Transactions of the American Fisheries Society 115:115–127, 1986
© Copyright by the American Fisheries Society 1986

Functional Locomotor Morphology of Early Life History Stages of Fishes

PAUL W. WEBB

School of Natural Resources, University of Michigan
Ann Arbor, Michigan 48109, USA

DANIEL WEIHS

Department of Aeronautical Engineering, Technion
Haifa 32000, Israel

Abstract.—Routine activities of early life history stages of fishes occur in an intermediate hydrodynamic environment (as identified by Reynolds numbers), between a zone where drag is linearly dependent on velocity and resistive forces make large contributions to thrust, and a zone where inertial forces dominate except in the boundary layer immediately adjacent to the body surface. Sprint performance carries larvae into this latter zone; thus, locomotor activities important for survival of both larvae and adults occur in the same hydrodynamic environment and similar selective pressures would be expected to influence locomotor morphology of larvae and adults. The simplest framework for evaluating and interpreting development of larvae recognizes the parental form as the developmental terminus and uses adult forms as references to identify similarities and discrepancies in larva structure. Three measures of locomotor structure are used to examine changes during development: (a) the ratio of caudal peduncle depth to maximum body depth, which is small in thunniform fish; (b) a body shape factor, which is small in chaetodontiform fishes; and (c) a transient swimming thrust factor, which is large in esociform fish. Similarities in form are found in yolk-bearing larvae and are attributed to oxygen demand. Similarities in the pattern of development of larvae directly towards the parental form are found for fusiform species, except for delayed development of the caudal fin in tunas that probably is due to the hydrodynamic regime of the tail. Convergence with parents does not occur during the larva stage of deep-bodied, compressed species. This is attributed to high drag of compressed forms at low Reynolds numbers and diet differences between larvae and parents. Although this framework is successful in identifying and interpreting problems, comparative studies of form, kinematics, and performance during biologically important activities are essential.

The early life stages of fishes are relatively difficult to study compared to later stages. Nevertheless, current knowledge of the biology of early life stages is remarkably extensive, especially that concerning ecological aspects. This may be attributed in large part to the early focus provided by the problem of high larva mortality, for which Hjort's (1914) critical-period hypothesis provided a conceptual framework for research. As the need expands to examine other factors contributing to larva mortality, new frameworks are required that address a wider range of adaptations that affect survival.

There are many possible approaches to understanding the biology of the early life stages of fishes. One is functional morphology: the analysis of the structure, function, and role of structural traits (Gans, in press). A functional morphological approach has a proven record in articulating testable hypotheses (Feder and Lauder 1985). This is especially true for locomotion, because movement is central to behaviors such as feeding and predator-avoidance that are of major importance for survival (Webb, in press). Our purpose is to review some of the major ideas on the functional locomotor morphology of fish, emphasizing structure, with the object of determining an initial foundation for framing questions concerning developmental changes in the capabilities and roles of locomotor systems.

Hydrodynamic Environment

Many authors have emphasized that the small size of larval fishes places them in a hydrodynamic regime with somewhat different properties than that occupied by adults (Vlymen 1974; Weihs 1980a, 1980b; Batty 1981, 1984). Therefore, in order to understand the development of locomotor form and function, the logical starting point is the hydrodynamic environment.

The hydrodynamic environment depends on two physical properties of water and the size and speed of objects moving through the water. The physical properties are viscosity and density, often ex-

pressed together as the kinematic viscosity (the ratio of viscosity to density). These are used with size and speed to calculate the relative magnitudes of inertial and frictional forces, whose ratio is expressed as the nondimensional Reynolds number:

$$R = U \cdot L/\nu; \quad (1)$$

R = Reynolds number based on some characteristic linear dimension, often indicated by a subscript;
U = velocity;
L = length;
ν = kinematic viscosity.

The Reynolds number based on total fish length, R_L, has been used most often by fishery biologists to understand how form interacts with flow to determine drag. When $R_L < 20$, viscous forces spread through the water for a large distance from the body and inertial forces can be neglected. At these low Reynolds numbers, drag of any given body is proportional to viscosity and velocity (Wu 1976; Weihs 1980a).

At $R_L > 200$ inertial (Newton's Law) forces dominate. Viscous effects are confined to a thin region close to the body surface called the boundary layer, where most of the resistance to motion (drag) arises. Outside the boundary layer, viscous forces are negligible and inertial forces dominate. In this R_L zone, the drag of a given body is proportional to the square of its velocity and to a nondimensional drag coefficient that is usually determined empirically.

The region $20 < R_L < 200$ is an intermediate zone in the sense that flow characteristics gradually change from those typical of the viscous zone to that where inertial effects dominate. In this intermediate zone, predicting resistive forces is difficult, but drag lies between that calculated for the viscous and inertial zones (Weihs 1980a). Where viscous forces dominate at the low-R_L end of the intermediate zone, a small surface-area-to-volume ratio is desirable for nonpropulsive parts of the body. This is because viscosity acts only on the body surface. Rounded and spherical shapes would be expected for nektonic animals, whereas planktonic animals should have large areas that increase drag so they may be better carried with the current. Yolk-bearing larvae tend towards the shape of a sphere with a tail, and move at low speeds, when the appropriate dimension for calculating Reynolds number is the diameter of the yolk sac. Thus, the Reynolds number is small for yolk-bearing larvae, but as the yolk is absorbed, the larva both grows and its reference length changes. As a result, larvae tend to "snap through" to higher values of the intermediate Reynolds number range at the start of feeding.

Newly hatched larvae, about 3 mm long, only move in the viscous zone at swimming speeds up to about 1 body length per second (Figure 1). Routine swimming is primarily in the intermediate zone for the first few weeks of life. However, even earliest yolk-bearing larvae can accelerate to speeds high enough to swim at $R_L \gg 200$ (Webb and Corolla 1981).

The Reynolds number not only illustrates the nature and magnitude of resistive forces, it is also useful, for similar reasons, in considering the mechanics of propulsors. Three hydrodynamic approaches are used to understand relations between undulatory body–caudal fin propulsors (the usual propulsion mechanism for larvae) and the water. These approaches are (a) resistive, (b) reactive, and (c) lift models (see Lighthill 1975, Wu et al. 1975, and Yates 1983 for details).

The resistive model describes resistance forces that counteract movements of the body; a component of these forces contributes to thrust. The force acting at any point on the body can be resolved into components normal and parallel to the surface. The normal component is approximately twice as large as that parallel to the surface. Therefore, pushing or paddling motions are preferred at low R_L, which can be achieved for body–caudal fin undulation by large-amplitude waves passing along the body. The body and tail should be flexible along the body length so that each section can more effectively push water backwards relative to the direction of motion. Such swimming movements are described as eel-like, or anguilliform, motions characterized by two or more half-wavelengths within the length of the body and large-amplitude lateral movements over most of the body length (Lighthill 1975).

The reactive model describes the forces acting on the body due to the acceleration of water by body movements. It is most appropriate at higher R_L for trout-like swimmers (historically, subcarangiform propulsion: Breder 1926; Yates 1983) whose tail-beat amplitude increases rapidly over the posterior one-half to one-third of the body and whose body cross-sections are compressed or extended by median fins.

Larvae swim in the intermediate R_L zone where both resistive and reactive forces contribute to thrust. Vlymen (1974) calculated that about a third of the total thrust would result from resistive forces

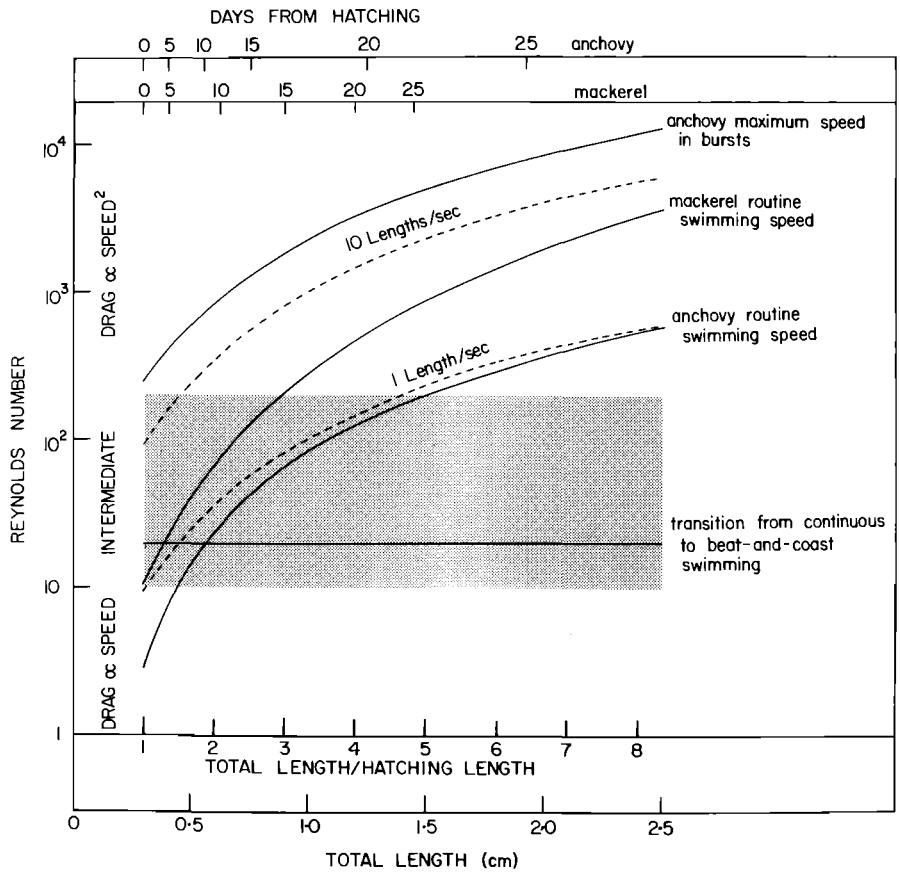

FIGURE 1.—Relationships between length of larvae and Reynolds number (based on total length) to show the various hydrodynamic zones occupied during development. The dotted lines show relationships for speeds of 1 and 10 lengths per second, speeds frequently considered typical of routine and maximum sprint activity. Lengths are shown as absolute values and as multiples of length at hatching, and a time scale is included at the top for northern anchovy *Engraulis mordax* and chub mackerel *Scomber japonicus*. Data were obtained from Hunter (1972, 1976), Weihs (1980a), Webb and Corolla (1981), and Hunter and Kimbrell (1980).

for northern anchovy *Engraulis mordax* at routine swimming speeds of 14-mm-long larvae. This proportion would probably be larger for smaller larvae, but lower at sprint speeds.

The lift model concerns discrete fins that act like hydrofoils to generate a lift force, a large component of which is thrust. The lunate tail has been studied most (Yates 1983), and is characteristic of fish such as tunas (Scombridae). Lift is generated when a certain flow pattern (circulation) is established outside the boundary layer of appropriately shaped bodies such as fins, oriented at a small angle to the flow. The Reynolds number, R_C, is now based on the mean length or chord C of the fin used to generate lift. The R_C must be in the hundreds, and preferably greater than 1,000 before lift-based mechanisms can be effective (Prandtl and Tietjens 1934; Von Mises 1959; Ellington 1984). Furthermore, because R_C is calculated on the basis of fin chord, it will be at least an order of magnitude lower than R_L for a given fish. The fin chords of early larvae are small and larva speeds are low, so lift-based propulsors are not expected.

In general, fish spend most of their first few weeks swimming at intermediate R_Ls. However, all are capable of swimming at high R_L, when inertial forces are dominant. Furthermore, the high R_Ls occur during activities that are crucial for survival. Larvae fleeing particle-feeding predators swim at high speeds (Webb 1981) typical of bursts of swimming such as those illustrated for northern anchovy larvae in Figure 1. Similar high levels of performance probably affect vulnerability to vertebrate filter feeders and nets (Webb and Corolla

1981) and presumably invertebrate predators such as chaetognaths. Burst speeds of yolk-bearing larvae would be required to escape relatively slow invertebrate filter feeders such as *Aurelia* medusae (Bailey and Batty 1983) because larva speeds are small compared to the dimensions of the bell they must avoid. Finally, burst performance is used to capture food particles (Rosenthal and Hempel 1970; Hunter 1972, 1981).

The above discussion suggests that larvae and adults move in the same hydrodynamic zone for locomotor behaviors important for survival. This conclusion has some support in observations on the development of larva swimming behavior. Hunter (1972) described a shift in swimming behavior of northern anchovy, and Weihs (1980a) showed this is related to changes in the hydrodynamic regime, as characterized by R_L. Thus, at $R_L < 20$, larvae tend to be stationary between occasional periods of continuous swimming. At $R_L > 20$, beat-and-coast swimming occurs. The latter reduces the net cost of transport when inertial forces are larger than viscous forces. Thus, routinely swimming larvae behave as if inertial forces were most important at $R_L > 20$, and hence through most of the intermediate zone.

Because adults and larvae move in the same hydrodynamic regime for important activities, locomotor form and behavior of all life history stages should be subject to similar physical constraints and form should reflect the effects of analogous selective pressures. Under these circumstances, the principles used to elucidate the functional morphology of adults should be applicable throughout ontogeny, such that similar forms correlate with similar behavior.

Young fish grow into adults, so that the parental form is the terminus for all development trajectories. Most fish also lack true metamorphosis (Balon 1975), so that the degree of structural variability during development cannot be very large. As a result, larvae are expected to be more similar to their parents than to other larvae. This implies that larvae should differ among each other in form and behavior in the same way as their parents, as found for the body form of cottids by Strauss and Fuiman (1985). Therefore, the simplest starting framework for studying locomotor development takes parental forms, for which there are many data, as references, and determines how form approaches this reference during development. The analysis consequently identifies relevant similarities and differences while providing tools to assist in evaluating their functional importance.

Body and Fin Form

Before discussing how form changes during development, we must establish relationships between form and swimming activity. Recent theoretical and experimental studies and various field observations on juvenile and adult fish suggest that the functional locomotor morphology of most bony fish can be understood in terms of three activity patterns. These are (1) *transient swimming* during acceleration and powered turns, (2) *periodic* or *cyclic swimming* during cruising and sprinting at relatively constant speed, and (3) *slow swimming* and maneuvering (Webb 1984a, 1984b). It has become traditional to use exemplary species to name morphologies associated with various locomotor patterns, and those relevant here are included in Table 1. Each of these activities is distinct in the way thrust is generated and in the nature of resistance forces. Consequently each is distinct in the structures and forms that are optimal for the activity. Furthermore, optimal body–fin shapes and configurations along the body length are mutually exclusive for each of the three activity patterns (Weihs 1972, 1973; Lighthill 1975; Webb 1982, 1984a, 1984b) so that fish emphasizing a form correlating with one of the three activity patterns sacrifices performance in the others. Such fish are defined as specialists for an activity. Most fish have body–fin forms that show characters intermediate among those of specialists. These are generalists in that they perform in several areas of locomotor activity, although performance in each area is lower than that of the relevant specialist. Locomotor specialists illustrate most clearly how principles of drag, thrust, and form correlate, and developmental changes are most appropriately examined in these groups.

Many characters could be used to quantify the functional morphology of fish (Table 1). In practice, many individual structural traits are correlated within a functional type. Therefore, morphologies can be identified with a few simple measures. Furthermore, the hydrodynamic regimes of adults and feeding larvae are described in terms of Reynolds number, based on the same characteristic dimension (total length), when morphologies of these life history stages should be described by similar characters. On the basis of hydrodynamic theories for thrust and drag and examination of the measures of form listed in Table 1, we suggest that most developmental trajectories can be described with as few as three characters. These are described below, together with a

TABLE 1.—Body form characters of teleostean locomotor specialists for three activity patterns. Characters are the main entries; a method of quantifying each is shown in parentheses.[a] The mechanical basis for the characters and their measurement are described elsewhere (Weihs 1972, 1973; Lighthill 1975; Webb 1982, 1984a).

CHARACTER (index)[a]	Thunniform (cruiser)	Esociform (accelerator)	Chaetodontiform (maneuverer)
Body shape (shape factor)	Streamlined (intermediate)	Elongate (large)	Gibbose (small)
Caudal peduncle (d_{cp}/d_b)	Narrow (small)	Deep (large)	Intermediate (intermediate)
Caudal fin (aspect ratio)	Lunate (large)	Rounded or square shape; indented or square trailing edge (small)	Rounded or square shape; indented or square trailing edge (small)
Effective area of posterior of body (transient swimming thrust factor)	Small (small)	Large (large)	Intermediate (intermediate)
Muscle mass (percent muscle mass)	Large (large)	Large (large)	Small (small)
Position of dorsal fin(s) (L_a/L_t) and (L_p/L_t)	Anterior (small) (small)	Posterior (large) (large)	Anterior to posterior (small) (large)
Location of pectoral fins (L_{pec}/L_t)	Various (various)	Various (various)	Lateral (small)
Location of pelvic fins (L_{pel}/L_t) and (d_{pel}/d_b)	Various (various) (various)	Various (various) (various)	Anterior and ventrolateral (small) (small)

[a] Key:
d_{cp} depth of caudal peduncle.
d_b maximum depth of body.
d_{pel} distance of pelvic fins from ventral surface.
L_a distance from nose to anterior edge of dorsal fin.
L_p distance from nose to posterior edge of dorsal fin.
L_{pec} distance from nose to pectoral fin base.
L_{pel} distance from nose to pelvic fin base.
L_t total length.

fourth to examine a special case for lift-based propulsors.

In order to facilitate comparisons over the wide range of sizes of larvae and of adult fishes, each measure of body and fin form is reduced to a nondimensional factor by standardizing with appropriate dimensions of the fish. A nondimensional length is also obtained by dividing total length, L, by the average length at hatching, L_h.

The three primary measures of locomotor body–fin form used are as follows.

Caudal peduncle depth factor is the ratio of the minimum depth of the caudal peduncle to the maximum depth of the body. The ratio would be more appropriately based on caudal fin depth instead of body depth, but this would make the measure particularly sensitive to the quality of larval material and the methods used in the single measure of caudal fin depth. However, it is usually desirable for the tail to span the wake generated by sharp anterior edges in order to maximize potential advantages to thrust and drag from wake interactions (Lighthill 1975); under such conditions, caudal fin depth should be correlated with body depth. The use of maximum body depth is, therefore, a pragmatic compromise least likely to be affected by methods and material. The caudal peduncle depth factor will be most effective in characterizing thunniform (tuna-like) fish, for which it takes small values. These fish use an axially oscillating caudal fin to generate large thrust forces for cruising and sprinting at relatively constant high speed. A relatively small caudal peduncle is necessary for the fin motions required to generate lift, to reduce drag where this resistance force is increased most due to propulsive movements, and to reduce energy-wasting recoil movements (Lighthill 1975).

Body shape factor is the ratio of total length to maximum body depth. The shape factor is well known as one measure of streamlining (fineness ratio), but the measure is used here as a simple body shape character. Low values are typical of chaetodontiform fish, slow-swimming maneuverers named after butterflyfish (Chaetodontidae). The truncated, gibbose body of these fish minimizes resistance during turns about the body axis (Alexander 1967) while providing for the insertion of various median and paired fins around the center of mass to generate thrust forces in a wide range of directions (Webb 1975, 1984a).

Transient swimming thrust factor was devel-

oped to identify such transient swimmers as esociform or pike-like fishes (Esocidae) that use short, nonrepeating bursts of activity in fast starts and powered turns. Each small length of the body, called a propulsive element, contributes to mean thrust. The force on each propulsive element is proportional to the mass and acceleration of the water influenced by the element's motion (Weihs 1972, 1973). The mass of water affected is the added mass:

$$m_a \propto \rho \cdot d^2; \quad (2)$$

m_a = added mass per unit length;
ρ = density of water;
d = depth of the element.

The acceleration given to the water by a propulsive element depends on the amplitude of the element's motion. The amplitude of lateral movements of the body tends to increase during swimming as a quadratic function with distance over the posterior of the body (see figures in Weihs 1973, Webb 1976, Videler 1981, and Batty 1984). Therefore, more posterior propulsive elements of a given size will give a greater acceleration to the water and hence contribute more to thrust. As a result, the transient swimming thrust factor was determined to account for both the depth and the position of propulsive elements.

The transient swimming thrust factor was measured as follows. The posterior two-thirds of the body length was divided into 10 vertical strips of equal width. Emphasis on the posterior portion of the body that generates thrust, generally the part posterior to the center of mass, simplifies the calculation. The depth was measured for the anterior and posterior edges of each strip, and the mean depth was taken as the average of these two values. The added mass associated with each strip was then calculated by equation (2) and the length of a strip. These results for the added mass were weighted by multiplying the added mass by the square of the element number, the trailing edge element being the tenth. The numerical integral of these 10 estimates of the relative thrust represents the potential of the longitudinal profile of the fish to generate thrust in transient swimming.

The resistance to acceleration is a function of fish mass, which is usually not known with accuracy for larvae. However, mass will be proportional to volume. A volume measure was calculated as the product of total length and maximum body depth squared. In the absence of adequate data for the width of fish, depth was arbitrarily substituted.

The transient swimming thrust factor is the numerical integral of the weighted added masses of the posterior strips divided by the volume (mass) measure. Hence, it is a ratio of those factors dominating thrust to those dominating resistance. The transient swimming thrust factor should be large in esociform fish because a large caudal area is required to generate large forces for high performance in linear and centripetal acceleration. Thunniform fish will have low values for this factor because of their reduced caudal areas; chaetodontiform fish should have low values because their bodies tend to be relatively short.

The fourth factor measured was the *aspect ratio* of the tail, defined as the area of the tail divided by the square of the tail depth (Von Mises 1959).

Appropriate data to determine changes in form of larvae during development of representatives of the principal locomotor patterns are rare, but can be found in works on systematics. The paucity of data is due in large part to the difficulty of collecting and identifying the larvae of the species of greatest interest here. Measurements of larvae and adults were made from published drawings of larval tunas (Fahay 1983), northern pike *Esox lucius* (Fuiman 1982), and sunfish *Lepomis* spp. (Hardy 1978). The centrarchid sunfish were selected to represent chaetodontiform fish because adequate material could not be located for chaetodontids. The systematic drawings represent compilations of many different individual larvae collected in different areas with various gear, preserved by various methods, and drawn after various periods of time. All these factors affect the quality of the material, and substantial variation in the data is to be expected. The limited number of samples relevant to the current problem and the variation in the quality of material mean that the following analysis and discussion must be considered preliminary and suggestive. We hope they lead to directed studies that address the problems and hypotheses raised by the existing limited observations.

Ontogenetic Changes in Body and Fin Shape

Larvae are initially similar to each other, and begin to diverge in form when they reach a length of approximately 1.5 times hatching length L_h (Figure 2), close to the size at which first feeding occurs. Although observations on the length of

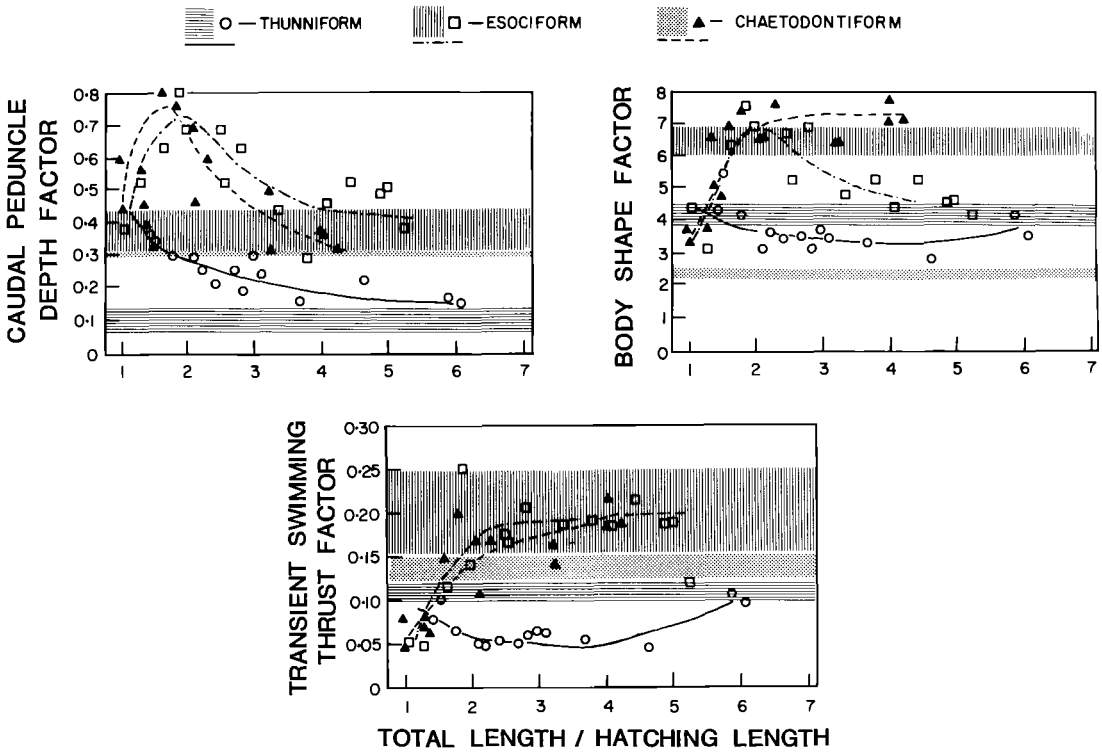

FIGURE 2.—Three form factors related to the functional locomotor morphology of larval fish from thunniform, esociform, and chaetodontiform adults. Parental values are shown by the shaded strips. The caudal peduncle depth factor is minimum peduncle depth/maximum body depth; the body shape factor is total body length/maximum body depth; the transient swimming thrust factor is capacity for thrust/resistance.

larvae at first feeding are more sparse than those on length at hatching, first-feeding lengths average $1.6L_h$ (range 1.2 to 2.2) for groups illustrated in Figure 2 (Hardy 1978; Fuiman 1982; Fahay 1983).

For thunniform species, form factors attain adult values by a length of about $6L_h$, except for the aspect ratio of the caudal fin. This begins to diverge from that of other larvae at 4 to $5L_h$ (Figure 3), but does not reach adult proportions during the larva stages.

For esociform species, caudal peduncle depth and transient swimming thrust factors also attain adult values by $6L_h$. The caudal peduncle depth factor initially diverges from values for the adults, due to the persistent large depth of the fin fold associated with the development of the median fins close to the caudal peduncle. The larvae measured are also deeper anteriorly in the gut region than adults, resulting in smaller shape factors. This may relate to the fullness of the gut.

Development patterns of larval sunfish (chaetodontiform) are similar to those of the esociform larvae, and hence do not converge with the adults for any of the form factors. Instead, the various factors diverge from expectations based on the adults up to a length of $3L_h$. Only the caudal peduncle depth factor declines towards adult values within the larva period.

Discussion

These measurements of the body form factors were undertaken to examine the utility of a framework for identifying functional patterns during fish development. The framework is based on the similarity of hydrodynamic regimes for critical activities through ontogeny to the parental forms. Any such framework must not only allow patterns of similarities, differences, and apparent discrepancies in form and function to be analyzed quantitatively, it must also facilitate their explanation. The above analysis shows similarities in the form of the yolk-bearing larvae and in the developmental pattern of fusiform species. A discrepancy is found in the delayed development of the caudal

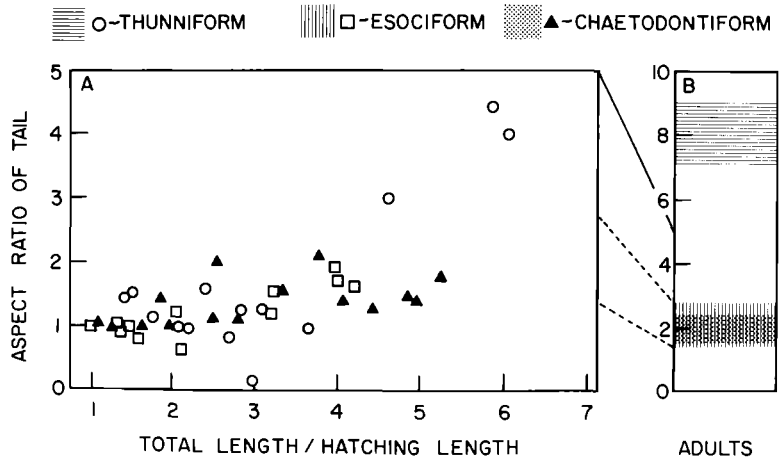

FIGURE 3.—Relationships between body size and the aspect ratio of the tail (caudal fin area/square of fin depth) for the larvae of thunniform, esociform, and chaetodontiform adults.

fin in young of thunniform species compared to other characters of these species, and a difference is found in the pattern of development of chaetodontiform species. We examine these in turn.

The dominant external morphological features of yolk-bearing larvae are the yolk sac and the fin fold. Feeding is unnecessary and sensory–motor systems are still undergoing rapid development (Eaton et al. 1977; O'Connell 1981; Webb 1981; Forstner et al. 1983). A large fin fold might develop large thrust forces to accelerate away from predators, but mortality of these larvae is similar to that of eggs (Hunter 1984) so the motor system has little demonstrable utility in reducing predation. Thus, there appears to be little locomotor reason for the presence of a fin fold in these early larvae.

Alternatively, the fin fold might be essential for locomotor functions after the yolk-bearing stages. It might be necessary to generate large thrust forces in the acceleration lunges characteristic of feeding (Rosenthal and Hempel 1970; Hunter 1972; Hunter and Kimbrell 1980). If this were the case, however, one would expect the fin fold to be retained or even expanded at the time of first feeding whereas, in practice, differentiation begins at or before this time (Figure 2; Balon 1975). In addition, general retention of a large fin fold through first feeding would exclude other body and fin forms, such as those of thunniform fish, that are associated with various prey search and capture strategies, and hence would preclude different ecological roles among larvae (Hunter 1972, 1981; Hunter and Kimbrell 1980). The fin fold is generally considered to be important in the evolution of such diverse fin patterns. Although the fin fold undoubtedly allows the development of a wide range of median fin patterns and associated behaviors among species, it is hardly necessary for any discrete median fin configuration. It seems more likely that the fin fold serves a nonlocomotor function.

The common body–fin shape of yolk-bearing larvae is likely to be related to common, nonlocomotor problems. One such problem for early larvae appears to be respiration (Weihs 1980a, 1980b; Liem 1981). The metabolic rate of eggs increases during embryogenesis and plateaus as hatching approaches; metabolism increases thereafter in larvae (Hempel 1979). The leveling-off of metabolic rate before hatching is attributed to limiting diffusion resistance of the egg membranes (Robertson 1974; Hempel 1979). The gills develop relatively slowly (Webb and Brett 1972; Batty 1984) and probably would not be very effective at very low Reynolds numbers for small larvae (Langille et al. 1983). Therefore, it seems likely that hatching of altricial young of most bony fish is related to oxygen needs and that the fin fold is a necessary gas exchange area (Liem 1981).

With the onset of feeding, locomotion becomes important in locating and catching prey, and body forms and foraging behaviors diverge (Figure 2; Hunter 1981). It is important to recognize that substantial energetic advantages can accrue to foraging larvae from beat-and-coast swimming behavior, if larvae can achieve sufficiently large R_L. Increasing foraging speed would be one way to

achieve higher R_L, but would be the least likely means of doing so. The length of the glide would not be improved much and, in addition, drag begins to increase with the square of speed. It would be energetically most economical to increase R_L by increasing length, which suggests that there should be a minimum length that first-feeding larvae should achieve to minimize foraging costs. The advantages that accrue with large R_L are first felt in the R_L range of 10 to 20. Therefore, at typical foraging speeds of larvae, the minimum size is about 3 mm. Most first-feeding larvae are larger (Fritzsche 1978; Hardy 1978; Martin and Drewry 1978; Fuiman 1982; Fahay 1983). There are some exceptions. White mullet *Mugil curema* are reported to complete the yolk-bearing stages at 2.5 to 2.7 mm (Martin and Drewry 1978), when feeding presumably begins. Such exceptions warrant further study to determine if small larvae do forage at relatively higher speeds, and if this affects early growth rates. In general, however, a variety of mechanisms should be expected to increase length, and hence R_L, at first feeding. The change in shape of larvae from the more spherical form of slow-swiming yolk-bearing larvae to the elongate form of feeding larvae also results in a change in the characteristic dimension, leading to a higher R_L, as mentioned above. Early larvae are typically elongate with a relatively small depth so food material may be preferentially used to grow in length, adjustments in body dimensions occurring later (Fuiman 1983). Indeed, Fuiman (1983) speculated that the elongation of larvae compared to adults might relate to larva locomotion. The large increase in the water content of larvae (Brett 1983) may facilitate increase in length without large demands on limited materials. Such questions are extremely speculative, but warrant further research.

A second problem focused by the analysis of form during development is the late differentiation of the caudal fin of thunniform species. A high aspect ratio for the caudal fin is characteristic of thunniform adults (Table 1; Lindsey 1978). The late development of the caudal fin is presumably related to the poor effectiveness of lift mechanisms at very low R_C. If so, the timing of the onset of differentiation of a high-aspect-ratio tail should occur when R_C takes values in the higher hundreds, perhaps greater than 500. The problem then becomes to determine if tail development occurs as larvae grow into the required hydrodynamic regime.

A first crude estimate of larva size at which the tail should differentiate can be made. Hunter and Kimbrell (1980) measured the relationship of tail-beat frequency and amplitude with swimming speed for chub mackerel larvae *Scomber japonicus* of 4.3 mm standard length. Chub mackerel are not thunniform but are structurally less specialized cruisers, and use of data from this species should give conservative results. Hunter (1972) found tail-beat frequency and amplitude were independent of size for northern anchovy, and a conservative assumption would be that the same applies to chub mackerel. Hunter's data give

$$f \cdot a = 1.47 + 0.72U; \tag{3}$$

f = tail-beat frequency (Hz);
a = tail-beat amplitude (cm);
U = swimming speed (cm/s).

Equation (3) can be used to calculate the lateral velocity of the tail, if simple harmonic motion is assumed, and hence the resultant velocity of the caudal fin at any swimming speed. For estimates of R_C, sprint speeds would provide a boundary on values at any size. Sprint speeds are not known for thunniform larvae, so again use, probably conservative, was made of northern anchovy maximum speeds (Webb and Corolla 1981).

The caudal fin chord length C is related to length of tuna larvae according to

$$C = 0.077L^{0.29}. \tag{4}$$

The Reynolds number R_C (equation 1) for tuna larvae increases rapidly during development (Figure 4) and reaches minimal values required for a lift-based propulsor to work at sprint speeds when L/L_h is about 5, similar to the size at which the caudal fin aspect ratio increases. Although the calculation of R_C is extremely crude, it suggests that differentiation of the caudal fin is related to the hydrodynamic regime, and strongly suggests that further research might lead to an explicit test of the hypothesis.

A third problem revealed by the analysis of changes in form is the developmental pattern of the chaetodontiform larvae, which showed no convergence with parental form factors over the size range studied, although convergence obviously must occur when a large enough size range is examined. This is probably related in part to resistance penalties associated with such a form for larvae. The compressed, gibbose body form of chaetodontiform adults has a large surface area compared to the muscle mass, and the locomotor muscle is a small proportion of total body mass

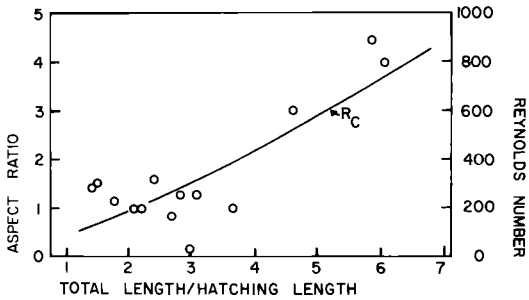

FIGURE 4.—Relationship between size of tuna larvae and both aspect ratio of the caudal fin and Reynolds number R_C at sprint speeds.

(Webb 1978). This means that the ratio of thrust to resistance is small for both transient and periodic swimming activities. For larvae with a chaetodontiform shape, the frictional resistance would be particularly great because drag coefficients are large at low R_L (Prandtl and Tietjens 1934). This might represent an excessive energy drain when relatively long periods are spent searching for food, as expected for larvae because of their high total energy requirements, small sighting distances, and low food-capture success rates. However, other factors are involved. Adult chaetodontiform fish live in habitats with many small or encrusting food items, often in structurally complex locations, where maneuverability is essential for feeding (O'Brien 1979; Webb 1984a). Analogous habitats on a comparable scale are not available for larvae, which are often pelagic and occupy habitats that, on their scale, are more homogeneous.

Parental diet options are also not available for the larvae of chaetodontiform fish. Compared with chaetodontiform adults, larvae feed on items that are always relatively large and, when motile, relatively fast. As a result, larvae strike at their food using fast starts that are not only mechanically similar among larvae (Rosenthal and Hempel 1970; Hunter 1972; Hunter and Kimbrell 1980) but also similar to strikes made by adult fish at prey with the same characteristics of relative size and mobility (Weihs and Webb 1983). The thunniform and esociform adults and their larvae take prey with similar relative (i.e., scaled) characteristics, and convergence of larva and adult form factors is not surprising. Chaetodontiform adults and their larvae consume food with different characteristics, so differences in form are not unexpected. Therefore, the developmental pattern of chaetodontiform larvae appears to be related to diet options made possible by increasing size during ontogeny.

Locomotor morphology of the larvae of fusiform species rapidly converges with adults. In certain situations, this should substantially influence life history patterns. The greatest problems are likely to occur for thunniform animals because their shape is specialized for constant high speed swimming but is not conducive to the high rates of acceleration commonly employed in predator avoidance (Weihs and Webb 1983). Although predator pressure on adults is likely to be small because of their size, larvae and juveniles are particularly vulnerable. Under these circumstances, life history strategies should minimize vulnerability of early stages. Nonteleostean thunniform animals (elasmobranchs, extinct ichthyosaurs, and cetaceans) are viviparous (Breder and Rosen 1966; Romer 1966) so that young must fend for themselves only after reaching relatively large sizes. Tunas, in contrast, reduce the period of vulnerability by spawning in warm, locally productive patches where high foraging speeds and large mouth and prey size lead to extremely rapid growth. As a result, tunas typically attain lengths of 30 to 40 cm by the end of their first year (Fritzsche 1978). Relationships between functional properties of fish larvae and life history strategies seem likely to be a particularly rewarding area for research in fish.

Conclusions

The objective of this paper was to establish a framework to identify and interpret locomotor development during the early life history of fishes. Based on the hydrodynamic environment and observed performance levels in various behaviors, we argue that the hydrodynamic environment for critical activities is constant through ontogeny. This appears to be correct within certain constraints, reservations that are usual and taken into account in interpreting results in functional morphological studies. First, a propulsor must be mechanically feasible, which is not the case for lift-based mechanisms in small larvae. Second, high performance levels must be possible and essential for survival, which apparently does not apply to yolk-bearing larvae. Third, different requirements at various life history stages, especially in terms of diet characteristics, may result in different optimal forms at different times, and hence developmental trajectories that diverge from direct paths to adult forms. The need to expand fields of inquiry in functional morphology to recognize multiple system needs (Gans, in press), however, does not negate a more restricted study, provided integration is ultimately made at the organismic level. Indeed,

by targeting a study on an initially restricted area (here locomotor structure), the relative importance of other functions (e.g., feeding) and situations (e.g., development patterns in larvae and parents with different diet breadths) can be focused. Therefore, the simple approach described above undoubtedly has utility and could be used more extensively to explore the biology of early life stages.

However the previous discussion has two weaknesses: it is based on the very limited and variable data that are currently available, as discussed above; and it emphasizes morphology. This approach is necessary at this time. Nevertheless, there is an implicit assumption that larvae behave as expected from their structure alone. The only data on this point are those on beat-and-coast swimming (Weihs 1980a) and observations on foraging by chub mackerel and northern anchovy (Hunter 1981). On the basis of structure, chub mackerel would be expected to be the superior cruisers and hence forage more widely and at higher speeds than northern anchovy (Webb 1984a). Larval forms of these species do indeed separate in the same way as adult forms; chub mackerel larvae and adults have different foraging patterns from northern anchovy as expected from their structures (Hunter 1981). Therefore, the little evidence available suggests that form and function are well correlated. However, this hardly mitigates the weakness of an approach that focuses on form alone. It is clear that comparative studies are essential on form, kinematics, and performance, especially on the ontogenetic changes in those motor activities stimulated by predators and feeding.

Acknowledgments

We thank Lee A. Fuiman, for his critique of the manuscript, and R. Lasker and J. R. Hunter, who share equal blame for introducing us to fish larvae. D. Weihs thanks the National Research Council and the National Aeronautics and Space Administration–Ames for providing the opportunity for this research. This work was supported by National Science Foundation grants PCM77-14664 and PCM-8401650.

References

Alexander, R. McN. 1967. Functional design in fishes. Hutchinson, London.

Bailey, K. M., and R. S. Batty. 1983. A laboratory study of predation by *Aurelia aurita* on larval herring (*Clupea harengus*): experimental observations compared with model predictions. Marine Biology 72: 295–301.

Balon, E. K. 1975. Terminology of intervals in fish development. Journal of the Fisheries Research Board of Canada 32:1663–1670.

Batty, R. S. 1981. Locomotion of plaice larvae. Symposium of the Zoological Society of London 48:53–69.

Batty, R. S. 1984. Development of swimming movements and musculature of larval herring (*Clupea harengus*). Journal of Experimental Biology 110:217–229.

Breder, C. M. 1926. The locomotion of fishes. Zoologica 4:159–256.

Breder, C. M., and D. E. Rosen. 1966. Modes of reproduction in fishes. American Museum of Natural History, Garden City, New York.

Brett, J. R. 1983. Life energetics of sockeye salmon, *Oncorhynchus nerka*. Pages 29–63 *in* W. P. Aspey and S. I. Lustick, editors. Behavioral energetics. Ohio State University Press, Columbus.

Eaton, R. C., R. D. Farley, C. B. Kimmel, and E. Schabtach. 1977. Functional development in the Mauthner cell system of embryos and larvae of the zebra fish. Journal of Neurobiology 8:151–172.

Ellington, C. P. 1984. The aerodynamics of hovering insect flight. Philosophical Transactions of the Royal Society of London B, Biological Sciences 305:1–181.

Fahay, M. P. 1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. Journal of Northwest Atlantic Fishery Science 4:1–423.

Feder, M. E., and G. V. Lauder. 1985. Predator–prey relationships. Chicago University Press, Chicago.

Forstner, H., S. Hinterleitner, K. Mahr, and W. Weiser. 1983. Towards a better definition of "metamorphosis" in *Coregonus* sp.: biochemical, histological, and physiological data. Canadian Journal of Fisheries and Aquatic Sciences 40:1224–1232.

Fritzsche, R. A. 1978. Development of fishes of the Mid-Atlantic Bight. V. Chaetodontidae through Ophidiidae. U.S. Fish and Wildlife Service Biological Services Program FWS/OBS-78/12.

Fuiman, L. A. 1982. Esocidae. Pages 155–173 *in* N. A. Auer, editor. Identification of larval fishes of the Great Lakes Basin with emphasis on the Lake Michigan drainage. Great Lakes Fishery Commission Special Publication 82-3, Ann Arbor.

Fuiman, L. A. 1983. Growth gradients in fish larvae. Journal of Fish Biology 23:117–123.

Gans, C. In press. Functional morphology as a tool in the study of predator–prey interactions. *In* M. E. Feder and G. V. Lauder, editors. Predator–prey relationships. Chicago University Press, Chicago.

Hardy, J. D. 1978. Development of fishes of the Mid-Atlantic Bight. III. Aphredoderidae through Rachycentridae. U.S. Fish and Wildlife Service Biological Services Program FWS/OBS-78/12.

Hempel, G. 1979. The early life history of marine fish. The egg stage. University of Washington Press, Seattle.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological

research. Rapports et ProcèsVerbaux des Réunions, Internationale Conseil pour l'Exploration de la Mer 20:1–228.

Hunter, J. R. 1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. U.S. National Marine Fisheries Service Fishery Bulletin 70:821–838.

Hunter, J. R. 1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. U.S. National Marine Fisheries Service Fishery Bulletin 74:81–88.

Hunter, J. R. 1981. Feeding ecology and predation of marine fish larvae. Pages 33–77 *in* R. Lasker, editor. Marine fish larvae. University of Washington Press, Seattle.

Hunter, J. R. 1984. Inferences regarding predation on the early life stages of cod and other fishes. Flodevigen Rapportserie 1:533–562.

Hunter, J. R., and C. A. Kimbrell. 1980. Early life history of Pacific mackerel, *Scomber japonicus*. U.S. National Marine Fisheries Service Fishery Bulletin 78:89–101.

Langille, B. L., E. D. Stevens, and A. Anantaraman. 1983. Cardiovascular and respiratory flow dynamics. Pages 92–139 *in* P. W. Webb and D. Weihs, editors. Fish biomechanics. Praeger Scientific, New York.

Liem, K. F. 1981. Larvae of air-breathing fishes as counter-current flow devices in hypoxic environments. Science (Washington, D.C.) 211:1177–1179.

Lighthill, M. J. 1975. Mathematical biofluiddynamics. Society for Industrial and Applied Mathematics, Philadelphia.

Lindsey, C. C. 1978. Form, function, and locomotory habits in fish. Pages 1–100 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology, volume VII. Locomotion. Academic Press, New York.

Martin, F. D., and G. E. Drewry. 1978. Development of fishes of the Mid-Atlantic Bight. VI. Stromateidae through Ogcocephalidae. U.S. Fish and Wildlife Service Biological Services Program FWS/OBS-78/12.

O'Brien, W. J. 1979. The predator–prey interaction of planktivorous fish and zooplankton. American Scientist 67:572–581.

O'Connell, C. P. 1981. Development of organ systems in the northern anchovy, *Engraulis mordax*, and other teleosts. American Zoologist 21:429–446.

Prandtl, L., and O. G. Tietjens. 1934. Applied hydro- and aeromechanics. Dover, New York.

Robertson, D. A. 1974. Developmental energetics of the southern pigfish (Teleostei: Congiopodidae). New Zealand Journal of Marine and Freshwater Research 8:611–620.

Romer, A. S. 1966. Vertebrate paleontology. University of Chicago Press, Chicago.

Rosenthal, H., and G. Hempel. 1970. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus*). Pages 344–364 *in* J. H. S. Steele, editor. Marine food chains. University of California Press, Berkeley.

Strauss, R. E., and L. A. Fuiman. 1985. Quantitative comparisons of body form and allometry in larval and adult Pacific sculpins (Teleostei: Cottidae). Canadian Journal of Zoology 63:1582–1589.

Videler, J. J. 1981. Swimming movements, body structure and propulsion in cod *Gadus morhua*. Symposium of the Zoological Society of London 48:1–27.

Vlymen, W. J. 1974. Swimming energetics of the larval anchovy, *Engraulis mordax*. U.S. National Marine Fisheries Service Fishery Bulletin 72:885–899.

Von Mises, R. 1959. Theory of flight. Dover, New York.

Webb, P. W. 1975. Hydrodynamics and energetics of fish propulsion. Fisheries Research Board of Canada Bulletin 190.

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. Journal of Experimental Biology 65:157–177.

Webb, P. W. 1978. Fast-start performance and body form in seven species of teleost fish. Journal of Experimental Biology 74:211–226.

Webb, P. W. 1981. Responses of northern anchovy, *Engraulis mordax*, larvae to predation by a biting planktivore, *Amphiprion percula*. U.S. National Marine Fisheries Service Fishery Bulletin 79:727–735.

Webb, P. W. 1982. Locomotor patterns in the evolution of actinopterygian fishes. American Zoologist 22:329–342.

Webb, P. W. 1984a. Body form, locomotion and foraging in aquatic animals. American Zoologist 24: 107–120.

Webb, P. W. 1984b. Form and function in fish swimming. Scientific American 251(7):72–82.

Webb, P. W. In press. Locomotion and predator–prey relationships. *In* M. E. Feder and G. V. Lauder, editors. Predator–prey relationships. Chicago University Press, Chicago.

Webb, P. W., and J. R. Brett. 1972. Respiratory adaptations of prenatal young in the ovary of two species of viviparous seaperch, *Rhacochilus vacca* and *Embiotoca lateralis*. Journal of the Fisheries Research Board of Canada 29:1525–1542.

Webb, P. W., and R. T. Corolla. 1981. Burst swimming performance of northern anchovy, *Engraulis mordax*, larvae. U.S. National Marine Fisheries Service Fishery Bulletin 79:143–150.

Weihs, D. 1972. A hydrodynamic analysis of fish turning manoeuvres. Proceedings of the Royal Society of London B, Biological Sciences 182:59–72.

Weihs, D. 1973. The mechanism of rapid starting of slender fish. Biorheology 10:343–350.

Weihs, D. 1980a. Energetic significance of changes in swimming modes during growth of anchovy larvae, *Engraulis mordax*. U.S. National Marine Fisheries Service Fishery Bulletin 77:597–604.

Weihs, D. 1980b. Respiration and depth control as possible reasons for swimming of northern anchovy, *Engraulis mordax*, yolk-sac larvae. U.S. National

Marine Fisheries Service Fishery Bulletin 78:109–117.

Weihs, D., and P. W. Webb. 1983. Optimization of locomotion. Pages 339–371 *in* P. W. Webb and D. Weihs, editors. Fish biomechanics. Praeger Scientific, New York.

Wu, T. Y. 1976. Introduction to the scaling of aquatic animal locomotion. Pages 203–232 *in* T. J. Pedley, editor. Scale effects in animal locomotion. Academic Press, New York.

Wu, T. Y., C. J. Brokaw, and C. Brennen. 1975. Swimming and flying in nature. Plenum Press, New York.

Yates, G. T. 1983. Hydrodynamics of body and caudal fin propulsion. Pages 177–213 *in* P. W. Webb and D. Weihs, editors. Fish biomechanics. Praeger Scientific, New York.