



SYMPOSIUM

What Fish Can Teach Us about the Feeding Functions of Postcranial Muscles and Joints

Ariel L. Camp^{1,*†}

*Department of Musculoskeletal Biology, Institute of Ageing and Chronic Disease, University of Liverpool, Liverpool, UK; †Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA

From the symposium “Multifunctional structures and multistructural functions: Functional coupling and integration in the evolution of biomechanical systems” presented at the annual meeting of the Society of Integrative and Comparative Biology, January 3–7, 2019 at Tampa, Florida.

¹E-mail: Ariel.Camp@liverpool.ac.uk

Synopsis Studies of vertebrate feeding have predominantly focused on the bones and muscles of the head, not the body. Yet, postcranial musculoskeletal structures like the spine and pectoral girdle are anatomically linked to the head, and may also have mechanical connections through which they can contribute to feeding. The feeding roles of postcranial structures have been best studied in ray-finned fishes, where the body muscles, vertebral column, and pectoral girdle attach directly to the head and help expand the mouth during suction feeding. Therefore, I use the anatomy and motion of the head–body interface in these fishes to develop a mechanical framework for studying postcranial functions during feeding. In fish the head and body are linked by the vertebral column, the pectoral girdle, and the body muscles that actuate these skeletal systems. The morphology of the joints and muscles of the cranio-vertebral and hyo-pectoral interfaces may determine the mobility of the head relative to the body, and ultimately the role of these interfaces during feeding. The postcranial interfaces can function as anchors during feeding: the body muscles and joints minimize motion between the head and body to stabilize the head or transmit forces from the body. Alternatively, the postcranial interfaces can be motors: body muscles actuate motion between the head and body to generate power for feeding motions. The motor function is likely important for many suction-feeding fishes, while the anchor function may be key for bite- or ram-feeding fishes. This framework can be used to examine the role of the postcranial interface in other vertebrate groups, and how that role changes (or not) with morphology and feeding behaviors. Such studies can expand our understanding of muscle function, as well as the evolution of vertebrate feeding behaviors across major transitions such as the invasion of land and the emergence of jaws.

Introduction

Vertebrate feeding studies have focused on the bones and muscles of the head, with much less known about the interaction between the head and body or the roles of postcranial bones and muscles. This is not surprising, as it is the cranial structures—tongues, jaws, beaks, teeth—that directly contact food, and the muscles of the head that attach directly to these elements. Cranial motions are often externally visible and can be directly related to acquiring and ingesting food, while postcranial structures such as the vertebral column, pectoral girdle, and associated body muscles are usually neither visible nor directly interacting with the food. However, these

postcranial structures may also be acting as part of the feeding apparatus.

The head and body are anatomically linked, and there is reason to expect they are also mechanically linked. In tetrapods, the head is connected to the trunk and limbs by the neck, while in non-tetrapod fishes the body muscles of the trunk attach directly to the cranial skeleton (Evans 1939; Shubin et al. 2015). By linking the head and body, this postcranial interface has the potential to transmit forces or even power from the body to the head. What role the postcranial musculoskeletal system plays in feeding will depend on the morphology of these muscles and joints, as well as their behavior during feeding.

Understanding the role of postcranial structures during feeding can bring new insights into the mechanics and evolution of vertebrate feeding behaviors, as well as how the demands of feeding may have shaped the head–body interface.

The feeding role of the postcranial interface has been most widely recognized in suction-feeding fishes. In non-tetrapod bony fishes (“bony fishes” hereafter) that primarily capture food by suction the body muscles and pectoral girdle have long been studied as part of the feeding apparatus (Gregory 1933; Tchernavin 1953; Alexander 1967), as they are capable of contributing to mouth expansion during suction feeding. First, the dorsal body muscles (epaxials) are the only muscles that cross the craniovertebral joint and can rotate the head dorsally to increase the dorsoventral height of the mouth cavity (Fig. 1A). Second, the ventral body muscles (hypaxials) can retract the pectoral girdle to expand the mouth cavity ventrally and caudally, via linkages with the hyoid apparatus and lower jaw (Fig. 1A). As a result, the body muscles, vertebral column, and pectoral girdle have been studied during feeding in a wide range of suction-feeding fishes (reviewed in Schaeffer and Rosen 1961; Anker 1974; Lauder 1985; Ferry-Graham and Lauder 2001; Westneat 2006). Therefore, bony fishes are an excellent system for exploring the role of postcranial musculoskeletal systems during feeding, and may offer insights that can be applied to other vertebrate systems as well.

Outside of bony fishes, relatively little is known about the feeding functions of postcranial structures, nor is there a mechanical framework for understanding postcranial motion and morphology in the context of feeding. This is due in part to the difficulty of visualizing the *in vivo* motion of deep structures like the pectoral girdle, vertebral column, and the muscles actuating them. Additionally, measuring motion between the head and body requires a new frame of reference. Many feeding studies measure motion relative to the cranium, making it impossible to determine how the cranium itself is moving relative to the body. X-ray Reconstruction of Moving Morphology (XROMM) has made it possible to visualize bones like the vertebral column and pectoral girdle in live animals, by combining biplanar X-ray video with 3D digital bone models (Brainerd et al. 2010). The skeletal animation produced by XROMM also allows bone motions to be measured in multiple, anatomically relevant frames of reference (e.g., Camp and Brainerd 2014; Menegaz et al. 2015). Additionally, sonomicrometry and fluoromicrometry use sound or biplanar X-ray video, respectively, to measure *in vivo* muscle length.

With the ability to directly image and measure postcranial structures now available, the mechanical interface between head and body is an exciting area for exploration. The goal of this paper is to propose a framework for how the postcranial body structures can contribute to feeding, based on our knowledge from bony fishes. I first describe the anatomical connections between the head and body in bony fishes, and then propose mechanical functions for the postcranial interfaces during feeding. Lastly, I examine how this mechanical framework may be applied across the major vertebrate groups, highlighting areas that are ripe for further research.

Anatomy of the postcranial interface

Cranio-vertebral interface

In bony fishes, the head and body are connected by two musculoskeletal systems: dorsally by the cranio-vertebral interface and ventrally by the hyoid–pectoral interface. The cranio-vertebral interface consists of the bones, joints, and muscles that connect the cranium and the vertebral column. The neurocranium and the vertebral column directly articulate in most fish at the craniovertebral joint (but see Schnell et al. 2008) between the basioccipital and the rostralmost vertebral body (Fig. 1A). This joint is crossed dorsally and laterally by the epaxials: segmented body muscles whose W-shaped myomeres extend along the vertebral column from the neurocranium to the caudal fin (Fig. 1). Thus, the epaxial muscles, and only these muscles, have a line of action to produce flexion between the head and body. This flexion is usually described as dorsal rotation or elevation of the neurocranium relative to the body, and has been measured in many bony fishes (reviewed in Schaeffer and Rosen 1961; Lauder 1985).

It remains unclear which vertebral joints contribute to cranial elevation in suction-feeding fishes, or how this role relates to vertebral morphology. Traditionally, the vertebral column of fish has been split into abdominal and caudal regions (Rockwell et al. 1938), but there is developmental (Morin-Kensicki et al. 2002; Johanson et al. 2005) and morphological (Nowroozi et al. 2012) evidence for a cervical region immediately caudal to the head (Fig. 1B) in at least some species. The presence and extent of a cervical region has not yet been broadly examined across bony fishes, nor whether it contributes to cranial elevation. Nevertheless, morphologically distinct anterior vertebrae are found in many fishes, such as the Weberian apparatus of ostariophyans (e.g., Bird and Hernandez 2007), and some have

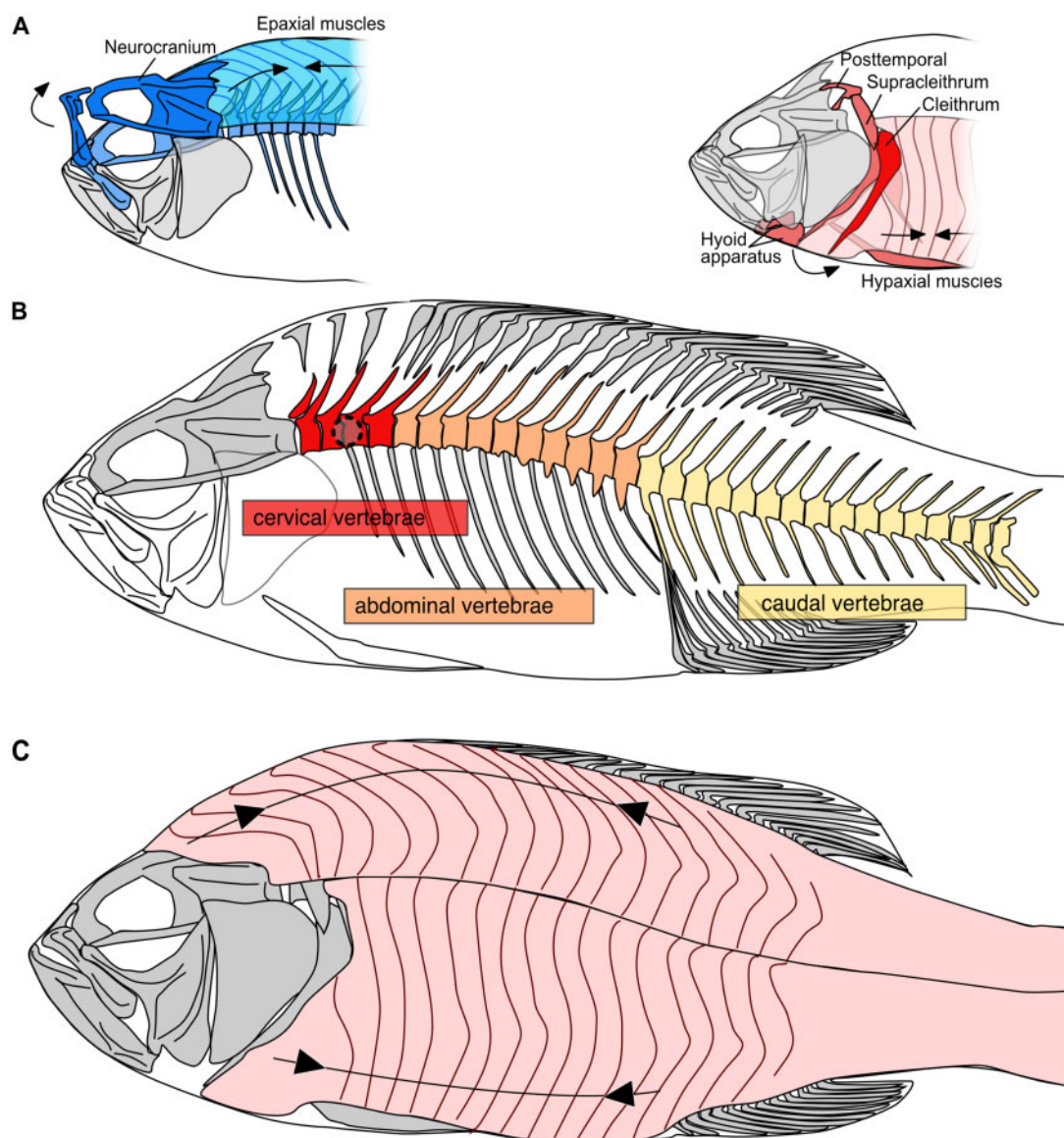


Fig. 1 Anatomy and function of the postcranial interface during feeding in fish, based on largemouth bass (*Micropterus salmoides*). **A**) The dorsal, cranio-vertebral interface (in blue) can contribute to mouth expansion as epaxial muscle shortening produces dorsal flexion at the craniovertebral joint to rotate (elevate) the cranium. The ventral, hyo-pectoral interface (in red) can contribute to expansion by hypaxial muscle shortening to caudally rotate (retract) the pectoral girdle, which in turn retracts and depresses the hyoid. **B**) The vertebral column can be divided into three regions: caudal (yellow), abdominal (orange), and cervical (red) as defined by Nowroozi et al. (2012). The average center of neurocranial rotation measured from largemouth bass (Jimenez et al. 2018) is indicated by a black, dashed circle. **C**) The epaxial and hypaxial musculature, with the regions that shorten during feeding indicated with black arrows (Camp and Brainerd 2014) extend far beyond the cervical vertebrae and center of neurocranial rotation shown in **B**.

been hypothesized to directly relate to cranial elevation (Lesiuk and Lindsey 1978; Lauder and Liem 1981; Huet et al. 1999; Jimenez et al. 2018). For most fishes cranial elevation is likely not achieved by flexion at the craniovertebral joint alone, and the center of cranial rotation is further posterior at approximately the level of the pectoral girdle's post-temporal-supracleithrum joint (Fig. 1A) based on morphology, specimen manipulation (Gregory 1933), 2D (Carroll et al. 2004), and 3D (Jimenez et al. 2018)

kinematics analysis. This implies that some number of intervertebral joints on either side of that center are also dorsally flexed to generate cranial elevation. For example, in largemouth bass (*Micropterus salmoides*), the center of cranial rotation was between the second and fourth vertebrae (Jimenez et al. 2018), within the cervical region (Fig. 1B). Alternatively, the pivot-feeding sygnathiform fishes have centers of cranial rotation at, or rostral to, the craniovertebral joint (Roos et al. 2010), and may achieve cranial elevation

by flexion primarily about this joint (de Lussanet and Muller 2007). Given the morphological and behavioral diversity of fishes, the number and location of intervertebral joints contributing to the dorsal postcranial interface likely varies among species or even feeding behaviors.

Large regions of the epaxial muscles may contribute to cranial elevation, and therefore be considered part of the cranio-vertebral interface. The epaxial muscles have long been known to activate during suction feeding in many fishes (Wainwright et al. 1989), and in the largemouth bass that activity extends over halfway down the body (Thys 1997). These muscles are not only active, but also shorten from the head to about halfway down the body in at least two species: largemouth bass (Camp and Brainerd 2014) and bluegill sunfish (Camp et al. 2018). This demonstrates that large regions of the epaxial muscles, likely extending beyond the region of dorsally flexing intervertebral joints, can contribute to the cranio-vertebral interface during feeding. Like the vertebrae, no morphological distinction has been found to indicate which regions of the epaxial muscles contribute to cranial elevation.

Hyo-pectoral interface

Ventrally, the head and body are linked by the hyo-pectoral interface: the bones of the pectoral girdle, and the muscles that connect it to the hyoid apparatus and the body. In most bony fishes the pectoral girdle is made up of a series of articulated bones, the most dorsal of which typically articulates with the epiotic bones in the caudal region of the neurocranium (Gosline 1977) (Fig. 1A). Ventrally, the cleithrum is linked to the hyoid apparatus by the sternohyoideus muscle and to the body and vertebral column by the hypaxial muscles (Fig. 1A). These muscles control the cranio-caudal position of the cleithrum and can generate rostradorsal (protraction) or caudoventral (retraction) sagittal-plane rotations at the cleithrum–supracleithrum joint. During feeding, the hypaxial muscles can shorten to retract the pectoral girdle, which in turn retracts and depresses the hyoid apparatus and contributes to mouth expansion (Muller 1987; Van Wassenbergh et al. 2007b; Camp and Brainerd 2014). The sternohyoideus muscle may also shorten during pectoral girdle retraction as in bluegill sunfish (Camp et al. 2018), or it may act as a ligament to transmit motion to the hyoid, as in largemouth bass (Camp and Brainerd 2014) and clariid catfishes (Van Wassenbergh et al. 2007b). It has also been proposed that the sternohyoideus could shorten against an

immobile cleithrum—held in place by the hypaxials—to retract the hyoid apparatus (Lauder and Lanyon 1980), but this has yet to be demonstrated experimentally.

As with the epaxial muscles, it is not anatomically obvious what proportion of the hypaxial muscles are involved. Activity has only been recorded in the rostralmost regions of the hypaxials (Lauder and Lanyon 1980; Lauder and Norton 1980; Lauder 1981), but large regions (from the pectoral girdle to halfway down the body) of the hypaxial muscles shorten during pectoral girdle retraction in largemouth bass (Camp and Brainerd 2014) and bluegill sunfish (Camp et al. 2018). While cleithrum retraction has been measured in multiple species, it is unknown whether this is due solely to rotation about the cleithrum–supracleithrum joint or whether more dorsal pectoral girdle joints also contribute (Gosline 1977; Muller 1987).

Mechanical framework

As described above, the postcranial interface has multiple anatomical connections to the head and can contribute kinematically to mouth expansion through cranial elevation and/or hyoid retraction. These mechanical connections lead to two proposed feeding functions of the postcranial interface.

First, the postcranial interface may act as a motor: generating power that is then transmitted to the head during mouth expansion (Fig. 2). In order to generate power (the product of force and velocity), muscles must actively shorten to generate force and positive velocity. To allow this muscle shortening and power transmission to the head, there must also be flexion of the skeleton at the postcranial interface. Thus, for the cranio-vertebral interface to act as a motor, there should be motion (dorsal flexion) at the craniovertebral and/or intervertebral joints, and epaxial muscle shortening. Similarly, for the hyo-pectoral system power production must be accompanied by rotation (retraction) of the pectoral girdle and hypaxial shortening. In summary, if the postcranial interface is functioning as a motor to power feeding motions, then the interfacing body muscles should be active and shortening, and the neurocranium or pectoral girdle should rotate relative to the body (Fig. 2).

Second, the postcranial interface may act as an anchor to stabilize the head and transmit forces from the body (Fig. 2). The interfacing muscles may actively generate force, but not shorten or generate power, which would move rather than stabilize the head. Therefore, there is no joint motion at the interface: no dorsal flexion of the neurocranium or

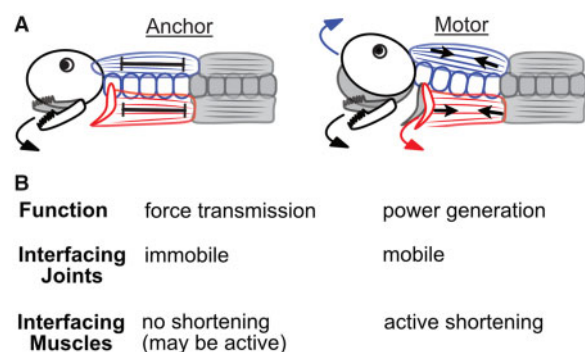


Fig. 2 Mechanical roles of the cranio-vertebral and hyo-pectoral systems during feeding. **A**) Schematic of the postcranial interfaces (unfilled, shapes) as either motors or anchor, relative to the rest of the body (filled, shapes). **B**) Each role is hypothesized to have distinct mechanical functions, interfacing joints motions (relative to the body), and interfacing muscle behaviors. (Online figure in color.)

retraction of the pectoral girdle. In this way the postcranial interfaces can provide stable attachment sites for the cranial muscles that insert on the neurocranium or pectoral girdle. Such stability may also be important for transferring forces from the locomotion system (body and fins) to the head. Anchoring is also required during suction feeding: if either the neurocranium or pectoral girdle were free to move, they would be sucked toward the center of the mouth by the sub-ambient pressure in the mouth cavity (e.g., Carroll et al. 2004). The postcranial interfaces must at least generate force to overcome this pressure. In summary, if the postcranial interface is functioning as an anchor, then the muscles should be active but not shortening and the neurocranium and pectoral girdle should not move relative to the body (Fig. 2).

The mechanical functions of “motor” and “anchor” are somewhat simplistic and likely represent two extremes along a spectrum of roles for the postcranial interface during feeding. These musculo-skeletal systems can do more than just generate force or power, and may switch roles within or between feeding behaviors. However, the motor and anchor roles still provide a useful framework for examining postcranial function in suction-feeding bony fishes and other vertebrates. The motor function is clearly important for suction feeding fishes, as substantial power is required to expand the mouth fast and forcefully enough to accelerate a bolus of water and prey into the mouth. While it has long been recognized that the muscles of the head are too small to be the sole source of suction power (Alexander 1970; Elshoud-Oldenhave 1979; Aerts et al. 1987), recent studies have shown that epaxial and hypaxial

muscles generate over 90% of the required power for suction strikes (Camp et al. 2015, 2018). In some suction feeding fishes, however, cranial elevation is minimal or absent (Van Wassenbergh et al. 2009), implying the cranio-vertebral interface may have an anchoring role in these species. Anchoring the postcranial interface may function to transmit force or stabilize cranial muscle attachment sites, but it prevents the body muscles from contributing power. Given the predicted importance of body muscle power for mouth expansion, it seems unlikely that both postcranial interfaces would act as anchors during suction feeding. However, if only one interface is acting as a motor to power suction expansion, then the other must be an anchor to resist the mouth cavity collapsing. For example, if the hyo-pectoral interface alone powers suction expansion, then the cranio-vertebral interface must anchor the neurocranium so it is not accelerated ventrally by the sub-ambient pressure of the mouth cavity. In order to expand the mouth cavity dorsoventrally, i.e., by increasing the angle between the neurocranium and the pectoral girdle, both interfaces must function together as motors or a motor-anchor pair. Suction feeding fish may even be able to modify the role (anchor vs. motor) of an interface depending on prey type and position (Van Wassenbergh et al. 2006).

Postcranial feeding roles across vertebrates

While this framework has been developed based on suction feeding fishes, I expect it can be usefully applied to studying how the postcranial interface contributes to other feeding behaviors and vertebrates. All vertebrates have anatomical connections between the head and body—although the specific structures and muscles vary—and therefore have the potential for postcranial structures to contribute mechanically to feeding. While there are fewer studies outside of suction-feeding bony fishes, I use the motor–anchor framework to develop informed hypotheses about postcranial function during feeding.

Cartilaginous fishes

Chondrichthyans, the sharks, chimaeroids, and rays are the other major group of aquatic vertebrates, and while some are specialized suction feeders this is not the predominant mode of prey capture as in bony fishes (Wilga et al. 2007). The cranio-vertebral interface of chondrichthyans is broadly similar to that of bony fishes in that the chondrocranium directly articulates with the vertebral column at the

craniovertebral joint (Fig. 3A), which is spanned by the epaxial muscles. While a cervical region has not been identified in this group, the anterior vertebrae may have distinct morphologies, such as the synarcual of chimaeroids and rays formed by fusion of two or more of the most cranial vertebrae (Claeson 2011; Johanson et al. 2015), and expanded basiventrals in some sharks and rays (Claeson and Hilger 2011). It remains unclear how or if these vertebral morphologies contribute to motion between the chondrocranium and vertebral column (Claeson and Hilger 2011), although cranial elevation is usually minimal in most sharks and rays including suction-feeding specialists (Wu 1994; Ajemian and Sanford 2007; Wilga and Sanford 2008) (but see Fouts and Nelson 1999). This suggests that in most chondrichthyans the cranio-vertebral interface, including specialized anterior vertebrae like the synarcual, may function as an anchor to stabilize the head during feeding. The ram- and bite-and-tear feeding behaviors of sharks rely on accelerating the body to ram into prey (Motta and Wilga 2001), so transmitting force from the body to the head may be an important function of the postcranial interface.

The pectoral girdle of sharks does not articulate with the cranium at all and is caudally displaced compared with bony fishes (Fig. 3). Despite this, in at least one suction-feeding shark (the white-spotted bamboo shark) pectoral girdle retraction and hypaxial muscle shortening were recorded during feeding (Camp et al. 2017), consistent with a motor function for the hyo-pectoral interface. This pectoral girdle retraction occurred relatively late (Camp et al. 2017), and mouth expansion was likely powered by the hypobranchial muscles rather than the axial muscles as in bony fish (Ramsay 2012). The role of the pectoral girdle and axial muscles in suction-feeding rays (e.g., Dean and Motta 2004) has yet to be examined, although morphology suggests limited pectoral girdle mobility (Da Silva and De Carvalho 2015). Much remains to be discovered about the function of the postcranial interfaces in cartilaginous fishes, and studying this group may also help us understand the role of the postcranial interface for feeding in stem gnathostomes.

Bony fishes

The role of the postcranial interfaces during suction feeding in bony fishes is discussed above, but less is known about their role in other behaviors such as ram-feeding, biting, scraping, filtering, and winnowing. Mechanically, these behaviors rely less on powerful mouth expansion, and instead require force and

work to be exerted on the food. The epaxial muscles are often still active at least during biting (e.g., Alfaro et al. 2001), and anchoring of the postcranial interface may aid the function of cranial muscles during these feeding behaviors. For example, the interfaces may stabilize the head during ram and ram-filter feeding (as it is propelled forward by whole-body acceleration), or transmit body forces to the head during bite-and-tear feeding where food is gripped with the jaws, and pulled or twisted off by body motions. Alternatively, motor functions of the cranio-vertebral and hyo-pectoral interfaces may still be important for these feeding modes; more data on body muscle shortening and neurocranium and pectoral girdle kinematics are needed to test this. Most actinopterygian biters, scrapers, and filterers can also suction feed, with little evidence of performance trade-offs between these two behaviors (Liem 1980; Van Wassenbergh et al. 2007a). This suggests that the body muscles may be quite versatile and multi-functional within a single individual, as well as across species.

Tetrapods

Unlike bony and cartilaginous fishes, tetrapods have an anatomically distinct postcranial interface: the neck, which spans from the head to the pectoral girdle. The cervical vertebrae of the neck allow three-dimensional motion and positioning of the head during feeding (e.g., Gussekloo and Bout 2005; Snively et al. 2014). In addition to driving head motions, the postcranial interface may contribute mechanically to feeding. Suction-feeding salamanders and turtles can use the cranio-vertebral and hyo-pectoral interfaces as motors, with cranial elevation and pectoral girdle retraction as in suction-feeding fishes (Lauder and Shaffer 1985; Lauder and Prendergast 1992; Van Damme and Aerts 1997; Aerts et al. 2001). Presumably this allows the body muscles to contribute power to suction feeding, as in bony fishes, despite the separation of the head and body by the neck. For at least the cranio-vertebral interface, this motor function is not limited to suction feeding as cranial elevation has also been observed during feeding in lizards (Herrel et al. 1995; Herrel and Vree 1999) and caiman (Cleuren and de Vree 1992), although in these ram- and bite-feeders it is most likely used to widen the mouth opening before biting down on food.

The craniovertebral interface is also likely to be used by many tetrapods as an anchor to stabilize the head and transmit forces from the body. There are qualitative and anecdotal reports of tetrapods

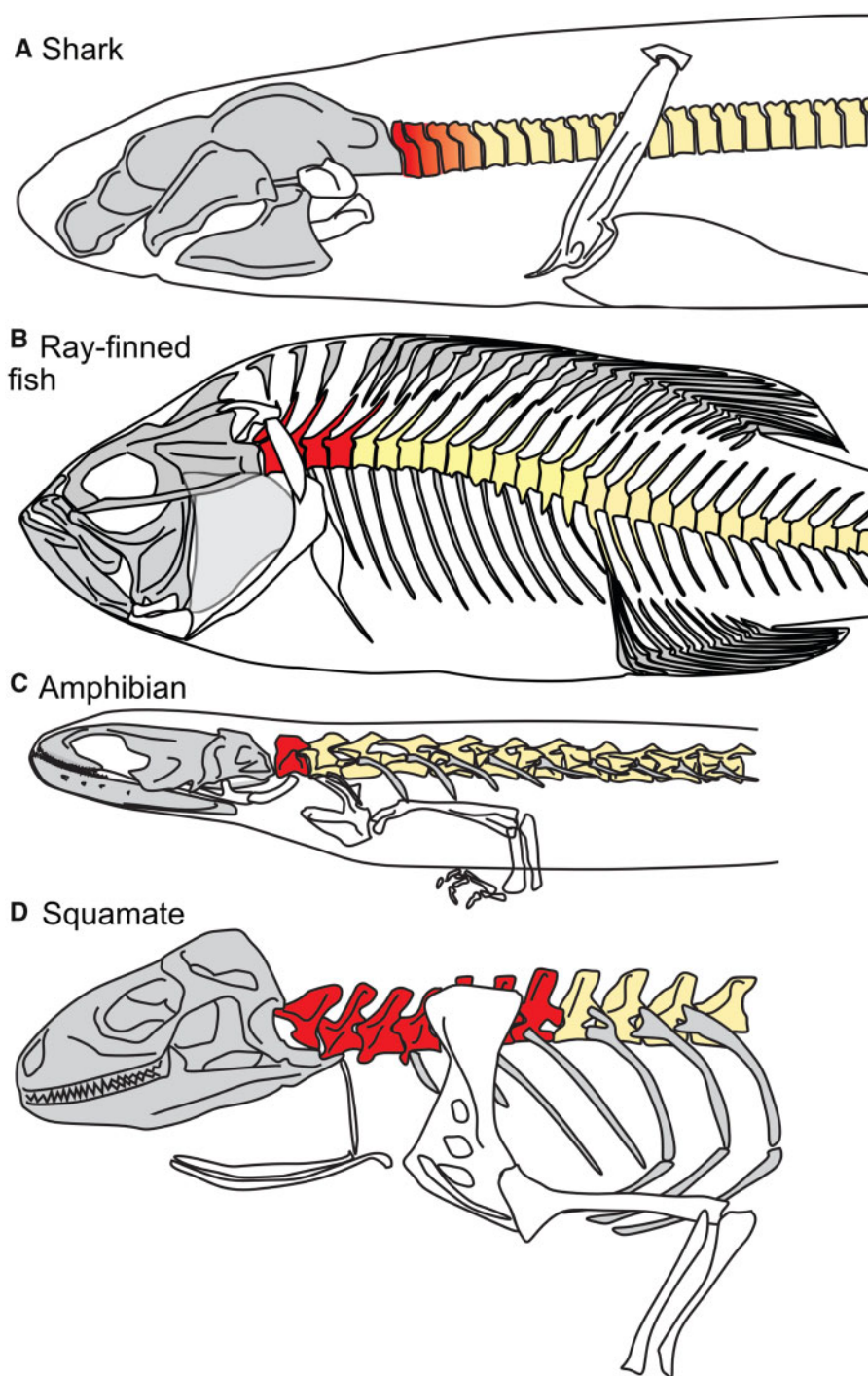


Fig. 3 Comparative skeletal anatomy of the postcranial interfaces from different vertebrate groups. The pectoral girdle and hyoid apparatus are shown in white (unfilled) and the cervical vertebrae highlighted in darker tones. The gradient of tones in the shark (A) indicates vertebrae that may be morphologically distinct, although not referred to as a cervical region (see Claeson and Hilger 2011). Schematic diagram of (A) shark (*Chiloscyllium plagiosum*), (B) ray-finned fish (*Micropterus salmoides*), (C) salamander (*Pleurodeles waltl*), and (D) lizard (*Iguana iguana*). Online version in color.

holding food in the jaws while motions of the neck and/or body are used to dislodge or tear the food (e.g., Van Valkenburgh 1996). In some feeding behaviors—like diving at high speeds or the precise occlusion of mammalian chewing—head stabilization

may be crucial, and the anchoring of the craniovertebral interface may be important. However, more studies are needed to better understand how tetrapods use the craniovertebral interface, and how these functions correspond to vertebral morphology. For

example, does all cranial elevation in salamanders result from rotation about their single cervical vertebrae (Fig. 3C), or are more caudal intervertebral joints also contributing? Conversely, are all the cervical vertebrae in lizards (Fig. 3D) contributing to cranial elevation?

The hyo-pectoral interface has received even less study in tetrapods, but is most often associated with anchor functions in these vertebrates. The morphology of the pectoral girdle skeleton varies widely across tetrapods and some elements (Jenkins 1974) or even the entire girdle may be absent (e.g., Tsuihiji et al. 2012). Not only is the pectoral girdle of tetrapods separated from the head, but its roles supporting the rib cage or forelimbs may prevent substantial motion of the girdle (Heiss et al. 2018). And unlike bony and cartilaginous fishes, tetrapods have a muscular tongue, derived from hypobranchial muscles which still attach to elements of the pectoral girdle and/or hyoid apparatus (Diogo et al. 2008). One possibility is that stability of the pectoral girdle may be important for the tongue's functions during feeding. More research is needed to examine the role of the hyo-pectoral interface during feeding in tetrapods, and understand how pectoral girdle morphology relates to feeding behaviors.

A broader understanding of the feeding roles of the postcranial interface across vertebrates, not just bony fishes, can lead to exciting and important evolutionary questions. First, there are good reasons to hypothesize that the axial muscles of the postcranial interface were involved in the feeding of early stem gnathostomes. Stem gnathostomes already possessed the musculoskeletal elements of the postcranial interfaces. The evolution of the epaxial and hypaxial muscles and the pectoral girdle predate the cranial muscles and vertebrate jaw (Forey and Janvier 1993; Kusakabe et al. 2011; Brazeau and Friedman 2015). Epaxial-powered cranial elevation is an important mechanism of mouth-opening—for suction, ram, and bite feeding—used across extant bony fishes, and inferred to be ancestral for this group (Schaeffer and Rosen 1961). Early jawed vertebrates such as the arthrodire placoderms may also have used epaxial-powered cranial elevation to feed (Anderson and Westneat 2007; Trinajstić et al. 2007, 2013; Anderson 2010). Although we don't yet know if the same is true of hypaxial-powered pectoral girdle retraction, this motion has been observed in bony and cartilaginous fishes (Camp and Brainerd 2014; Camp et al. 2017) and W-shaped hypaxial muscles were present in placoderms (Trinajstić et al. 2007). As we better understand the form–function relationships of the postcranial interface in

living fishes, we may be able to infer its role during feeding in early vertebrates.

Second, as vertebrates colonized terrestrial habitats, how did the function of the postcranial interface change, and how did this influence the evolution of postcranial morphology and feeding behaviors? The morphology and mechanics of the postcranial interface changed substantially in tetrapods. The pectoral girdle was initially separated from the head by the neck in tetrapodomorph fishes (Shubin et al. 2006; Shubin et al. 2015), and then co-opted to support the forelimbs and rib cage in terrestrially locomoting tetrapods. Suction feeding was no longer feasible in the low-density, low-viscosity air of the terrestrial environment, so food had to be captured by mouth-closing rather than powerful mouth expansion (Neenan et al. 2014; Heiss et al. 2018). As a result of these anatomical and mechanical changes, what happened to the role of the postcranial interface during feeding in tetrapods? Most studies of the pectoral girdle and vertebral column in early tetrapods and tetrapodomorph fishes have focused on their role in locomotion (e.g., Shubin et al. 2006; Pierce et al. 2013), while feeding studies have focused on the jaws and skull (e.g., Neenan et al. 2014). But could these interfaces have still acted as motors during feeding, as they do in many bony fishes? As we discover more about the feeding functions of the postcranial interfaces of modern tetrapods and bony fishes, we can start to answer these questions.

Conclusion

Understanding the feeding functions of the postcranial interface is an exciting research area, with much still to be discovered. This paper provides a preliminary framework for understanding the function of the postcranial interface during feeding—as an anchor or a motor—which may be revised or replaced as more data are collected. Currently, comparative data on musculoskeletal function of the cranio-vertebral and hyo-pectoral interfaces are scarce, and more studies are desperately needed. With recent advances in visualizing and recording musculoskeletal function, I hope more feeding studies will include these postcranial elements, leading to a more complete understanding of their form–function relationships, evolutionary morphology, and muscle function.

Acknowledgments

I am grateful to Peter Falkingham for discussions and feedback on early drafts, Emily Kane and Stacy Farina for organizing the associated symposium, and

two anonymous reviewers for their constructive suggestions.

Funding

This work was supported by the Biosciences and Biotechnology Research Council [Future Leaders Fellowship to A.L.C.] and the US National Science Foundation [IOS-1655756 to A.L.C. and E. L. Brainerd].

References

- Aerts P, Osse J, Verraes W. 1987. Model of jaw depression during feeding in *Astatotilapia elegans* (Teleostei: Cichlidae): mechanisms for energy storage and triggering. *J Morphol* 194:85–109.
- Aerts P, Van Damme J, Herrel A. 2001. Intrinsic mechanics and control of fast cranio-cervical movements in aquatic feeding turtles. *Am Zool* 41:1299–310.
- Ajemian MJ, Sanford CP. 2007. Food capture kinematics in the deep-water chain catshark *Scyliorhinus retifer*. *J Mar Biol Assoc UK* 87:1277–86.
- Alexander R. 1967. Feeding. In: Cain AJ, editor. *Functional design in fishes*. London: Hutchinson and Co. p. 89–114.
- Alexander R. 1970. Mechanics of the feeding action of various teleost fishes. *J Zool (Lond)* 162:142–56.
- Alfaro M, Janovetz J, Westneat M. 2001. Motor control across trophic strategies: muscle activity of biting and suction feeding fishes. *Integr Comp Biol* 41:1266–79.
- Anderson P. 1974. Using linkage models to explore skull kinematic diversity and functional convergence in arthrodire placoderms. *J Morphol* 271:990–1005.
- Anderson P, Westneat M. 2007. Feeding mechanics and bite force modelling of the skull of *Dunkleosteus terrelli*, an ancient apex predator. *Biol Lett* 3:77–80.
- Anker GC. 1974. Morphology and kinetics of the head of the stickleback, *Gasterosteus aculeatus*. *Tran Zool Soc (Lond)* 32:311–416.
- Bird NC, Hernandez LP. 2007. Morphological variation in the Weberian apparatus of Cypriniformes. *J Morphol* 268:739–57.
- Brainerd EL, Baier DB, Gatesy SM, Hedrick TL, Metzger KA, Gilbert SL, Crisco JJ. 2010. X-ray reconstruction of moving morphology (XROMM): precision, accuracy and applications in comparative biomechanics research. *J Exp Zool* 313A:262–79.
- Brazeau MD, Friedman M. 2015. The origin and early phylogenetic history of jawed vertebrates. *Nature* 520:490–7.
- Camp AL, Brainerd EL. 2014. Role of axial muscles in powering mouth expansion during suction feeding in largemouth bass (*Micropterus salmoides*). *J Exp Biol* 217:1333–45.
- Camp AL, Roberts TJ, Brainerd EL. 2015. Swimming muscles power suction feeding in largemouth bass. *Proc Natl Acad Sci U S A* 112:8690–5.
- Camp AL, Roberts TJ, Brainerd EL. 2018. Bluegill sunfish use high power outputs from axial muscles to generate powerful suction-feeding strikes. *J Exp Biol* 221:jeb178160 (doi:10.1242/jeb.178160).
- Camp AL, Scott B, Brainerd EL, Wilga CD. 2017. Dual function of the pectoral girdle for feeding and locomotion in white-spotted bamboo sharks. *Proc Biol Sci* 284:pii:20170847 (doi:10.1098/rspb.2017.0847).
- Carroll AM, Wainwright PC, Huskey SH, Collar DC, Turingan RG. 2004. Morphology predicts suction feeding performance in centrarchid fishes. *J Exp Biol* 207:3873–81.
- Claeson KM. 2011. The synarcual cartilage of batoids with emphasis on the synarcual of Rajidae. *J Morphol* 272:1444–63.
- Claeson KM, Hilger A. 2011. Morphology of the anterior vertebral region in elasmobranchs: special focus, Squatiniformes. *Fossil Record* 14:129–40.
- Cleuren J, de Vree F. 1992. Kinematics of the jaw and hyolingual apparatus during feeding in *Caiman crocodilus*. *J Morphol* 212:141–54.
- Da Silva JPCB, De Carvalho MR. 2015. Morphology and phylogenetic significance of the pectoral articular region in elasmobranchs (Chondrichthyes). *Zool J Linn Soc* 175:525–68.
- de Lussanet MH, Muller M. 2007. The smaller your mouth, the longer your snout: predicting the snout length of *Syngnathus acus*, *Centriscus scutatus* and other pipette feeders. *J R Soc Interface* 4:561–73.
- Dean MN, Motta PJ. 2004. Feeding behavior and kinematics of the lesser electric ray, *Narcine brasiliensis* (Elasmobranchii: Batoidea). *Zoology* 107:171–89.
- Diogo R, Abdala V, Lonergan N, Wood BA. 2008. From fish to modern humans—comparative anatomy, homologies and evolution of the head and neck musculature. *J Anat* 213:391–424.
- Elshoud-Oldenhave MJW. 1979. Prey capture in the Pike-Perch, *Stizostedion lucioperca* (Teleostei, Percidae) structural and functional analysis. *Zoomorphologie* 93:1–32.
- Evans FG. 1939. The morphology and functional evolution of the atlas-axis complex from fish to mammals. *Ann N Y Acad Sci* 39:29–104.
- Ferry-Graham L, Lauder G. 2001. Aquatic prey capture in ray-finned fishes: a century of progress and new directions. *J Morphol* 248:99–119.
- Forey P, Janvier P. 1993. Agnathans and the origin of jawed vertebrates. *Nature* 361:129–34.
- Fouts WR, Nelson DR. 1999. Prey capture by the Pacific angel shark, *Squatina californica*: visually mediated strikes and ambush-site characteristics. *Copeia* 1999:304–12.
- Gosline J. 1977. The structure and function of the dermal pectoral girdle in bony fishes with particular reference to ostariophysines. *J Zool (Lond)* 183:328–38.
- Gregory WK. 1933. *Fish skulls: a study of the evolution of natural mechanisms*. New York (NY): Noble Offset Printers.
- Gussekkloo SW, Bout RG. 2005. The kinematics of feeding and drinking in palaeognathous birds in relation to cranial morphology. *J Exp Biol* 208:3395–407.
- Heiss E, Aerts P, Van Wassenbergh S. 2018. Aquatic-terrestrial transitions of feeding systems in vertebrates: a mechanical perspective. *J Exp Biol* 221:pii: jeb154427 (doi:10.1242/jeb.154427).
- Herrel A, Vree FD. 1999. Kinematics of intraoral transport and swallowing in the herbivorous lizard *Uromastix acaanthinurus*. *J Exp Biol* 202:1127–37.
- Herrel A, Cleuren J, De Vree F. 1995. Prey capture in the lizard *Agama stellio*. *J Morphol* 224:313–29.

- Huet L, Goosse V, Parmentier E, Vandewalle P. 1999. About some skeletal particularities of the first vertebrae relate Trin to the mode of prey capture in *Uranoscopus scaber* (Uranoscopidae). *Cybiurn* 23:161–7.
- Jenkins FA. 1974. The movement of the shoulder in clavicate and a clavicate mammals. *J Morphol* 144:71–83.
- Jimenez YE, Camp AL, Grindall JD, Brainerd EL. 2018. Axial morphology and 3D neurocranial kinematics in suction-feeding fishes. *Biol Open* 7:pii: bio036335 (doi: 10.1242/bio.036335).
- Johanson Z, Sutija M, Joss J. 2005. Regionalization of axial skeleton in the lungfish *Neoceratodus forsteri* (Dipnoi). *J Exp Zool B Mol Dev Evol* 304:229–37.
- Johanson Z, Boisvert C, Maksimenko A, Currie P, Trinajstic K. 2015. Development of the synarcual in the elephant sharks (Holocephali; Chondrichthyes): implications for vertebral formation and fusion. *PLoS ONE* 10:e0135138.
- Kusakabe R, Kuraku S, Kuratani S. 2011. Expression and interaction of muscle-related genes in the lamprey imply the evolutionary scenario for vertebrate skeletal muscle, in association with the acquisition of the neck and fins. *Dev Biol* 350:217–27.
- Lauder G, Lanyon L. 1980. Functional anatomy of feeding in the bluegill sunfish, *Lepomis macrochirus*: in vivo measurement of bone strain. *J Exp Biol* 84:33–55.
- Lauder G, Norton SF. 1980. Asymmetrical muscle activity during feeding in the gar, *Lepisosteus oculatus*. *J Exp Biol* 84:17–32.
- Lauder G, Liem KF. 1981. Prey capture by *Luciocephalus pulcher*: implications for models of jaw protrusion in teleost fishes. *Environ Biol Fishes* 6:257–68.
- Lauder GV. 1985. Aquatic feeding in lower vertebrates. In: Hildebrand M, editor. *Functional vertebrate morphology*. Cambridge, MA: Harvard University Press. p. 185–229.
- Lauder GV, Shaffer HB. 1985. Functional morphology of the feeding mechanism in aquatic ambystomatid salamanders. *J Morphol* 185:297–326.
- Lauder GV, Prendergast T. 1992. Kinematics of aquatic prey capture in the snapping turtle *Chelydra serpentina*. *J Exp Biol* 164:55–78.
- Lauder GV. 1981. Intraspecific functional repertoires in the feeding mechanism of the characoid fishes *Lebiasina*, *Hoplias* and *Chalceus*. *Copeia* 1981:154–68.
- Lesiuk T, Lindsey C. 1978. Morphological peculiarities in neck-bending Amazonian characoid fish *Rhaphiodon vulpinus*. *Can J Zool* 56:991–7.
- Liem KF. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am Zool* 20:295–314.
- Menegaz RA, Baier DB, Metzger KA, Herring SW, Brainerd EL. 2015. XROMM analysis of tooth occlusion and temporomandibular joint kinematics during feeding in juvenile miniature pigs. *J Exp Biol* 218:2573–84.
- Morin-Kensicki EM, Melancon E, Eisen JS. 2002. Segmental relationship between somites and vertebral column in zebrafish. *Development* 129:3851–60.
- Motta PJ, Wilga CD. 2001. Advances in the study of feeding behaviors, mechanisms, and mechanics of sharks. *Environ Biol Fishes* 60:131–56.
- Muller M. 1987. Optimization principles applied to the mechanism of neurocranium levation and mouth bottom depression in bony fishes (Halecostomi). *J Theor Biol* 126:343–68.
- Neenan JM, Ruta M, Clack JA, Rayfield EJ. 2014. Feeding biomechanics in *Acanthostega* and across the fish–tetrapod transition. *Proc Biol Sci* 281:20132689.
- Nowroozi BN, Harper CJ, De Kegel B, Adriaens D, Brainerd EL. 2012. Regional variation in morphology of vertebral centra and intervertebral joints in striped bass, *Morone saxatilis*. *J Morphol* 273:441–52.
- Pierce SE, Hutchinson JR, Clack JA. 2013. Historical perspectives on the evolution of tetrapodomorph movement. *Integr Comp Biol* 53:209–23.
- Ramsay JB. 2012. A comparative investigation of cranial morphology, mechanics, and muscle function in suction and bite feeding sharks [dissertation]. Biological Sciences, Doctor of Philosophy. University of Rhode Island.
- Rockwell H, Evans FG, Pheasant HC. 1938. The comparative morphology of the vertebrate spinal column. Its form as related to function. *J Morphol* 63:87–117.
- Roos G, Van Wassenbergh S, Herrel A, Adriaens D, Aerts P. 2010. Snout allometry in seahorses: insights on optimisation of pivot feeding performance during ontogeny. *J Exp Biol* 213:2184–93.
- Schaeffer B, Rosen D. 1961. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. *Am Zool* 1:187–204.
- Schnell NK, Bernstein P, Maier W. 2008. The “pseudo-craniovertebral articulation” in the deep-sea fish *Stomias boa* (Teleostei: Stomiidae). *J Morphol* 269:513–21.
- Shubin N, Daeschler EB, Jenkins FA. 2015. Origin of the tetrapod neck and shoulder. In: Dial KP, editor. *Great transformations in vertebrate evolution*. Chicago: The University of Chicago Press. p. 63–76.
- Shubin NH, Daeschler EB, Jenkins FA. 2006. The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb. *Nature* 440:764–71.
- Snively E, Russell AP, Powell GL, Theodor JM, Ryan MJ. 2014. The role of the neck in the feeding behaviour of the Tyrannosauridae: inference based on kinematics and muscle function of extant avians. *J Zool* 292:290–303.
- Tchernavin VV. 1953. *The feeding mechanisms of a deep sea fish Chauliodus sloani* Schneider. London: British Museum.
- Thys T. 1997. Spatial variation in epaxial muscle activity during prey strike in largemouth bass (*Micropterus salmoides*). *J Exp Biol* 200:3021.
- Trinajstic K, Marshall C, Long J, Bifield K. 2007. Exceptional preservation of nerve and muscle tissues in Late Devonian placoderm fish and their evolutionary implications. *Biol Lett* 3:197–200.
- Trinajstic K, Sanchez S, Dupret V, Tafforeau P, Long J, Young G, Senden T, Boisvert C, Power N, Ahlberg PE. 2013. Fossil musculature of the most primitive jawed vertebrates. *Science* 341:160–4.
- Tsuihiji T, Kearney M, Rieppel O. 2012. Finding the neck–trunk boundary in snakes: anteroposterior dissociation of myological characteristics in snakes and its implications for their neck and trunk body regionalization. *J Morphol* 273:992–1009.
- Van Damme J, Aerts P. 1997. Kinematics and functional morphology of aquatic feeding in Australian snake-necked turtles (Pleurodira; Chelodina). *J Morphol* 233:113–25.

- Van Valkenburgh V. 1996. Feeding behavior in free-ranging large African carnivores. *J Mammal* 70:240–54.
- Van Wassenbergh SV, Herrel A, Adriaens D, Aerts P. 2006. Modulation and variability of prey capture kinematics in clariid catfishes. *J Exp Zool A* 305:559–69.
- Van Wassenbergh S, Herrel A, Adriaens D, Aerts P. 2007. No trade-off between biting and suction feeding performance in clariid catfishes. *J Exp Biol* 210:27–36.
- Van Wassenbergh S, Herrel A, Adriaens D, Aerts P. 2007. Interspecific variation in sternohyoideus muscle morphology in clariid catfishes: functional implications for suction feeding. *J Morphol* 268:232–42.
- Van Wassenbergh S, Lieben T, Herrel A, Huysentruyt F, Geerinckx T, Adriaens D, Aerts P. 2009. Kinematics of benthic suction feeding in Callichthyidae and Mochokidae, with functional implications for the evolution of food scraping in catfishes. *J Exp Biol* 212:116–25.
- Wainwright PC, Sanford CP, Reilly SM, Lauder GV. 1989. Evolution of motor patterns: aquatic feeding in salamanders and ray-finned fishes. *Brain Behav Evol* 34:329–41.
- Westneat MW. 2006. Skull biomechanics and suction feeding in fishes. In: Shadwick RE, Lauder G, editors. *Fish physiology*. San Diego (CA): Academic Press. p. 29–75.
- Wilga CD, Sanford CP. 2008. Suction generation in white-spotted bamboo sharks *Chiloscyllium plagiosum*. *J Exp Biol* 211:3128–38.
- Wilga CD, Motta PJ, Sanford CP. 2007. Evolution and ecology of feeding in elasmobranchs. *Integr Comp Biol* 47:55–60.
- Wu E. 1994. Kinematic analysis of jaw protrusion in orectolobiform sharks: a new mechanism for jaw protrusion in elasmobranchs. *J Morphol* 222:175–90.