# SYMPOSIUM

# Origins, Innovations, and Diversification of Suction Feeding in Vertebrates

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**Synopsis** We review the origins, prominent innovations, and major patterns of diversification in suction feeding by vertebrates. Non-vertebrate chordates and larval lamprey suspension-feed by capturing small particles in pharyngeal mucous. In most of these lineages the gentle flows that transport particles are generated by buccal cilia, although larval lamprey and thaliacean urochordates have independently evolved a weak buccal pump to generate an oscillating flow of water that is powered by elastic recovery of the pharynx following compression by buccal muscles. The evolution of jaws and the hyoid facilitated powerful buccal expansion and high-performance suction feeding as found today throughout aquatic vertebrates. We highlight three major innovations in suction feeding. Most vertebrate suction feeders have mechanisms that occlude the corners of the open mouth during feeding. This produces a planar opening that is often nearly circular in shape. Both features contribute to efficient flow of water into the mouth and help direct the flow to the area directly in front of the mouth's aperture. Among several functions that have been identified for protrusion of the upper jaw, is an increase in the hydrodynamic forces that suction feeders exert on their prey. Protrusion of the upper jaw has evolved five times in ray-finned fishes, including in two of the most successful teleost radiations, cypriniforms and acanthomorphs, and is found in about 60% of living teleost species. Diversification of the mechanisms of suction feeding and of feeding behavior reveals that suction feeders with high capacity for suction rarely approach their prey rapidly, while slender-bodied predators with low capacity for suction show the full range of attack speeds. We hypothesize that a dominant axis of diversification among suction feeders involves a trade-off between the forces that are exerted on prey and the volume of water that is ingested.

## Introduction

Suction feeding, the ability to generate a strong pressure gradient inside the oral cavity that draws water and prey into the mouth, is nearly ubiquitous in aquatic-feeding vertebrates but is known in only a few non-vertebrate animals. This dominance within aquatic vertebrates reflects both effectiveness and constraints as even the aquatic lineages that have abandoned capturing prey by suction feeding retain the mechanism and use it at some stage in the feeding process, during the processing and manipulation of prey, if not during capture. The stark contrast between the extensive use of suction feeding by vertebrates and its near absence outside vertebrates calls for explanation. Why is suction feeding so entrenched within vertebrates but rare outside the group? Also, once suction feeding evolved in vertebrates what were the key subsequent innovations that have helped it to flourish? Finally, given that a large fraction of the roughly 32,000 aquatically feeding vertebrates are suction feeders, how has the mechanism diversified to support such extreme species richness? In the sections below we address these issues in a review of the origins, innovations, and diversification of suction feeding. While the first topic is approached from a broad phylogenetic perspective across vertebrates, the second and third sections emphasize the literature on ray-finned fishes (Actinopterygii) with a few insights from other fishes and tetrapods.

# The origins of suction feeding by vertebrates

Some insight into the origins of suction feeding in vertebrates can be gained from considering the feeding mechanisms in the lineages of living animals most closely related to the suction-feeding vertebrates. It appears that suction feeding evolved before the last common ancestor of living gnathostomes (Fig. 1), suggesting that living jawless vertebrates (lamprey and hagfish) and non-vertebrate chordates (Urochordata and Cephalochordata) may provide useful comparisons. Cephalochordates and most urochordates have pharyngeal slits and suspension-feed on tiny, water-born particles such as bacteria and phytoplankton. Particles are trapped in mucous in the pharynx after being transported through an entry siphon or mouth by a steady flow of water generated by the actions of many cilia inside the branchial chamber. The water passes through the pharyngeal slits into postbranchial chambers of some sort and ultimately exits the body through separate openings (cephalochordates) or a common excurrent siphon (urochordates).

In contrast to the steady flow of water generated by cephalochordates and most urochordates, thaliacean urochordates (salps) and larval lamprey apparently have independently evolved a pump-based
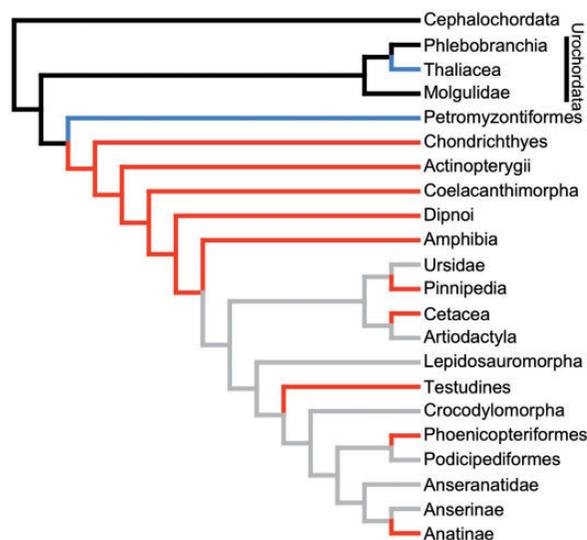


Fig. 1 Diagram of the phylogenetic distribution across chordates of high-powered suction feeding (red), no suction feeding (gray), oscillating pump-based suspension feeding (blue), and cilia-based steady-flow suspension feeding (black). Note that high powered suction feeding is only found in gnathostomes and was lost with full terrestriality in tetrapods but independently gained in most lineages of secondarily aquatic-feeding tetrapods. Traits are informally mapped on the phylogeny (note that many vertebrate lineages are not shown).

system that generates a pulsatile flow of water into the pharynx. In the salps' system, contraction of the entire body with the oral siphon closed is used to jet water from the excurrent siphon (Madin 1990; Sutherland and Madin 2010). This jet is used for propulsion and feeding flows are generated as the body and pharynx elastically recover their shape due to stiffness in connective tissue in the body wall, while the atrial siphon is closed and the oral siphon opened (Sutherland and Madin 2010). These flows transport small particles into the pharynx where they are trapped in a sheet of mucous and eaten. Salps produce a stronger pressure gradient across the filtering structures than do taxa that generate the flows with cilia (Madin 1990). Larval lamprey also pump to produce feeding flows and may produce more forceful suction powered by elastic recoil of their cartilaginous branchial skeleton following compression by cranial muscles (Mallatt 1981), in a fashion reminiscent of the pumping mechanism in salps. Thus, while gentle flows based on beating cilia drive flows in cephalochordates and most urochordates, a transition to a pump-based mechanism is seen in salps within the urochordates and is apparently independently evolved in gnathostomes. Among urochordates, a third mechanism of generating the flow of water is seen in appendicularians that beat a large tail to drive the movement of water (Bochdansky and Deibel 1999).

There are many extinct lineages of jawless vertebrates and it has proven a challenge to deduce feeding mechanisms in these lineages, including conodonts and the many radiations referred to collectively as ostracoderms. Weak suction was likely widespread in jawless fishes such as heterostracans and other ostracoderms (Purnell 2001). However, the origin of jaws, the hyoid arch, and the other visceral arches, and their subsequent stiffening via mineralization, was a key event that set the stage for a greatly enhanced mechanism of suction feeding. Anatomical enhancement of the suction-feeding mechanism and the capacity to generate strong suction pressures evolved in parallel in several lineages of gnathostomes, including multiple lineages of chondrichthyans (Motta and Wilga 2001), actinopterygians (Lauder 1985), basal sarcopterygians (Bemis 1986, Bemis and Lauder 1986; Dutel et al. 2013), and several groups of secondarily aquatic tetrapods. The origin of opposable jaws with muscular control probably immediately provided an enhanced ability to feed by suction. The ability to forcefully open and close the jaws alone ensures that suction will be involved at least minimally when feeding aquatically because opening stiff jaws generates some flow of

water into the mouth (Heiss et al. 2013). However, all major radiations of vertebrate suction feeders primarily depend on movement of the hyoid bar of the second visceral arch to expand the buccal cavity, independently of the opening and closing jaws, thereby permitting a level of independence of the expansion of buccal volume and the opening of the mouth that is one key to high-performance suction feeding.

Interestingly, there is very little evidence of a major reliance on suction feeding among the first successful radiations of gnathostomes. This is especially surprising for placoderms, given the extent of their radiation, their apparent ecological diversity, and the long period of time over which they were successful aquatic predators (Long 1995; Anderson 2009). Placoderms' hyoid bars appear to have been present but not ossified and while placoderms' jaws were extremely diverse (Anderson et al. 2011) they do not appear to have become specialized for suction feeding. The earliest elaboration of suction feeding within extant vertebrates may have occurred within Chondrichthyes. Although capture of prey by most living sharks and extinct lineages is dominated by raptorial biting and ram, several modern lineages have evolved high-performance suction feeding and a number of associated morphological modifications (Motta et al. 2002; Dean and Motta 2004; Wilga et al. 2007). These modifications include more pronounced labial cartilages that allow control of the shape of the mouth's aperture, hypertrophied coracohyoideus, and coracobranchial muscles that expand the buccal cavity ventrally, reduced dentition, and a relatively small mouth (Motta and Wilga 1999; Motta et al. 2002, 2008).

Members both of extinct and living Dipnoi and Coelacanthimorpha are thought to employ suction feeding. Empirical data show that Dipnoi are capable of generating relatively large forces through rapid depression of an enlarged and mineralized hyoid apparatus (Bemis and Lauder 1986). Experimental data have not been collected for coelacanths and their capacity for suction feeding is a subject of debate (Lauder 1980; Dutel et al. 2013). The presence of a pseudomaxillary fold in *Latimeria* is thought to occlude the mouth laterally during influx of water (Yabumoto et al. 2012), but recent inspection of a preserved specimen suggests that the hyoid apparatus has limited mobility (Dutel et al. 2013). Direct observations of *Latimeria* are badly needed to determine its mechanism of capturing prey.

The most extensive radiation of suction feeding within aquatic vertebrates is seen within Actinopterygii, the ray-finned fishes. Actinopterygian suction feeding is characterized by a rapid wave of expansion that starts with opening of the mouth followed by nearly concomitant depression of the hyoid and a lateral expansion of the suspensorium, ending with water flowing out the opercular openings (van Leeuwen 1984; Lauder 1985). Within ray-finned fishes, morphological features such as shape of the mouth interact with the physical characteristics of the flow (e.g., volume, velocity, and acceleration of flow) to affect suction feeding (Wainwright and Day 2007; Holzman et al. 2008a). Actinopterygians that are powerful suction feeders are characterized by high cross-sectional area of the muscles that power suction feeding (either epaxial muscles or ventral hypaxial musculature, or both), high mechanical advantage in linkage systems that transmit muscular contractions into an expanding buccal cavity, and relatively small buccal cavities over which the expansive force is distributed (Wainwright et al. 2007).

Among tetrapods, aquatic amphibians also generally use suction feeding. The ancient radiation of temnospondyl amphibians included several lineages, including *Plagiosuchus* and *Gerrothorax*, with skeletal features indicative of suction feeding (Damini et al. 2009; Witzmann and Schoch 2013). In the living groups it is unclear in most cases whether their suction-feeding abilities are secondarily derived or represent retention of traits from more aquatic ancestors. In modern amphibians, suction feeding is seen in most aquatic larvae that have been studied. For instance, the pipid larva *Hymenochirus* uses hyoid depression to drive water into the mouth (Deban and Olson 2002). Aquatic salamanders (Miller and Larsen 1989) and some larval caecilians (O'Reilly 2000; Kleinteich 2010) are also known to use suction feeding. In those species in which the hyoid drives movement of the water, the hyobranchial apparatus is well mineralized.

While most amphibians are generally assumed to power suction by forceful depression of the hyobranchial apparatus, some aquatic amphibians emphasize the use of the jaws to generate suction. An example is seen in the Chinese giant salamander, *Andrias davidianus* (Heiss et al. 2013). High-speed video combined with computational modeling of fluid flow clearly showed that hyoid depression significantly lagged behind concomitant rotation of the skull dorsally and lower jaw ventrally. Such a decoupled system may have allowed the evolution of terrestrial feeding modes without compromising the capacity for suction feeding (Heiss et al. 2013).

Because amniotes have lost the openings to the gill slits, their secondary invasion into aquatic environments and utilization of suction poses a significant hydrodynamic challenge. In unidirectional suction

feeding (as seen in fishes and most aquatic amphibians), water enters through the mouth and exits via gill slits or the opercular opening. Advantages of this unidirectional flow are obvious, as estimates suggest that largemouth bass, *Micropterus salmoides*, capture 2.5 times the volume of their oral and buccal cavities during a strike (Higham et al. 2006). In groups without the opercular opening, water must both enter and exit via the mouth, creating novel challenges (Reilly and Lauder 1992), such as the capacity to temporarily hold an extremely large volume of water in their buccal region.

Most aquatic lineages of tetrapods have secondarily evolved suction feeding as their dominant mode of capturing prey. Turtles show considerable diversity in their use of aquatic habitats and their ability to obtain food via suction. Turtles that are largely terrestrial are able to modulate the kinematics of hyoid-depression depending on whether they are feeding in air or in water (Summers et al. 1998). The morphological constraints associated with bidirectional feeding also manifest themselves in the need for compensatory suction during ram feeding in cryptodiran turtles (Summers et al. 1998); this type of suction keeps the prey from being pushed or alerted by a bow wave as the mouth is moved closer to the prey. Within fully aquatic turtles, the challenges of bidirectional feeding are met by a large and heavily ossified hyoid apparatus with a greatly reduced muscular tongue, coupled with a highly extensible neck and expanding pharynx (Bramble and Wake 1985; Lemell et al. 2002).

Within marine mammals at least four odontocete families exhibit suction feeding (Werth 2000a) (Ziphiidae [beaked whales]-Heyning and Mead 1996; Delphinidae [pilot whales]-Kane and Marshall 2009; Kogiidae [pygmy and dwarf sperm whales]-Bloodworth and Marshall 2007; Monodontidae [belugas and narwhals]-Kane and Marshall 2009). A fifth family, the monotypic Eschrichtiidae, which includes the gray whale, *Eschrichtius robustus*, exhibits an unusual form of lateral suction feeding, often used to feed in the benthos (Nerini 1984). However, in a phylogenetic treatment using data from both fossil and extant taxa Johnston and Berra (2011) argued that suction feeding evolved only once early in the evolutionary history of Cetacea. While all use a similar tongue-powered mechanism to expand the buccal cavity and draw in water, there is variation in the shape both of the skull and the jaw among groups. Suction-feeding odontocetes exhibit shortened jaws (Bloodworth and Marshall 2007). Bloodworth and Marshall (2007) mentioned a novel fibrous ridge of tissue

found in pygmy whales that are assumed to be involved in lateral occlusion of the mouth's opening. Within pilot whales, facial muscles help form and modulate a more circular mouth by occluding lateral gape (Werth 2000b). Finally, unusually large oral cavities and throats accommodate the expansion of volume required in these bidirectional suction feeders. An increased palatal vault into which the tongue can be displaced significantly increases intraoral volume and concomitant change in volume (Bloodworth and Marshall 2007). Pleating of the throat also serves to increase distention of the throat during suction feeding (Heyning and Mead 1996; Bloodworth and Marshall 2007), a feature that is most developed in the non-suction feeding rorqual whales (Goldbogen et al. 2013). In a large multivariate analysis, gular grooves along with foreshortened mandibles have been correlated with increased suction feeding within Cetacea (Johnston and Berta 2011).

Among pinnipeds, leopard seals, bearded seals, and walruses exhibit shortened jaws, more mineralized hyoids, and considerable capacity for suction feeding (Kastelein and Gerrits 1990; Kastelein et al. 1991, 1997; Marshall et al. 2008; Hocking et al. 2013). As in cetaceans, pinnipeds' suction feeding is powered primarily by rapid hyolingual depression (Marshall et al. 2008). Walruses can generate sufficient suction pressure to pull molluscs from their shells, a feat helped by the relatively large buccal chamber of the walrus, which allows for a large change in volume during retraction of the tongue (Kastelein and Gerrits 1990). As in other pinnipeds the flexible lips allow the walrus to carefully hold the shell while forming a restricted aperture that enhances flow during buccal expansion (Kastelein et al. 1991, 1997). Bearded and leopard seals both purse their rostral and lateral lips to create a small circular opening of the mouth during suction (Marshall et al. 2008; Jones et al. 2013). Structural modifications for improved generation of suction may negatively affect raptorial biting performance in those pinnipeds adapted to a suction-feeding lifestyle (Hocking et al. 2013).

Avian suction feeders are suspension feeders that separate small prey that are drawn into the mouth through suction, performing both functions with the bill and the tongue (Jenkin 1957; Zweers et al. 1995). There have been at least two separate origins of suction feeding within Aves, within Phoenicopteriformes (flamingoes) and Anatidae (ducks and geese) (Fig. 1). As with cetaceans and pinnipeds a large tongue is used as a lingual piston pump in birds to draw water into the anterior end of the beak and

then the tongue is used to force water laterally out of the buccal cavity past filtering lamellae (Mascitti and Kravetz 2002). Flexible skin at the base of the throat allows for retraction of the enlarged and relatively stiff tongue (Zweers et al. 1995). As seen in suction-feeding mammals, an enlarged hyoid apparatus and increased buccal cavity characterize many ducks (Rylander and Bolen 1974).

No modern crocodylomorphs are known to use suction as a primary means of capturing prey, but several extinct lineages possessed features indicative of suction feeding. The sea-going metriorhynchid crocodile *Dakosaurus*, thought to be analogous to modern killer whales (Young et al. 2012), evolved a series of traits associated with suction feeding in odontocetes (Werth 2006). Another crocodylomorph lineage, the stomatosuchids, possessed several features, including unusually large jaw-opening musculature and reduced dentition, which suggest a suction-feeding lifestyle (Holiday and Gardner 2012).

## Innovations in suction feeding

There are a number of major innovations in suction feeding that have been identified over the years. In some of these, such as the protrusion of the upper jaw, we have a strong idea of the phylogenetic history of the trait, but in other cases, such as the shape of the mouth's aperture during suction feeding, there are relatively few quantitative comparative data, and therefore there are opportunities for future studies to help us understand better the evolutionary history of some features that are known to have a major impact on the performance of suction feeding.

### Planar and circular aperture of the mouth

It has long been recognized that many fishes are able to form an almost planar and circular aperture of the mouth during suction feeding. An early experiment in which the aperture of a hose draining a bucket was made planar or bilaterally notched, found that the planar opening drained the bucket more rapidly (Lauder 1979). More recently, using computational modeling of fluid dynamics, the impact of a circular mouth on flows during suction feeding was found to enhance the net rate of flow relative to an elliptical opening; also, a planar opening produced a much different, and more efficient, flow from a bilaterally notched aperture (Skorczewski et al. 2012). While a circular, planar aperture resulted in a symmetrical flow field focused anteriorly with peak flow occurring in the center of the aperture, the circular, bilaterally notched shape

produced a more diffuse flow field and two foci of peak flow occurred dorsally and ventrally in the aperture of the mouth (Skorczewski et al. 2012). Such a marked departure from the single, large focus of flow in the center of the mouth, confirms that the mouth's shape has a major impact on the effectiveness of suction flows, and supports the notion that the many specializations seen in chondrichthyans, actinopterygians, and tetrapods for producing a planar, circular opening to the mouth are adaptations that generate efficient suction-flow fields that are maximally effective.

### Protrusion of the upper jaw

Protrusion of the upper jaw is variable in extent but found in many chondrichthyans and actinopterygians (Motta 1984). It occurs in most elasmobranchs and is quite extensive in some batoids (Motta and Wilga 2001). Within actinopterygians, it has evolved five times (Fig. 2). Two origins of jaw protrusion are associated with very large, successful radiations: Acanthomorpha and Cypriniformes (Fig. 2). Acanthomorphs comprise about 17,000 species and have invaded virtually all major aquatic habitats and feeding niches throughout the water column while many of the 3200 cypriniforms are benthic feeders. Three additional origins of jaw protrusion are seen in much less diverse groups: Acipenseriformes (Carroll and Wainwright 2003), the characiform genus *Bivibranchia* (Vari 1985; Vari and Goulding
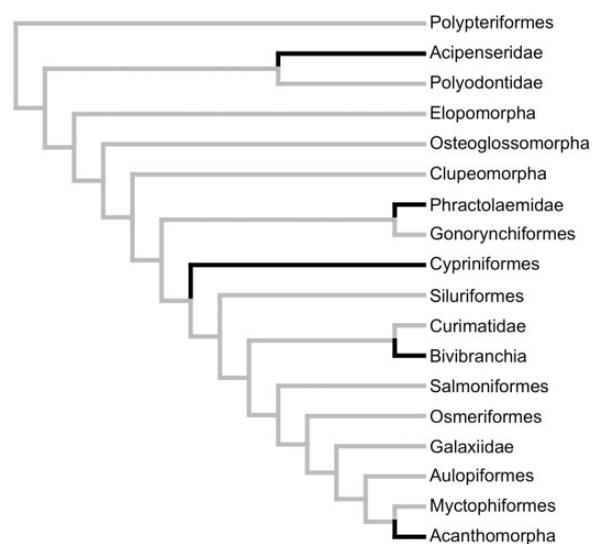
**Fig. 2** Diagram of the phylogenetic distribution of upper jaw protrusion in ray-finned fishes (Actinopterygii). Five independent origins of upper jaw protrusion are known in ray-finned fishes. Two of these five groups are extremely successful, diverse groups of fishes: Acanthomorpha (∼17,000 species) and Cypriniformes (∼3200 species). Phylogenetic topology is from Near et al. (2012).

1985), and the gonorynchiform *Phractolaemus ansorgei* (Grande and Poyato-Ariza 1999) (Fig. 2). Although the mechanism of protrusion is different in each case, all three groups are able to protrude the opened mouth toward the prey during feeding.

Protrusion of the jaw in sturgeon (Acipenseridae) results from rostromedial rotation of hyomandibulae that transfers force to the palatoquadrates, moving them forward (Carroll and Wainwright 2003), while in *Bivibranchia* spp. protrusion appears to result from a ligamentous connection of the upper jaw to the mesethmoid (Langeani 1998) as well as to a unique ectopterygoid-quadrate finger-and-ring joint (Roberts 1974) that together allow the upper jaw to protrude anteriorly.

Acanthomorphs and cypriniforms evolved divergent mechanisms of effecting premaxillary protrusion. In Acanthomorpha an elongated ascending process of the premaxilla bears a rostral cartilage and slides down a long groove within the rostrum during opening of the mouth (Motta 1984). As the lower jaw is depressed, ligaments that connect it to the distal regions of the maxilla cause the maxilla to swing anterolaterally occluding the lateral gape. Proximally, the head of the maxilla interacts with the ventral surface of the premaxilla in a diversity of ways that force the premaxilla into a protruded position. In cypriniforms, premaxillary protrusion is not directly caused by depression of the lower jaw, but is driven largely by the kinethmoid, a novel ossification within the rostral skeleton of these fishes. Located between the ascending processes of the premaxillae and the neurocranium, this bone also has ligamentous attachments to the palatines and maxillae. Tension produced either through opening of the mouth or by a ventral shift of the maxilla (Gidmark et al. 2012) produces a 90–180° rotation of the kinethmoid that pushes the premaxilla anteriorly. While high levels of jaw protrusion in acanthomorphs are typically associated with suction feeding on elusive prey (Hulsey et al. 2010), many cypriniforms that show extensive protrusion are benthic feeders, and rely on protrusion to help fluidize and stir detritus layers through which they sort (Gidmark et al. 2012). A conspicuous feature of cypriniform premaxillary protrusion is its extensive use during the processing of prey while the fish maintains a closed mouth (Staab et al. 2012).

Protrusion of the upper jaw is a key aspect of many biting mechanisms in fishes and plays important roles in suction feeding. Protrusion has been hypothesized to increase the speed at which the jaws can approach the prey (Motta 1984) and increase the hydrodynamic force exerted on the prey

by the suction flow (Holzman et al. 2008b). Data from both acanthomorphs and cypriniforms support the inference that premaxillary protrusion significantly improves suction feeding both by increasing the speed of attack (Oufiero et al. 2012) and by increasing hydrodynamic forces on the prey (Holzman et al. 2008b; Staab et al. 2012). Estimates of the magnitude of this effect indicate that protrusion of the jaw can increase the hydrodynamic forces experienced by prey by up to 40%, suggesting that it significantly enhances the capture of prey.

### Anterior-to-posterior wave of buccal expansion

The recent use of flow-visualization techniques to study suction feeding has allowed precise determination of the timing of skull kinematics with the time-course of suction flows. It has been shown both in bluegill (*Lepomis macrochirus*) and in largemouth bass (*M. salmoides*) that peak flow generated during suction feeding occurs very close to the time of peak gape (Day et al. 2005; Higham et al. 2006). This relationship has been shown to be more variable, but similar, in goldfish (*Carassius auratus*) (Staab et al. 2012) and is found in *Polypterus* sp. (R. S. Mehta and P. C. Wainwright, unpublished observations). The mechanism that allows peak flow to occur as peak gape is reached was considered in a modeling study (Bishop et al. 2008). Because the flow field developed by suction feeders is directly proportional to the size of the mouth's opening (Day et al. 2005), it would be advantageous for suction feeders to synchronize maximum flow speed with peak gape, but if the buccal cavity expands synchronously along its anterior-to-posterior axis, peak flow will always occur well before peak gape is reached (Bishop et al. 2008). The presence of an anterior-to-posterior wave of expansion is required to generate peak flow speed at the time that maximum gape is established (Bishop et al. 2008). Such a wave of expansion is thought to be a general feature of actinopterygian suction feeders, but considerable comparative data will be required to explore the phylogenetic distribution of this feature and any tradeoffs that may be present in taxa specialized in other behaviors. This observation underscores the importance of the hyoid arch in suction feeding. The hyoid arch is as integral to buccal expansion during suction feeding as is the role of stiff jaw-elements in maintaining an open aperture to the mouth.

### Diversification of suction feeding

Suction feeding is a unifying feature of aquatic vertebrates. Nearly every aquatic vertebrate uses suction

in capturing or processing prey. Any vertebrate that is a suction feeder faces a similar set of constraints and challenges when trying to capture prey, and while some features of suction feeders seem to be almost universal, such as the planar, circular aperture of the mouth, and an anterior-to-posterior wave of buccal expansion, there is nevertheless tremendous diversity in form of the mouth, shape of the body, and attack behavior. In addition to using suction to capture prey, many species also employ various forms of biting during feeding and trade-offs in the design of the jaws for biting and suction appear to be one major source of this morphological and kinematic variation.

Many fish have a distinct bilateral notch in the mouth's aperture, in spite of the negative consequences that this shape has for efficient suction (Skorczewski et al. 2012). A notched mouth is found in several fish and tetrapod species that employ high-speed, frontal attacks on large elusive prey and may be accompanied by sharp, raptorial, or cutting teeth. Examples include *Esox*, *Sphyraena*, *Hepsetus*, *Tylosurus*, *Gempylus*, some mackerel species, and many piscivorous snakes and birds. In these taxa, the notched mouth is thought to have a beneficial hydrodynamic consequence because during the frontal attack, water passes freely past the anterior end of the jaws and spills laterally, thereby allowing the animal to avoid producing a large bow wave such as would be expected with a planar opening to the mouth in the absence of strong suction (Herrel et al. 2008). In this case, what is good for ram-biting results in reduced performance in suction feeding and as a consequence these taxa place relatively little emphasis on the use of suction during capture of prey. It is worth noting, however, that all of these taxa continue to use some suction during capture of prey and particularly during processing it (e.g., Porter and Motta 2011).

While the evolution of various biting behaviors is expected to impact suction feeding, it is also apparent that there is considerable diversity in the morphology and behavior related to feeding in taxa that predominantly rely on suction feeding. What is the nature of this diversity and in what way does it reflect adaptation to different challenges? We focus here on two types of variation: variation in the morphological basis of the capacity to generate suction pressure and the behaviors used to approach prey, as well as the relationship between these variables.

An index of the capacity to generate suction pressure (Carroll et al. 2004) has shown that a common axis of variation in size of the body and mouth is also associated with variation in the ability to generate suction pressure. Centrarchid species with a more slender, elongate body and a large mouth have a low capacity to generate suction pressure, while deep-bodied species with a small mouth are predicted to generate the highest suction pressures (Carroll et al. 2004; Collar and Wainwright 2006). This axis of variation also has been described formally for damselfishes, Pomacentridae (Holzman et al. 2012b) and grunts, Haemulidae (Price et al. 2013), and is thought to apply broadly to suction-feeding taxa that are not specialized for biting (Holzman et al. 2012b). Species with a deep body and small mouth have relatively high cross-sectional area of the epaxial musculature that can generate a large expansive force distributed over a small buccal cavity, thus generating a strong pulse of suction pressure (Carroll et al. 2004; Collar and Wainwright 2006).

Species with a more slender body and a large mouth generate less force by the epaxial muscles, and this force is distributed over a larger buccal cavity during expansion, resulting in a lower pressure gradient. The trade-off is that slender-bodied, large-mouthed species ingest larger volumes of water and have a higher volumetric rate of ingestion (Higham et al. 2006). It is believed that the small-mouthed, deep-bodied morph is most effective in exerting high forces on small, clinging prey (Holzman et al. 2012a) while the slender-bodied, large-mouthed species often attack elusive prey at high speed. At least within centrarchids, this difference in speed of attack is also associated with differences in accuracy of the strike, as the small-mouthed taxa are more precise in positioning prey in the center of the suction-flow field, and the slender-bodied species are less accurate (Higham et al. 2006).

Consideration of how the predator closes the distance between itself and the prey during the strike led to the recognition of the importance of swimming toward the prey during suction feeding (Norton and Brainerd 1993; Wainwright et al. 2001). Movement of the mouth toward the prey can be accomplished by swimming or by protrusion of the jaw and hence the terms "body ram" and "jaw ram". Most suction feeders cover a much greater distance with body ram or jaw ram than they do by drawing the prey toward them by suction (Wainwright et al. 2001). This reflects an important constraint on suction feeding—that the flows generated during suction feeding are near-field (Day et al. 2005). In fact, the maximum distance from which a suction feeder can be expected to draw prey into its mouth is about 1 mouth-diameter (Wainwright et al. 2001; Day et al. 2005; Holzman et al. 2012a). Since
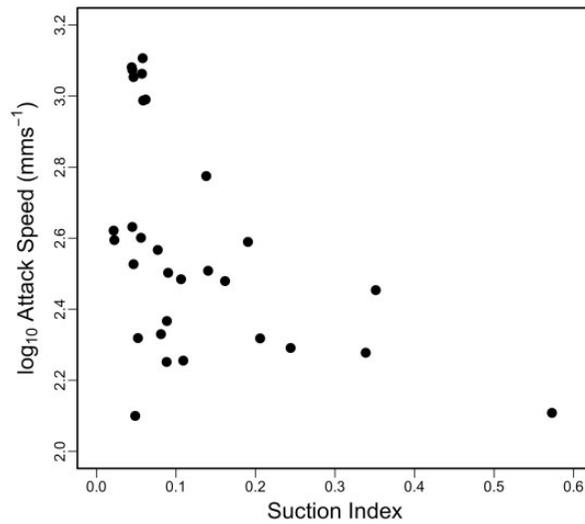
**Fig. 3** The relationship between the capacity to generate suction pressure and to press home rapid attacks in 30 species of serranid fishes suggests that the capacity for suction feeding constrains attack behavior. Each point represents averages for a single species. Speed of attack was measured from video recordings of sequences of attacks by fishes feeding on small fish as prey. Fish with the highest capacity to generate suction show the least diversity in speed of attack, being confined to low speeds, while species with weak potential for suction show the full range of attack speeds. Data are from Oufiero et al. (2012).
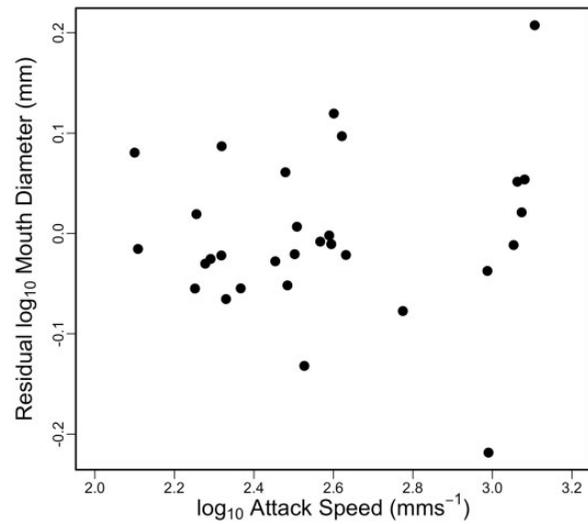


**Fig. 4** The relationship between speed of attack and diameter of the mouth (corrected for body size) in 30 species of serranid fishes during filmed sequences of prey-capture. Each point in the graph represents the average value for a single species. Although morphological construction for generating suction pressure shows a strong relationship with speed of attack, the diameter of the mouth does not. Data were taken from Oufiero et al. (2012).

many suction feeders cover far more than 1 mouth-diameter during the strike it becomes clear that suction is frequently a minor contributor to closing the distance between predator and prey.

Relatively few large comparative datasets of strike kinematics and morphology have been analyzed in the literature (Carroll et al. 2004; Gibb and Ferry-Graham 2005; Holzman et al. 2012b; Oufiero et al. 2012). Within suction-feeding lineages that do not use biting behaviors as a major mechanism of apprehending prey, a very common morphological axis of diversity is the previously mentioned contrast between deep-bodied species with small mouths and more slender, elongate species with larger mouths (Collar and Wainwright 2006; Claverie and Wainwright 2014). Indeed, a survey of diversity in body shape in 56 families of tropical reef fishes showed that the primary axis of variation in two-thirds of the families studied was along this axis from deep-bodied, to slender-bodied (Claverie and Wainwright 2014). In serranid fishes, this axis of morphological variation is associated with a major shift in the diversity of attack strategies (Oufiero et al. 2012). Deep-bodied serranids (high suction index) only attack at low speeds of swimming speeds (Fig. 3) while slender-bodied species with larger mouths (low suction index) exhibit the full

range of attack speeds, some rushing in at the prey during the strike and others creeping up to the prey before using an explosive strike (Fig. 3). It appears that high-speed attacks may be ineffective for deep-bodied serranid suction feeders with a high capacity to generate suction, limiting these taxa to slower attacks that cover less distance. It is tempting to imagine that this is because a deep body is correlated with a smaller mouth, but in fact this is not the case; among these serranids there is no relationship between speed of attack and relative size of the mouth (Fig. 4).

The magnitude of jaw protrusion varies considerably among serranid species and is weakly, but significantly, positively associated with attack speed but not with the capacity to generate suction (Fig. 5). Thus, jaw protrusion in serranids appears to evolve independently of attack strategy, and the capacity for suction, is used to augment the final approach to the prey both in slow-attacking and fast-attacking species.

## Conclusions

The dominance of suction feeding among aquatic vertebrates stands in stark contrast to the rarity of this mechanism of capturing prey across the rest of Metazoa. This dominance appears to relate to the capacity among vertebrates for powerful suction
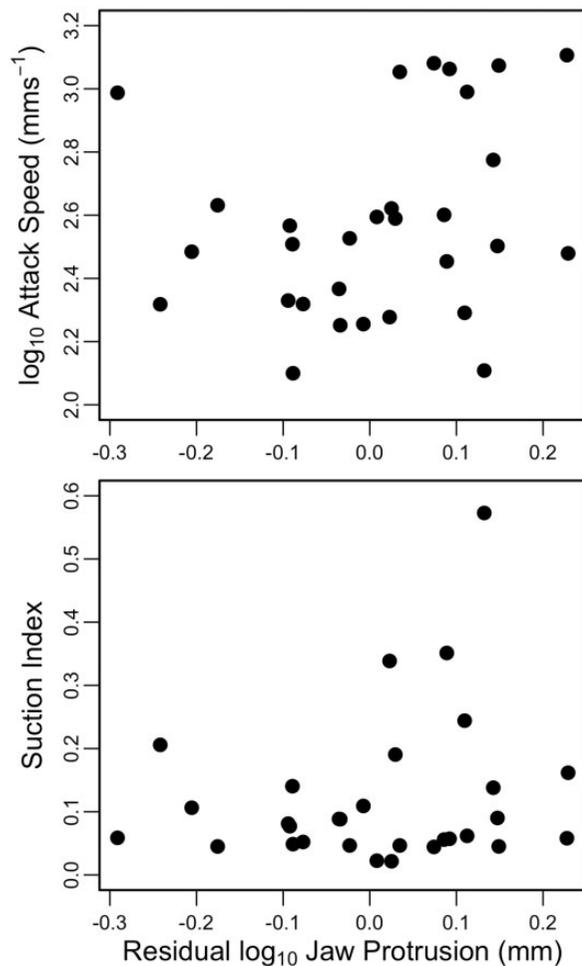
**Fig. 5** The relationship between the distance the jaw is protruded (corrected for body size), attack speed, and the capacity to generate suction in 30 species of serranid fishes. These plots emphasize the relative independence of these traits and hence the high diversity of combinations of behavior and functional morphology across species of serranids. Data are from Oufiero et al. (2012).

feeding, which is powered by axial muscles and depends on stiff jaw and hyoid elements for rapid, forceful expansion of the buccal cavity. Among ray-finned fishes and aquatic tetrapods, several major innovations have enhanced the performance of suction feeding, including a planar, circular opening of the mouth, upper jaw protrusion, and an anterior-to-posterior wave of buccal expansion during suction feeding. In ray-finned fishes, diversification of the feeding mechanism primarily involves adding additional behaviors to the suction-feeding repertoire, such as various biting behaviors. Diversity among suction feeders reflects a trade-off between the capacity to generate high speeds of suction flow and the volume of water that can be ingested during the strike. In terms of mechanisms for closing the

distance between the predator and prey during the strike, body ram by locomotion and jaw ram by movements of the jaw or head are more significant than suction, which is limited to a short distance in front of the mouth.

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