AMER. ZOOL., 28:709–725 (1988)

Simple Physical Principles and Vertebrate Aquatic Locomotion[1]

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SYNOPSIS. Swimming is a common and important component of vertebrate behavior. Therefore the study of swimming form and function is essential to understanding vertebrate biology. An interactive process between biologists and hydrodynamicists has proven extremely successful in providing such understanding. This process starts with a definition of forces that may act on an animal; viscous and pressure drag, acceleration reaction, lift and body inertia, and ground reaction. Dominant force components are selected on the basis of ground contact, Reynolds number, reduced frequency, and shape. Conservation of momentum requires forces and their moments be in balance leading to models describing swimming motions and associated forces. These provide the bridge between the hydrodynamics studies and biological applications. Numerical solutions to models estimate thrust and drag, and rates of working, which are several times greater than expected for man-made non-flexing bodies. These solutions are used in prediction of optimal two-phase swimming behaviors, alternating high resistance swimming with low resistance behavior such as gliding. Qualitative predictions from models define optimal forms for various behaviors and habitats. Optimal forms tend to be mutually exclusive, providing benchmarks for analyses relating form and function in an ecological context. Life history patterns are also affected by locomotor capabilities of various morphologies. Scale effects limit the distribution of propulsors. Numerical solutions to models are probably only good within an order of magnitude because of the assumptions in their formulation, but rankings of mechanisms or organisms are adequate for comparative study. Predictions must be tempered by consideration of non-locomotor function, developmental limitations of structural options, and non-equilibrium community structures.

INTRODUCTION

Many vertebrates live in or near water, and most vertebrates can swim if necessary. Indeed, since fish are the most speciose vertebrates (Nelson, 1976), swimming is probably the common means of vertebrate locomotion. Swimming is basic to many activities, including agonistic and reproductive behavior, foraging and predator avoidance, and numerous mechanisms are recognized for effective swimming. In contrast to moving around in water, aquatic vertebrates are also exposed to currents. Consequently, avoiding moving in water is as important, or more important than swimming for many vertebrates, and has a large effect on form and function (Arnold and Weihs, 1978). Both moving and avoiding swimming are considered here.

In order to understand the role of swimming in the biology of vertebrates, research has been largely directed by two major questions. The first question concerns the magnitudes of the forces that determine speed, linear acceleration and turning rate. These are performance measures which ultimately place boundaries on behavior and hence the range of hydrodynamic environments that a vertebrate is physically competent to occupy (Webb, 1986; Daniel and Webb, 1987). The second question considers the energy changes associated with these forces. These costs take into account interactions with organisms and other habitat features. They must be met from consumed food energy and hence affect functional features such as the diet breadth providing for an energy surplus (Werner, 1986) and fitness through the use of surplus energy for reproduction (Ware, 1984).

Answering these two general questions of performance magnitude and locomotor costs requires knowledge of how animals interact with their hydrodynamic environment. The diversity of hydrodynamic environments occupied and of swimming and flow avoidance mechanisms among verte-

[1] From the Symposium on *Science as a Way of Knowing—Form and Function* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1987, at New Orleans, Louisiana.

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TABLE 1. *Summary of functional-morphological study process for aquatic vertebrate locomotion.*

Ideal goal	Description of pressure and flow around a swimming animal
Current practical starting points	Description of force components and their moments
Practical procedure	Identify dominant force component(s), using Re, σ, shape, ground contact
Bridge from hydrodynamics to biological applications	Hydrodynamic models
Applications	Calculation of forces, moments, and rates of working Optimal design Optimal behavior Ecomorphology Life history Scaling

brates is very large since vertebrates use all possible axial and appendicular structures for swimming, range in size from fish larvae, 2–3 mm in length, to adult blue whales, over 10 m long, and live in habitats containing various structural features variously affecting flow. As a result, answering questions about aquatic locomotion may initially appear to be overwhelming. Fortunately, there are a relatively small number of basic principles that underlie this diversity of locomotor habitats, and these provide the foundation for studies of vertebrate swimming. The basic ideas have been elucidated for locomotion in general by Daniel and Webb (1987), and their analysis provides the starting point for the present discussion. Here I emphasize process whereby hydrodynamic principles are used to identify principal forces acting on swimmers and their use in models to estimate thrust and resistance. Since these models contain parameters for the motion and shapes of propulsors and the body, they form the basis for prediction of optimal form to be tested against observation and experiment to elucidate vertebrate swimming form and function. These studies lead in turn to analyses of various behavioral and ecological relationships (Table 1).

BASIC PRINCIPLES

Momentum transfer

Swimming, like all forms of locomotion, is the result of transfer of momentum from some part of an animal, the propulsor, to the environment. Momentum, which is also transferred from the water to the animal, and the animal inertia, appear as forces resisting motion (Daniel and Webb, 1987). Ideally, momentum changes would be determined from direct observations of flow patterns or pressure fields around a swimming animal. Adequate techniques are rarely available to do this (an exception is McCutcheon, 1977), but attempts continue to be made to achieve a breakthrough (Allan, 1961; DuBois *et al.*, 1974; Aleyev, 1977; Dubois and Ogilvy, 1978). The alternative is to use a momentum or force balance approach (Daniel and Webb, 1987).

Forces acting on swimming animals

Momentum transfers are mediated by certain physical properties of water (density and viscosity) and solid boundaries (friction, compliance). Viscosity is a measure of the resistance of a fluid to the rate of its distortion, ultimately related to molecular attractions, and giving rise to fluid "friction." Density affects inertial and pressure forces in a fluid. Thus the physical properties of fluids relevant to momentum transfer are few, so that a small number of momentum transfer mechanisms can be defined, each associated primarily with a certain general flow pattern (Fig. 1). Momentum transfer mechanisms are most conveniently described in terms of the rates of change of momentum, or force components acting on an animal. For aquatic vertebrates, the pertinent force components are (Fig. 1); friction and pressure drag, lift, acceleration reaction and ground reaction (Daniel and Webb, 1987).

Viscous drag always contributes to the total force acting on an animal. When animals are small and move slowly, accelerations in the fluid are small. Then viscous forces alone are significant and inertial, density related force components can be neglected (Vogel, 1981; Daniel and Webb,

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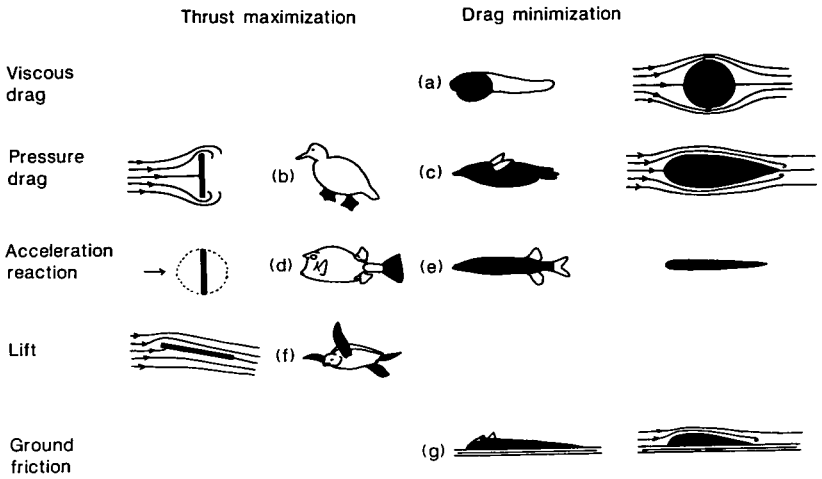

FIG. 1. Diagrammatic representation of the flow patterns associated with thrust and resistance components most important to aquatic vertebrates. Examples of mechanisms (shaded) for thrust maximization and for resistance minimization are illustrated by some vertebrates. Key: a—anuran tadpole; b—duck; c—penguin; d—boxfish, *Ostracion*; e—pike; f—sea turtle; g—plaice. All examples of propulsors are for oscillatory appendages.

1987). For big and fast animals, large velocity gradients, and hence viscous forces, are restricted to a small region close to the body or an appendage. This region is defined as the boundary layer. However, viscous effects in the boundary layer cause it to separate, greatly distorting the flow outside the boundary layer. The resultant asymmetry of the flow fore and aft of a body is associated with a pressure difference which is the basis of pressure drag (Hoerner, 1965; Schlichting, 1968).

Lift also arises from asymmetries in the flow, again originating from water viscosity. Lift is usually induced by orienting a body or an appendage at a small angle to the flow. The asymmetry in the flow generates a pressure difference across the body nearly normal to the incident flow (Hoerner, 1975; Vogel, 1981).

Acceleration reaction results from changes in the kinetic energy of water affected by an accelerating (or decelerating) body. A body accelerating in water must obey Newton's Laws. Therefore, acceleration reaction is conveniently calculated as an additional inertial mass, the added mass, that when added to the inertia of a body accelerating in water gives the momentum changes expected from Newton's Laws (Daniel, 1984; Daniel and Webb, 1987).

Ground reaction depends on the physical properties of a surface with which an animal is in contact. It is resolved into two orthogonal force components. The force parallel to the ground is the frictional force resisting slippage. As with fluid friction, this force results from molecular attractions between an object and the surface. Normal to the surface is an elastic force resulting from molecular distortion of a body or propulsor pushing directly against the ground (Daniel and Webb, 1987).

One additional factor, body inertia, affects rates of acceleration. However, body inertia is not a mechanism for momentum transfer. Therefore, while body inertia may make starting hard and tend to maintain motion once begun, it cannot propel an animal.

The force balance

Further analysis of locomotion is based on the principle of conservation of linear and angular momentum. This requires that the rate of change of the linear and angular momentum of the body is equal to all the forces and moments of forces generated by the propulsors acting on the body (Yates,

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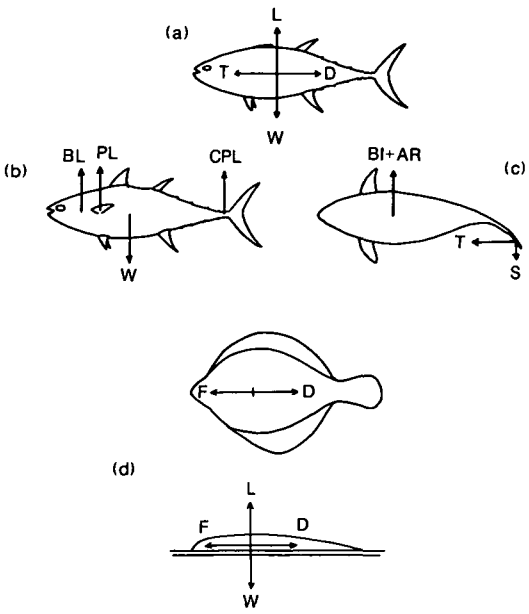

FIG. 2. Force and moment balances for swimming vertebrates. a) Force balance for rectilinear swimming. b) Moment balance for forces in the horizontal plane (after Magnuson, 1978). c) Recoil moment balance. d) plan and side views with force balance for a benthic fish holding station on the bottom (after Arnold and Weihs, 1975). a–c show tuna and d plaice, *Pleuronectes platessa*. Key: AR—acceleration reaction; BI—center of body inertia; BL—center of body lift; CPL—caudal peduncle lift; D—drag; F—ground friction; L—lift; PL—pectoral fin lift; S—side force; T—thrust; W—weight.

1983). Therefore, the forces propelling an animal, the *thrust forces*, must balance retarding forces, the *resistance forces*. This leads to a statement of the force balance (Fig. 2) as a central concept in the analysis of locomotion (Daniel and Webb, 1987);

$$\text{Thrust} = \text{Resistance} \qquad \text{(eq. 1)}$$

$$\text{Thrust} = \text{drag} + \text{lift} + \text{acceleration reaction} + \text{ground reaction} \qquad \text{(eq. 2)}$$

$$\text{Resistance} = \text{drag} + \text{acceleration reaction} + \text{ground reaction} + \text{body inertia.} \qquad \text{(eq. 3)}$$

Any of the momentum transfer mechanisms can contribute to thrust and drag, but body inertia contributes only to resistance. In addition, lift generation requires appropriate volitional movements of propulsors, and animals typically prevent lift contributing to resistance, except for rapid braking. Therefore, this force component is not usually relevant to the resistance equation.

Thrust and resistance moments must also balance and equations 1 to 3 can be rewritten with each force component replaced with its moment about the center of mass. Compared to swimming forces, swimming moments have received little attention, although they may have a major effect on animal form and function (Harris, 1936, 1938; Lighthill, 1975; Thompson and Simanek, 1977; Magnuson, 1978; Lauder, 1987; Weihs, 1987).

Factors affecting the magnitude of force components

All the mechanisms for momentum transfer may operate simultaneously. However, a variety of factors affect their relative magnitudes which are usually sufficiently different that analysis often can be simplified by consideration of dominant force components. Determination of the dominant force component is thus a critical step in studies of locomotion. Four major criteria are used for aquatic animals (Daniel and Webb, 1987): 1) contact with the ground, 2) Reynolds number, 3) reduced frequency, 4) shape.

Ground Contact. The magnitude of the force between an animal and the bottom depends on the animal's excess weight in water. Since the ratio of the densities of water and of an animal is close to unity, this excess weight is always small. As a result, friction forces with the ground cannot be high. Nevertheless, Arnold and Weihs (1978) have shown that friction with the ground can be sufficiently large relative to hydrodynamic drag that animals can hold station in currents without swimming (Fig. 2). Current speeds at which animals begin to slip downstream can be increased when friction with the surface is increased by suckers, or appendages used as grapples (Hora, 1930; Hubbs, 1940).

Hydrodynamic forces normal to the flow

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cannot be neglected for animals on the bottom because of a lift force opposite to weight (Arnold and Weihs, 1978). Station holding is facilitated by using fins as hydrofoils to orient the lift force downwards, adding to weight (Feldmeth, 1983; Rimmer *et al.*, 1985). Otherwise, lift on a body in contact with the bottom reduces weight, and hence the slip speed. A number of behaviors, such as body arching and fin fluttering, have been described for the benthic plaice, *Pleuronectes platessa,* that induce flow beneath the body reducing the flow asymmetry and hence the magnitude of the lift force (Arnold and Weihs, 1978).

Ground reaction is eliminated from the force balance whenever an animal is not in contact with a surface. However, this does not mean that surfaces become unimportant. Streamlines are compressed near a surface, altering the magnitude of thrust and resistance forces. An increase in effective lift is most important for free-living animals (Hoerner, 1965, 1975; Blake, 1983), and can improve locomotor efficiency (Blake, 1983). Ground effect falls off rapidly with distance, being negligible when a propulsor is more than one span length from the surface (Lighthill, 1979; Alexander, 1983; Blake, 1983).

Reynolds number. Size and speed affect the relative importance of viscous and inertial forces. A non-dimensional scaling factor relating these is given by Reynolds number, Re;

$$Re = L \cdot u / \nu \qquad \text{(eq. 4)}$$

where

L = measure of length of a body or propulsor,
u = speed of the body or propulsor,
ν = kinematic viscosity of water.

Viscous forces dominate at small Re, for practical purposes Re < 20–30. This Re boundary is based on the onset of burst-and-coast swimming behavior of fish larvae, a behavior which cannot occur until inertial forces are sufficiently large relative to viscous forces (Weihs, 1980). Acceleration reaction similarly becomes important at greater Re (Vlymen, 1974). Effective lift also requires that viscous forces are small relative to inertial forces, which occurs when Re exceeds about 500 (Webb and Weihs, 1986).

Viscous (friction) drag is restricted to the boundary layer over most of the range of Re for vertebrate swimmers. Boundary layer flow may be laminar or turbulent, and friction drag is greater for the latter. Transition from laminar to turbulent flow occurs when randomly occurring disturbances cannot be damped by viscous forces and are amplified by inertial forces (Schlichting, 1968). Thus conditions under which transition occurs are related to Re and well designed bodies can delay transition up to Re of about 10^6 (Hoerner, 1965; Wardle, 1977).

Reduced frequency. Pressure drag and lift dominate the force balance only when movements are reasonably steady. Both depend on viscous effects so that their full magnitude develops with time from the start of movement. Therefore, when movements are highly time dependent, drag and lift can be substantially reduced. In contrast, as motions become more time dependent, accelerations become large, and the magnitude of the acceleration reaction increases (Daniel and Webb, 1987).

The relative importance of acceleration reaction compared to pressure drag and lift is indicated by the reduced frequency. This essentially compares the time taken for a particle of water to traverse the length of an object with the time taken to complete one movement cycle (Yates, 1983). Reduced frequency, σ, is given by;

$$\sigma = \omega \cdot L / u \qquad \text{(eq. 5)}$$

where

ω = radian velocity, equal to $2 \cdot pi \cdot f$,
f = frequency,
L = characteristic length.

The effects of time dependent motion can be ignored when $\sigma < 0.1$ (Lighthill, 1975; Yates, 1983, Daniel, 1984). Then the motion at any instant is considered similar to an equivalent steady motion. Such motions are called quasi-steady or freeze-frame (Yates, 1983) because the net forces acting on an object can be obtained by summing the steady-state forces for all flow

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situations through a cycle. In the range $0.1 < \sigma < 0.4$, both acceleration reaction and lift and pressure drag make contributions to the force balance. At larger values of σ, acceleration reaction dominates (Yates, 1983).

Reduced frequencies of swimming propulsors usually exceed 0.1, and are only likely to fall below this value for propulsors of very large animals, perhaps the tail flukes of the larger cetaceans.

Shape. Shape, including orientation to the incident flow, has a large effect on the magnitude of the force components at any Reynolds number and reduced frequency. Relationships between shape and steady state lift and drag forces have been extensively studied, especially by engineers, and their methods and results are used by biologists (see Hoerner, 1965, 1975; Webb, 1975*a*; Aleyev, 1977; Vogel, 1981; Blake, 1983). For acceleration reaction, see Vogel (1981), Blake (1983, 1986), and Daniel (1984).

FORCE COMPONENTS AND PROPULSION MODELS

Forces during swimming

The bridge between hydrodynamics principles and their application to biological problems is provided by a variety of models combining the force components with propulsor and body motions. Thrust is usually calculated using one of four basic approaches: 1) wing theory, 2) blade element theory, 3) slender body theory, 4) bulk flow theory. There is also promise for direct modeling of pressure and flow fields using high speed computers, but this is at an early stage of development (W. W. Schultz, personal communication).

Wing theory is used with some propulsors, for example, the tail or caudal fin of tuna-like (thunniform) animals, which move as units with little spanwise variation in speed and orientation to the incident water (angle of attack). Re is typically large, $>10^5$ for the caudal fin, and σ may approach values <0.1. Lift dominates thrust. Engineering data and direct measurements on wings (see Hoerner, 1975) are used to determine thrust forces and associated resistance forces (Lighthill, 1975; Chopra and Kambe, 1977).

Blade element theory can be used where there is substantial span-wise variation in velocity and angle of attack and simple wing theory is not applicable. Examples include penguin wings, mammal and duck feet, and stiff fins of fish. A propulsor is divided into strips (elements) along its span. The forces acting on each element at any instant are summed along the span and through the time for a complete propulsive cycle. Forces may be determined from engineering data, or from measurements using models or excised propulsors themselves. The method is used at large Re, with σ typically >0.1. Thus lift or drag forces as appropriate plus acceleration must be taken into account (Blake, 1983, 1986).

Slender body theory is currently the method of choice for analyzing the motions of the body and caudal fin of most fish, and is being applied to snakes (Jayne, 1985; Graham *et al.*, 1987) and may also be used to analyze the motions of long-based fins (Blake, 1976; Yates, 1983). The theory considers motions of elongate systems which undergo small perturbations with respect to a characteristic length. For fish and other aquatic vertebrates this assumes that the maximum amplitude of the tip of the tail (the trailing edge) is less than 0.2, preferably <0.1 of the length of the propulsive wave, and amplitude does not grow too rapidly near the trailing edge (Lighthill, 1975; Yates, 1983). Span is similarly small with respect to length (<0.2), although values up to 0.4 are tolerable (Yates, 1983). Variations in span along the length should not be large (Wu, 1971*a*, *b*; Lighthill, 1975). Many of the vertebrates to which the theory is applied meet these assumptions only marginally.

Slender body theory is applicable to vertebrates with substantially compressed non-tapering bodies, at large Re and σ, and viscous effects on thrust can be neglected. Hence the acceleration reaction force is determined. As a result, these models are inadequate to describe thrust forces for elongate eel-like (anguilliform) animals, including many deepwater fish, and salamanders, snakes, crocodiles etc., because

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pressure drag forces also contribute substantially to the force balance (Lighthill, 1975). Neither are the models adequate for fish larvae where Re is relatively small (Vlymen, 1974). Lighthill (1975, 1983) has consistently pointed to the need for an acceleration reaction/drag model for these animals, which is still to be developed.

Bulk flow theories consider the net effect of the propulsor on the water. Blade-element and slender body theories can quickly become tedious or unwieldy if the time intervals must be small or the number of elements large. A bulk flow approach is an attractive alternative because less detailed information is needed on propulsor movements. This lends itself especially to comparative work where replicate measurements are required on numerous specimens from several species.

The bulk flow theory most commonly used for aquatic animals is derived from slender body theory, and calculates the mean rate at which the trailing edge sheds momentum to the wake. Another bulk flow model applied to fish is helicoper theory (Blake, 1983). This theory treats fins as an actuator disc that instantaneously accelerates water passing through the disk, thereby generating thrust.

Resistance of propulsors must be calculated from models such as those used to determine thrust. When the body is held rigid and appendages are used for propulsion, body resistance is frequently measured or calculated from Newton's Equation for Drag and engineering data (Blake, 1983; Williams, 1983; Fish, 1984; Williams and Kooyman, 1985). These techniques typically neglect interference between the propulsor and the body and possible behavioral effects on surface characteristics and shape (Webb, 1975*a*; Blake, 1983).

APPLICATIONS OF PRINCIPLES AND MODELS

Body and propulsor form and function

Effective propulsion requires:

1) propulsors orient one or more force components to propel an animal in some desired direction;
2) propulsor morphology and movements maximize the thrust and minimize moments that cause the body to recoil (Table 2);
3) propulsor morphology and movements and body morphology minimize resistance forces in the direction of motion; body morphology maximizes resistance forces that reduce recoil (Table 3).

All models for determining thrust and resistance include variables for morphology (shape), and movement (velocity and/or acceleration rates) and hence provide the framework for interpreting propulsor and body form.

Propulsor movements. Aquatic vertebrate propulsors can be classified as undulatory or oscillatory (Webb and Blake, 1985). Undulatory propulsors are the body/tail of most fish, salamanders and tadpoles, crocodilians, and perhaps some seals (see Fig. 3), and the long-based fins of fish. Consider an animal moving forward. The propulsor is bent into a wave which travels caudally and at a velocity greater than the mean velocity of the body. Each propulsor element faces caudally at a large angle to the direction of mean body motion. As a result, the thrust is the major component of the total force acting on the element, and only a small side component produces recoil (Gray, 1933; Webb, 1975*a*; Wardle and Videler, 1980; Videler, 1981; Blake, 1983).

Oscillatory propulsors include short-based fins of fish, legs and feet of anuran amphibians, reptiles, birds and most mammals, and the lunate tails of thunniform lamnid sharks, tuna, ichthyosaurs, reptiles and cetaceans (Figs. 2, 3). Oscillatory propulsors attach to the body by narrow connections providing freedom for the propulsor to move at high speeds relative to the body and to direct the normal forces as appropriate to maximize thrust.

Propulsor shape. Both undulatory and oscillatory propulsors have greater span when large thrust is required. This increases area, and hence lift and drag, and increases the volume of water entrained during accelerations, and hence acceleration reaction.

Propulsors that use drag and acceleration reaction for thrust typically increase

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TABLE 2. *Shape factors maximizing thrust and reducing resistance and energy wastage for propulsors.*

Propulsor and kinematic pattern	Dominant thrust force component	Thrust maximization	Resistance or source of energy loss	Resistance minimization
Undulation of the body/ caudal fin	Viscous and pressure drag and acceleration reaction	Large span increasing caudally correlating with velocity and increasing in the same direction	Enhanced viscous drag ("boundary layer thinning")	Reduce body area anterior to caudal fin
			Lateral recoil	Reduce body area anterior to the caudal fin
Undulation of appendage	Drag and acceleration reaction	Large span	Enhanced viscous drag	No special mechanisms recognized
Oscillation of caudal fin or tail	Lift	High aspect ratio	Lateral recoil	Narrow necking; tail attached to body by streamlined caudal peduncle
			Induced drag	Large aspect ratio tail
Oscillation of appendage	Drag and acceleration reaction	Triangular, oscillating about apex	Drag during recovery stroke	Feather paddle blade and/or slow speed recovery stroke
			Interference drag	Triangular fin oscillating about apex
	Lift	High aspect ratio	Induced drag	High aspect ratio
			Acceleration reaction	Distal tapering (high aspect ratio)
			Interference drag	Narrow tapering body connection

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TABLE 3. *Predicted optimal morphologies for various behavior patterns in different habitats.*

	Behavioral pattern				
	Cruising and sprinting	Cruising	Acceleration	Station holding	Low speed maneuvering
Typical habitat	pelagic	pelagic	various	benthic	structurally complex
Typology	thunniform	carchariniform	none	pleuronectiform	chaetodontiform
Vertebrate groups	thunnids, lamnids, ichthyosaurs, cetaceans	many selachians	esocids, cottids, etc.	pleuronectiformes, rays	acanthopterygian fishes; *e.g.*, chaetodontids, centrarchids
Morphological characteristics					
Thrust maximization					
Caudal fin	high AR lunate	moderate to high AR	small AR, large area	—	small AR
Body cross section	—	variable along length	elliptical	—	elliptical
Body flexibility	—	large	large	—	variable
Anterior median fins	slot effect possible	large fins spaced to enhance thrust	large along body length	—	large in caudal region
Paired fins	medial hydrofoils	ventral hydrofoils	variable	variable	anterior and ventrolateral
Resistance minimization					
Body shape	streamlined rigid	fusiform, flexible	elongate, flexible	streamlined, gibbose	streamlined gibbose
Fineness ratio (L/H)	4–5	4–5	<4	12–14	1–2
L_H/L	0.5–0.7	0.3–0.5	0.3–0.4	0.2–0.3	0.3–0.5
Anterior median fins	large over center of mass	large fins widely spaced	—	large along body length for faring	—
Caudal area	small	small	—	—	—
Recoil minimization					
Caudal peduncle	narrow	narrow	—	—	—
Anterior median fins	large over center of mass	large anteriorly	large anteriorly	—	large anteriorly

Key: AR = aspect ratio; H = maximum depth, or height from the ground in benthic species; L = total length; L_H = distance of H from nose. Based on Alexander (1967), Weihs (1973b), Bone (1974), Lighthill (1975), Webb (1977), Arnold and Weihs (1978), Blake (1983), Weihs and Webb (1983), and Webb and Weihs (1986).

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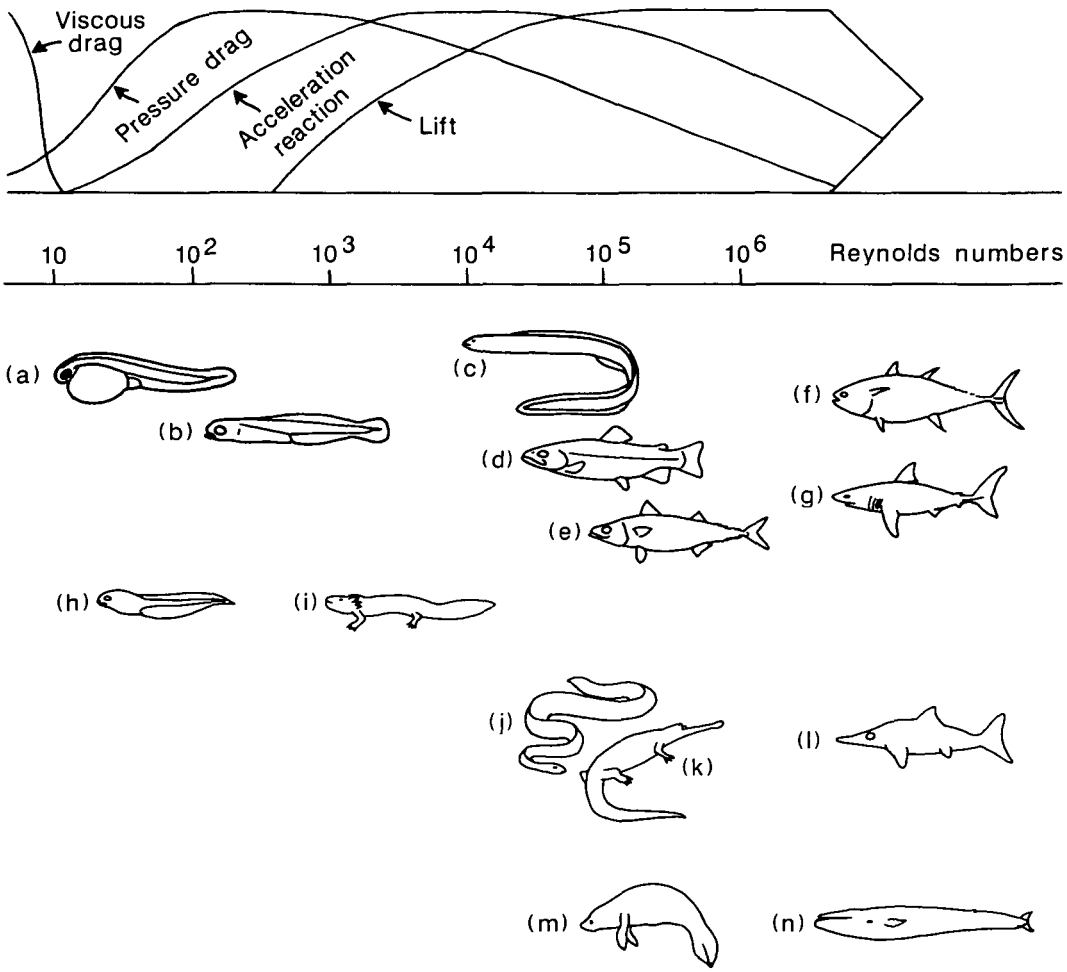

FIG. 3. Diagrammatic representation of the relative importance of force components used by vertebrates swimming distant from a boundary, placed crudely on a Reynolds number, Re, scale. Examples of body/tail swimming fish (a–g), amphibia (h,i), reptiles (j–l) and mammals (m,n) are shown to illustrate the shapes of vertebrates to which the various Re and force components apply. Key: a—yolk-sac walleye, *Stizostedion*, larva; b—10-mm walleye larva; c—eel, *Anguilla*; d—salmon, *Salmo*; e—mackerel, *Scomber*; f—tuna, *Thunnus*; g—lamnid shark; h—anuran tadpole; i—newt, *Necturus*; j—sea snake, *Pelamis*; k—short-nosed crocodile, *Caiman*; l—ichthyosaur; m—sea cow, *Manatus*; n—blue whale, *Balaenoptera*. f,g,l and n are thunniform animals, swimming with oscillatory movements of a wing-like lunate tail. The other vertebrates are undulatory swimmers, using the body/tail.

in depth along the propulsor length. Span (width normal to the flow) increases caudally in undulatory propulsors and chord (width parallel to the flow) increases distally in oscillatory propulsors. Since speed and acceleration rate increase in the same direction, this ensures maximum element size correlates with maximum element speed and acceleration rate. Thus the depth of the body and median fins increase caudally in strong cruisers such as trout compared to eels (see Fig. 3), and for strong accelerators such as pike compared to eels. Drag-based oscillatory propulsors tend to be triangular in shape, with the propulsor rotating directly about the apex (*e.g.*, *Synchropus* pectoral fins; Blake, 1983), or more distally on limb bones (*e.g.*, duck feet; Prange and Schmidt-Nielsen, 1970).

Lift-based oscillating appendages, with

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large spanwise variations in angular velocity, again tend to rotate about a narrow base, but are obtuse angled or curved on the leading edge. This shape has a high aspect ratio (span^2/area) to maximize the lift coefficient (Hoerner, 1975), while reducing acceleration reaction, which in this case wastes energy (Blake, 1983). Lift-based oscillating appendages such as tails of thunniform animals experience little spanwise variation in velocity. These propulsors are high aspect ratio, lunate-shaped wings, providing for high lift (Chopra and Kambe, 1975).

There are always costs associated with thrust generation as some component of the normal force typically retards motion or adds to energy costs; *e.g.*, induced drag and acceleration reaction for lift-based propulsors; interference drag for appendage propulsors; lateral recoil for body/caudal fin propulsion; resistance during recovery strokes of drag-based systems. These costs are reduced by appropriate shape (Table 2) and orientation of the propulsor as noted above.

Body shape. The objective of the propulsors is to propel the body by generating thrust equal to total resistance. Therefore, performance, measured as one or more of speed, acceleration, efficiency, and energy expenditure (Daniel and Webb, 1987) is improved by minimizing body resistance. The swimming resistance of vertebrates has been extensively studied as a result of early, but never convincingly supported, suggestions that their resistance might be lower than that possible from the best human engineering (Gray, 1936; Bainbridge, 1961; Osborne, 1961; Brett, 1963). In the search to prove animal superiority, many mechanisms have been identified to reduce body resistance in the direction of motion. These include streamlining the body, minimizing surface area in the tail region, fish mucus reducing viscous resistance, and a variety of mechanisms to prevent transition and separation (Table 3).

Minimizing recoil remains a major problem for body/caudal fin swimmers. Movements normal to the axis of progression induced by the side-force component of the propulsor are typically reduced by an anterior large resistance (Lighthill, 1975; 1977). The large resistance is achieved by concentrating body inertia near the center of mass, and usually by enhancing this inertial resistance with lateral flattening and median fins to greatly increase the added mass in the same region. Paired fin propulsion also avoids recoil, but oscillating appendages incur costs so that they appear to provide no net gains in performance (Webb, 1975*b*; Blake, 1983).

Optimal behavior

A consistent result from analyses of the force balance and rates of working during swimming and physiological measures of energy expenditure is that the total swimming resistance (=thrust) of aquatic vertebrates is several times higher than that possible for man-made rigid, but otherwise similar bodies (Brett, 1964; Alexander, 1967; Webb, 1975*a*; Blake, 1983). However, the resistance of an animal's body while gliding or coasting may be similar to that of such a rigid man-made reference (Webb, 1975*b*; Blake, 1983; Williams, 1983; Fish, 1984; Williams and Kooyman, 1985).

A number of behaviors take advantage of the different resistance during swimming and coasting. All involve two-phase swimming movements, alternating high resistance swimming with low resistance coasting. Such discontinuous swimming can lead to energy savings of up to about 80%, more commonly 30–50%, for traversing unit distance compared to continuous swimming at the same average speed; alternatively range increases of the same order are possible for a given fuel load (Weihs, 1973, 1974, 1980; Au and Weihs, 1980; Videler and Weihs, 1982; Blake, 1983). The advantages of discontinuous swimming are greatest when the swimming resistance is high compared to coasting resistance. For example, large energy savings could be made by anguilliform swimmers which are believed to have the highest swimming energy costs (Weihs, 1974). Similarly, larger advantages accrue (in theory) when acceleration rates must be high during the active swimming phase (Blake, 1983).

A different application of hydrodynamic

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principles and the models for forces acting on swimming fish has been the prediction of optimal strike behavior for piscivorous fish. This recognizes that the response of prey to a predator strike is typically a maximal acceleration turn. Then an optimal target can be defined as that point of the body which moves least, and an optimal strike path as the relatively invariant trajectory of this target for the prey's motor response. Piscivorous fish strike behavior is generally consistent with these predictions (Webb, 1986).

Optimum form and ecomorphology

Mechanical principles can be used to predict optimal designs for various swimming activities. Broad categories of swimming activity are defined by recognizing that an animal's path is determined by a state variable, velocity, and two control variables, linear and angular acceleration. Then optimal forms, typically named after an exemplary species (Breder, 1926; Lindsey, 1978; Webb, 1984*a*), are those that maximize performance (magnitude) of these variables (Table 3). Most work to date has focused on optimal design of body/caudal fin swimmers for high speed cruising/sprinting and for acceleration. The typology for the former is thunniform (Lindsey, 1978). No single species combines all the desirable features to maximize acceleration because many other locomotor and non-locomotor needs force compromises (Webb, 1977, 1984*a*, *b*). Design optima for other activities (station holding on the bottom, slow swimming and maneuvering) have not been as well researched, but expected features are summarized in Table 3.

Design features optimizing various behaviors and exploiting different habitats overlap. However, for any given behavior pattern and habitat, the desirable design features are sufficiently different that optimal morphologies appear to be exclusive. Consequently, morphologies that have evolved to maximize some activity, for example acceleration, are believed to result in diminished performance in other areas, for example cruising (Webb, 1982, 1984*a*; Weihs and Webb, 1983). The idea of exclusive optimal morphologies provides a framework for predicting the form expected of animals living in various habitats and for interpreting observed ecological roles.

Several studies have correlated various aspects of locomotor morphology with feeding ecology. Keast and D. Webb (1966) found diet segregation among fish living in a small temperate lake, correlating in part with body and fin form. They concluded that differences in locomotor performance associated with the thrust and drag properties of the various forms contributed to reduction of interspecific feeding competition. Webb (1984*b*) showed that vertebrates with locomotor morphologies typical of specialists for cruising, accelerating and manuevering typically took certain food types, defined on the basis of food particle size, dispersion and evasive capability. Thus cruising specialists tend to feed on dispersed food items, accelerators take locally concentrated evasive items while manueverers exploit less evasive food in structurally complex habitats. This study also showed that there were limitations imposed on foraging locomotor specialization due to predation risk, and suggested that this may be an important factor underlying the adaptive radiation of various mechanisms for inertial suction feeding.

Life history

Many animals grow through a range of habitats, often correlating with size, with different physical and biological characteristics. As a result, life history patterns of many aquatic vertebrates appear to be affected by the difficulty of achieving generalized locomotor morphologies that provide high performance in successive habitats.

Among vertebrates, fish traverse the largest range of physical habitats during ontogeny. For example, a tuna hatching as a 2–3 mm larva can reach a length of 50 cm in its first year of life alone, while the adult may be 2 m in length (Fritzsche, 1978; Rivas, 1978). This spans a Re range of $10 < Re < 10^6$. The most rapid change in hydrodynamic regime occurs during early larval life. Newly hatched, slow swimming larvae

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live in a habitat dominated by viscous forces, with Re typically less than 20–30 (Webb and Weihs, 1986; Fuiman and Webb, 1987). The optimal form to minimize viscous body resistance at these Re is spherical, with minimal area per unit volume, and this shape is typical of the globular yolked stage of development (Fig. 1). However, at first feeding it is desirable to use behaviors dependent on inertial forces; economical burst-and-coast swimming to search for prey and fast starts for more powerful strikes at evasive prey. These behaviors are only possible at higher Re, >20–30, and require a more elongate, flexible form with large body depth (Table 3). However, this results in a large area, quite inappropriate for a predominantly viscous habitat. Thus a rapid change in form, or "snap-through" (Webb and Weihs, 1986) is characteristic of early fish development from a globular non-feeding yolk-sac stage more suitable for life at low Re to an elongate feeding form suitable to higher Re.

Once feeding has begun, ontogenetic habitat shifts appear to occur when the balance of benefits (measured in terms of growth) to risks (vulnerability to predation) reaches higher values for a new habitat. Swimming affects both benefits and risks, so that changes in locomotor morphology would be expected to correlate with ontogenetic habitat shifts. However, morphological characteristics beneficial in one habitat may be suboptimal for life in the next. At the same time, anticipatory development prior to a shift may be essential to making the shift. However, this may reduce the ability of an animal to grow to an adequate size to make the shift if the preparatory changes reduce competitive ability in the present habitat. This leads to bottlenecks in development and movement of individuals to juvenile or adult habitats (Werner, 1986).

The most extreme examples of ontogenetic habitat shifts among vertebrates undoubtedly occur in anurans at metamorphosis. Wassersug and Sperry (1977) have shown that the resorption of the tail reduces swimming performance at a time when resistance is increased by the emerging limbs, while at the same time terrestrial performance is impaired by the tail. Reduced locomotor performance makes metamorphosing anurans very vulnerable to predation, which is only partly ameliorated by cryptic behavior during the locomotor transition.

Less extreme situations are probably more common. An example is given by habitat shifts in centrarchid (sunfish) communities (Werner, 1986). The young of most sunfish species live among the weeds, competing for similar food resources, while adults occupy a more diverse range of trophic and structural habitats. Transitions to more adult morphologies begin before the shift to the adult habitat. Green sunfish (*Lepomis cyanellus*), for example, develops the piscivorous adult locomotor and mouth forms while still in the weed beds. This reduces the fish's competitive ability compared to other species creating a bottleneck delaying the shift of this sunfish to the adult habitat.

Many vertebrates appear to avoid or minimize such problems associated with habitat shifts by modifying their life histories. Among mammals, birds, reptiles, and elasmobranch fishes, viviparity or telolecithal eggs ensure that young are relatively large when they first swim. As a result they begin life in the same, or very similar, hydrodynamic regimes as their parents. Most of the tetrapods, and perhaps some sharks (Breder and Rosen, 1966), show parental care. This would ameliorate remaining risks for early stages which may be less well adapted for their habitat than morphologically similar adults for theirs.

Scale

Aquatic vertebrates span a wide size range, not only within their life histories, but also among species. Size affects the nature of the force balance, and hence optimal morphology for various behaviors. As noted above, these underlie certain ontogenetic habitat shifts, such as that from non-feeding yolked larva to feeding larva in fish.

In addition, scale may place size limits on certain morphologies. For example, lift forces are not very effective for swimming

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at Re less than about 500. Therefore, there is a lower size limit for this mechanism, and shapes typical of lift-based mechanisms would not be expected below this size. Provisional analysis of the development of thunniform fish suggests that the caudal fin does not begin to adopt its high aspect ratio form until Re >500, when larvae are at least 10mm in length (Webb and Weihs, 1986). Similar development patterns are expected for other lift-based fins, but data are lacking.

Acceleration reaction appears to have upper limits for effectiveness. As size increases, the ability of the muscles to generate stresses relative to inertial forces decreases (Daniel and Webb, 1987; Webb and Johnsrude, 1988). Large vertebrates, lacking the ability or need for high rates of acceleration, and with sigma reaching low values, use sophisticated lift-based propulsors. Thus large vertebrates are not merely thunniform, but thunniform vertebrates must also be large.

CONCLUSIONS

The study of aquatic vertebrate locomotion follows a well-established pattern (Table 1) commonly used by functional morphologists. The process has long proven successful in postulating and testing likely functions for various systems, leading to predictions of performance at a wide range of biological levels of organization. Model formulation is a critical step in the process of evaluating the importance of swimming to general vertebrate biology. Superficially, hydrodynamic models appear to drive research because they provide the framework for interpretation and prediction of biological phenomena. In practice, close interaction among contributing disciplines has been essential, although evidence for the cooperation must often be found in the acknowledgements to papers. For example, Sir James Gray was clearly influential in recruiting several emminent fluid dynamicists to work on animal locomotion (*e.g.*, Taylor, 1952; Gray and Hancock, 1955; Lighthill, 1975). Thus a feedback loop links hydrodynamicist with biological tests of reality (Table 1) and such interaction remains essential to advance in the area.

The interaction between hydrodynamicists and biologists has provided an evolving, but still incomplete, set of models applicable to overlapping hydrodynamic and morphological ranges (Fig. 3). These models continue to form the basis for analyzing vertebrate swimming. They may be used in two ways: quantitative and qualitative. Quantitative applications of models give numerical solutions for thrust or resistance, rates of working and efficiency, while qualitative uses consider the significance of model parameters on performance in various biological settings (Daniel and Webb, 1987).

Quantitative analyses usually give results of the order expected from measurements of metabolic rate and muscle mechanics. They also rank efficiency of swimming mechanisms in accord with expectation; for example, from low efficiency lift-based paddles to high efficiency acceleration reaction and lift-based propulsors (Magnuson, 1978; Blake, 1983; Williams, 1983; Fish, 1984). However other predictions do not seem correct. For example, the slender body theory usually used by biologists (Lighthill, 1975) typically gives Froude efficiencies above about 0.5, while inferences from biological studies suggest smaller values at low speeeds (Webb, 1984*b*). In addition, this efficiency is based mainly on propulsive wave velocity relative to swimming velocity. As a result, tadpoles, tunas, salmon, etc., appear equally efficient (Wassersug and Hoff, 1985) which seems improbable given the different shapes of their propulsors and the nature of their effects on the water (Wu, 1971*b*; Lighthill, 1975; Alexander, 1983; Blake, 1983). Furthermore, thrust coefficients calculated for thunniform organisms are typically large compared to less specialized cruisers such as trout (Webb, 1975; Magnuson, 1978). This is contrary to belief.

Such discrepancies should not be surprising. As noted above, all methods for determining thrust and resistance make assumptions, and sometimes fish are close to violating axioms of various theories.

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Indeed, large discrepancies between different methods for obtaining thrust and resistance may be considered reasonable and acceptable (Magnuson, 1978). Thus it is essential to keep in mind that the numeric solutions are probably only good *order of magnitude* estimates.

Apparent contradictions or inaccuracies of numerical solutions to models are not necessarily problematic for qualitative analysis and prediction providing *relative* solutions are correct. This appears to be the situation for the models used. For example, slender body theory ranks eels below salmonids on the basis of thrust coefficients (*e.g.*, Webb, 1975*a*). Rankings also appear faithful for comparisons among some models. Thus drag-based paddles analyzed using blade element theory are consistently less efficient than body/caudal fin swimmers analyzed using slender body theory (Blake, 1983; Williams, 1983; Fish, 1984). Similarly, models give correct ranking for propulsor designs, such as ranking thrust generated by paddles with different area distributions (Blake, 1983). Under these circumstances, *comparative predictions* are reasonably reliable, so that the models remain effective for comparisons such as those illustrated above.

The use of faithfully ranking but numerically uncertain models for accurate qualitative prediction is not confined to functional morphology and locomotor studies. Slender-ship theory was used in the development of the *Stars & Stripes*, the eventual victor in the 1987 America's Cup races (Lecher *et al.*, 1987). The theory was found to be inaccurate in *absolute* terms, but became a foundation for hull design because model predictions of *relative* performance were correct. Similarly, Schoener(1986) notes that modern ecology uses a family of overlapping quantitative models, yet argues that they can only describe qualitative reality because of their assumptions.

Finally, single area form and function studies are, of course, inadequate to understand the biology of any organism. While movement is central in many fitness-critical events, animals must perform many other functions, which may constrain locomotor options, and developmental trajectories may limit variability from which locomotor structures might be selected. In addition, tests of prediction of ecomorphological distributions may apparently fail through lack of understanding of the factors that structure communities. For example, communities may not be in equilibrium, and stochastic events may result in apparently optimal forms being absent from habitats for which they appear well suited. Thus a community is a subset of organisms from among those physically capable of living in a given habitat (Diamond and Case, 1986), and while locomotor structures may set ultimate limits on swimming performance, they rarely exclude organisms from a particular habitat (Keast and Webb, 1966). Interactions with other organisms, with differing performance profiles in different habitats ultimately determine membership from among physically and physiologically competent, and temporally available candidates (Diamond and Case, 1986).

ACKNOWLEDGMENTS

This work follows from an analysis of common principles in locomotion with Dr. T. L. Daniel, to whom I remain indebted for his discussions and insights. The manuscript was prepared during leave from the University of Michigan at the Ministry of Agriculture, Fisheries and Food Fisheries Laboratory, Lowestoft to whom I am grateful for their hospitality and support. Financial support was provided by the National Science Foundation Grants PCM-8401650 and DCB-8701923.

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