

West Chester University  
**Digital Commons @ West Chester University**

---

Biology Faculty Publications

Biology

---

12-1-2017

# Control surfaces of aquatic vertebrates: active and passive design and function

Frank E. Fish

*West Chester University of Pennsylvania*, [ffish@wcupa.edu](mailto:ffish@wcupa.edu)

George V. Lauder

*Harvard University*

Follow this and additional works at: [https://digitalcommons.wcupa.edu/bio\\_facpub](https://digitalcommons.wcupa.edu/bio_facpub)



Part of the [Biomechanics Commons](#)

---

## Recommended Citation

Fish, F. E., & Lauder, G. V. (2017). Control surfaces of aquatic vertebrates: active and passive design and function. *Journal of Experimental Biology*, 220(23), 4351-4363. <http://dx.doi.org/10.1242/jeb.149617>

This Article is brought to you for free and open access by the Biology at Digital Commons @ West Chester University. It has been accepted for inclusion in Biology Faculty Publications by an authorized administrator of Digital Commons @ West Chester University. For more information, please contact [wcressler@wcupa.edu](mailto:wcressler@wcupa.edu).

## REVIEW

# Control surfaces of aquatic vertebrates: active and passive design and function

Frank E. Fish<sup>1,\*</sup> and George V. Lauder<sup>2</sup>

## ABSTRACT

Aquatic vertebrates display a variety of control surfaces that are used for propulsion, stabilization, trim and maneuvering. Control surfaces include paired and median fins in fishes, and flippers and flukes in secondarily aquatic tetrapods. These structures initially evolved from embryonic fin folds in fishes and have been modified into complex control surfaces in derived aquatic tetrapods. Control surfaces function both actively and passively to produce torque about the center of mass by the generation of either lift or drag, or both, and thus produce vector forces to effect rectilinear locomotion, trim control and maneuvers. In addition to fins and flippers, there are other structures that act as control surfaces and enhance functionality. The entire body can act as a control surface and generate lift for stability in destabilizing flow regimes. Furthermore, control surfaces can undergo active shape change to enhance their performance, and a number of features act as secondary control structures: leading edge tubercles, wing-like canards, multiple fins in series, finlets, keels and trailing edge structures. These modifications to control surface design can alter flow to increase lift, reduce drag and enhance thrust in the case of propulsive fin-based systems in fishes and marine mammals, and are particularly interesting subjects for future research and application to engineered systems. Here, we review how modifications to control surfaces can alter flow and increase hydrodynamic performance.

**KEY WORDS:** Flippers, Flukes, Fins, Hydrodynamics

## Introduction

Control surfaces are structures that allow for adjustment and control of the attitude (i.e. position with respect to orientation axes, see Glossary) of a free body in a fluid. We are most familiar with the concept in relation to aeronautical and hydrodynamic engineering (Barnard and Philpott, 1995; Weihs, 2002). Control surfaces for airplane flight include the ailerons, elevator, rudder, flaps, slats, spoilers, canard wings (see Glossary) and air brakes (Wegener, 1991; Barnard and Philpott, 1995). For submarines, control surfaces are limited to the rudder and dive planes, which are rigid elements (Burcher and Rydill, 1994; Gabler, 2000). These control surfaces can be mobile to provide course adjustments and correct for trajectory-changing (see Glossary) instabilities, or can remain stationary once motion is stabilized.

Although not typically described in engineering terms, control surfaces in animals are used for all major modes of locomotion (i.e. flight, running, swimming). Wings can change shape (morphing) for maneuvering in flight by birds and bats, and their tail feathers

and uropatagium (see Glossary) can, respectively, stabilize the body and control longitudinal static stability (Norberg, 1990; Warrick et al., 2002; Iriarte-Díaz and Swartz, 2008). Even in terrestrial locomotion, the tail of vertebrates can actively function as an aerodynamic and inertial control surface for rapid turning (Libby et al., 2012; Patel et al., 2016).

Control surfaces in aquatic animals can regulate both stability and maneuverability in the water (Webb, 2006). Stability promotes steady movement along a predictable trajectory (Fish, 2002). Stability in aquatic vertebrates is a dynamic equilibrium and ultimately is dependent on the creation of control forces (Webb, 2006). Control surfaces are necessary for the production of the forces to resist instabilities and make corrections in attitude and trajectory, and are so named because they are used to control body position. However, the same control surfaces that foster stability also can be used to create instabilities to promote maneuverability. Changes in the rate of movement and trajectory characterize maneuverability (Webb, 1997). Animals have been characterized formally as ‘agile’ when exhibiting maneuvers of high velocities in small space volumes (Walker, 2000; Webb, 2006). Webb (2004) considered that aquatic animals are capable of high maneuverability with little loss of stability. Maneuverability is generally defined as the ability to make a series of changes in direction and position (Webb, 2004). The maintenance of stability is important for aquatic animals: when they are suspended in the water column, they are free to move with about six degrees of freedom.

Aquatic vertebrates can use their control surfaces to manipulate water flow both actively and passively (Fish and Lauder, 2006). Active flow control mechanisms use movement of propulsive appendages driven by activation of intrinsic and extrinsic musculature to modify wake flow structure. Vorticity is used to vector hydrodynamic forces during propulsion, maneuvering and trim control (see Glossary) when shed from the body or appendages as structured vortices or shear layers. By contrast, passive mechanisms rely on the structural and morphological components of the control surfaces, which dictate flow over the surface and vortex shedding.

Here, we review the various types of active and passive control surfaces used by aquatic vertebrates to promote stability and maneuverability. Although control surfaces can in some cases also be used for propulsion and to generate thrust, it is useful to separate the control and propulsive functions of animal structures as a way of focusing attention on one key role of features that are often multifunctional. Thus, this Review will focus predominantly on those structures that are non-propulsive and not used in active thrust generation. The evolution of the diverse groups of aquatic vertebrates has placed constraints on the structures that can be used to control body attitude. These constraints have, in some cases, produced novel morphological solutions. An understanding of the performance attributes, and their limitations, of control surfaces provides an understanding of the causative factors that shaped the design and function of aquatic vertebrates.

<sup>1</sup>Department of Biology, West Chester University, West Chester, PA 19383, USA.

<sup>2</sup>Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA.

\*Author for correspondence (ffish@wcupa.edu)

 F.E.F., 0000-0001-5973-3282

**GLOSSARY****Aerodynamic center**

Point at which the lift force acts.

**Attack (angle)**

Angle between the incident water flow and the chord of a wing-like structure.

**Attitude**

Position of the body relative to defined orientation axes.

**Canard**

Additional wing that is anterior (forward) of the main wing.

**Center of pressure**

The point at which all the aerodynamic forces sum on a body.

**Cephalofoil**

Head of hammerhead sharks with a wing-like design.

**Dihedral**

Vertical tilting of wings.

**Fin (cf. flipper)**

Appendages of fish supported internally by fin rays, used for stability, maneuverability and propulsion.

**Fin fold**

Primordial median and ventro-lateral ridges of the integument that give rise to fins.

**Fin span**

Linear distance from base to tip of fin.

**Flipper (cf. fluke)**

A broad flat appendage modified from the arms and legs of secondarily aquatic vertebrates.

**Fluke**

Lateral wing-like extension of the tail of cetaceans.

**Heterocercal (tail)**

Caudal fin with upper lobe larger than lower lobe, as seen in most sharks.

**Peduncle**

Narrow base of tail anterior of the caudal fin or flukes.

**Pinniped**

Member of the mammalian order that includes seals, sea lions and the walrus.

**Planform area**

Two-dimensional projected area of a surface.

**Rostrum**

Anterior projection of the head.

**Spoiler**

Hydrodynamic structure that alters flow over the body.

**Trajectory**

Pathway of a moving body.

**Trim**

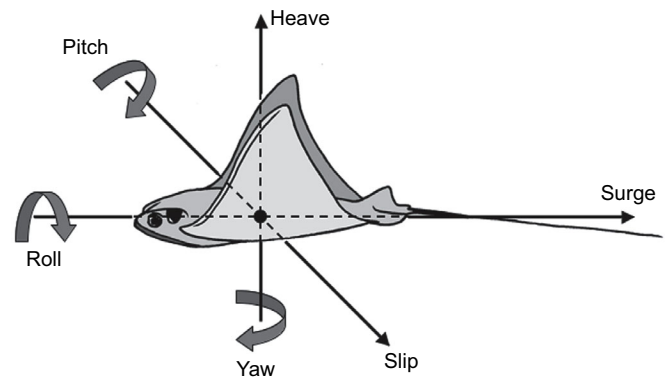
A balanced condition in which the body is in stable equilibrium.

**Tubercle**

A rounded bump projecting from the surface.

**Uropatagium**

Wing membrane from the skin of bats that is supported by the legs and tail.



**Fig. 1. The six degrees of freedom that specify the position and orientation of the batoid (ray) body.** Rotational movements include roll (rotation around the longitudinal axis), pitch (rotation around the transverse axis) and yaw (rotation around the vertical axis). Translational movements along the three axes include surge (longitudinal axis), heave (vertical axis) and slip (transverse axis). Reproduced with permission from Parson et al. (2011).

rotational movements that, combined, give rise to what is termed the ‘six degrees of freedom’. The degrees of freedom for the translational planes are surge (anterior-posterior movement), heave (vertical displacement) and slip (lateral displacement), whereas rotation about the rotational axes is termed roll for the longitudinal axis, pitch for the lateral axis and yaw for the vertical axis (Webb, 2004, 2006). Stability about the roll axis governs lateral stability, about the yaw axis controls directional stability and about the pitch axis imparts longitudinal stability. Longitudinal stability is associated with ‘trim’, which relates to the alignment of the COMs and buoyancy in the vertical axis, and the longitudinal axis of the horizontally oriented body (Burcher and Rydill, 1994).

Control of each degree of freedom by various combinations of control surfaces maintains stability in order to combat internal and external perturbations. Perturbations are forces and torques that cause undesired changes in attitude and trajectory (Webb, 2006). Internal perturbations are related to self-generated motions of the animal and changes in body density (e.g. muscle contraction, gas distribution). External perturbations are a function of forces impinging on the animal from the environment (e.g. waves, currents, vortices shed from structures in flow, interactions with other animals). The position, size and geometry of the control surfaces help to maintain stability and to regulate instabilities by generating the forces to counter perturbations. Alternatively, when deployed asymmetrically, these same stabilizing structures can initiate instabilities for maneuvering. It is this duality of function that makes control surfaces so important in the locomotor performance and evolution of aquatic vertebrates.

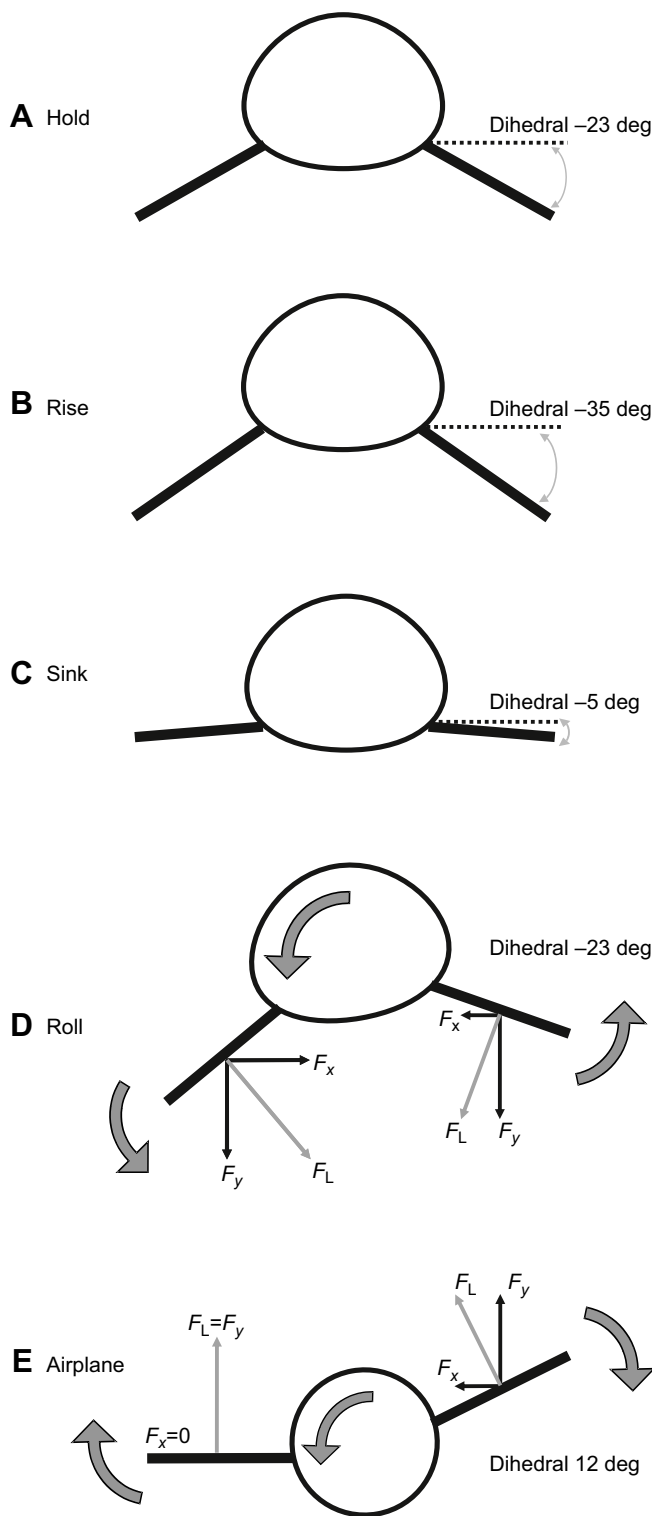
**The control of attitude**

To understand how variation in the morphology of control surfaces can affect stability and maneuverability, consideration should be given to parameters associated with stability that affects the attitude (i.e. position of the body relative to defined orientation axes). Maneuverability represents a controlled instability, and morphological characters that deviate from those of a stable design are expected to enhance maneuvering performance. Generally, the more stable a body is, the less maneuverable it is (Weihs, 1993; Fish, 2002, 2004). Here, we will first explain the basic principles in terms of one of the simplest models for assessing a stable design for movement through a fluid – that of the performance of an arrow (Harris, 1936; Wegener, 1991; Fish, 2002). Upon being shot from a

First we introduce the general principles governing movement in aquatic vertebrates, then discuss primary control surfaces such as fins and flippers (see Glossary), before describing what we term secondary (or specialized) structures for positional control. We will also briefly consider the evolution of control surfaces and its application to bio-inspired designs.

**Axes of motion and the need for control surfaces**

When suspended within the water column, animals can move freely about three translational planes and about three rotational axes that are orthogonally arranged and intersect at the center of mass (COM) (Fig. 1). The COM is the point where the weight of the animal is considered to be concentrated and acts as the ‘balance point’. Movement about the COM permits translational and



**Fig. 2. Pectoral fin orientation in sharks.** (A–C) Schematic of the dihedral orientation of the pectoral fins in a leopard shark during (A) holding body position in the water, (B) rising and (C) sinking swimming behaviors. The body and fin are represented as a cross-section at the level of the pectoral fin. Small double-headed arrows represent the dihedral angle between the horizontal (dotted line) and pectoral fins. (D,E) Forces during a roll are illustrated for (D) the pectoral fins of a leopard shark and (E) the wings of an airplane. Thick arrows show the direction of movement of the body and fins or wing during a roll. Positive dihedrals (such as those used in aircraft design; E) are self-stabilizing, whereas fins oriented at a negative dihedral angle, as in the leopard shark (D), are destabilizing in roll and tend to amplify roll forces.  $F_x$ , horizontal force;  $F_y$ , vertical force;  $F_L$ , resultant force. Graphic and caption modified with permission from Wilga and Lauder (2000).

about the control surface and the body determines the net force and its applied torque. Like the feathers of an arrow, control surfaces located far from the COM can generate large directionally correcting or destabilizing torques because of their long lever arms (Webb et al., 1996; Fish, 2002). The relative size of a control surface in relation to its location will also determine the magnitude of the torques (Aleyev, 1977). Stable forward movement occurs with posterior placement of the control surfaces relative to the COM (Wegener, 1991). This placement positions the center of pressure (COP, see Glossary) aft of the COM. The COP is the point where all the aerodynamic forces combine on a body (Wegener, 1991). The reverse position will create an unstable situation, and perturbations result in tumbling. Placing the tail fin well aft of the COM turns the body into the flow in a manner similar to a weathercock (Wegener, 1991).

Both dihedral (see Glossary) and sweep of control surfaces act similarly to stabilize roll and yaw, respectively (Fig. 2; Breder, 1930; Harris, 1936; Webb, 1975; Weihs, 1993; Fish, 2004). Dihedral is a positive or negative vertical tilting of the control surface or wing relative to the body long axis. Sweep is a rearward or forward sloping of the leading edge. Dihedral designs are good at resisting sideslip (Fish, 2004). When the trajectory of an arrow deviates from a straight flight (i.e. pitch or yaw), the velocity of fluid will be oriented obliquely to each member of a paired control surface. The control surface with a more perpendicular orientation to the flow will generate larger forces than the other control surfaces and produce stabilizing moments (Fish, 2004). Rearward sweep results in a backward shift in the COP, providing increased stability with respect to yaw (Weihs, 1993). Alternatively, forward swept control surfaces increase maneuverability (Anderson and Eberhardt, 2001). Swept wings can be combined with negative dihedral, also called ‘anhedral’, to combat coupled instabilities of yaw and roll (Barnard and Philpott, 1995), although anhedral control surfaces are considered to be destabilizing in aerial flight (Anderson and Eberhardt, 2001). Reduced motion of control surfaces and reduced flexibility of the attached body can restrict self-generated perturbations (Walker, 2000; Fish, 2002, 2004; Fish and Nicastro, 2003).

Although dihedral control surface designs tend to be self-stabilizing, some fishes have control surfaces oriented with an anhedral, and such a condition is destabilizing. Many sharks (Wilga and Lauder, 2000) have pectoral fins oriented with a negative dihedral (anhedral), and roll instability is amplified in this configuration. Sharks can also alter the extent of the negative dihedral. Wilga and Lauder (2000) showed that, as leopard sharks move up in the water column, pectoral fins are held at a greater anhedral angle than sharks moving toward the bottom, and the dihedral angle approaches 90 deg (Fig. 2). When swimming at night, the great hammerhead shark (*Sphyrna mokarran*) rolls 50 to

bow, an arrow becomes self-stabilizing with respect to pitch, yaw and roll.

Features associated with the placement and design of control surfaces provide stability by producing torques to maintain a constant attitude by counteracting perturbations (Harris, 1936; Aleyev, 1977; Weihs, 1993; Bandyopadhyay et al., 1997; Fish, 2002, 2004). Control surfaces in animals act as either wing-like structures to generate lift, or as paddles and spoilers to disrupt flow and increase drag. In both cases, the pressure distribution from flow

70 deg to reconfigure the lifting surfaces with one pectoral fin and a large dihedral dorsal fin (Payne et al., 2016). This reorientation generates increased lift that counteracts sinking of the dense body. Payne et al. (2016) asserted that this orientation of the body and fins should reduce the cost of transport by 10%. However, the large dorsal fin could potentially produce more lift than the pectoral fins, generating an asymmetry in forces that would induce roll and return the body to its normal swimming orientation. The energy necessary for the generation of compensatory forces to maintain roll could negate any energy savings.

The highly streamlined bodies of animals (e.g. fish, dolphins) should be unstable and necessitate the addition of control surfaces for stability (Triantafyllou, 2017). This unstable morphology is due to the position of the aerodynamic center (see Glossary), which is anterior to the COM. The aerodynamic center is an imaginary point where the lift force acts through a fixed point in which the pitching torque remains constant (Wegener, 1991; Barnard and Philpott, 1995). To compensate for the unstable morphology as in an arrow, the position of stabilizing hydrofoils and the COP is toward the rear of the body (Fish, 2002; Triantafyllou, 2017).

But unlike an arrow, the animal body is responsible for producing its own propulsive forces. Flexibility of the body and the appendages, by undulation and oscillation, are necessary in the generation of thrust (Lighthill, 1975; Webb, 1975; Fish, 1996). These propulsive motions produce transverse recoil forces that must be balanced along the body to maintain stability and minimize energy expenditure during locomotion (Lighthill, 1975; Webb, 1992). But increased flexibility for propulsion can also induce destabilizing perturbations. The various forms of cyclical and symmetrical movements of the body and appendages can act as dynamic stabilizers (Harris, 1937; Fish, 1982; Ferry and Lauder, 1996; Fish et al., 2003a,b; Hedrick et al., 2009). In dynamic stabilization, the movements generate the stabilizing forces by active control. When symmetrically applied, the time-averaged propulsive forces maintain an animal on course, although oscillations in the body are apparent. In elongate animals, recoil forces are balanced by multiple body flexures (Webb, 1975). However, the animal pays a penalty in terms of increased drag and by generating large side forces that do not contribute to thrust (Lighthill, 1975). Animals with short or inflexible bodies reduce recoil by changes in the distribution of the projected area in the direction normal to flexure (Lighthill, 1975; Aleyev, 1977; Fish et al., 2003a,b).

As opposed to maintaining stability, control surfaces can also promote maneuvering performance. Banking is required for fully submerged animals to turn without a substantial reduction in speed (Watts, 1961; Hui, 1985; Fish and Battle, 1995; Fish, 2002; Fish et al., 2003a,b). A banking turn is initiated by a rolling maneuver to direct the lift created by the control surfaces towards the center of the turn (Fig. 2). Lift forces are used to generate the centripetal force required to accomplish the turn. The effectiveness of a banking turn is determined mainly by the bank angle (i.e. degree of roll), size and lift characteristics of the control surfaces, and the square of the speed (Weihs, 1981b). Maintaining a curved trajectory is difficult at low speeds. As speed decreases, the lift generated by control surfaces also decreases relative to the required force necessary to turn. Low-speed maneuvers can be accomplished by asymmetrical alignment of paired control surfaces. By using one control surface as a spoiler, drag is created to generate a yawing torque about the COM (Edel and Winn, 1978; Segre et al., 2016).

Rolling maneuvers (i.e. when the center of rotation runs through the longitudinal axis of the body) can be accomplished by alternate or simultaneous canting of the paired control surfaces. Cetaceans, for example, induce spinning by using the lift produced by pectoral

flippers (Fish et al., 2006; Goldbogen et al., 2013; Segre et al., 2016).

### Primary control surfaces

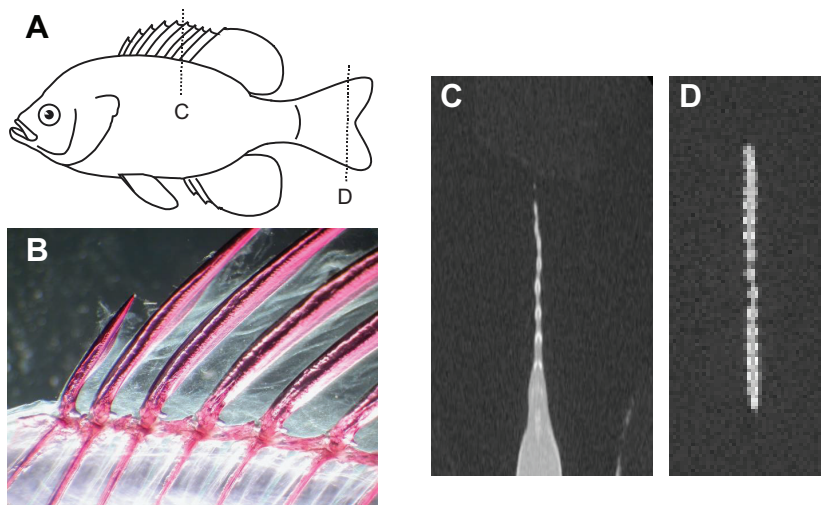
#### The function of lift- and drag-based primary control surfaces

Primary control surfaces in aquatic vertebrates consist of paired and unpaired fins in fishes, and paired flippers and the unpaired dorsal fin in secondarily aquatic tetrapods. In addition to these paired structures, the propulsive caudal flukes (see Glossary) of cetaceans (whales, dolphins, porpoises) and sirenians (manatee, dugong), and the laterally compressed caudal peduncle (see Glossary) of cetaceans function as primary control structures (Fish, 2002). In addition, various structures serve as secondary modifiers of the primary locomotor control surfaces – these will be discussed later. Primary control structures can be rigid or flexible, and are generally either both thin and flat (e.g. fish fins) or have a fusiform (spindle-like) cross-sectional design (e.g. flippers of penguins, sea lions and cetaceans) (Felts, 1966; Lang, 1966; Magnuson, 1970; Fish, 2002). Many fish fins have a ‘bumpy’ or uneven surface caused by fin ray-supporting elements interspersed between a thin membrane (Fig. 3; Lauder, 2011). The forces that these control surfaces produce can be ‘lift-based’ or ‘drag-based’, or both.

Control surfaces that are primarily ‘lift-based’ act as wing-like planing devices. The control surface generates a lift force that can be directed in a particular direction for stabilization or to generate an instability in any combination of pitch, roll and yaw. The lift force created by the control surface is a function of the surface area reflected in the planform (i.e. shape, see Glossary), hydrofoil shape and aspect ratio (=fin span<sup>2</sup>/planform area), where fin span (see Glossary) is defined as the linear distance from base to tip of the control surface. Well-performing hydrofoils maximize the lift to drag ratio (L/D) (von Mises, 1945; Webb, 1975; Vogel, 1994; Weber et al., 2009, 2014). Increased lift can be fostered by cambering (i.e. asymmetry between dorsal and ventral surfaces of a hydrofoil). Although most control surfaces for vertebrates have a hydrofoil shape that is nearly symmetrical in cross-section, the pectoral fins of tuna and wings of penguins are cambered (Magnuson, 1970; Bannasch, 1994), suggesting a predictable bias in the direction of the lift vector resulting from flow over the surface.

Control surfaces that act in a primarily ‘drag-based’ mode have a paddle-like design in which the planform area is directed perpendicular to the motion of the paddle. This design and orientation produce a large pressure differential between forward and leeward surfaces, resulting in substantial pressure drag. With this increased drag, control surfaces can be engaged as a brake to slow down or to stop motion (Harris, 1936, 1937; Felts, 1966; Webb, 1983, 1984; Lauder and Drucker, 2004; Higham, 2007; Oliver et al., 2013), and dampen recoil from propulsive oscillations (Fish et al., 2003a,b). Tests on models of fish demonstrated that fins with circular and triangular planforms produced greater pressure drag than square or rectangular planforms (Blake, 1981).

Most control surfaces act with a combination of lift-based and drag-based effects, and this can be clearly seen in the directionality of vortex-induced flows produced by control surfaces as they act to modify body position or generate propulsive forces (e.g. Drucker and Lauder, 1999; Wilga and Lauder, 2000). Control surfaces, as they deform and move, generate fluid momentum that can be manifest as discrete vortex rings with a central momentum jet. The reaction force to this fluid momentum jet can have a lift component, directed vertically (acting to counteract body weight, for example) and a drag component directed anteriorly in the direction of travel that contributes to thrust. Analyzing the directional components of



**Fig. 3. Anatomy of bluegill sunfish fins to illustrate the shape and textured surface of fins in ray-finned fishes, which are not often streamlined in cross-section (also see Fig. 4).** The position of fin sections for C and D are indicated in A for a fish 15 cm in length. (B) Light micrograph of skeletal elements of dorsal fin spines, stained red, and the collagenous membrane that connects the spines. (C,D) Enlarged anterior views of the dorsal and caudal fins show the 'bumpy' texture caused by the fin rays and intervening membrane that connects the rays. Fish fins can be composed of rigid spines as well as more flexible regions supported by fin rays. Figure elements modified with permission from Lauder (2011).

fluid momentum generated by the control surfaces of aquatic vertebrates shows that most surfaces function to generate both lift and drag forces, and the surfaces are able to modify L/D through conformational changes, depending on the particular locomotor situation.

#### Structure of primary control surfaces

Ray-finned fishes (Actinopterygii) have fins composed of a thin membrane supported by proximal bony radial elements and more distally by bony spines and fin rays (lepidotrichia). The skeletal arrangement of the lepidotrichia is composed of two columns of bony segments (Geerlink and Videler, 1986; Alben et al., 2007; Lauder and Drucker, 2004; Flammang et al., 2013; Taft and Taft, 2012). Muscles pulling on either column of lepidotrichia causes fin rays to flex, which allows for active surface control driven by musculature that remains within the body wall.

Scombrid fishes (e.g. tuna) can erect the median dorsal fins with a musculo-vascular complex (Pavlov et al., 2017). The combination of fin muscles, bones and extensive lymphatic vessels work to hydraulically control the shape and area of the fin affecting stability and maneuverability. Sharks and rays have cartilaginous basal elements at the base of the fin and numerous smaller radial cartilages extending distally. The majority of fin area is composed of collagenous ceratotrichia (Kemp, 1977), which cannot be actively bent. There are no muscles extending to the distal elements of fins, with the exception of sarcopterygian fishes (e.g. lungfish) and batoid rays (e.g. stingrays, skates, manta rays). It has been proposed that an increase in the hydrostatic pressure within the body may be transferred through the collagen fibers around the body and into the dorsal fin of the white shark (*Carcharodon carcharias*) to stiffen this control surface (Wainwright et al., 1978; Lingham-Soliar, 2005).

The flippers of aquatic tetrapods are modifications of the fore- and hindlimbs of terrestrial animals, which have become adapted for use in water. These limbs enclose a bony skeleton homologous with the bones of terrestrial tetrapods (Williston, 1914; Howell, 1930; Cooper et al., 2007). Pectoral limbs have a proximal humerus, which articulates at the shoulder joint with the scapula (Howell, 1930; Walker, 1971; English, 1977; Bannasch, 1994; Wyneken, 1997; Fish, 2004). This joint is a multiaxial ball-and-socket articulation, permitting various movements, including protraction, retraction, adduction, abduction and rotation. In reptiles and birds, the shoulder joint also includes the coracoid, and in cetaceans also can involve the sternum (Klima et al., 1987).

Distally, the humerus articulates with two bones – the radius and the ulna. The ulna and radius terminate at the wrist joint and articulate distally with the carpal bones that are followed distally by the metacarpals and the phalanges. In the terrestrial condition, there are five digits, with the exception of large whales in the family Balaenopteridae, which lack a thumb, and birds, which have lost digits in the evolution of the wing for flight. In flippers, the digits are not separated. The number of phalanges in each digit of the flipper is variable among species. Hyperphalangy is the condition found in cetaceans and ichthyosaurs in which the maximum number of phalanges in the digits exceeds the terrestrial number (Williston, 1914; Howell, 1930; Riess, 1986; McGowan, 1991; Fish and Battle, 1995).

Control surfaces without internal bony support, such as the dorsal fin, flukes and peduncle keels in ichthyosaurs, sirenians and cetaceans are reinforced by dense arrays of collagen fibers (Felts, 1966; Lingham-Soliar, 2001; Lingham-Soliar and Plodowski, 2007). The keels of the peduncle of dolphins are composed of blubber containing structural fibers composed of collagen and elastic fibers (Hamilton et al., 2004). These fibers act as tensile stays. Collagen fibers with high tensile strength are found in the flukes of cetaceans (Sun et al., 2010a,b). Fibers are arranged in a dense array of chordwise-oriented thin crossing fibers, which make up the inner core layer, sandwiched between two layers of spanwise-oriented thick fibers, which make up the outer ligamentous layers (Felts, 1966; Sun et al., 2010a,b, 2011; Gough et al., 2016). This sandwich composite beam provides rigidity with some bending (Sun et al., 2010b).

The caudal fin of fishes can be used as a rudder to stabilize the body in the yaw axis or to generate torques to effect a turn (Harris, 1936; Webb, 1975; Walker, 2000). The peduncle and flukes of dolphins can be twisted to produce turns (Fish, 2002). By laterally deflecting the position of the tail, crocodilians can induce a spinning maneuver that is used to dismember large prey when feeding (Fish et al., 2007a,b). This maneuver is a turn of zero angular momentum created by an imbalance from the respective positions of the masses of the body and tail segments. A zero angular momentum maneuver is where the vector sum of all the momenta balances for the motion of the animal from the start to the termination of the spin with a lack of external torques (Frohlich, 1980; Fish et al., 2007a,b).

Some control surfaces can be stored to minimize the surface area exposed to the flow to control instabilities and reduce drag. For example, the hind flippers of pinnipeds (see Glossary) can be folded to minimize drag or spread to act as a rudder during turning (Fish et al., 2003a,b). Penguins, pinnipeds and humpback whales can fold

the pectoral flippers against the body to increase streamlining. Both tuna and some deep-diving toothed whales can place their pectoral fins and flippers, respectively, into shallow depressions on the sides of the body to further increase streamlining. The dorsal fins of tuna can be folded into a dorsal slot when not needed (Fig. 4). Folding of the dorsal fin can control its sweep and move the aerodynamic center of the tuna either posteriorly to increase stability or anteriorly for maneuverability by reducing stability (Triantafyllou, 2017). Most ray-finned fish species can fold the dorsal anal, pectoral and pelvic fins or hold them against the body to minimize surface area to control lift and drag.

In addition to movement of the entire control surface, active fin surface deformation is well documented, and such conformational changes can alter flow direction to effect maneuvers. Ray-finned fishes, in particular, can exhibit considerable fin surface deformation when fins are used as control surfaces, and many shark species also are capable of altering fin conformation to alter body pitch and roll (Fig. 2; Wilga and Lauder, 1999, 2000).

### The evolution of control surfaces

Control surfaces first evolved in aquatic organisms and appeared to have been associated with swimming stability and maneuvering (Radinsky, 1987). The earliest chordates are considered to have lacked paired fins for control surfaces (Jarvik, 1965; Maderson, 1967; Webb, 2006), although the tail and ventro-lateral fin folds (see Glossary) could have generated control forces. In modern jawless fishes (e.g. hagfish, lamprey) that lack pectoral fins, undulation of the elongate flexible body can be used to stabilize the swimming trajectory. Nevertheless, yawing moments at the head and instabilities in roll might reflect a lack of three-dimensional body control due to the arrangement of control surfaces (Ullén et al., 1995; Webb, 2004).

The evolution of armor and ornamentation in early ostracoderm fishes (i.e. Silurian and Devonian jawless fishes) led to the development of hydrodynamic control surfaces (Webb, 2004). Lateral extensions of large head shields in Osteostraci and Heterostraci (Moy-Thomas and Miles, 1971; Long, 1995) were immobile and probably acted as simple planing structures for pitch and roll control. During the subsequent evolution of jawed fishes, there was a general trend towards increased mobility and independent control of individual fins. Early pectoral fins presumably were capable of independent movement from the

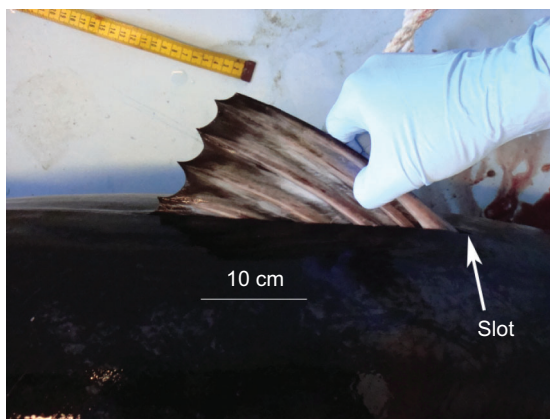
body and could be used to control body position (Nursall, 1962; Moy-Thomas and Miles, 1971; Hopson, 1974; Long, 1995). Pectoral and pelvic fin movements are somewhat limited in sharks and basal Actinopterygii (e.g. sturgeon) relative to teleost fishes, but can still be repositioned to allow directional force vectoring (Harris, 1936, 1937, 1938; Wilga and Lauder, 1999, 2000, 2001; Fish and Shannahan, 2000). In teleost fishes, fins have considerable mobility, which is achieved by muscular control of individual skeletal elements (Lauder et al., 2006; Westneat and Walker, 1997). This mobility permits active control to generate stabilizing forces as well as propulsive forces (Webb, 1994, 2006; Lauder and Drucker, 2004). In derived teleost fish clades, positioning the pectoral fins laterally and the pelvic fins anteroventrally moved these control surfaces near to the COM to promote maneuverability and braking (Harris, 1938; Drucker and Lauder, 2002; Schrank et al., 1999).

In fishes, median fins (e.g. dorsal, anal, caudal) likely evolved before paired fins, ~400 million years ago (Coates, 1994; Mabee et al., 2002). Caudal fins could have developed as an extension of the trailing edge fin flap (Webb and Smith, 1980) and became the major propulsive structure in fishes functioning in concert with undulations of the body. The evolution of the other median fins might have been represented first by dorsal spines (Moy-Thomas and Miles, 1971) before the development of a fin membrane, with the subsequent addition of skeletal supportive elements. Median fins appear to have initially lacked mobility independently of the body (Webb, 1994).

The paired fins of sarcopterygian fishes are homologous with the pectoral and pelvic limbs of tetrapods, which were used originally for mobility underwater and subsequently for terrestrial locomotion. Various lineages of terrestrial vertebrates, however, reinvaded the aquatic realm, resulting in the convergent evolution of fin-like structures in derived species (Howell, 1930; Kelley and Pyenson, 2015). These secondarily aquatic vertebrates included extant sea turtles, penguins, cetaceans, sirenians and pinnipeds, and extinct ichthyosaurs, mosasaurs and plesiosaurs (Fish, 2002, 2004, 2016). Flippers represent modifications of the pectoral and pelvic limbs, with limited mobility within the appendage, except at the shoulder and hip joints, respectively (Williston, 1914; Howell, 1930; Felts, 1966; Raikow et al., 1988; Fish, 2004; Slack et al., 2006; Cooper et al., 2008). Flippers are used to control stability and maneuverability, but the pectoral flippers of sea turtles, penguins and sea lions (otariids) are also the primary propulsive structures. Both the pectoral and pelvic flippers of extinct plesiosaurs probably functioned for propulsion as well as providing stability and maneuverability (Robinson, 1975; Lingham-Soliar, 2000; O'Keefe, 2001; Carpenter et al., 2010). Dorsal fins are present in ichthyosaurs and most cetaceans, and, unlike the flippers of aquatic tetrapods, relatively immobile dorsal fins developed anew without internal bony supports. Similarly, the caudal flukes of cetaceans and sirenians lack internal skeletal stiffening (Felts, 1966; Fish et al., 2007a,b; Sun et al., 2010a).

### The body as a control surface

Appendages are the primary control surfaces in aquatic vertebrates, but the geometry of some body configurations can generate lift in the vertical plane, and a flexible body can also act as a control surface. The forward 'snout', or rostrum (see Glossary), of many sharks has a cross-sectional profile that is wider than it is high, with its maximum thickness close to the ventral side (Weihs, 1981a). This design provides increased streamlining laterally that reduces drag on the head arising from the yawing motions due to recoil from the propulsive lateral undulations of the body and caudal fin.



**Fig. 4. Slot for storage of dorsal fin in a Pacific bluefin tuna (*Thunnus orientalis*).** The slot is indicated by the arrow. In this image, the dorsal fin is being pulled out of the slot to expose the fin spines and membrane. Scale bar: 10 cm. Photograph taken by F.E.F.

Furthermore, the position of the maximum thickness close to the ventral side produces a flattening of the ventral aspect of the animal that can serve as a lifting surface. Harris (1936, 1938) demonstrated that the body of a shark (*Mustelus canis*) could generate positive and negative lift at positive and negative angles of attack (see Glossary), respectively. However, greater lift was produced when the paired fins were present (Harris, 1936). Both the leopard shark (*Triakis semifasciata*) and sturgeon (*Acipenser transmontanus*) angle the flattened undersides of the anterior body to deflect the momentum of the water downwards to generate lift and counter downward pitching induced by the motions of the extended heterocercal tail (see Glossary) (Wilga and Lauder, 1999, 2000; Liao and Lauder, 2000). Flying fish (Exocoetidae) of the genus *Cypselurus* have a flattened venter, which could generate lift underwater, at the surface and in the air (Breder, 1930; Fish, 1990). Finally, data from three-axis accelerometers placed on free-diving elephant seals (*Mirounga angustirostris*) indicate that the body generates lift as the animal descends in order to reduce sinking rates and allow the body to glide horizontally (Davis et al., 2001; Davis and Weihs, 2007).

Benthic animals often have body shapes or use their fins in ways that produce negative lift. Plaice (*Pleuronectes platessa*) have a semi-ellipsoid shape with a flat venter when oriented into a flow (Arnold and Weihs, 1978), and this can act to generate forces to press the body into the bottom. To prevent the fish being dislodged in high-speed flows, plaice beat their fins rapidly to increase flow under the fish and reduce the pressure differential between the dorsal and ventral surfaces of the fish. This action prevents the flow-induced lift forces from pulling fish off the bottom (Arnold and Weihs, 1978). Demersal rays (e.g. *Dasyatis sabina*, *Potamotrygon motoro*) similarly hold station on the bottom in opposition to advancing waves by undulating the posterior margin of the enlarged pectoral fins (Fish and Hoffman, 2015). Pectoral fins of benthic and stream-dwelling fishes can also act to generate negative lift forces and increase friction between the body and substrate in flow (Arnold and Weihs, 1978; Carlson and Lauder, 2011; Wilga and Lauder, 2001).

### Secondary control structures

As discussed above, appendages that extend from the body serve as the primary control structures for aquatic locomotion, and can modify flow and generate the forces and torques to control body attitude. These control surfaces can be modified to enhance performance, and, in this section, we consider a number of intriguing features that serve as secondary modifications to locomotor control surfaces – some such as tubercles (see Glossary) originate as modifications to the primary control structures, whereas others such as keels and finlets are non-propulsive secondary structures in their own right.

### Modifications of primary structures

#### Tubercles of whale flippers

A remarkable feature on the leading edge of humpback whale flippers is the presence of 10 to 11 prominent rounded bumps, called tubercles (Fig. 5; Fish and Battle, 1995). Tubercles are large near the body, but decrease in size towards the tip of the flipper. The intertubercular distance is relatively uniform, between 6.5% and 8.6% of the span over the mid-span of the flipper and decreasing towards the tip (Fish et al., 2011).

The position and number of tubercles on the humpback flipper suggest that tubercles serve as leading-edge control devices lending improvements in hydrodynamic performance (Bushnell and Moore, 1991; Fish and Battle, 1995; Fish et al., 2011). The elongate flippers in whales function as ‘wings’ to generate the centripetal force



**Fig. 5. Flipper of the humpback whale (*Megaptera novaeangliae*) showing tubercles along the leading edge.** These tubercles modify the flow over the wing-like flipper to enhance the hydrodynamic performance of this control surface. Photograph courtesy of W. Rossitier (Cetacean Society International).

necessary for turning maneuvers in the capture of elusive prey (Fish et al., 2011). Fish and Battle (1995) considered that tubercles generate vortices by unsteady excitation of flow to maintain lift and prevent stall at high angles of attack. A delay in stall at high angles of attack allows the whale to turn tightly. Stall is postponed because vortices exchange momentum within the boundary layer to keep it attached over the wing surface (Miklosovic et al., 2004; Fish and Lauder, 2006). Wind tunnel tests showed that wings with tubercles improved maximum lift by over 6%, increased the ultimate stall angle by 40% and decreased drag by as much as 32% (Miklosovic et al., 2004).

The occurrences of biological leading-edge structures with possible hydrodynamic effects, such as tubercles, although rare, are not unique. Paleozoic fishes of the order Iniopterygia had an array of large fish-hook-shaped denticles along the leading edge of the elongate pectoral fins (Zangerl and Case, 1973). The genus *Protosphyraena* was a member of a group of swordfish-like predatory marine fishes from the Upper Cretaceous period. These fishes possessed high-aspect-ratio pectoral fins with serrated leading edges (Fish et al., 2011).

The scalloped hammerhead (*Sphyrna lewini*) has a cephalofoil (see Glossary) with a scalloped shape reminiscent of the tubercles of the humpback whale flipper. Bushnell and Moore (1991) proposed that the scalloped leading edge could have hydrodynamic benefits with regard to drag reduction. Although drag reduction has not been tested, the scalloping of the cephalofoil could act like the humpback whale tubercles and delay stall at high angles of attack (Miklosovic et al., 2004), which would permit the shark to make sharp pitching maneuvers.

Small tubercles ( $\geq 1.1$  mm) occur along the leading edge of the dorsal fin of porpoises (Ginter et al., 2011). These tubercles could act as passive flow-regulating structures to reduce disturbances at the surface of the water. Alternatively, microtubercles could help the fin pierce thin ice at the water surface or play a role in tactile social interactions (Kastelein et al., 2016).

#### Fin surface texture in ray-finned fish

The fins of ray-finned fishes are often thought of as being smooth and airfoil-like. But as Fig. 3 shows, fish fins can be far removed from having a streamlined shape and they often have blunt leading



edges with a ‘bumpy’ surface formed by the individual fin rays or spines and the thin intervening membrane. This design could be considered as a secondary control feature, although the effect of this roughened control surface on fluid flow dynamics and force generation is, at this point, entirely unknown. In addition, because fish can alter the position of their fins, the direction of the textured surface relative to the incident flow can be altered. For example, as the dorsal fin is erected during acceleration behaviors (Tytell and Lauder, 2008; Tytell et al., 2010; Chadwell et al., 2012), the orientation of the fin ray ‘bumps’ on the fin will change. The effect of fin surface textures on control surface function in fishes is a particularly fascinating area for future research.

#### Tip and trailing edge structures

Although rarely considered in the literature, the shape of the trailing edge of control surfaces can have significant hydrodynamic effects. In the ‘bulk momentum’ model from Lighthill’s (1975) elongate body theory, the trailing edge of an oscillating caudal fin is considered to be the site where momentum is shed into the wake for propulsion. The trailing edge is often modeled as a straight edge. However, the trailing edges of fins, flippers and flukes are rarely straight. These control surfaces can have fin tips that will extend well beyond the posterior margin of the fin and a ragged or crenelated trailing edge.

Fin tips are the sites where the tip vortices are formed. As fins are canted at an angle to the oncoming flow, tip vortices are created from the pressure difference between the suction and pressure sides of the fin as fluid moves around the tip and is convected into the wake. Tip vortices represent a loss of energy and are associated with induced drag in the generation of lift (Webb, 1975). The morphology of fin tips can therefore influence the strength of tip vortices and the resulting drag force. Flexibility at the fin tips could further control flow by allowing them to act as flexible ‘winglets’ (Blevins and Lauder, 2012). Winglets are modification of the tips of wings that modify wing tip vortices and effectively increase wingspan, which improves aerodynamic efficiency. Furthermore, the tips of the caudal fin of tuna and dolphins lag the oscillatory movements of the center of the fin (Fierstine and Walters, 1968; Curren and Lien, 1994) and could be acting effectively as winglets.

The flukes of humpback whales possess crenellations along their span, which could act as trailing-edge control surface modifications. These small extensions of the trailing edge are larger in height near the fluke midspan and then sharply decrease towards the tip of each fluke (Wolfe, 2017). It is unknown what the hydrodynamic effects of such crenellations are, but studies of wavy and serrated trailing edges, including those of owl wings, have implicated drag reduction, stall alleviation and noise abatement (Werle et al., 1987; Bachmann and Wagner, 2011; Wolfe, 2017).

#### Secondary structures

##### Canard wings, foils and rostra

Canards are small forewings on aircraft located anterior to the main wing that add lift anteriorly and reduce the load on the main wing (Barnard and Philpott, 1995; Anderson and Eberhardt, 2001). An additional hydrofoil may act as a canard wing when positioned upstream of the main control surfaces (e.g. pectoral fins).

The broad cephalofoil of the hammerhead sharks (family Sphyrnidae) has been hypothesized primarily to be an adaptation to improve sensory capabilities (Nakaya, 1995; Abel et al., 2010). However, the wing-like shape of the cephalofoil may act also as a canard wing. Species of sphyrnid sharks with the broadest cephalofoils (e.g. *Sphyrna lewini*) have proportionally the smallest

pectoral fins, whereas smaller cephalofoil species (e.g. *Sphyrna tiburo*) possess the largest fins (Moss, 1984; Fish and Shannahan, 2000). The symmetrical cross-sectional geometry has the appearance of an engineered hydrofoil. The cephalofoil is not used in banking turns (Kajiura et al., 2003). Cephalofoils, acting as canards, may modify the flow over the body and pectoral fins. Cephalofoils could shed vorticity into its wake that could be used to enhance vertical lift by wake energy recapture by the more posterior fins, and thereby counteract gravity due to the high body density of the shark (Triantafyllou et al., 2000; Payne et al., 2016). In addition, lift generation could be employed to enhance pitching maneuvers (Nakaya, 1995). Added lift from the cephalofoil could help to maintain trim and counter any downward pitch of the head owing to action of the posterior heterocercal caudal fin (Harris, 1936; Alexander, 1965; Fish and Shannahan, 2000; Wilga and Lauder, 2000).

Paddlefish (*Polyodon spathula*) possess a rostrum that is broad and paddle-like, and serves an electroreceptive function (Fig. 6). Hydrodynamic analysis of the paddlefish rostrum showed that it also generates substantial lift (Allen and Riveros, 2013). The presence of this lift-generating canard may be related to pitching moments created by the heterocercal caudal fin or to the filter feeding strategy of paddlefish. Minke whales (*Balaenoptera acutorostrata*) may use the upper palate in concert with the pectoral flippers to generate a lifting torque as the lower jaw is opened during engulfment feeding (Cooper et al., 2008; Cade et al., 2016). The lifting torque cancels out the downward torque produced from opening the mouth and filling the throat pouch during feeding.

#### Multiple control surfaces in series

It has not escaped the notice of biologists or engineers that arranging control surfaces in series can greatly alter the performance of swimming bodies (Yates, 1983). Flow leaving an upstream control surface will have altered velocity and vorticity characteristics as it then encounters the next downstream surface. Downstream control surfaces thus do not encounter undisturbed free-stream flow, and instead experience a greatly altered flow environment compared with that of the upstream fin. For the engineer, configuring control surfaces in this manner could be considered a secondary or additional design criterion to designing individual control surfaces.

Well-studied examples of multiple control surfaces include the dorsal fins of both sharks (Maia and Wilga, 2013a,b, 2016) and bony fishes (Drucker and Lauder, 2001, 2005). Dorsal fins can interact hydrodynamically with each other, when multiple fins are present, or with the caudal fin. In aquatic mammals, hydrodynamic



**Fig. 6.** Paddlefish (*Polyodon spathula*) exhibiting the front-protruding flattened rostrum that can function as a canard to generate lift. The paddlefish was swimming in an aquarium. Photograph taken by F.E.F.

interactions between flippers and dorsal fins and the flukes are possible, but have not yet been studied in detail. Experimental studies in ray-finned fishes (e.g. Drucker and Lauder, 2005; Tytell, 2006) have quantified wake flows leaving the dorsal fin, and determined how this altered flow encountered by the tail might change thrust generation. Estimating such effects on thrust and swimming efficiency from experimental studies is challenging, and computational approaches have served to fill this gap. For example, computational analyses based on bluegill sunfish dorsal and caudal fin movement patterns (Akhtar et al., 2007) showed that a shear layer separating from the dorsal fin is capable of increasing the apparent angle of attack on the caudal fin, and enhancing formation of the leading edge vortex on the tail – hence increasing thrust. This effect was, however, sensitive to the phasing of dorsal and caudal fin motion, and not all phase relationships resulted in increased thrust.

Both computational and engineered models of dual or tandem flapping foils can relieve some of the constraints of working with living animals, where *in vivo* force measurement is difficult, and an increasing number of studies have addressed the effects of dual in-line flapping surfaces to better understand the dynamics of multiple propulsors (Alben, 2009; Deng et al., 2007; Lauder et al., 2007; Yuan et al., 2015).

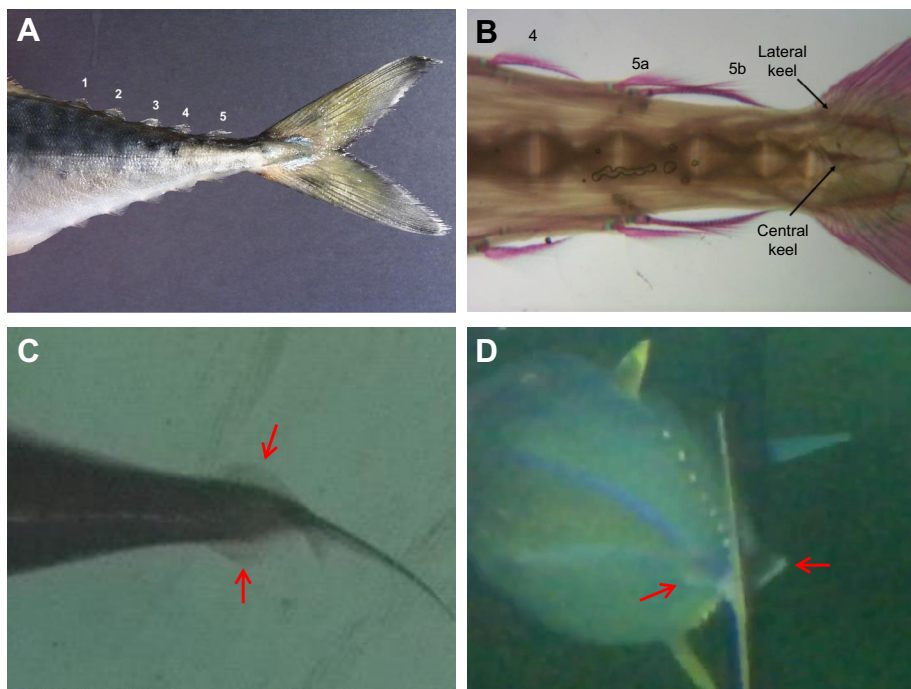
#### Finlets

One of the most remarkable features of ray-finned fishes in the scombrid clade (tuna and relatives) is the presence of small individual finlets located posterior to the dorsal fin and anterior to the tail along both the dorsal and ventral midlines (Fig. 7). Finlets represent a novel and enigmatic type of secondary control surface that total ~15% of the tail surface area in mackerel (Nauen and Lauder, 2000). Each finlet has its own array of intrinsic musculature that allows independent movement, is generally triangular in shape, with a longer trailing edge near the body surface, and is attached to the body at one anterior location that allows rotational motion. Fishes with finlets are generally high-performance swimmers, capable of fast sustained locomotion. Finlets have been generally hypothesized to play some, as yet undetermined, role in increasing

locomotor efficiency. Previous hypotheses of finlet function were summarized by Nauen and Lauder (2001a,b) and include: (1) reducing drag by preventing boundary layer separation in the posterior region of the fish; (2) directing flow towards the caudal keels and thus contributing to lift produced by the keels; and (3) directing flow into the vortex generated by the caudal fin, increasing its circulation and thrust production. Nauen and Lauder (2001b) quantified flow around the finlets of chub mackerel (*Scomber japonicus*) by tracking particle motion in the water and estimated that flow was not significantly redirected by finlet motion during steady swimming. However, finlets move in a complex three-dimensional space, and the most posterior finlets oscillate from side to side, and may also sweep down along the lateral sides of the caudal peduncle. The most posterior finlets in mackerel might thus function to alter local flow in the region of the tail. Finlets have also been observed to function during gliding behavior to reposition the body angle relative to oncoming flow, without involving motion of the tail or other median fins, and in this manner they function as small maneuvering ‘thrusters’.

#### Keels

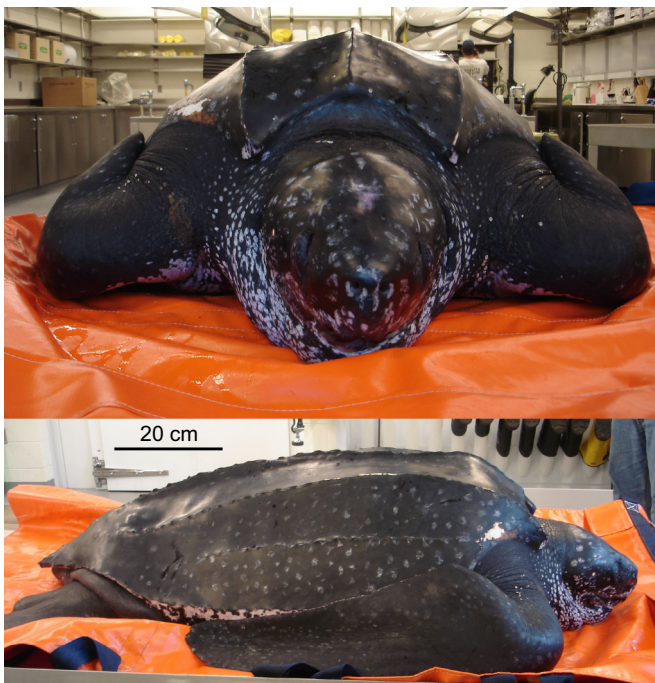
Keels, or ridges along the body (most often in a lateral or dorsal direction), are found in several groups of fishes and provide another class of potential secondary control structures, although keels are generally passive and not under active conformational control. Boxfishes (Ostraciidae, Tetradontiformes) are a group of fishes encased in a rigid bony carapace, which is equipped with keels that are located dorsally and ventrolaterally. It has been proposed that these keels aid in passively stabilizing and trimming the body (Gordon et al., 2000; Bartol et al., 2002, 2003, 2005, 2008). Leading edge vortices are generated as water flows past the keels, in a manner similar to that of delta wing aircraft (Bartol et al., 2003, 2008). These vortices generate a low pressure as the fish is pitched into the flow. Thus, the vortices produce a correcting force, which opposes pitching motions and maintains trim for the body of the fish (Bartol et al., 2002). In addition, yawing was stabilized by the production of dorsal and ventral vortices from the keels (Bartol



**Fig. 7. Peduncle and caudal fin of a scombrid fish, as illustrated in chub mackerel, *Scomber japonicus*, and yellowfin tuna, *Thunnus albacares*.** (A) The peduncle has an array of dorsal and ventral finlets to control flow, here numbered 1 to 5 in chub mackerel. (B) The internal skeleton of the post-posterior two finlets and keels are cleared of muscle tissue and pigment cells, and stained to show the internal skeleton. The most posterior finlet contains two fin rays (labeled 5a and 5b). The two lateral and one central keels in chub mackerel are visible on the lateral aspect of the peduncle. (C,D) In free-swimming yellowfin tuna, the large laterally projecting central keels (indicated by red arrows) are visible from dorsal (C) and posterior views (D). Keels might act to streamline the peduncle in the direction of lateral tail oscillation and hence reduce drag. Modified with permission from Nauen and Lauder (2000).

et al., 2003). This passive stabilization was considered paradoxical as boxfishes operate in complex environments (i.e. coral reef communities) and demonstrate enhanced maneuvering capabilities (Walker, 2000; Van Wassenbergh et al., 2015). Stabilizing torques by vortices have recently been considered negligible compared with torques generated by the head, which can enhance maneuverability (Van Wassenbergh et al., 2015). However, yawing maneuvers by boxfish are relatively limited (Fish and Nicasro, 2003). Keels might be important in helping to stabilize boxfish when they are exposed to external perturbations (i.e. currents), whereas the multiple propulsors that are distributed about the COM induce maneuvering torques.

Interestingly, another rigid-bodied swimmer, the leatherback sea turtle (*Dermochelys coriacea*), possesses keel-like ridges that could be an adaptation for flow control (Fig. 8; Bang et al., 2016). Five dorsal ridges are longitudinally arranged on the carapace of leatherbacks. These ridges could have a hydrodynamic effect with regard to drag, lift and flow separation. Like the leading edge tubercles of the flipper of the humpback whale, the leatherback ridges may delay stall from separation of the flow over the carapace, which can reduce drag (Miklosovic et al., 2004; Fish and Lauder, 2006; Bang et al., 2016). Drag is reduced up to 32% at negative angles of attack, but drag increases by 5.6% at a positive angle of attack. The greater drag reduction with negative angles of attack is associated with the head down/tail up swimming posture of hatchling leatherback turtles (Davenport, 1987). Unpaired streamwise vortices are generated by the ridges and delay separation by conducting momentum to the flow near the surface of the turtle to overcome adverse pressure gradients (Bang et al., 2016). This mechanism differs from the humpback whale tubercles, which generate paired vortices with opposite spins to energize the attached flow on the surface of the flipper to delay stall (Fish and Lauder, 2006).



**Fig. 8.** Leatherback sea turtle (*Dermochelys coriacea*) showing keels from anterior (top) and lateral (bottom) views. Scale bar: 20 cm. The turtle stranded on Cape Cod (MA, USA) before dying. Photographs taken by F.E.F.

Tuna and many scombrid fishes possess keel-like structures along the caudal peduncle (Collette and Nauen, 1983), and these can be large single fleshy structures projecting laterally or multiple keels positioned along the peduncle (Fig. 7). In fresh tuna specimens, these keels are remarkably flexible, and are quite a bit larger than might be suspected from side-view images of live fish. But it remains unclear what hydrodynamic function they have, if any, as previous analysis showed that, in mackerel (Nauen and Lauder, 2001b), keels were unlikely to redirect flow near the tail. Magnuson (1970) proposed that tuna keels could generate lift, but no direct experimental evidence for this hypothesis exists. It remains unclear what the hydrodynamic function of the larger flexible keels in tuna is, and, although other species such as jacks (Carangidae) possess relatively rigid but smaller lateral keels at the peduncle, the function of those structures similarly remains unknown.

### Concluding remarks

The addition of control surfaces (e.g. fins, flukes, flippers, peduncle, finlets, keels) to the vertebrate axial body has been instrumental to the ability of animals to maintain stability and maneuver in the three-dimensional aquatic environment. These control surfaces provide the torques necessary to counter internally generated perturbations associated with recoil from the propulsive mechanics of the animal, and to counter external perturbations (e.g. currents, waves, turbulence) that are encountered in the physical environment.

In ray-finned fishes, median and paired fins act as control surfaces, and have bony supporting fin ray structures with a bilaminar design that allows active control of fin surface shape, but only through muscles acting at the fin base. By contrast, sharks control fin conformation using internal musculature and cartilaginous rays, although these fin rays do not possess the bilaminar structure that allows active surface alteration. In aquatic tetrapods, control surfaces, such as flippers in sea turtles, penguins and pinnipeds, can be highly mobile at a single articulation point, whereas the flippers of most cetaceans have limited movement. The addition of secondary control surfaces (e.g. multiple control surfaces, leading and trailing edge features, deformable surfaces) can aid in overcoming limitations of particular control surface designs. The extent to which active or passive control of surface shape occurs to modify flow during swimming to affect locomotor forces is still a matter of ongoing research.

The analysis of natural control surfaces has technical application in the biomimetic development of aquatic robotic systems (Bandyopadhyay, 2004; Fish, 2006; Tangorra et al., 2010; Moored et al., 2011; Fish and Kocak, 2011; Triantafyllou, 2017). Studies of aquatic vertebrate control surfaces can serve as ‘lessons learned’ from nature to be applied to the design of flexible surfaces with high performance under a variety of locomotor conditions for biomimetic vehicles.

An understanding of the biological roles and potential applications of control surfaces will be elucidated with further research, particularly as new technologies (e.g. flow mapping, accelerometers, miniaturized video cameras, computational fluid dynamics) are applied to studies of animal locomotion. New and novel mechanisms of flow control in animals are to be discovered. Questions regarding the ecological importance of control surfaces will provide insight into foraging efficiency, predator and prey interactions, and energy economy for swimming. As much as an understanding by biologists of the function and mechanics of control surfaces is based on engineering principles, engineers are taking their cue from biology to design future control surfaces based on animals.

**Acknowledgements**

We are highly indebted to the students and collaborators who have helped us attain a greater understanding of the function of aquatic control surfaces.

**Competing interests**

The authors declare no competing or financial interests.

**Funding**

Preparation of this Review was supported by an Office of Naval Research MURI grant (N00014-14-1-0533 monitored by Dr Bob Brizzolara).

**References**

- Abel, R. L., Maclaine, J. S., Cotton, R., Xuan, V. B., Nickels, T. B., Clark, T. H., Wang, Z. and Cox, J. P. L. (2010). Functional morphology of the nasal region of a hammerhead shark. *Comp. Biochem. Physiol. A* **155**, 464–475.
- Akhtar, I., Mittal, R., Lauder, G. V. and Drucker, E. (2007). Hydrodynamics of a biologically inspired tandem flapping foil configuration. *Theor. Comput. Fluid Dyn.* **21**, 155–170.
- Alben, S. (2009). Simulating the dynamics of flexible bodies and vortex sheets. *J. Comput. Phys.* **228**, 2587–2603.
- Alben, S., Madden, P. G. A. and Lauder, G. V. (2007). The mechanics of active fin-shape control in ray-finned fishes. *J. Roy. Soc. Interface* **4**, 243–256.
- Alexander, R. M. N. (1965). The lift produced by the heterocercal tails of Selachii. *J. Exp. Biol.* **43**, 131–138.
- Aleyev, Y. G. (1977). *Nekton*. The Hague: Junk.
- Allen, J. B. and Riveros, G. (2013). Hydrodynamic characterization of the *Polyodon spathula* rostrum using CFD. *J. Appl. Math.* **2013**, 1–8.
- Anderson, D. F. and Eberhardt, S. (2001). *Understanding Flight*. New York: McGraw Hill.
- Arnold, G. P. and Weihs, D. (1978). The hydrodynamics of rheotaxis in the plaice (*Pleuronectes platessa* L.). *J. Exp. Biol.* **75**, 149–169.
- Bachmann, T. and Wagner, H. (2011). The three-dimensional shape of serrations at barn owl wings: towards a typical natural serration as a role model for biomimetic applications. *J. Anat.* **219**, 192–202.
- Bandyopadhyay, P. R. (2004). Trends in biorobotic autonomous undersea vehicles. *J. Ocean Eng.* **29**, 1–32.
- Bandyopadhyay, P. R., Castano, J. M., Rice, J. Q., Philips, R. B., Nedderman, W. H. and Macy, W. K. (1997). Low-speed maneuvering hydrodynamics of fish and small underwater vehicles. *Trans. ASME* **119**, 136–144.
- Bang, K., Kim, J., Lee, S.-I. and Choi, H. (2016). Hydrodynamic role of longitudinal dorsal ridges in a leatherback turtle swimming. *Sci. Rep.* **6**, 34283.
- Bannasch, R. (1994). Functional anatomy of the 'flight' apparatus in penguin. In *Mechanics and Physiology of Animal Swimming* (ed. Q. Bone, L. Maddock and J. M. V. Rayner), pp. 163–192. Cambridge: Cambridge University Press.
- Barnard, R. H. and Philpott, D. R. (1995). *Aircraft Flight*. Essex: Longman Scientific & Technical.
- Bartol, I. K., Gordon, M. S., Gharib, M., Hove, J. R., Webb, P. W. and Weihs, D. (2002). Flow patterns around the carapaces of rigid-bodied, multi-propulsor boxfishes (Teleostei: Ostraciidae). *Integr. Comp. Biol.* **42**, 971–980.
- Bartol, I. K., Gharib, M., Weihs, D., Webb, P. W., Hove, J. R. and Gordon, M. S. (2003). Hydrodynamic stability of swimming in ostraciid fishes: role of the carapace in the smooth trunkfish *Lactophrys triquetter* (Teleostei: Ostraciidae). *J. Exp. Biol.* **206**, 725–744.
- Bartol, I. K., Gharib, M., Webb, P. W., Weihs, D. and Gordon, M. S. (2005). Body-induced vortical flows: a common mechanism for self-corrective trimming control in boxfishes. *J. Exp. Biol.* **208**, 327–344.
- Bartol, I. K., Gordon, M. S., Webb, P., Weihs, D. and Gharib, M. (2008). Evidence of self-correcting spiral flows in swimming boxfishes. *Bioinspir. Biomim.* **3**, 014001.
- Blake, R. W. (1981). Influence of pectoral fin shape on thrust and drag in labriform locomotion. *J. Zool.* **194**, 53–66.
- Blevins, E. L. and Lauder, G. V. (2012). Rajiform locomotion: three-dimensional kinematics of the pectoral fin surface during swimming in the freshwater stingray *Potamotrygon orbignyi*. *J. Exp. Biol.* **215**, 3231–3241.
- Breder, C. M. Jr. (1930). On the structural specialization of flying fishes from the standpoint of aerodynamics. *Copeia* **1930**, 114–121.
- Burcher, R. and Rydill, L. (1994). *Concepts in Submarine Design*. Cambridge: Cambridge University Press.
- Bushnell, D. M. and Moore, K. J. (1991). Drag reduction in nature. *Ann. Rev. Fluid Mech.* **23**, 65–79.
- Cade, D. E., Friedlaender, A. S., Calambokidis, J. and Goldbogen, J. A. (2016). Kinematic diversity in orqual whale feeding mechanisms. *Curr. Biol.* **26**, 2617–2624.
- Carlson, R. L. and Lauder, G. V. (2011). Escaping the flow: boundary layer use by the darter *Etheostoma tetrazonum* (Percidae) during benthic station holding. *J. Exp. Biol.* **214**, 1181–1193.
- Carpenter, K., Sanders, F., Reed, B., Reed, J. and Larson, P. (2010). Plesiosaur swimming as interpreted from skeletal analysis and experimental results. *Tran. Kansas Acad. Sci.* **113**, 1–34.
- Chadwell, B. A., Standen, E. M., Lauder, G. V. and Ashley-Ross, M. A. (2012). Median fin function during the escape response of bluegill sunfish (*Lepomis macrochirus*): I: fin-ray orientation and movement. *J. Exp. Biol.* **215**, 2869–2880.
- Coates, M. I. (1994). The origin of vertebrate limbs. *Development* **1994** Suppl., 169–180.
- Collette, B. B. and Nauen, C. E. (1983). *Scombrids of the World*. Rome: Food and Agriculture Organization of the United Nations.
- Cooper, L. N., Dawson, S. D., Reidenberg, J. S. and Berta, A. (2007). Neuromuscular anatomy and evolution of the cetacean forelimb. *Anat. Rec.* **290**, 1121–1137.
- Cooper, L. N., Sedano, N., Johansson, S., May, B., Brown, J. D., Holliday, C. M., Kot, B. W. and Fish, F. E. (2008). Hydrodynamic performance of the minke whale (*Balaenoptera acutorostrata*) flipper. *J. Exp. Biol.* **211**, 1859–1867.
- Curren, K. and Lien, J. (1994). Swimming kinematics of a harbor porpoise (*Phocoena phocoena*) and an Atlantic white-sided dolphin (*Lagenorhynchus acutus*). *Mar. Mamm. Sci.* **10**, 485–492.
- Davenport, J. (1987). Locomotion in hatchling leatherback turtles *Dermochelys coriacea*. *J. Zool.* **212**, 85–101.
- Davis, R. W. and Weihs, D. (2007). Locomotion in diving elephant seals: physical and physiological constraints. *Philos. Trans. R. Soc. B* **362**, 2141–2150.
- Davis, R. W., Fuiman, L. A., Williams, T. M. and Le Boeuf, B. J. (2001). Three-dimensional movements and swimming activity of a northern elephant seal. *Comp. Biochem. Physiol. A* **129**, 759–770.
- Deng, J., Shao, X.-M. and Yu, Z.-S. (2007). Hydrodynamic studies on two traveling wavy foils in tandem arrangement. *Phys. Fluids* **19**, 113104.
- Drucker, E. G. and Lauder, G. V. (1999). Locomotor forces on a swimming fish: three-dimensional vortex wake dynamics quantified using digital particle image velocimetry. *J. Exp. Biol.* **203**, 2393–2412.
- Drucker, E. G. and Lauder, G. V. (2001). Locomotor function of the dorsal fin in teleost fishes: experimental analysis of wake forces in sunfish. *J. Exp. Biol.* **204**, 2943–2958.
- Drucker, E. G. and Lauder, G. V. (2002). Wake dynamics and locomotor function in fishes: interpreting evolutionary patterns in pectoral fin design. *Integr. Comp. Biol.* **42**, 997–1008.
- Drucker, E. G. and Lauder, G. V. (2005). Locomotor function of the dorsal fin in rainbow trout: kinematic patterns and hydrodynamic forces. *J. Exp. Biol.* **208**, 4479–4494.
- Edel, R. K. and Winn, H. E. (1978). Observations on underwater locomotion and flipper movement of the humpback whale *Megaptera novaeangliae*. *Mar. Biol.* **48**, 279–287.
- English, A. W. M. (1977). Structural correlates of forelimb function in fur seals and sea lions. *J. Morph.* **151**, 325–352.
- Felts, W. J. L. (1966). Some functional and structural characteristics of cetacean flippers and flukes. In *Whales, Dolphins, and Porpoises* (ed. K. S. Norris), pp. 255–276. Berkeley, CA: University of California Press.
- Ferry, L. A. and Lauder, G. V. (1996). Heterocercal tail function in leopard sharks: a three-dimensional kinematic analysis of two models. *J. Exp. Biol.* **199**, 2253–2268.
- Fierstine, H. L. and Walters, V. (1968). Studies in locomotion and anatomy of scombroid fishes. *Mem. S. Cal. Acad. Sci.* **6**, 1–31.
- Fish, F. E. (1982). Function of the compressed tail of surface swimming muskrats (*Ondatra zibethicus*). *J. Mamm.* **63**, 591–597.
- Fish, F. E. (1990). Wing design and scaling of flying fish with regard to flight performance. *J. Zool.* **221**, 391–403.
- Fish, F. E. (1996). Transitions from drag-based to lift-based propulsion in mammalian aquatic swimming. *Am. Zool.* **36**, 628–641.
- Fish, F. E. (2002). Balancing requirements for stability and maneuverability in cetaceans. *Integr. Comp. Biol.* **42**, 85–93.
- Fish, F. E. (2004). Structure and mechanics of nonpiscine control surfaces. *IEEE J. Ocean. Eng.* **29**, 605–621.
- Fish, F. E. (2006). Limits of nature and advances of technology: what does biomimetics have to offer to aquatic robots? *Appl. Bionics Biomech.* **3**, 49–60.
- Fish, F. E. (2016). Secondary evolution of aquatic propulsion in higher vertebrates: validation and prospect. *Integr. Comp. Biol.* **56**, 1285–1297.
- Fish, F. E. and Battle, J. M. (1995). Hydrodynamic design of the humpback whale flipper. *J. Morph.* **225**, 51–60.
- Fish, F. E. and Hoffman, J. L. (2015). Stability design and response to waves by batoids. *Integr. Comp. Biol.* **55**, 648–661.
- Fish, F. E. and Kocak, D. M. (2011). Biomimetics and marine technology: an introduction. *Mar. Tech. Soc. J.* **45**, 8–13.
- Fish, F. E. and Lauder, G. V. (2006). Passive and active flow control by swimming fishes and mammals. *Annu. Rev. Fluid Mech.* **38**, 193–224.
- Fish, F. E. and Nicastro, A. J. (2003). Aquatic turning performance by the whirligig beetle: constraints on maneuverability by a rigid biological system. *J. Exp. Biol.* **206**, 1649–1656.
- Fish, F. E. and Shannahan, L. D. (2000). The role of the pectoral fins in body trim of sharks. *J. Fish Biol.* **56**, 1062–1073.

- Fish, F. E., Hurley, J. and Costa, D. P.** (2003a). Maneuverability by the sea lion, *Zalophus californianus*: turning performance of an unstable body design. *J. Exp. Biol.* **206**, 667–674.
- Fish, F. E., Peacock, J. E. and Rohr, J. J.** (2003b). Stabilization mechanism in swimming odontocete cetaceans by phased movements. *Mar. Mamm. Sci.* **19**, 515–528.
- Fish, F. E., Nicasastro, A. J. and Weihs, D.** (2006). Dynamics of the aerial maneuvers of spinner dolphins. *J. Exp. Biol.* **209**, 590–598.
- Fish, F. E., Beneski, J. T. and Ketten, D. R.** (2007a). Examination of the three-dimensional geometry of cetacean flukes using CT-scans: hydrodynamic implications. *Anat. Rec.* **290**, 614–623.
- Fish, F. E., Bostic, S. A., Nicasastro, A. J. and Beneski, J. T.** (2007b). Death roll of the alligator: mechanics of twist feeding in water. *J. Exp. Biol.* **210**, 2811–2818.
- Fish, F. E., Weber, P. W., Murray, M. M. and Howle, L. E.** (2011). The tubercles on humpback whales' flippers: application of bio-inspired technology. *Integr. Comp. Biol.* **51**, 203–213.
- Flammang, B. E., Alben, S., Madden, P. G. A. and Lauder, G. V.** (2013). Functional morphology of the fin rays of teleost fishes. *J. Morph.* **274**, 1044–1059.
- Frohlich, C.** (1980). The physics of somersaulting and twisting. *Sci. Am.* **242**, 154–164.
- Gabler, U.** (2000). *Submarine Design*. Bonn: Bernard & Graefe.
- Geerlink, P. J. and Videler, J. J.** (1986). The relation between structure and bending properties of teleost fin rays. *Neth. J. Zool.* **37**, 59–80.
- Ginter, C. C., Böttger, S. A. and Fish, F. E.** (2011). Morphology and microanatomy of harbor porpoise (*Phocoena phocoena*) dorsal fin tubercles. *J. Morph.* **272**, 27–33.
- Goldbogen, J. A., Calambokidis, J., Friedlaender, A. S., Francis, J., DeRuiter, S. L., Stimpert, A. K., Falcone, E. and Southall, B. L.** (2013). Underwater acrobatics by the world's largest predator: 360° rolling manoeuvres by lunge-feeding blue whales. *Biol. Lett.* **9**, 20120986.
- Gordon, M. S., Hove, J. R., Webb, P. W. and Weihs, D.** (2000). Boxfishes as unusually well-controlled autonomous underwater vehicles. *Physiol. Biochem. Zool.* **73**, 663–671.
- Gough, W. T., Fish, F. E. and Bart-Smith, H.** (2016). Physical properties of the subdermal fibrous layers in cetacean tail flukes. *Integr. Comp. Biol.* **56**, E293.
- Hamilton, J. L., Dillaman, R. M., McLellan, W. A. and Pabst, D. A.** (2004). Structural fiber reinforcement of keel blubber in harbor porpoise (*Phocoena phocoena*). *J. Morph.* **261**, 105–117.
- Harris, J. E.** (1936). The role of the fins in the equilibrium of the swimming fish. I. Wind-tunnel tests on a model of *Mustelus canis* (Mitchill). *J. Exp. Biol.* **13**, 476–493.
- Harris, J. E.** (1937). The mechanical significance of the position and movements of the paired fins in the Teleostei. *Pap. Tortugas Lab.* **31**, 173–189.
- Harris, J. E.** (1938). The role of the fins in the equilibrium of the swimming fish. II. The role of the pelvic fins. *J. Exp. Biol.* **15**, 32–47.
- Hedrick, T. L., Cheng, B. and Deng, X.** (2009). Wingbeat time and the scaling of passive rotational damping in flapping flight. *Science* **324**, 252–255.
- Higham, T. E.** (2007). Feeding, fins and braking maneuvers: locomotion during prey capture in centrarchid fishes. *J. Exp. Biol.* **210**, 107–117.
- Hopson, J. A.** (1974). The functional significance of the hypocercal tail and lateral fin folds of anaspid ostracoderms. *Feldiana* **33**, 83–93.
- Howell, A. B.** (1930). *Aquatic Mammals*. Springfield, IL: Charles C. Thomas.
- Hui, C. A.** (1985). Maneuverability of the Humboldt penguin (*Spheniscus humboldti*) during swimming. *Can. J. Zool.* **63**, 2165–2167.
- Iriarte-Díaz, J. and Swartz, S. M.** (2008). Kinematics of slow turn maneuvering in the fruit bat *Cynopterus brachyotis*. *J. Exp. Biol.* **211**, 3478–3489.
- Jarvik, E.** (1965). On the origin of girdles and paired fins. *Israel J. Zool.* **14**, 141–172.
- Kajiura, S. M., Forni, J. B. and Summers, A. P.** (2003). Maneuvering in juvenile carcharhinid and sphyrnid sharks: the role of the hammerhead shark cephalofoil. *Zoology* **106**, 19–28.
- Kastelein, R. A., Triesscheijn, R. J. V. and Jennings, N.** (2016). Reversible bending of the dorsal fins of harbor porpoises (*Phocoena phocoena*) and a striped dolphin (*Stenella coeruleoalba*) in captivity. *Aquat. Mamm.* **42**, 218–226.
- Kelley, N. P. and Pyenson, N. D.** (2015). Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. *Science* **348**, aaa3716.
- Kemp, N. E.** (1977). Banding pattern and fibrillogenesis of ceratotrichia in shark fins. *J. Morph.* **154**, 187–203.
- Klima, M., Oelschläger, H. A. and Wüensch, D.** (1987). Morphology of the pectoral girdle in the amazon dolphin *Inia geoffrensis* with special reference to the shoulder joint and the movements of the flippers. *Z. Saugtierkunde* **45**, 288–309.
- Lang, T. G.** (1966). Hydrodynamic analysis of dolphin fin profiles. *Nature* **209**, 1110–1111.
- Lauder, G. V.** (2011). Swimming hydrodynamics: ten questions and the technical approaches needed to resolve them. *Exp. Fluids* **51**, 23–35.
- Lauder, G. V. and Drucker, E. G.** (2004). Morphology and experimental hydrodynamics of fish fin control surfaces. *IEEE J. Ocean. Eng.*, **29**, 556–571.
- Lauder, G. V., Madden, P. G., Mittal, R., Dong, H. and Bozkurtas, M.** (2006). Locomotion with flexible propulsors: I. Experimental analysis of pectoral fin swimming in sunfish. *Bioinspir. Biomim.* **1**, S25.
- Lauder, G. V., Anderson, E. J., Tangorra, J. and Madden, P. G. A.** (2007). Fish biorobotics: kinematics and hydrodynamics of self-propulsion. *J. Exp. Biol.* **210**, 2767–2780.
- Liao, J. A. and Lauder, G. V.** (2000). Function of the heterocercal tail in white sturgeon: flow visualization during steady swimming and vertical maneuvering. *J. Exp. Biol.* **203**, 3585–3594.
- Libby, T., Moore, T. Y., Chang-Siu, E., Li, D., Cohen, D. J., Jusufi, A. and Full, R. J.** (2012). Tail-assisted pitch control in lizards, robots and dinosaurs. *Nature* **481**, 181–184.
- Lighthill, J.** (1975). *Mathematical Biofluidynamics*. Philadelphia, PA: Society for Industrial and Applied Mathematics.
- Lingham-Soliar, T.** (2000). Plesiosaur locomotion: is the four-wing problem real or merely an atheoretical exercise? *N. Jb. Geol. Paläont. Abh.* **217**, 45–88.
- Lingham-Soliar, T.** (2001). The ichthyosaur integument: skin fibers, a means for a strong, flexible and smooth skin. *Lethaia* **34**, 287–302.
- Lingham-Soliar, T.** (2005). Dorsal fin in the white shark, *Carcharodon carcharias*: a dynamic stabilizer for fast swimming. *J. Morph.* **263**, 1–11.
- Lingham-Soliar, T. and Plodowski, G.** (2007). Taphonomic evidence for high-speed adapted fins in thunniform ichthyosaurs. *Naturwissenschaften* **94**, 65–70.
- Long, J. A.** (1995). *The Rise of Fishes*. Baltimore, MD: Johns Hopkins University Press.
- Mabee, P. M., Crotwell, P. L., Bird, N. C. and Burke, A. C.** (2002). Evolution of median fin modules in the axial skeleton of fishes. *J. Exp. Zool.* **294**, 77–90.
- Maderson, P. F.** (1967). A comment on the evolutionary origin of vertebrate appendages. *Amer. Nat.* **101**, 71–78.
- Magnuson, J. J.** (1970). Hydrostatic equilibrium of *Euthynnus affinis*, a pelagic teleost without a gas bladder. *Copeia* **1970**, 56–85.
- Maia, A. and Wilga, C. D.** (2013a). Anatomy and muscle activity of the dorsal fins in bamboo sharks and spiny dogfish during turning maneuvers. *J. Morph.* **274**, 1288–1298.
- Maia, A. and Wilga, C. A.** (2013b). Function of dorsal fins in bamboo shark during steady swimming. *Zoology* **116**, 224–231.
- Maia, A. and Wilga, C. A.** (2016). Dorsal fin function in spiny dogfish during steady swimming. *J. Zool.* **298**, 139–149.
- McGowan, C.** (1991). *Dinosaurs, Spitfires, & Sea Dragons*. Cambridge, MA: Harvard University Press.
- Miklošovic, D. S., Murray, M. M., Howle, L. E. and Fish, F. E.** (2004). Leading-edge tubercles delay stall on humpback whale (*Megaptera novaeangliae*) flippers. *Phys. Fluids* **16**, L39–L42.
- Moored, K. W., Fish, F. E., Kemp, T. H. and Bart-Smith, H.** (2011). Batoid fishes: inspiration for the next generation of underwater robots. *Mar. Tech. Soc. J.* **45**, 99–109.
- Moss, S. A.** (1984). *Sharks: An Introduction for the Amateur Naturalist*. Englewood, NJ: Prentice-Hall.
- Moy-Thomas, J. A. and Miles, R. S.** (1971). *Palaeozoic Fishes*, 2nd edn. London: Chapman and Hall.
- Nakaya, K.** (1995). Hydrodynamic function of the head in the hammerhead sharks (Elasmobranchii: Sphyrnidae). *Copeia* **1995**, 330–336.
- Nauen, J. C. and Lauder, G. V.** (2000). Locomotion in scombrid fishes: morphology and kinematics of the finlets of the Chub mackerel *Scomber japonicus*. *J. Exp. Biol.* **203**, 2247–2259.
- Nauen, J. C. and Lauder, G. V.** (2001a). Three-dimensional analysis of finlet kinematics in the Chub mackerel (*Scomber japonicus*). *Biol. Bull.* **200**, 9–19.
- Nauen, J. C. and Lauder, G. V.** (2001b). Locomotion in scombrid fishes: visualization of flow around the caudal peduncle and finlets of the chub mackerel *Scomber japonicus*. *J. Exp. Biol.* **204**, 2251–2263.
- Norberg, U. M.** (1990). *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution*. Berlin: Springer-Verlag.
- Nursall, J. R.** (1962). Swimming and the origin of paired appendages. *Am. Zool.* **2**, 127–141.
- O'Keefe, F. R.** (2001). Ecomorphology of plesiosaur flipper geometry. *J. Evol. Biol.* **14**, 987–991.
- Oliver, S. P., Turner, J. R., Gann, K., Silvosa, M. and Jackson, T. D.** (2013). Thresher sharks use tail-slaps as a hunting strategy. *PLoS ONE* **8**, e67380.
- Parson, J. M., Fish, F. E. and Nicasastro, A. J.** (2011). Turning performance of batoids: limitations of a rigid body. *J. Exp. Mar. Biol. Ecol.* **402**, 12–18.
- Patel, A., Boje, E., Fisher, C., Louis, L. and Lane, E.** (2016). Quasi-steady state aerodynamics of the cheetah tail. *Biol. Open* **5**, 1072–1076.
- Pavlov, V., Rosental, B., Hansen, N. F., Beers, J. M., Parish, G., Rowbotham, I. and Block, B. A.** (2017). Hydraulic control of tuna fins: a role for the lymphatic system in vertebrate locomotion. *Science* **357**, 310–314.
- Payne, N. L., Iosilevskii, G., Barnett, A., Fischer, C., Graham, R. T., Gleiss, A. C. and Watanabe, Y. Y.** (2016). Great hammerhead sharks swim on their side to reduce transport costs. *Nat. Commun.* **7**, 12289.
- Radinsky, L. B.** (1987). *The Evolution of Vertebrate Design*. Chicago, IL: University of Chicago Press.
- Raikow, R. J., Bicanovsky, L. and Bledsoe, A. H.** (1988). Forelimb joint mobility and the evolution of wing-propelled diving in birds. *Auk* **100**, 446–451.
- Riess, J.** (1986). Fortbewegungsweise, Schwimmbiophysik und Phylogenie der Ichthyosaurier. *Palaeontographica A* **192**, 93–155.

- Robinson, J. A.** (1975). The locomotion of plesiosaurs. *N. Jb. Geol. Paläont. Abh.* **149**, 286–332.
- Schrank, A. J., Webb, P. W. and Mayberry, S.** (1999). How do body and paired-fin positions affect the ability of three teleost fishes to maneuver around bends? *Can. J. Zool.* **77**, 203–210.
- Segre, P. S., Cade, D. E., Fish, F. E., Potvin, J., Allen, A. N., Calambokidis, J., Friedlaender, A. S. and Goldbogen, J. A.** (2016). Hydrodynamic properties of fin whale flippers predict maximum rolling performance. *J. Exp. Biol.* **219**, 3315–3320.
- Slack, K. E., Jones, C. M., Ando, T., Harrison, G. A., Fordyce, R. E., Arnason, U. and Penny, D.** (2006). Early penguin fossils, plus mitochondrial genomes, calibrate avian evolution. *Mol. Biol. Evol.* **23**, 1144–1155.
- Sun, Q., Morikawa, H., Kobayashi, S., Ueda, K., Miyahara, H. and Nakashima, M.** (2010a). Structure and mechanical properties on tail flukes of dolphin. *J. Aero. Aqua. Bio-mech.* **1**, 45–50.
- Sun, Q., Morikawa, H., Kobayashi, S., Ueda, K., Miyahara, H. and Nakashima, M.** (2010b). Structure and bending properties of central part of tail fin of dolphin. *J. Biomech. Sci. Eng.* **5**, 388–398.
- Sun, Q., Morikawa, H., Kobayashi, S., Ueda, K., Miyahara, H. and Nakashima, M.** (2011). Bending properties of tail flukes of dolphin. *J. Biomech. Sci. Eng.* **6**, 15–25.
- Taft, N. K. and Taft, B. N.** (2012). Functional implications of morphological specializations among the pectoral fin rays of the benthic longhorn sculpin. *J. Exp. Biol.* **215**, 2703–2710.
- Tangorra, J. L., Lauder, G. V., Hunter, I. W., Mittal, R., Madden, P. G. A. and Bozkurttas, M.** (2010). The effect of fin ray flexural rigidity on the propulsive forces generated by a biorobotic fish pectoral fin. *J. Exp. Biol.* **213**, 4043–4054.
- Triantafyllou, M. S.** (2017). Tuna fin hydraulics inspire aquatic robotics. *Science* **357**, 251–252.
- Triantafyllou, M. S., Triantafyllou, G. S. and Yue, D. K. P.** (2000). Hydrodynamics of fishlike swimming. *Annu. Rev. Fluid Mech.* **32**, 33–53.
- Tytell, E. D.** (2006). Median fin function in bluegill sunfish *Lepomis macrochirus*: streamwise vortex structure during steady swimming. *J. Exp. Biol.* **209**, 1516–1534.
- Tytell, E. D. and Lauder, G. V.** (2008). Hydrodynamics of the escape response in bluegill sunfish, *Lepomis macrochirus*. *J. Exp. Biol.* **211**, 3359–3369.
- Tytell, E. D., Borazjani, I., Sotiropoulos, F., Baker, T. V., Anderson, E. J. and Lauder, G. V.** (2010). Disentangling the functional roles of morphology and motion in the swimming of fish. *Integr. Comp. Biol.* **50**, 1140–1154.
- Ullén, F., Deliagina, T. G., Orlovsky, G. N. and Grillner, S.** (1995). Spatial orientation in the lamprey. I. Control of pitch and roll. *J. Exp. Biol.* **198**, 665–673.
- Van Wassenbergh, S., van Manen, K., Marcroft, T. A., Alfaro, M. E. and Stamhuis, E. J.** (2015). Boxfish swimming paradox resolved: forces by the flow of water around the body promote manoeuvrability. *J. R. Soc. Interface* **12**, 20141146.
- Vogel, S.** (1994). *Life in Moving Fluids*. Princeton, NJ: Princeton University Press.
- Von Mises, R.** (1945). *Theory of Flight*. New York: Dover.
- Wainwright, S. A., Vosburgh, F. and Hebrank, J. H.** (1978). Shark skin: function in locomotion. *Science* **202**, 747–749.
- Walker, J. A.** (2000). Does a rigid body limit maneuverability? *J. Exp. Biol.* **203**, 3391–3396.
- Walker, W. F. Jr.** (1971). Swimming in sea turtles of the family cheloniidae. *Copeia* **1971**, 229–233.
- Warrick, D. R., Bundle, M. W. and Dial, K. P.** (2002). Bird maneuvering flight: blurred bodies, clear heads. *Integr. Comp. Biol.* **42**, 141–148.
- Watts, E. H.** (1961). The relationship of fish locomotion to the design of ships. *Symp. Zool. Soc. Lond.* **5**, 37–41.
- Webb, P. W.** (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd. Can.* **190**, 1–158.
- Webb, P. W.** (1983). Speed, acceleration and manoeuvrability of two teleost fishes. *J. Exp. Biol.* **102**, 115–122.
- Webb, P. W.** (1984). Body and fin form and strike tactics of four teleost predators attacking fathead minnow (*Pimephales promelas*) prey. *Can. J. Fish. Aquat. Sci.* **41**, 157–165.
- Webb, P. W.** (1992). Is the high cost of body/caudal fin undulatory swimming due to increased friction drag or inertial recoil. *J. Exp. Biol.* **162**, 157–166.
- Webb, P. W.** (1994). The biology of fish swimming. In *Mechanics and Physiology of Animal Swimming* (ed. L. Maddock, Q. Bone and J. M. V. Rayner), pp. 45–62. Cambridge: Cambridge University Press.
- Webb, P. W.** (1997). Designs for stability and maneuverability in aquatic vertebrates: What can we learn? Proceedings of the Tenth International Symposium on Unmanned Untethered Submersible Technology: Proceedings of the special session on bio-engineering research related to autonomous underwater vehicles, pp. 86–103. Lee, NH: Autonomous Undersea Systems Institute.
- Webb, P. W.** (2004). Maneuverability-general issues. *IEEE J. Ocean Eng.* **29**, 547–555.
- Webb, P. W.** (2006). Stability and maneuverability. In *Fish Biomechanics* (ed. R. E. Shadwick and G. V. Lauder), pp. 281–332. Amsterdam: Academic Press.
- Webb, P. W. and Smith, G. R.** (1980). Function of the caudal fin in early fishes. *Copeia* **1980**, 559–562.
- Webb, P. W., LaLiberte, G. D. and Schrank, A. J.** (1996). Does body and fin form affect the maneuverability of fish traversing vertical and horizontal slits? *Environ. Biol. Fish.* **46**, 7–14.
- Weber, P. W., Howle, L. E., Murray, M. M. and Fish, F. E.** (2009). Lift and drag performance of odontocete cetacean flippers. *J. Exp. Biol.* **212**, 2149–2158.
- Weber, P. W., Howle, L. E., Murray, M. M., Reidenberg, J. S. and Fish, F. E.** (2014). Hydrodynamic performance of the flippers of large-bodied cetaceans in relation to locomotor ecology. *Mar. Mamm. Sci.* **30**, 413–432.
- Wegener, P. P.** (1991). *What Makes Airplanes Fly?* New York: Springer-Verlag.
- Weis, D.** (1981a). Body section variations in sharks: an adaptation for efficient swimming. *Copeia* **1981**, 217–219.
- Weis, D.** (1981b). Effects of swimming path curvature on the energetics of fish motion. *Fish. Bull.* **79**, 171–176.
- Weis, D.** (1993). Stability of aquatic animal locomotion. *Cont. Math.* **141**, 443–461.
- Weis, D.** (2002). Stability versus maneuverability in aquatic locomotion. *Integr. Comp. Biol.* **42**, 127–134.
- Werle, M. J., Paterson, R. W. and Resz, W. M. Jr.** (1987). Trailing-edge separation/stall alleviation. *AIAA J.* **25**, 624–626.
- Westneat, M. W. and Walker, J. A.** (1997). Motor patterns of labriform locomotion: kinematic and electromyographic analysis of pectoral fin swimming in the labrid fish *Gomphosus varius*. *J. Exp. Biol.* **200**, 1881–1893.
- Wilga, C. D. and Lauder, G. V.** (1999). Locomotion in the sturgeon: function of the pectoral fins. *J. Exp. Biol.* **202**, 2413–2432.
- Wilga, C. D. and Lauder, G. V.** (2000). Three-dimensional kinematics and wake structure of the pectoral fins during locomotion in Leopard sharks, *Triakis semifasciata*. *J. Exp. Biol.* **203**, 2261–2278.
- Wilga, C. D. and Lauder, G. V.** (2001). Functional morphology of the pectoral fins in bamboo sharks, *Chiloscyllium plagiosum*: benthic vs. pelagic station-holding. *J. Morph.* **249**, 195–209.
- Williston, S. W.** (1914). *Water Reptiles of the Past and Present*. Chicago, IL: University of Chicago Press.
- Wolfe, T. M.** (2017). Review of fluid dynamic and acoustic performance of biologically inspired passive flow control trailing edge devices for design applications. 55th AIAA Aerospace Sciences Meeting, AIAA SciTech Forum, AIAA 2017-0542. <http://dx.doi.org/10.2514/6.2017-0542>.
- Wyneken, J.** (1997). Sea turtle locomotion: mechanisms, behavior, and energetics. In *The Biology of Sea Turtles* (ed. P. L. Lutz and J. A. Musick), pp. 165–198. Boca Raton, FL: CRC Press.
- Yates, G. T.** (1983). Hydromechanics of body and caudal fin propulsion. In *Fish Biomechanics* (ed. P. W. Webb and D. Weis), pp. 177–213. New York: Praeger.
- Yuan, C., Liu, G., Ren, Y. and Dong, H.** (2015). Propulsive performance and vortex interactions of multiple tandem foils pitching in line. 45th AIAA Fluid Dyn. Conf. p. 3220.
- Zangerl, R. and Case, G. R.** (1973). Iniopterygia, a new order of chondrichthyan fishes from the Pennsylvanian of North America. *Fieldiana Geol. Mem.* **6**, 1–67.