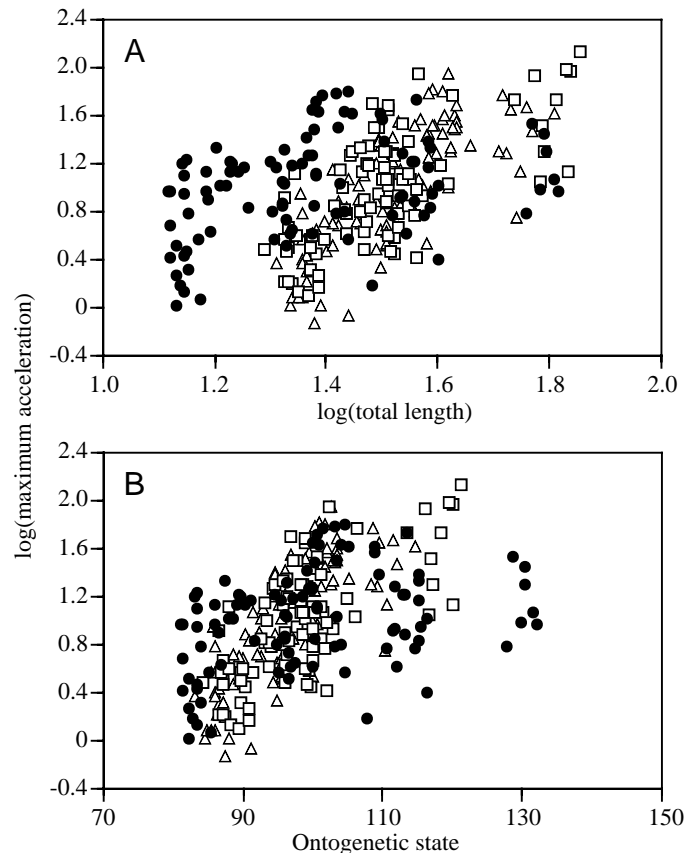


Fig. 9. Maximum acceleration of the center of mass. Log-transformed maximum acceleration ( $\text{mm ms}^{-2}$ ) of chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) salmon and brown trout (*Salmo trutta*) plotted against (A) log-transformed total length (mm) and (B) ontogenetic state (calculated using equation 1).  $\Delta$ , chinook salmon;  $\square$ , coho salmon;  $\bullet$ , brown trout. For *O. tshawytscha*,  $N=100$ ; for *O. kisutch*,  $N=91$ ; for *S. trutta*,  $N=97$ .

The slope of maximum velocity against total length was not significantly different from zero through the juvenile period ( $r^2=0.109$ ,  $P=0.073$ ).

Maximum acceleration ranged from  $1 \text{ m s}^{-2}$  to over  $100 \text{ m s}^{-2}$ . Maximum acceleration did not show a strong trend though early development (Fig. 9A; Table 3). Although the slopes are significantly greater than zero ( $P < 0.05$ ), the  $r^2$  values are low for all three species. Maximum acceleration differed significantly between brown trout and pooled chinook and coho salmon data ( $P < 0.05$ ) when compared at the eleutheroembryo size range at which they overlap (the same ranges as described for the maximum velocity data), but there was no significant difference after ontogenetic state transformation (Fig. 9B).

## Discussion

There are two central results of this study. First, fast-start kinematic variables differ in their relationship to ontogenetic state and to size. A number of kinematic variables of the fast-

Table 3. Results of regressions of  $\log(\text{distance traveled during stage 2})$ ,  $\log(\text{maximum velocity})$  and  $\log(\text{maximum acceleration})$  against  $\log(\text{total length})$  for chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*) and brown trout (*Salmo trutta*)

	Species	N	OLS slope	OLS y-intercept	RMA slope	RMA slope 95% C.I.		RMA y-intercept	RMA intercept 95% C.I.		$r^2$	F-ratio	P-value	
						Low	High		Low	High				
Distance	Chinook	100	1.219	-0.049	1.537	1.374	1.717	-1.185	-1.465	-0.934	0.623	163.537	<0.0001	
	Chinook <sup>1</sup>	72	1.099	-0.533	1.837	1.556	2.147	-1.612	-2.069	-1.194	0.349	39.121	<0.0001	
	Coho	91	1.317	0.124	1.487	1.296	1.711	-1.062	-1.392	-0.775	0.474	83.856	<0.0001	
	Coho <sup>1</sup>	69	1.555	-1.151	2.168	1.876	2.462	-2.038	-2.473	-1.609	0.517	71.763	<0.0001	
	Brown <sup>1</sup>	57	1.764	-1.354	2.125	1.777	2.527	-1.803	-2.319	-1.356	0.689	121.619	<0.0001	
	Brown <sup>2</sup>	40	1.301	-0.742	1.419	1.271	1.569	-0.925	-1.160	-0.684	0.850	216.117	<0.0001	
	Velocity	Chinook	100	1.849	-2.395	2.048	1.897	2.211	-3.454	-3.695	-3.229	0.816	443.639	<0.0001
	Chinook <sup>1</sup>	72	1.934	-3.282	2.295	2.073	2.526	-3.811	-4.144	-3.490	0.712	173.416	<0.0001	
	Coho	91	1.633	-2.102	1.878	1.680	2.114	-3.156	-3.501	-2.862	0.706	222.012	<0.0001	
	Coho <sup>1</sup>	69	2.395	-3.897	2.790	2.483	3.128	-4.463	-4.956	-4.013	0.733	183.818	<0.0001	
	Brown <sup>1</sup>	57	1.678	-2.599	2.065	1.824	2.300	-3.082	-3.381	-2.776	0.660	106.608	<0.0001	
	Brown <sup>2</sup>	40	0.209	-0.529	0.678	0.528	0.933	-1.264	-1.663	-1.027	0.082	3.393	0.0733	
Acceleration	Chinook	100	3.316	-5.900	4.326	3.847	4.843	-5.571	-6.349	-4.855	0.569	132.946	<0.0001	
	Chinook <sup>1</sup>	72	3.945	-6.872	5.609	4.963	6.294	-7.396	-8.397	-6.465	0.485	67.827	<0.0001	
	Coho	91	2.558	-4.804	3.684	3.239	4.195	-4.549	-5.283	-3.899	0.462	79.983	<0.0001	
	Coho <sup>1</sup>	69	3.199	-6.786	5.673	4.887	6.509	-7.366	-8.574	-6.235	0.321	31.659	<0.0001	
	Brown <sup>1</sup>	57	2.075	-4.537	4.159	3.567	4.752	-4.289	-5.031	-3.531	0.247	18.0218	<0.0001	
	Brown <sup>2</sup>	40	-0.455	0.518	-3.139	-4.322	-2.281	4.706	-3.950	7.288	0.021	0.8298	0.3681	

OLS, ordinary least squares; RMA, reduced major axis; C.I., confidence interval.

Eleutheroembryo and juvenile data was separated for some analyses.

When the entire data set was not used, <sup>1</sup> indicates only eleutheroembryo data, <sup>2</sup> indicates only juvenile data.

start (i.e. durations, maximum velocity and maximum acceleration) depend on ontogenetic state. In contrast, distance traveled during stage 2 depends on body length, regardless of the fish's ontogenetic state. Second, trends in many fast-start variables change at the end of yolk-sac absorption. For example, the durations of the fast-start stages decrease during eleutheroembryo development in brown trout and increase during juvenile development, reconciling trends found in larvae and adults.

Although there are considerable changes in the values of many kinematic variables through development in these species, the overall pattern of the fast-start as assessed by movement angles does not change markedly. Both eleutheroembryos and juvenile salmonids used double-bend C-starts with large stage 1 angles and smaller stage 2 angles to move away from the stimulus. Overall, they tended to move over an angle of slightly more than 100° from their initial position. The similarity in escape trajectory angle among the fishes is probably due to the consistent stimulus direction used

in this study. Domenici and Blake (1993a,b) similarly found that adult angelfishes varying in size prefer the same trajectories away from a stimulus. However, their study, in which stimulus direction differed relative to fish orientation, shows that the fish vary their movement angles in order to achieve those trajectories.

While in juvenile fishes there were no changes in any of the angle variables, in eleutheroembryo salmonids, the stage 1 angle (A1) and the escape trajectory angle (ETA) decrease with length increase, although correlations were low. This suggests either that the preferred escape trajectory changes through early development or that changes in morphology and other kinematic variables cause the fish to turn a greater angle than is optimal. Although the second possibility seems more likely, since eleutheroembryos are well protected from predators during early post-hatching development, the neural circuitry and body muscles used for the fast-start may also be important during hatching (Eaton and Nissanov, 1985) for which larger movement angles may be better suited.

*Size, stage and fast-start ability*

Improvements in stage 1 and stage 2 durations, maximum velocity and maximum acceleration during eleutheroembryo development are not due primarily to changes in body length. When the kinematics are compared at the same body length among species, these aspects of fast-start performance differ substantially. When the data are compared at the same ontogenetic state, there is little difference in these variables among the taxa. The values of these variables therefore reflect primarily ontogenetic state, at least in the closely related taxa examined here in which developmental trajectories are similar.

The changes in scaling of fast-start performance variables suggest that different factors may be affecting performance through a fish's life history. In adults, although body length continues to increase, the basic locomotor apparatus has been established and remains relatively constant. In contrast, during early development, not only does body length increase but body shape also changes, and the basic morphological components of the locomotor systems are formed and integrated (e.g. van Raamsdonk et al., 1982; Batty, 1984). For example, in salmonines, the yolk, which can be over 75% of the total mass at hatching (Fig. 1), is gradually absorbed through the eleutheroembryo phase. Fin folds extending along dorsal, caudal and ventral surfaces of the body also decrease in size as true fins develop (Fig. 1). Internal changes include chondrification and ossification of the axial skeleton and fins (Fig. 2) and the addition and subsequent modification of myomeres. Changes in muscle physiology have been studied during periods of development for many fishes including Atlantic salmon (*Salmo salar*) (e.g. Higgins and Thorpe, 1990; Usher et al., 1994), rainbow trout (*Oncorhynchus mykiss*) (e.g. Nag and Nursall, 1972) and brown trout (*Salmo trutta*) (Proctor et al., 1980). These studies show changes in the numbers and size of red and white muscle fibers from embryo through juvenile stages.

The scaling patterns observed for stage 1 and 2 durations, maximum velocity and maximum acceleration are probably related to the development of myomeres or aspects of the force generation and force transmission systems used for body bending. The durations of fast-start stages are analogous to cycle period, the inverse of cycle frequency (Webb, 1976). In adult fishes, cycle frequency is related to muscle contraction time, which increases with body length (Wardle, 1975). Duration would be expected to increase (cycle frequency to decrease) with body length if the properties of the myomeres remained the same. This is the relationship observed in juvenile and adult fishes. During pre-juvenile development, many changes occur in larval muscle in addition to an increase in length. In salmonids, the myomeres are still forming and changing shape through eleutheroembryo development. The muscle fibers also change with the continued development of white muscle fibers and with the differentiation of superficial fibers (Proctor et al., 1980). The tissues that transmit the forces generated by the myomeres (including the fins and backbone)

chondrify and ossify during this period (Fig. 2) and probably improve the transmission of muscle forces during body bending. The effects of changes in the composition and form of locomotor morphology may outweigh the effects of size on fast-start performance and cause the improvement in performance through reduced fast-start duration.

For the salmonids examined in the present study, distance traveled during stage 2 appears to be influenced less by the physiological changes occurring through development than by the physics of swimming, which is more directly related to overall size. Unlike other kinematic variables, distance traveled in stage 2 did not differ among species in its scaling with body length, but did differ significantly in its scaling with ontogenetic state. Distance traveled in stage 2 scales with the square of length (RMA slopes of the log-transformed values are not significantly different from 2.0), suggesting a relationship with propulsive surface area. Webb (1976, 1978) found that distance traveled during the fast-start of adult fishes was length-dependent but that the scaling exponents were indistinguishable from 1.0. Differences in scaling exponents between this study and studies of scaling in adults (Webb, 1976, 1978) may be due to differences in Reynolds number. In the eleutheroembryos studied, changes in the instantaneous Reynolds number are likely to have a greater effect on swimming performance because the sizes and speeds of these fishes place them in or close to the range of Reynolds numbers dominated by viscous rather than inertial forces (Hale, 1996). Other factors, such as body surface area and shape, are likely to be important determinants of performance in eleutheroembryos and larvae (Webb and Weihs, 1986) and need to be investigated in conjunction with kinematics.

Studies of life history often examine trade-offs in resource allocation (e.g. Partridge and Sibly, 1991; Bernardo, 1994). One factor found to be important in determining how resources are used is risk of predation. Predation pressure has been demonstrated to influence resource allocation in relation to reproduction in guppies (*Poecilia reticulata*) (Reznick and Endler, 1982). The results presented here suggest that the effects of resource allocations on the rate and timing of morphological development may also have important implications for fast-start swimming performance. Since kinematic variables differ in their relationships with size and developmental stage, there are potential trade-offs between putting energy resources into growing and into maturing as developmental strategies for improving performance. For example, if a fish grows quickly but remains ontogenetically immature, the distance it can move will be large, but its maximum velocity will be relatively low. If a fish matures rapidly, but at a smaller size, it may be able to move relatively quickly, but for a smaller distance. Although the differences in scaling among kinematic variables would make it theoretically possible to improve one at the expense of another, ecological and morphological studies are necessary to determine whether developing fishes actually manipulate resource allocation for competing locomotor functions.

*Transition in fast-start performance between life history stages*

Data on the C-start performance of brown trout through the eleutheroembryo period and into the juvenile developmental period show that the allometric trends seen in independent studies of eleutheroembryos (Hale, 1996) and adults (Webb, 1976, 1978; Domenici and Blake, 1993b) are reconciled at the end of eleutheroembryo development. The durations of the fast-start stages decrease during early post-hatching development, level off at the end of eleutheroembryo development and then increase during juvenile development. Distance traveled during stage 2, maximum velocity and maximum acceleration during stage 2 increase steeply with eleutheroembryo development. Distance traveled during stage 2 continues to increase through juvenile development, but the slope of the increase is significantly lower ( $P < 0.0001$ ) than during eleutheroembryo development. The slopes of maximum velocity and maximum acceleration *versus* length also change at the end of eleutheroembryo development, becoming independent of length through juvenile development.

Webb (1978) presents equations relating kinematic variables to total length for a wide variety of species adult fishes. For comparison, I converted the distance data for juvenile brown trout into the same form and calculated regressions comparable with those of Webb (1978). Although the overall trends in the two sets of data are the same, an increase in distance with increasing body length, there is a significant difference ( $P < 0.0001$ ) in slopes between the juvenile brown trout distance data and that presented for adult fishes by Webb (1978), with the slope for juveniles being significantly greater. Although the most dramatic ontogenetic changes in the salmonids studied occur during pre-hatching and eleutheroembryo development, body shape and other aspects of morphology continue to change, albeit less strikingly, after the eleutheroembryo stage and probably account for the difference in scaling between the data presented here and those for interspecific adult comparisons (Webb, 1978).

As with the data for juvenile brown trout presented here, Domenici and Blake (1993b) found in their intraspecific study of adult angelfish that maximum velocity and maximum acceleration are independent of body length. However, Webb (1976, 1978) found that maximum acceleration was independent of length but that maximum velocity scaled in proportion to length. It is unclear why these different studies found different patterns of scaling of maximum velocity. One possibility suggested by Domenici and Blake (1993b) is that Webb (1976, 1978) examined scaling of adults over a greater length range and, therefore, that his study had more power to reveal a trend in the data.

The peak in fast-start performance occurs at the end of eleutheroembryo development, indicating that, at this time, relative to its size, a fish is best able to perform the C-start escape response. During eleutheroembryo development, distance traveled during stage 2, maximum velocity and acceleration improve relative to total length (regression slopes are greater than 1). Similarly, during the eleutheroembryo

period, the durations of stage 1 and 2 decrease with regression slopes of less than  $-1$ , indicating an increase in performance relative to total length. During juvenile development, the performance of these kinematic variables relative to decreases in body length (except for stage 1 duration, which increases with a slope of less than 1). Carrier (1996) points out that, because of the relatively higher predation on juvenile animals than on adults, locomotor performance in juveniles should also be better than might be expected for their size. This seems to be the case for fast-start behavior in the species studied here; the period of maximal performance relative to body size coincides with the time when fast-start performance is likely to be especially important for survival.

In salmonids, good fast-start performance may be related to both predator avoidance and food acquisition. Early in development (eggs and eleutheroembryos), many salmonids are well protected in the gravel nest. They have a strong photonegative response during early post-hatching development, which generally keeps them buried in the gravel and less accessible to predators (e.g. Mason, 1976; Carey and Noakes, 1981). Also, during this period, they obtain nutrients through yolk-sac absorption so have no need to forage for food. Little is known about predation during this life history period; however, survival rates are high (approximately 80% for chinook and coho salmon under good conditions; Briggs, 1953), and mortality has generally been attributed to environmental effects such as oxygen deprivation rather than predation.

A trend of increased mortality at the end of yolk-sac absorption called the 'critical period' (Hjort, 1914) has been described for many fish species including salmonids (Elliot, 1989). The cause of mortality is generally thought to be either predation (for a review, see Bailey and Houde, 1989) or starvation (Hjort, 1914, 1928; Cushing, 1972). Predation on post-emergent salmonines is very high (Healey, 1991; Sandercock, 1991). Many vertebrate predators, including fish (e.g. Larkin, 1977; Patten, 1977; Logan, 1968), snakes (Shapovalov and Taft, 1954), birds and mammals (Sandercock, 1991), prey upon fry and juvenile coho salmon (for a review, see Sandercock, 1991). Starvation, or weakening due to starvation, which may result directly or indirectly in death through increased predation (Yin and Blaxter, 1987), is also likely to be an important factor in the post-emergent survival of salmonids (Elliot, 1989, 1990). Elliot (1989, 1990) and Sandercock (1991) discuss the behavior of, respectively, post-emergent brown trout and coho salmon in defending territories against intraspecifics, suggesting that these species may be defending limited resources. Although C-starts are generally thought of as escape maneuvers, they have also been implicated in territorial agonistic encounters in other species (cichlids) (Fernald, 1975). S-starts, which are generally used during feeding, like the C-start, are directional, high-acceleration locomotor behaviors involving rapid body bending. Although the behavior pattern is very different, I suggest that ontogenetic change and growth may affect aspects of these two fast-start types similarly. Thus, regardless of whether predation or starvation is the primary cause of death

in young fishes, fast-start performance may be an important factor affecting survival. Examining the movements of these fishes under natural conditions will be critical for determining the use and effectiveness of fast-start behavior.

This work was supported by an NSF dissertation grant (IBN 9423525) and a predoctoral fellowship from the Howard Hughes Medical Institute. Additionally, the high-speed video system was purchased with a NSF equipment grant (BIR 9318129) to A. Biewener (PI), M. Dickinson, M. LaBarbera and M. Westneat. The Illinois Department of Natural Resources, particularly Steve Krueger and The Jake Wolf Fish Hatchery, provided the specimens necessary for this work. Comments from and discussions with many people have influenced and improved this work. Much thanks to Drs M. LaBarbera, A. Biewener, B. Chernoff, M. Dickinson, M. Martindale, J. Walker, M. Westneat, J. Bernardo, P. Magwene, the biomechanics discussion groups at the University of Chicago and two anonymous reviewers.

### References

- Bailey, K. M. and Houde, E. D.** (1989). Predation on eggs and larvae of marine fishes and the recruitment problem. *Adv. Mar. Biol.* **25**, 1–83.
- Balon, E. K.** (1975). Terminology of intervals of fish development. *J. Fish. Res. Bd Can.* **32**, 1663–1670.
- Batty, R. S.** (1984). Development of swimming movements and musculature in the larval herring (*Clupea harengus*). *J. Exp. Biol.* **110**, 217–229.
- Bernardo, J.** (1994). Experimental analysis of allocation in two divergent, natural salamander populations. *Am. Nat.* **143**, 14–38.
- Briggs, J. C.** (1953). The behavior and reproduction of salmonid fishes in coastal streams. *Calif. Dept Fish. Game Fish. Bull.* **94**, 62pp.
- Carey, W. E. and Noakes, D. L. G.** (1981). Development of photobehavioural responses in young rainbow trout, *Salmo gairdneri* Richardson. *J. Fish Biol.* **19**, 285–296.
- Carrier, D. R.** (1996). Ontogenetic limits on locomotor performance. *Physiol. Zool.* **69**, 467–488.
- Cushing, D. H.** (1972). The production cycle and the numbers of marine fish. *Symp. Zool. Soc. Lond.* **29**, 213–232.
- Domenici, P. and Blake, R. W.** (1991). The kinematics and performance of the escape response in the angelfish (*Pterophyllum eimekei*). *J. Exp. Biol.* **156**, 187–205.
- Domenici, P. and Blake, R. W.** (1993a). Escape trajectories in angelfish (*Pterophyllum eimekei*). *J. Exp. Biol.* **177**, 253–272.
- Domenici, P. and Blake, R. W.** (1993b). The effect of size on the kinematic performance of angelfish (*Pterophyllum eimekei*) escape responses. *Can. J. Zool.* **71**, 2319–2326.
- Domenici, P. and Blake, R. W.** (1997). The kinematics and performance of fish fast-start swimming. *J. Exp. Biol.* **200**, 1165–1178.
- Eaton, R. C. and Emberley, D. S.** (1991). How stimulus direction determines the trajectory of the Mauthner-initiated escape response in a teleost fish. *J. Exp. Biol.* **161**, 469–487.
- Eaton, R. C., Farley, R. D., Kimmel, C. B. and Schabtach, E.** (1977). Functional development in the Mauthner cell system of embryos and larvae of the zebrafish. *J. Neurobiol.* **8**, 151–172.
- Eaton, R. C. and Nissanov, J.** (1985). A review of Mauthner-initiated escape behavior and its possible role in hatching in the immature zebrafish, *Brachydanio rerio*. *Env. Biol. Fish.* **12**, 265–279.
- Efron, B. and Tibshirani, R. J.** (1993). *An Introduction to the Bootstrap*. New York: Chapman & Hall. 236pp.
- Elliot, J. M.** (1989). Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. I. The critical time for survival. *J. Anim. Ecol.* **58**, 987–1001.
- Elliot, J. M.** (1990). Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. III. The role of territorial behavior. *J. Anim. Ecol.* **59**, 803–818.
- Fernald, R. D.** (1975). Fast body turns in cichlid fish. *Nature* **258**, 228–229.
- Foreman, M. B. and Eaton, R. C.** (1993). The direction change concept for reticulospinal control of goldfish escape. *J. Neurosci.* **13**, 4101–4133.
- Fuiman, L. A.** (1993). Development of predator evasion in Atlantic herring, *Clupea harengus* L. *Anim. Behav.* **45**, 1101–1116.
- Fuiman, L. A.** (1994). The interplay of ontogeny and scaling in the interactions of fish larvae and their predators. *J. Fish Biol.* **45** (Suppl. A), 55–79.
- Fuiman, L. A. and Webb, P. W.** (1988). Ontogeny of routine swimming activity and performance in zebra danios (Teleostei: Cyprinidae). *Anim. Behav.* **36**, 250–261.
- Hale, M. E.** (1996). The development of fast-start performance in fishes: escape kinematics of the chinook salmon (*Oncorhynchus tshawytscha*). *Am. Zool.* **36**, 695–709.
- Harper, D. G. and Blake, R. W.** (1989a). A critical analysis of the use of high-speed film to determine maximum accelerations of fish. *J. Exp. Biol.* **142**, 465–471.
- Harper, D. G. and Blake, R. W.** (1989b). On the error involved in high-speed film when used to evaluate maximum accelerations of fish. *Can. J. Zool.* **67**, 1929–1936.
- Healey, M. C.** (1991). Life history of the chinook salmon (*Oncorhynchus tshawytscha*). In *Pacific Salmon Life Histories* (ed. C. Groot and L. Margolis), pp. 313–393. Vancouver: UBC Press.
- Higgins, P. J. and Thorpe, J. E.** (1990). Hyperplasia and hypertrophy in the growth of skeletal muscle in juvenile Atlantic salmon, *Salmo salar* L. *J. Fish Biol.* **37**, 505–519.
- Hjort, J.** (1914). Fluctuations in the great fisheries of northern Europe reviewed in the light of biological research. *Rapp. P.-V. Reun. Cons. Perm. Int. Expl. Mer.* **20**, 1–228.
- Hjort, J.** (1928). Fluctuations in the year classes of important food fishes. *J. Cons. Perm. Int. Expl. Mer.* **1**, 5–38.
- Jayne, B. C. and Lauder, G. V.** (1996). New data on axial locomotion in fishes: How speed affects diversity of kinematics and motor patterns. *Am. Zool.* **36**, 642–655.
- Kasapi, M. A., Domenici, P., Blake, R. W. and Harper, D.** (1993). The kinematics and performance of escape responses of the knifefish *Xenomystus nigri*. *Can. J. Zool.* **71**, 189–195.
- Kimmel, C. B., Patterson, J. and Kimmel, R. O.** (1974). The development and behavioral characteristics of the startle response in the zebra fish. *Devl. Psychobiol.* **7**, 47–60.
- LaBarbera, M.** (1989). Analyzing body size as a factor in ecology and evolution. *Annu. Rev. Ecol. Syst.* **20**, 97–117.
- Lanczos, C.** (1956). *Applied Analysis*. London: Isaac Pitman & Sons.
- Larkin, P. A.** (1977). Pacific salmon. In *Fish Population Dynamics* (ed. J. A. Gulland), pp. 156–186. New York: J. Wiley & Sons.
- Logan, S. M.** (1968). Silver salmon studies in the Resurrection bay area. *Prog. Rep. Alaska Dep. Fish Game Sport Fish Div.* **9**, 117–134.

- Mason, J. C.** (1976). Some features of coho salmon *Oncorhynchus kisutch*, fry emerging from simulated redds and concurrent changes on photobehavior. *Fishery Bull.* **74**, 167–175.
- McArdle, B. H.** (1988). The structural relationship: regression in biology. *Can. J. Zool.* **66**, 2329–2340.
- Nag, A. C. and Nursall, J. R.** (1972). Histogenesis of white and red muscle fibres of trunk muscle of a fish, *Salmo gairdneri*. *Cytobios* **6**, 227–246.
- Partridge, L. and Sibly, R.** (1991). Constraints in the evolution of life histories. *Phil. Trans. R. Soc. Lond. B* **332**, 3–13.
- Patten, B. G.** (1977). Body size and learned avoidance as factors affecting predation on coho salmon, *Oncorhynchus kisutch* fry by torrent sculpin, *Cottus rhotheus*. *Fishery Bull.* **75**, 25–41.
- Proctor, C., Mosse, P. R. L. and Hudson, R. C. L.** (1980). A histochemical and ultrastructural study of the development of the propulsive musculature of the brown trout, *Salmo trutta* L., in relation to swimming behaviour. *J. Fish Biol.* **16**, 309–329.
- Rayner, J. M. V.** (1985). Linear relations in biomechanics: the statistics of scaling functions. *J. Zool., Lond. A* **206**, 415–439.
- Reznick, D. and Endler, J. A.** (1982). The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* **36**, 160–177.
- Rice, W. R.** (1989). Analyzing tables of statistical tests. *Evolution* **43**, 223–225.
- Sandercock, F.** (1991). Life history of the coho salmon (*Oncorhynchus kisutch*). In *Pacific Salmon Life Histories* (ed. C. Groot and L. Margolis), pp. 397–445. Vancouver: UBC Press.
- Shapovalov, L. and Taft, A. C.** (1954). The life histories of the steelhead rainbow trout (*Salmo gairdneri*) and the silver salmon (*Oncorhynchus kisutch*) with special references to Waddle Creek, California and recommendations regarding their management. *Calif. Dept Fish Game Fish. Bull.* **98**, 375pp.
- Taylor, E. B. and McPhail, J. D.** (1985). Ontogeny of the startle response in young coho salmon *Oncorhynchus kisutch*. *Trans. Am. Fish. Soc.* **114**, 552–557.
- Usher, M. L., Stickland, N. C. and Thorpe, J. E.** (1994). Muscle development in Atlantic salmon (*Salmo salar*) embryos and the effects of temperature on muscle cellularity. *J. Fish Biol.* **44**, 953–964.
- van Raamsdonk, W., van't Veer, L., Veeken, K., Heyting, C. and Pool, C. W.** (1982). Differentiation of muscle fiber types in the teleost *Brachydanio rerio*, the zebrafish. *Anat. Embryol.* **164**, 51–62.
- Walker, J. A.** (1998). Estimating velocities and accelerations of animal locomotion: a simulation experiment comparing numerical differentiation methods. *J. Exp. Biol.* **201**, 981–995.
- Wardle, C. S.** (1975). Limit of fish swimming speed. *Nature* **255**, 725–727.
- Webb, P. W.** (1976). The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri* and a consideration of piscivorous predator–prey interactions. *J. Exp. Biol.* **65**, 157–177.
- Webb, P. W.** (1978). Fast-start performance and body form in seven species of teleost fish. *J. Exp. Biol.* **74**, 211–226.
- Webb, P. W.** (1981). Responses of northern anchovy, *Engraulis mordax*, larvae to predation by a biting planktivore, *Amphiprion percula*. *Fishery Bull.* **79**, 727–735.
- Webb, P. W. and Corolla, R. T.** (1981). Burst swimming performance of northern anchovy, *Engraulis mordax*, larvae. *Fishery Bull.* **79**, 143–150.
- Webb, P. W. and Weihs, D.** (1986). Functional locomotor morphology of early life history stages of fishes. *Trans. Am. Fish. Soc.* **115**, 115–127.
- Weihs, D.** (1973). The mechanism of rapid starting of slender fish. *Biorheology* **10**, 343–350.
- Westneat, M. W., Hale, M. E., McHenry, M. J. and Long, J. H., Jr** (1998). Mechanics of the fast-start: muscle function and the role of intermuscular pressure in the escape behavior of *Amia calva* and *Polypterus palmas*. *J. Exp. Biol.* **201**, 3041–3055.
- Williams, P. J. and Brown, J. A.** (1992). Development changes in the escape response of larval winter flounder *Pleuronectes americanus* from hatch through metamorphosis. *Mar. Ecol. Prog. Ser.* **88**, 185–193.
- Williams, P. J., Brown, J. A., Gotceitas, V. and Pepin, P.** (1996). Developmental changes in escape response performance of five species of marine larval fish. *Can. J. Fish. Aquat. Sci.* **53**, 1246–1253.
- Yin, M. C. and Blaxter, J. H. S.** (1987). Escape speeds of marine fish larvae during early development and starvation. *Mar. Biol.* **96**, 459–468.