Zoology 117 (2014) 86–92

Contents lists available at ScienceDirect

Zoology

journal homepage: www.elsevier.com/locate/zool

ZOOLOGY

Review

The fish tail as a derivation from axial musculoskeletal anatomy: an integrative analysis of functional morphology☆

B.E. Flammang*

Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA

ARTICLE INFO

Article history:
Received 16 August 2013
Received in revised form 8 October 2013
Accepted 9 October 2013
Available online 29 October 2013

Keywords:
Caudal fin musculature
Fish tail morphology
Fluid dynamics
Functional morphology
Tail evolution

ABSTRACT

The adult morphology of the tail varies greatly among extant fishes despite sharing both ontogenetic similarities and the functional need to propel the body through a fluid medium. Both sharks (Chondrichthyes) and ray-finned fishes (Actinopterygii) control caudal fin musculature independently of axial body myomere activity to modify the stiffness and shape of their tails. For example, sharks and bony fishes possess different structural elements and muscles and move their tails in different ways, resulting in different locomotory hydrodynamic effects and a range of performance variables including speed and maneuverability. The stiffness of the heterocercal, lobate tail of the shark can be modulated during the tail beat resulting in nearly continuous thrust production. In contrast, the highly flexible tail of ray-finned fishes can be manipulated into many different shape conformations enabling increased maneuverability for these fishes. Consequently, the developmental, morphological, and functional derivation of the tail from the axial trunk has resulted in a diversity of form, the attributes of which may be of ecological and evolutionary significance.

1. Evolution of the tail fin

As early as the Cambrian (approximately 530 mya), the chordate ancestors †*Pikaia* and †*Haikouichthys* exhibited some of the axial morphology we see in living fishes today. Both of these species were swimmers who had elongate bodies powered by myotomal muscle, the fossil preservation of which looks very much like the axial myomeres of living fishes (Shu et al., 1996, 2003; Morris and Caron, 2012). By the Devonian (approximately 420–350 mya), swimming vertebrates had evolved tails of many shapes and sizes. Evolution of a tapered caudal fin predates the evolution of jaws as evidenced by the anaspid †*Euphanerops longaevus* (Janvier and Arsenault, 2007). The rapid diversification of bony fishes continued with the development of fins supported by flexible rays; these fishes are known as the actinopterygians and make up approximately half of the vertebrate species we know to exist today (Near et al., 2012, 2013). And within this group, the 28,000 species known as Teleost fishes are united primarily by a synapomorphy of the skeletal morphology of their tail fins; specifically, the presence of a urohyal formed as an unpaired intramembranous bone (Patterson, 1968; Lauder and Liem, 1983; Arratia and Schultze, 1990; de Pinna, 1996).

Even a cursory survey of living fishes demonstrates the diversity in fish fin morphologies. Caudal fins, in particular, vary within and among species in shape, size, and structure (Fig. 1). For example, in the caudal fin, the number, length, width, ossification, segmentation, branching, and stiffness of fin rays that support the tail lobe differ among species (Lauder, 1989). Caudal fin shapes run the gamut of all imaginable conformations, ranging from nearly nonexistent in eel-like fishes, to rigid scythe-shaped in tunas and sharks, to large flexible deformable foils that would almost seem a hindrance to locomotion in some exotic goldfish. Variation in tail fin morphologies is noted to be a factor in sexual selection, functional specializations, and locomotor modalities (Affleck, 1950; Ameyaw-Akumal, 1975; Abou-Seedo, 1994; Hale, 1996; Arratia et al., 2001; Basolo and Alcaraz, 2003; Flammang, 2010). There are species-specific modifications to the morphology of the vertebrae; for example, structural modifications to the vertebral centra and spines are functionally important in extremely fast fishes (Long, 1992; Long and Nipper, 1996). However, there is surprisingly little diversity in the morphology of the vertebrae and myomeres along the long axis of the fish body (the trunk and peduncle, specifically) as compared to the morphology of the caudal fin skeleton (including fin rays) and musculature. The more anterior axial skeletal and muscular anatomy is far more similar among living and extinct fishes than is tail fin morphology. This raises the question: why are fish tail fins so diverse, while trunk morphology is comparatively not?

To examine the evolution and diversification of tail morphologies, several factors must be considered. It is important to understand the developmental processes of the trunk and tail to

---

☆ This article is part of a special issue entitled "Axial systems and their actuation: new twists on the ancient body of craniates".

* Tel.: +1 6174967199.
E-mail address: bflammang@post.harvard.edu

0944-2006/$ – see front matter © 2013 Elsevier GmbH. All rights reserved.
http://dx.doi.org/10.1016/j.zool.2013.10.001

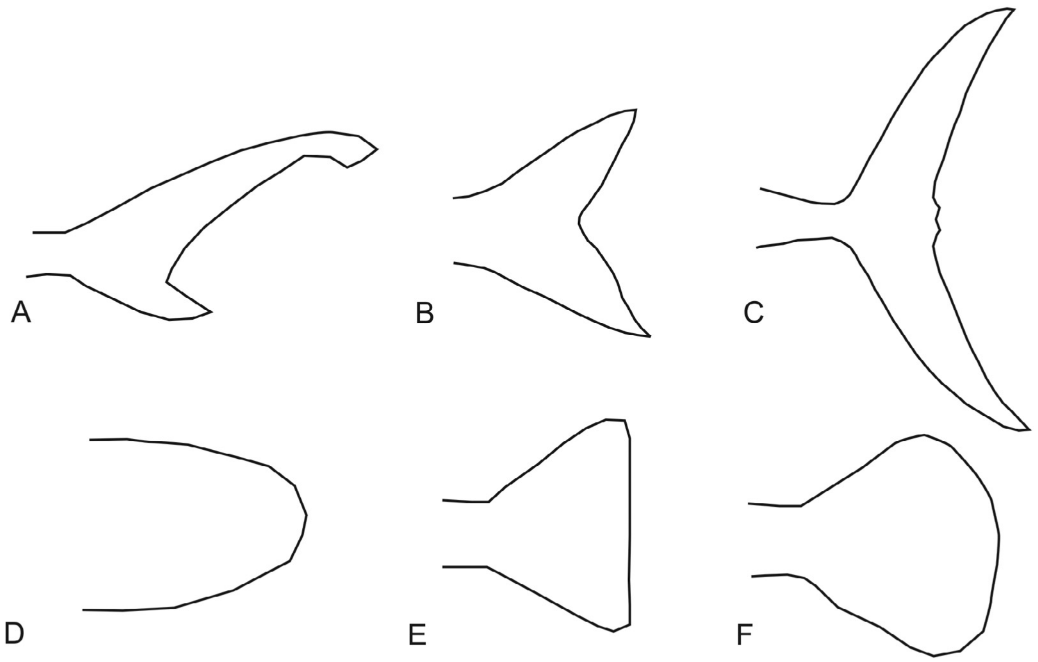

Fig. 1. Representative fish tail shapes: (A) heterocercal; (B) forked; (C) lunate; (D) eel-like; (E) truncate; (F) rounded.

know whether they are regulated by the same patterning and positioning modules or if they are independently organized. Anatomical differences in skeletal and muscular morphologies in tails result in functional differences in terms of how the tail fin will interact with the fluid environment. And as a result, different tail fin morphologies will exhibit specific performance traits which may be selected for under varied ecological circumstances.

2. Development of the tail

As in all vertebrates, the fish tail bud begins to form immediately following gastrulation, followed by a pattern of extension, protrusion, and eversion away from the yolk cell. The post-anal axial body of fish larvae is extended posteriorly and both somites and fin folds are symmetrical about the longitudinal axis (Fig. 2). However, within three days after hatching, this axial symmetry is lost as the ventral portion of the developing tail grows rapidly, displacing the notochord at an angle dorsally (Potthoff et al., 1988; Bird and Mabee, 2003; Britz and Johnson, 2005; Hilton and Johnson, 2007). This shift in axis orientation, aided by the migration of trunk neural crest cells (Smith et al., 1994), precipitates the formation of a caudal nerve plexus (Ishikawa and Iwamatsu, 1993; Schneider and Sulner, 2006), distinct muscle groups unlike the trunk myomeres, and cartilaginous or bony skeletal elements supporting the developing caudal fin (Bird and Mabee, 2003).

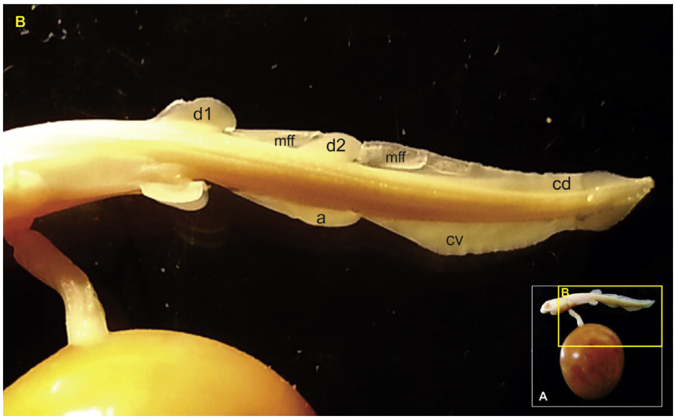

Fig. 2. Embryonic filetail catshark (*Parmaturus xaniurus*) of unknown age. (B) is a magnified image of the inset in (A). The first and second dorsal (d1 and d2, respectively), anal (a) and caudal (dorsal lobe, cd; ventral lobe, cv) fins have all formed, but a dorsal remnant of the median fin fold (mff) still remains.

The tail region in fishes develops via mechanisms that are distinct from those of the head and the trunk (Kanki and Ho, 1997; Griffin et al., 1998; Ahn and Gibson, 1999; Kimelman and Griffin, 2000; Morin-Kensicki et al., 2002; Holley, 2006). In fact, the tail has its own organizing center which acts independently of the dorsal organizer in larval zebrafish, *Danio rerio* (Agathon et al., 2003). Median fin patterning is regulated by *Hox* genes; expression boundaries in *Hox* groups 1–11 designate the anterior 17 somites in larval zebrafish as “trunk” and the remaining 14 posterior caudal somites as “tail” (Mabee et al., 2002). Further evidence supporting the tail region as a developmental entity separate from the trunk is the way *shh* and *bmp2b* modify bone patterning in the tail fin differently than in the more anterior axial skeleton (Quint et al., 2002).

3. Anatomy of the tail

The axial body of living fishes is supported by serially arranged vertebral elements which possess dorsal and ventral projections known as the neural and haemal arches, respectively. The “M”-shaped myomeres are anteriorly and posteriorly facing cones of muscle which attach to several vertebrae and their spines in series such that contraction of one myomere will manipulate the position of multiple vertebrae via a complex arrangement of myoseptal tendons (Winterbottom, 1974; Lauder, 1980; Koob and Long, 2000; Gemballa et al., 2003). This trunk morphology is conserved among fishes. However, in examining the evolution of tail fin morphologies of living fishes, there is a trend of increasing complexity of the structure of the tail relative to that of the trunk over time (Flammang and Lauder, 2009; cf. Fig. 3). In sharks and early actinopterygian fishes, the vertebral elements and myomeres curve dorsally into the tail (Gemballa, 2004). In both groups of fishes, with the exception of

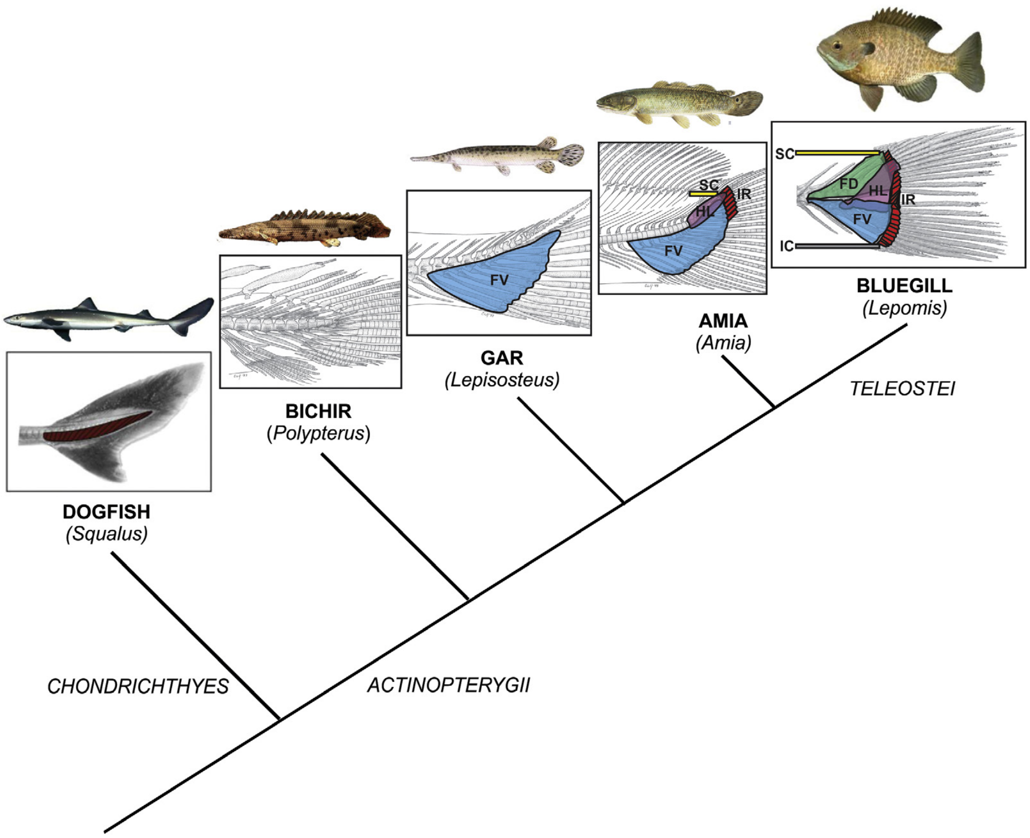

Fig. 3. Cladogram depicting tail morphology of a few extant fishes to illustrate the trend of increasingly complex intrinsic caudal musculature over time. Axial (epaxial and hypaxial) musculature is not depicted here. *Polypterus* do not have discrete intrinsic caudal musculature. Actinopterygians develop the m. flexor ventralis (FV, blue), m. hypochordalis longitudinalis (HL, purple), m. interradialis (IR, red), m. supracarinalis (SC, yellow), m. infracarinalis (IC, gray), and m. flexor dorsalis (FD).

Adapted from Flammang and Lauder (2009) (with permission).

Polypterus, novel intrinsic caudal muscles are positioned ventrally to the upward turned axial skeleton.

Sharks (Chondrichthyes) possess a heterocercal tail shape, meaning that the upper lobe is larger than the lower lobe of the tail (Fig. 4). The upper and lower lobes of the tail are supported by thin cartilaginous rods, or ceratotrichia, in a thin matrix of collagen. The vertebral column extends nearly to the end of the dorsal lobe of the tail and is surrounded by epaxial and hypaxial myomeres. Ventral to the axial (epaxial and hypaxial) musculature in the tail is an additional red muscle, the m. radialis (Flammang, 2010). The m. radialis is found in representatives of every family of shark species, regardless of swimming performance or habitat usage; fast oceanic predators and slow-moving epibenthic species all possess the m. radialis in equal proportion to the size of their tail (Flammang, 2010).

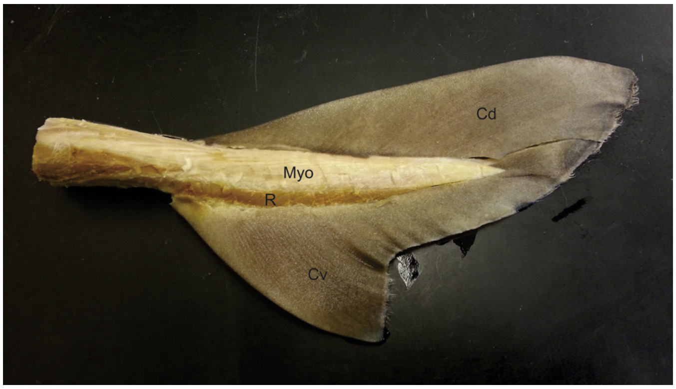

Fig. 4. Tail of adult spiny dogfish (*Squalus acanthias*) dissected to show the musculature extending into the dorsal lobe of the caudal fin (Cd). *Abbreviations*: Myo, axial myomeres; R, m. radialis; Cv, ventral lobe of caudal fin.

In most teleost fish, such as the bluegill sunfish (*Lepomis macrochirus*), the shape of the tail is described as homocercal, meaning that the upper and lower lobes of the tail fin are roughly equal in size. The vertebral column extends in a straight line posteriorly until the penultimate vertebra; the last vertebra is modified and more posterior axial elements form a fan composed of the uroneurals, epurals, parahypural, and hypural plates (Fig. 5A) during embryonic development. Without support by the vertebral column, the tail fin is composed of a thin membrane only, reinforced by fin rays, or lepidotrichia. The hypural plates are the origin for the large intrinsic caudal muscles that insert onto the tail fin. While the intrinsic caudal muscles are thought to be derived from the axial myomeres of the trunk (Schneider and Sulner, 2006), they bear little resemblance to them in structure and orientation (Fig. 5B). The bluegill sunfish has, in total, 46 discrete muscles that modulate the shape of the tail fin (Flammang and Lauder, 2008, 2009) by actuating each fin ray independently of its neighbor. Two large flexors, the m. flexor dorsalis and the m. flexor ventralis, originate on the dorsal, lateral, and ventral aspects of the last few vertebrae and neural and haemal spines and hypural plates and insert onto the lateral bases of the tail fin rays (Winterbottom, 1974; Flammang and Lauder, 2008). The m. hypochordalis longitudinalis originates on hypurapophyses and lower hypurals and inserts onto the four dorsal-most fin rays. Between every two neighboring fin rays is the m. interradialis, which originates on the fin ray closer to the axial

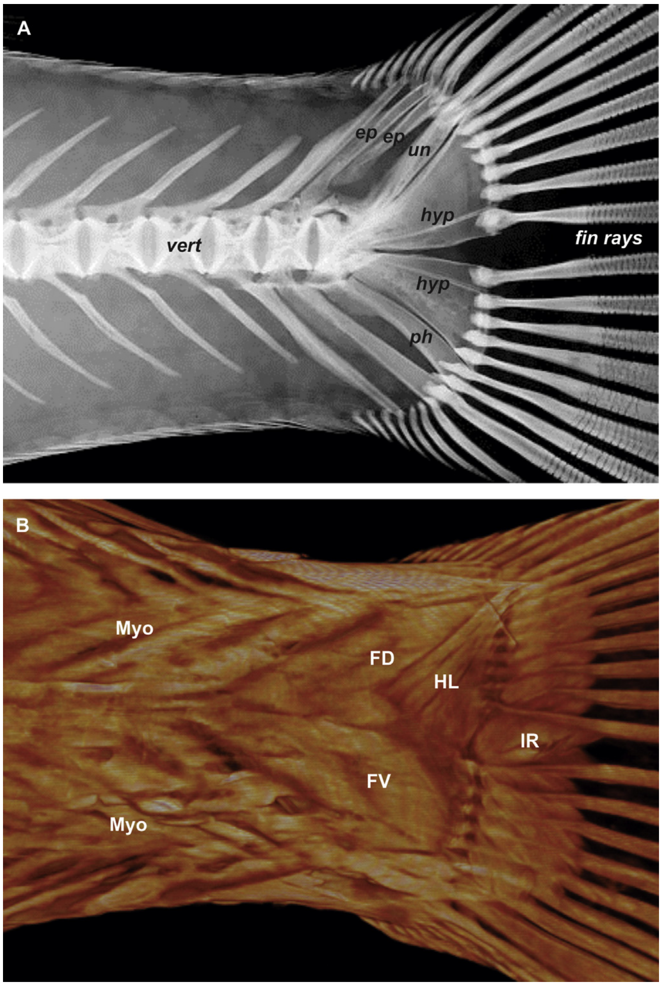

Fig. 5. Radiograph and computed microtomography (μCT) scan of bluegill sunfish (*Lepomis macrochirus*) tail and fin. (A) Radiograph of skeletal elements: epurals (ep), hypural plates (hyp), parahypural (ph), uroneural (un), vertebrae (vert). (B) μCT scan of musculature after soaking tail in 0.3% phosphotungstic acid for 6 days (Metscher, 2009) at approximately 12 μm voxel resolution. Individual myomeres (Myo) can be differentiated from the m. hypochordalis longitudinalis (HL), m. flexor dorsalis (FD), m. flexor ventralis (FV), and m. interradialis (IR). The ninth IR (from dorsal-most) is labeled here.

midline and inserts onto the dorsally adjacent fin ray in the dorsal lobe and the ventrally adjacent fin ray in the ventral lobe. These muscles are innervated via a caudal plexus which exhibits extensive branching after exiting the dorsal root at the penultimate vertebra (Ishikawa and Iwamatsu, 1993; Schneider and Sulner, 2006).

4. Muscular control of the tail

Fish swim by using a variety of fin and body movement patterns, but for those that swim by using their bodies, their motions are characterized by an undulatory wave that progresses from head to tail (Shadwick et al., 1998; Altringham and Ellerby, 1999). Undulation of the axial body is a hard-wired locomotor behavior driven by a central pattern generator (Cohen, 1988). Anterior to posterior activation of body undulation is observed in all species that use the body–caudal fin mode of swimming either as primary form of locomotion or for bouts of high-speed swimming.

In the shark, the axial skeleton and myomeres extend into the tip of the tail and the wave of body undulation is carried into the tail fin to power the lateral motion of the tail beat. The m. radialis, situated ventrally to the hypaxial musculature, produces little to no change to the shape of the tail when it is active. The m. radialis is active out of phase with the undulatory wave of activation that is directed posteriorly down the body (Flammang, 2010) and does not function in moving the tail. What, then, is the function of the m. radialis? The answer to this question is inherent to the anatomical architecture of the muscle and its association with the subdermal collagen fibers in the shark skin. Contraction of the m. radialis pulls taut the orthogonally arrayed mesh of subdermal collagen fibers while the isovolumetric nature of muscle causes the m. radialis to bulge and increase the tension in the skin. The end result is that the tail is stiffened on the side of m. radialis contraction. Most importantly, the m. radialis contracts as the tail reaches mid-stroke and passes behind the body of the swimming shark. This point in the tail beat is when the tail is moving at its greatest velocity, and therefore is incurring the greatest drag (Flammang, 2010; Lauder et al., 2012). Stiffening by the m. radialis counteracts bending from hydrodynamic loading; this is easily demonstrated by moving the tail of a dead or anaesthetized shark through the water and observing how the tail will yield to oncoming fluid.

The individual control of the approximately 50 distinct tail muscles in teleost fishes offers tremendous capacity to modulate the shape of the tail fin during both steady swimming and maneuvering (Flammang and Lauder, 2008, 2009). The m. flexor dorsalis and m. flexor ventralis swing the lobes of the tail laterally and independent of each other. The large m. hypochordalis longitudinalis inserts onto the dorsal-most caudal fin rays and rotates them laterally separately from the rest of the tail (Lauder, 1982; Flammang and Lauder, 2008), causing the dorsal edge of the tail to lead the tail beat and producing lift (Tytell, 2006; Flammang et al., 2011b; Esposito et al., 2012). The m. interradialis permits each fin ray to move individually and manipulate both the surface area and the overall three-dimensional conformation of the fin shape. Not only are all of these intrinsic caudal muscles activated independently of each other and of the myomeres, but their activity patterns exhibit recruitment patterns that vary with speed and swimming activity different from those observed in trunk muscles. In the trunk muscles of fishes, the red (slow oxidative) and white (fast glycolytic) muscle fibers are regionalized, i.e. separated from one another with the red fiber type condensed near the midline of a myomere. However, in the tail, developmental studies suggest that the red and white muscle fibers are more mixed (i.e. not regionalized) within a single muscle (Kimelman and Griffin, 2000). Recordings of the electrical activation of the intrinsic muscles demonstrate continuous recruitment within a single muscle as swimming speed increases (Flammang and Lauder, 2008), which is also suggestive of a mixed fiber-type muscle in which red and then white fibers might be recruited within the same muscle (Fig. 6). The regionalization of the red and white muscles of the trunk has made it possible to determine that the red fiber-type muscle is inactive at higher speeds (Jayne and Lauder, 1995); however, the non-regionalized nature of the caudal muscles has made it difficult to determine which motor units of which fiber types are active at a given time. Functionally, the mixed fiber composition ensures that the intrinsic caudal muscles will be active and control the tail regardless of speed.

5. Functional implications

The undulating body of the shark balances the lateral motion of the tail with the lateral motion of the anterior body in the opposite direction. And the downward and posteriorly directed forces produced by the tail are balanced by the lift provided by the 8–14° body angle maintained during forward swimming (Wilga and Lauder, 2002). It was previously thought that the fact that sharks produce downward oriented thrust forces was primarily a factor of their tail shape. Using two-dimensional hydrodynamic analysis methods

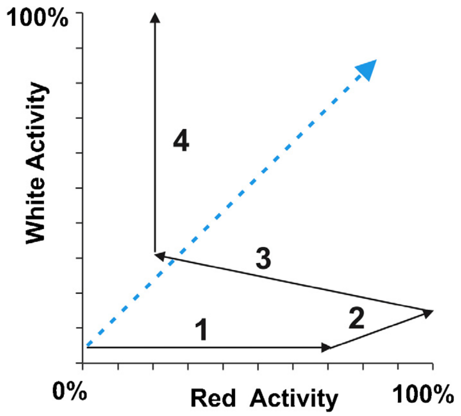

Fig. 6. Hypothesized whole muscle activity patterns of the intrinsic caudal muscle in teleost fishes. Axial swimming with increasing speed (solid line) is characterized by red muscle activity at slower speeds (1–2); at higher speeds, white muscle activity increases to power swimming (4) and red muscle activity is reduced (3). Because red and white muscle fibers may be non-regionalized in a single intrinsic caudal muscle, electromyographic studies suggest a linear increase in whole muscle activity is possible with increasing speed (dashed line).

Adapted from Jayne and Lauder (1995) (with permission).

and knowledge gained from engineering models of inclined exit vortex production, Wilga and Lauder (2004) hypothesized that the shark tail would form a single wake structure during a lateral pass of the tail and that this structure would be composed of two rings – one associated with the longer dorsal lobe inside another one associated with the whole tail. It was expected that this single wake structure would be released from the tail as it reaches maximum lateral excursion and changes direction, e.g. when the velocity equals zero, just as was known to be true for all undulating bodies in a fluid. However, with the use of three-dimensional hydrodynamic analysis methods that are able to capture an entire volume of the wake produced behind an undulating body (Flammang et al., 2011a), it became clear that a planar snapshot was not giving the full picture. Sharks produce two vortices at different times during a single tail pass. A vortex is a wake structure indicative of momentum being added to the water and resulting in thrust generation. As would be expected from an undulating body, sharks do produce a vortex as the tail changes direction. But sharks also produce an additional vortex midway through the lateral motion, just as the tail passes behind the shark body (Flammang et al., 2011a). This second vortex is released at the same time as the radialis muscle contracts and stiffens the tail. Multiple vortices being released through the tail beat means that momentum is being continuously added to the water behind the swimming shark, resulting in nearly constant thrust production.

Hydrodynamic analyses have shown that teleost fishes do not generate constant thrust; instead they produce a single vortex as the tail changes direction at maximum lateral excursion (Drucker and Lauder, 1999, 2000; Flammang et al., 2011b). The extremely flexible tail fin of the bluegill sunfish permits conformational changes that may facilitate the entrainment of flow generated by the upstream dorsal and anal fins, thereby increasing the momentum added to the fluid with every tail beat (Tytell, 2006; Flammang et al., 2011b). Perhaps most importantly, however, the flexible tail fin of teleost fishes helps make them more maneuverable than would be possible with a lobate tail. Modulation of flexible tail shapes varies the direction and magnitude of forces imparted upon the surrounding fluid (Esposito et al., 2012) allowing teleosts to accomplish difficult maneuvers such as swimming backwards (Flammang and Lauder, 2009).

6. Conclusions

6.1. Selective advantages of tail evolution

In both sharks and teleost fishes, undulation of the body generates forward locomotion. However, it is notable that while tail morphology differs greatly between these two groups of fishes, in both cases the tail still acts as a major locomotor control surface to manipulate fluid dynamics involved in swimming, albeit in different ways. But why should the tail of fishes have evolved a great deal of morphological differentiation amongst species when the trunk morphology has not specialized to the same degree? The answer to this question may lie in the functional attributes inherent in a given tail morphology which might have been selected for due to particular performance advantages.

An obvious performance advantage of the shark tail morphology is the contribution of the radialis muscle to continuous thrust generation. While not all shark species exhibit life histories necessitating long distance migrations or the capture of fast-swimming prey, they all profit from a metabolic advantage to continuous thrust production. When a fish swims, drag on the body causes deceleration whenever it is not producing thrust. Then, when thrust is produced, momentum created must overcome the inertial mass of the body in addition to providing forward propulsion. If the body does not decelerate between tail beats, then the momentum continuously drives the fish forward, thereby facilitating increases in velocity.

Certain fishes, like tunas and their relatives, are capable of long-distance high-speed propulsion but they typically have a specialized, less flexible tail structure than is seen in most other teleost fishes (Nauen and Lauder, 2000, 2001a,b, 2002). The very flexible tail fins observed in most teleost fishes may offer a selective advantage for maneuvering in a complex habitat. Before scleractinian corals began to form elaborate reef communities in the early Triassic (Stanley, 1981), the underwater habitat may not have offered a multitude of available locations to rear young, find food, and evade predation. Coincidentally, ray-finned fish diversity increased dramatically shortly after these reef communities began to form (Near et al., 2012). It is feasible that a fish that had the ability to maneuver through a complex habitat would be able to exploit a performance niche that other fishes unable to maneuver as well could not. Being able to make tight turns in place and swim backwards, for example, would be an advantage for moving around in a complex habitat.

6.2. Integrative functional morphology is the new evo-devo-eco

To understand the functional morphology of an organism, we need to take into consideration its evolutionary history and the developmental framework available to create the structures that we observe. We also need to place that organism in the context of its environment in order to understand what performance attributes may be under selection. In this way, experimental studies of functional morphology can act as a way to test hypotheses bridging an organism's evolution, development, and ecology.

Take the case of the tail presented here. Paleontology presents a number of ancestral milestones in the development of the axial skeleton and gives a glimpse into the morphology that existed under the ecological conditions relevant to the time of these early organisms. To understand the selective pressures that would have affected the fitness of an extinct organism, we need to know more about performance advantages inherent to their morphology. We can turn to similar morphologies of extant organisms, or use tools like bioinspired robotics and computational models if a good living analog does not exist.

Many developmental studies rely heavily on modifying a feature of a model organism and looking at the phenotypic effects of a genetic mutation. However, just because a mutation may be possible, in terms of evolutionary adaptation and selection, genetic mutations do not tell us anything without some knowledge on how the modifications to morphology affect function and performance. Using the zebrafish model to combine molecular studies, developmental physiology, and functional morphology will offer a wealth of opportunities to experimentally examine evolutionary processes.

Finally, to really understand how phenotype affects an organism's fitness, it is imperative to study the performance of a given morphology in the context of its environment. In this way we can learn how functional attributes contribute to advantages in feeding, evading predation, and rearing young – all of which are ultimately responsible for an individual to pass along its genes. Ecologically important questions, like those concerned with climate change and habitat modification, hinge upon our understanding of the functional morphology and adaptive physiology of the organisms in an ecosystem in question. For example, to understand how building or removing dams affects fish populations, we need not only data on the life of undisturbed populations, but also experimental data on how fishes respond to large-scale changes in flow velocity and perturbation within a short period of time. Here, again, bio-inspired robotics and computer models can help answer these broad questions by increasing the parameter space for forecasting anticipated conditions.

The recent trend in integrative biology has been to focus on the integration of research at the sub-organismal level. And while this no doubt offers researchers the opportunity to collaborate and combine resources enabling incredible discoveries with regard to the building blocks of vertebrate life, it should not be forgotten that the majority of evolutionary processes occurs at the organismal and population level. In the end, the functional morphology of an organism will impact its reproductive fitness and adaptive performance, thereby having the greatest impact on its evolution in the face of ecological changes.

Acknowledgements

The author is extremely thankful for many interesting discussions with George Lauder and other members of the Lauder lab, both past and present. John Long and Nadja Schilling provided the opportunity to present this material at the International Congress on Vertebrate Morphology in July 2013.

References

Abou-Seedo, F.S., 1994. An experimental study of the role of the caudal fin in the swimming performance of a tropical fish, *Eucinostomus lefroyi*. Cybium 17, 181–185.

Affleck, R.J., 1950. Some points in the function, development and evolution of the tail in fishes. Proc. Zool. Soc. Lond. 120, 349–368.

Agathon, A., Thisse, C., Thisse, B., 2003. The molecular nature of the zebrafish tail organizer. Nature 424, 448–452.

Ahn, D., Gibson, G., 1999. Expression patterns of threespine stickleback *Hox* genes and insights into the evolution of the vertebrate body axis. Dev. Genes Evol. 209, 482–494.

Altringham, J.D., Ellerby, D.J., 1999. Fish swimming: patterns in muscle function. J. Exp. Biol. 202, 3397–3403.

Ameyaw-Akumal, C., 1975. The functional morphology of the body and tail muscles of the tuna *Katsuwonus pelamis* Linnaeus. Zool. Anz. 194, 367–375.

Arratia, G., Schultze, H.-P., 1990. The urohyal: development and homology within osteichthyans. J. Morphol. 203, 247–282.

Arratia, G., Schultze, H.P., Casciotta, J., 2001. Vertebral column and associated elements in dipnoans and comparison to other fishes: development and homology. J. Morphol. 250, 101–172.

Basolo, A.L., Alcaraz, G., 2003. The turn of the sword: length increases male swimming costs in swordtails. Proc. R. Soc. Lond. B 270, 1631–1636.

Bird, N.C., Mabee, P.M., 2003. Developmental morphology of the axial skeleton of the zebrafish, *Danio rerio* (Ostariophysi: Cyprinidae). Dev. Dyn. 228, 337–357.

Britz, R., Johnson, G.D., 2005. Leis' conundrum: homology of the clavus of the ocean sunfishes. 1. Ontogeny of the median fins and axial skeleton of *Monotrete leiurus* (Teleostei, Tetraodontiformes, Tetraodontidae). J. Morphol. 266, 1–10.

Cohen, A.H., 1988. Evolution of the vertebrate central pattern generator for locomotion. In: Cohen, A.H., Rossignol, S., Grillner, S. (Eds.), Neural Control of Rhythmic Movements in Vertebrates. Wiley & Sons, New York, pp. 129–166.

de Pinna, M.C.C., 1996. Teleostean monophyly. In: Stiassny, M.L.J., Parenti, L.R., Johnson, G.D. (Eds.), Interrelationships of Fishes. Academic Press, San Diego, pp. 147–162.

Drucker, E.G., Lauder, G.V., 1999. Locomotor forces on a swimming fish: three-dimensional vortex wake dynamics quantified using digital particle image velocimetry. J. Exp. Biol. 202, 2393–2412.

Drucker, E.G., Lauder, G.V., 2000. A hydrodynamic analysis of fish swimming speed: wake structure and locomotor force in slow and fast labriform swimmers. J. Exp. Biol. 203, 2379–2393.

Esposito, C.J., Tangorra, J.L., Flammang, B.E., Lauder, G.V., 2012. A robotic fish caudal fin: effects of stiffness and motor program on locomotor performance. J. Exp. Biol. 215, 56–67.

Flammang, B.E., 2010. Functional morphology of the radialis muscle in shark tails. J. Morphol. 271, 340–352.

Flammang, B.E., Lauder, G.V., 2008. Speed-dependent intrinsic caudal fin muscle recruitment during steady swimming in bluegill sunfish, *Lepomis macrochirus*. J. Exp. Biol. 211, 587–598.

Flammang, B.E., Lauder, G.V., 2009. Caudal fin shape modulation and control during acceleration, braking and backing maneuvers in bluegill sunfish, *Lepomis macrochirus*. J. Exp. Biol. 212, 277–286.

Flammang, B.E., Lauder, G.V., Troolin, D.R., Strand, T., 2011a. Volumetric imaging of shark tail hydrodynamics reveals a three-dimensional dual-ring vortex wake structure. Proc. R. Soc. Lond. B 278, 3670–3678.

Flammang, B.E., Lauder, G.V., Troolin, D.R., Strand, T.E., 2011b. Volumetric imaging of fish locomotion. Biol. Lett. 7, 695–698.

Gemballa, S., 2004. The musculoskeletal system of the caudal fin in the basal Actinopterygii: heterocercy, diphycercy, homocercy. Zoomorphology 123, 15–30.

Gemballa, S., Ebmeyer, L., Hagen, K., Hannich, T., Hoja, K., Rolf, M., Treiber, K., Vogel, F., Weitbrecht, G., 2003. Evolutionary transformations of myoseptal tendons in gnathostomes. Proc. R. Soc. Lond. B 270, 1229–1235.

Griffin, K.J., Amacher, S.L., Kimmel, C.B., Kimelman, D., 1998. Molecular identification of spadetail: regulation of zebrafish trunk and tail mesoderm formation by T-box genes. Development 125, 3379–3388.

Hale, M.E., 1996. Functional morphology of ventral tail bending and prehensile abilities of the seahorse, *Hippocampus kuda*. J. Morphol. 2275, 51–65.

Hilton, E.J., Johnson, G.D., 2007. When two equals three: developmental osteology and homology of the caudal skeleton in carangid fishes (Perciformes: Carangidae). Evol. Dev. 9, 178–189.

Holley, S.A., 2006. Anterior–posterior differences in vertebrate segments: specification of trunk and tail somites in the zebrafish blastula. Genes Dev. 20, 1831–1837.

Ishikawa, Y., Iwamatsu, T., 1993. Development of a motor nerve in the caudal fin of the medaka (*Oryzias latipes*). Neurosci. Res. 17, 101–116.

Janvier, P., Arsenault, M., 2007. The anatomy of *Euphanerops longaevus* Woodward, 1900, an anaspid-like jawless vertebrate from the Upper Devonian of Miguasha, Quebec, Canada. Geodiversitas 29, 143–216.

Jayne, B.C., Lauder, G.V., 1995. Red muscle motor patterns during steady swimming in largemouth bass: effects of speed and correlations with axial kinematics. J. Exp. Biol. 198, 1575–1587.

Kanki, J.P., Ho, R.K., 1997. The development of the posterior body in zebrafish. Development 124, 881–893.

Kimelman, D., Griffin, K.J.P., 2000. Vertebrate mesendoderm induction and patterning. Curr. Opin. Genetics Dev. 10, 350–356.

Koob, T.J., Long Jr., J.H., 2000. The vertebrate body axis: evolution and mechanical function. Am. Zool. 40, 1–18.

Lauder, G.V., 1980. On the relationship of the myotome to the axial skeleton in vertebrate evolution. Paleobiology 6, 51–56.

Lauder, G.V., 1982. Structure and function in the tail of the pumpkinseed sunfish (*Lepomis gibbosus*). J. Zool. Lond. 197, 483–495.

Lauder, G.V., 1989. Caudal fin locomotion in ray-finned fishes: historical and functional analyses. Am. Zool. 29, 85–102.

Lauder, G.V., Liem, K.F., 1983. The evolution and interrelationships of the Actinopterygian fishes. Bull. Mus. Comp. Zool. 150, 95–197.

Lauder, G.V., Flammang, B., Alben, S., 2012. Passive robotic models of propulsion by the bodies and caudal fins of fish. Integr. Comp. Biol. 52, 576–587.

Long, J.H., 1992. Stiffness and damping forces in the intervertebral joints of blue marlin (*Makaira nigricans*). J. Exp. Biol. 162, 131–155.

Long, J.H., Nipper, K.S., 1996. The importance of body stiffness in undulatory propulsion. Am. Zool. 36, 678–694.

Mabee, P.M., Crotwell, P.L., Bird, N.C., Burke, A.C., 2002. Evolution of median fin modules in the axial skeleton of fishes. J. Exp. Zool. 294, 77–90.

Metscher, B.D., 2009. MicroCT for comparative morphology: simple staining methods allow high-contrast 3D imaging of diverse non-mineralized animal tissues. BMC Physiol. 9, 1–14.

Morin-Kensicki, E.M., Melancon, E., Eisen, J.S., 2002. Segmental relationship between somites and vertebral column in zebrafish. Development 129, 3851–3860.

Morris, S.C., Caron, J.B., 2012. *Pikaia gracilens* Walcott, a stem-group chordate from the Middle Cambrian of British Columbia. Biol. Rev. 87, 480–512.

Nauen, J.C., 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., Lauder, G.V., 2001a. 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.

Nauen, J.C., Lauder, G.V., 2001b. Three-dimensional analysis of finlet kinematics in the chub mackerel (*Scomber japonicus*). Biol. Bull. 200, 9–19.

Nauen, J.C., Lauder, G.V., 2002. Hydrodynamics of caudal fin locomotion by chub mackerel, *Scomber japonicus* (Scombridae). J. Exp. Biol. 205, 1709–1724.

Near, T.J., Eytan, R.I., Dornburg, A., Kuhn, K.L., Moore, J.A., Davis, M.P., Wainwright, P.C., Friedman, M., Smith, W.L., 2012. Resolution of ray-finned fish phylogeny and timing of diversification. Proc. Natl. Acad. Sci. U. S. A. 109, 13698–13703.

Near, T.J., Dornburg, A., Eytan, R.I., Keck, B.P., Smith, W.L., Kuhn, K.L., Moore, J.A., Price, S.A., Burbrink, F.T., Friedman, M., Wainwright, P.C., 2013. Pylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. Proc. Natl. Acad. Sci. U. S. A. 110, 12738–12743.

Patterson, C., 1968. The caudal skeleton in Lower Triassic pholidophorid fishes. Bull. Brit. Mus. (Nat. Hist.) Geol. 16, 201–239.

Potthoff, T., Kelley, S., Collins, A.L., 1988. Osteological development of the red snapper, *Lutjanus campechanus* (Lutjanidae). Bull. Mar. Sci. 43, 1–40.

Quint, E., Smith, A., Avaron, F., Laforest, L., Miles, J., Gaffield, W., Akimenko, M.A., 2002. Bone patterning is altered in the regenerating zebrafish caudal fin after ectopic expression of sonic hedgehog and bmp2b or exposure to cyclopamine. Proc. Natl. Acad. Sci. U. S. A. 99, 8713–8718.

Schneider, H., Sulner, B., 2006. Innervation of dorsal and caudal fin muscles in adult zebrafish *Danio rerio*. J. Comp. Neurol. 497, 702–716.

Shadwick, R.E., Steffensen, J.F., Katz, S.L., Knower, T., 1998. Muscle dynamics in fish during steady swimming. Am. Zool. 38, 755–770.

Shu, D.-G., Morris, S.C., Zhang, X.-L., 1996. A Pikaia-like chordate from the Lower Cambrian of China. Nature 384, 157–158.

Shu, D.-G., Morris, S.C., Han, J., Zhang, Z.-F., Yasui, K., Janvier, P., Chen, L., Zhang, X.-L., Liu, J.-N., Li, Y., 2003. Head and backbone of the Early Cambrian vertebrate *Haikouichthys*. Nature 421, 526–529.

Smith, M., Hickman, A., Amanze, D., Lumsden, A., Thorogood, P., 1994. Trunk neural crest origin of caudal fin mesenchyme in the zebrafish *Brachiodanio rerio*. Proc. R. Soc. Lond. B 256, 137–145.

Stanley, G.D., 1981. Early history of scleractinian corals and its geological consequences. Geology 9, 507–511.

Tytell, E.D., 2006. Median fin function in bluegill sunfish *Lepomis macrochirus*: streamwise vortex structure during steady swimming. J. Exp. Biol. 209, 1516–1534.

Wilga, C.D., Lauder, G.V., 2002. Function of heterocercal tail in sharks: quantitative wake dynamics during steady swimming and vertical maneuvering. J. Exp. Biol. 205, 2365–2374.

Wilga, C.D., Lauder, G.V., 2004. Hydrodynamic function of the shark's tail. Nature 430, 850.

Winterbottom, R., 1974. A descriptive synonymy of the striated muscles of the Teleostei. Proc. Acad. Nat. Sci. Phila. 125, 225–317.