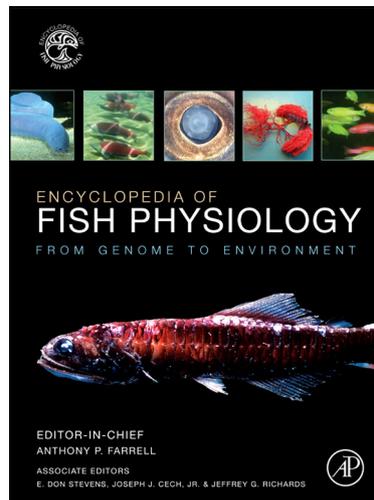


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Feeding Mechanics

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[How Do Fishes Capture Prey?](#)

[Feeding in Jawless Fishes](#)

[The Evolution of Suction Feeding](#)

[What Is Suction-Feeding Performance?](#)

[Hydrodynamics of Suction Feeding](#)

[Ecomorphology of Feeding](#)

[Jaw Protrusion](#)

[The Integration of Locomotion and Feeding](#)

[Future Directions](#)

[Further Reading](#)

Glossary

Buccal cavity The mouth (oral) cavity at the anterior end of the fish in front of the gills.

Digital particle image velocimetry (DPIV) A modern computational technique used to visualize the movement of fluids. Neutrally buoyant reflective particles are placed in the water, illuminated using a laser light sheet and are used to measure water

movement. The movements of the particles during feeding are captured using high-speed video.

Ecomorphology The relationship between morphology and ecology.

Exaptation A character, previously shaped by natural selection for a particular function, that later is co-opted for a new use.

Ram The forward movement of the fish.

How Do Fishes Capture Prey?

Suction (mouth expansion), ram (forward swimming), and manipulation are three mechanisms of prey capture in fishes. Despite the considerable diversity among the approximately 28 000 species of fishes, the most common mode of prey capture involves suction feeding. Although the general principles underlying suction feeding are relatively straightforward, several aspects of the feeding system can be modulated in order to alter feeding performance. For example, the rate and magnitude of mouth expansion, the distance between the fish's mouth and prey item, and body movements will influence suction-feeding performance. Jaw protrusion is an additional feature that can enhance suction-feeding performance. Based on recent evidence, intraoral processing (chewing) also appears to be a relatively common feature among fishes. For example, bowfin (*Amia calva*), salmonids (e.g., *Salmo salar*), and pike (e.g., *Esox niger*) all chew prey with their oral jaws. Modern experimental techniques, including sonomicrometry, digital particle image velocimetry (DPIV), *in vivo* pressure recordings, and computational fluid dynamics, all have propelled our understanding of the biomechanics of feeding in fishes. Some websites include videos that show examples of these features of fish feeding (see the Relevant Websites section).

The prevalence of suction feeding is the major focus of this article. The mechanisms underlying suction feeding in fishes are fairly complex. For example, the initial expansive phase is a result of hyoid depression, cranial rotation, jaw protrusion, and jaw opening. The musculature involved in feeding is discussed in other articles (see also **The Muscles: Cartilaginous Fishes Cranial Muscles and Bony Fish Cranial Muscles**).

Ram

Several species of fishes capture prey without generating suction or manipulating the prey. Ram feeding occurs when a fish swims over a prey item with its mouth open. Examples of fishes that employ ram include tunas and whale sharks.

Suction

As indicated above, suction feeding is the most common mode of prey capture. It involves the rapid expansion of the buccal cavity, which ultimately draws water into the mouth due to a pressure gradient formed (**Figure 1**). The majority of bony fishes (Osteichthyes) employs suction feeding in order to capture prey (see **Video Clip 1** for an example of a fish employing suction feeding).

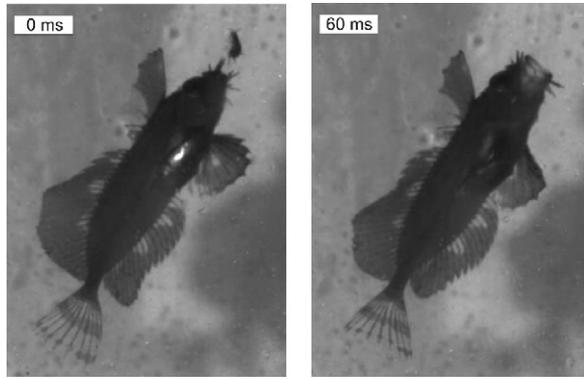


Figure 1 Suction feeding in the silverspotted sculpin, *Blepsias cirrhosus*. These images highlight the extent to which the jaw is protruded during suction feeding and the fact that ram (swimming) is not necessary for capturing prey with suction feeding.

Manipulation

In addition to suction and ram, fishes can obtain prey by physically contacting it and bringing it into the mouth, that is, biting. For example, biting is relatively common among shark and teleost fishes. Every species of heterodontid sharks is ecologically and functionally specialized for durophagy, which involves the consumption of hard prey such as mollusks or crabs. In many cases, the oral jaws of fishes are used to bite a prey item that is located on the substratum. Furthermore, some fishes will bite other animals (e.g., specialized for eating scales) and some will bite off small pieces of plants. As explained below, jawless fishes also use manipulation in order to obtain food.

Feeding in Jawless Fishes

Hagfishes and lampreys feed in a complex and very different way compared with other fishes (see also **Hagfishes and Lamprey: Energetics and Development, and Lampreys: Environmental Physiology**). The feeding system includes posteriorly directed keratinous teeth that are attached to dental plates, a paired series of cartilages. The dental plates are moved in and out of the mouth during feeding via retractor and protractor muscles. The movement of the dental plate acts in a similar way to a fixed pulley. This system appears to have both advantages and disadvantages relative to fishes with jaws. The pulley system allows maximal force transmission, but does not permit speed amplification. Speed amplification is likely a key aspect of jaws that has facilitated the success of jawed fishes.

The Evolution of Suction Feeding

The invasion of new habitats by early fishes was likely facilitated by the evolution of jaws. The diversity of gnathostomes (jawed fishes) exploded in the Silurian and gnathostomes is currently represented by the chondrichthyan and bony fishes. Later advances, such as jaw protrusion (discussed later) and pharyngeal jaws, then enhanced the basic feeding plan. However, it is important to discuss first the origin of jaws and ultimately suction feeding.

Jaws evolved in fishes over 460 million years ago. Recently, two hypotheses have been put forth explaining the origin of jaws. Several commonalities persist in both hypotheses. For example, both agree that jaws represent the first branchial arch, also termed the mandibular arch (**Figure 2**). The evidence supporting this includes the fact that most of the elements of the jaws (skeletal elements, muscles, etc.) resemble those of other branchial arches. Also, both agree that the lower jaw resides in the ancestral position of the mandibular arch, whereas the upper jaw

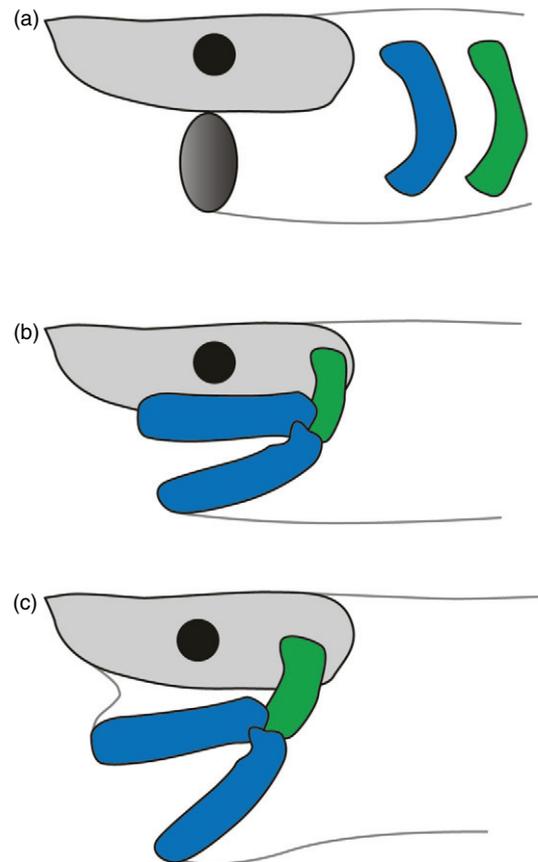


Figure 2 A hypothetical schematic the evolution of jaws for suction feeding. (a) Here the mandibular (blue) and hyoid (green) arches before being involved in the jaws. (b) Here the mandibular arch has become the jaws, which are suitable for respiration. In this amphistylic jaw suspension, the mandibular arch is directly connected to the cranium. (c) Here the mandibular arch is not directly connected with the cranium, which is more suitable for feeding.

stems from the forward extension (in front of the mouth opening) of the maxillary part of the mandibular arch (see also **The Skeleton: Bony Fish Skeleton**).

The first hypothesis for the origins of jaws is the neoclassical hypothesis, which asserts that the jaw first evolved for stronger ventilation and then to grasp prey. As ventilation increases, prey would be sucked in and potentially consumed. Thus, what originally began with a ventilatory function eventually became utilized for suction feeding, indicating that the current use in feeding is an exaptation. Eventually, the ability to grasp prey was improved when dentition became associated with the mandibular arches. In the neoclassical hypothesis, few or no oral structures were lost during the jawless-to-jawed transition.

The second hypothesis for the evolution of the jaws is the heterotopic hypothesis, which is based mainly on modern developmental studies. This hypothesis asserts that the upper jaw did not evolve through a series of intermediate stages. Instead, certain genes are expressed farther back in the head of gnathostomes compared with lamprey embryos, which leads to different skeletal structures being generated by different parts of the neural crest between the two clades.

What Is Suction-Feeding Performance?

In general, generating high fluid speeds (due to negative pressure in the mouth cavity) during suction feeding is a good indication of suction-feeding performance. However, several other factors have been implicated in suction-feeding performance, including the ingested volume of water (IVW), the volumetric flow rate, strike accuracy, and fluid acceleration. The importance of these metrics depends on the ecology of the fish. For example, largemouth bass (*Micropterus salmoides*) depend strongly on a large IVW and high ram speeds in order to capture prey. For this species, maximum fluid speed is likely not as important for capturing prey. Thus, species-dependent metrics of suction-feeding performance are necessary to understand the feeding diversity of fishes.

Hydrodynamics of Suction Feeding

Modern techniques have greatly enhanced our understanding of feeding mechanics in fishes. One such area that has contributed substantially is hydrodynamics. Advances have emerged in both experimental and modeling techniques.

Visualization of Fluid Movement

The flow of water generated during suction feeding can be quantified using DPIV, which is a modern computational technique used to visualize the flow of fluids. This technique has recently been utilized to study the flow

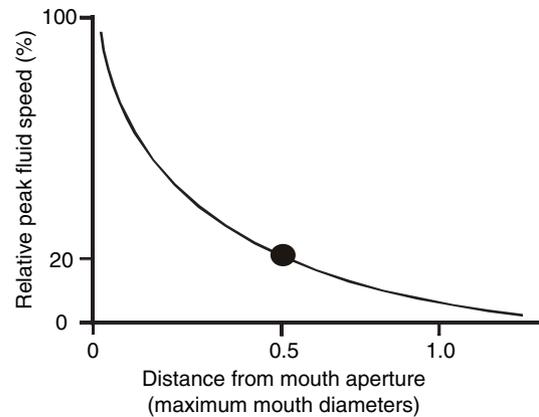


Figure 3 The general relationship between fluid speed and relative distance from the mouth opening (aperture). Fluid speed drops off exponentially going away from the mouth aperture, highlighting the importance of being close to the prey item for successful suction feeding. The black circle indicates the location that fluid speed is typically measured using digital particle image velocimetry (DPIV).

generated by suction in centrarchid fishes and sharks. The speed of the water being sucked into the fish's mouth is highest at the mouth aperture and decays rapidly moving away from the fish's mouth (**Figure 3**). Thus, suction feeding is most effective when the mouth of the predator is in very close proximity to the prey item.

Direct measurements of fluid flow permit the calculation of the ingested volume, which is strongly correlated with mouth size. Because the flow of water is unidirectional in fishes (i.e., flows in the mouth and out the opercular cavity), the amount of water ingested can exceed the size of the buccal cavity. In addition to the size, one can also calculate the shape of the IVW, which is strongly influenced by swimming speed.

Swimming during suction feeding can alter the hydrodynamics of suction feeding. Direct measurements from bluegill sunfish and largemouth bass indicate that, as swimming speed increases, the ingested volume becomes increasingly narrow and elongate (**Figure 4**). For further details, see section **The Integration of Locomotion and Feeding**.

Modeling

When experimental measurements are difficult (or impossible) to obtain, modeling the flow of water becomes increasingly informative. In addition, modeling allows one to predict the effects of manipulating a single variable while holding everything else constant. Modeling can ultimately provide insight into animal diversity and predator-prey interactions. Several attempts have been made to model the hydrodynamics of suction feeding in fishes. In the early 1980s, the expanding mouth cavity was

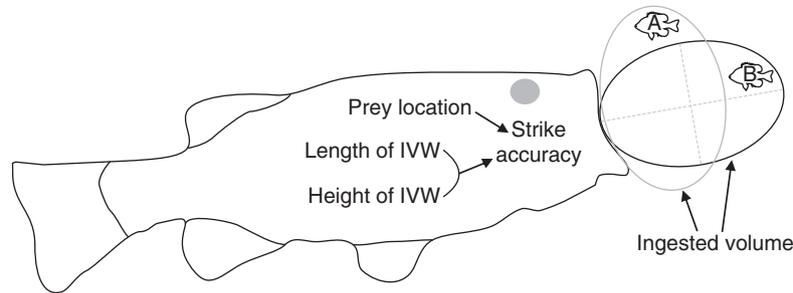


Figure 4 The influence of swimming (ram) speed on the shape of the ingested volume of water (IVW) and strike accuracy. In situation A, the forward swimming speed of the predator is negligible and prey item A is caught. However, prey B cannot be caught because the IVW is not long enough. In situation B, there is substantial ram speed and prey B is caught. However, prey A cannot be caught because the IVW is too narrow. Ultimately, the length of the IVW, and the location of the prey, will play a large role in capture success.

modeled as a single truncated cone with a gape (anterior end) and a posterior height. A number of input parameters define how the buccal cavity expands. This model yielded pressure and fluid speed for given dimensions and expansion profile of the feeding event. More than 20 years later, the model was modified to include three truncated cones connected in series.

Recently, the early model was tested by measuring both pressure and fluid speed simultaneously during suction feeding in largemouth bass and bluegill sunfish (*Lepomis macrochirus*). Pressure transducers were implanted through the dorsal aspect of the skull and they ultimately protruded into the buccal cavity. DPIV was used to quantify fluid speed. The dimensions of the buccal cavity, and the profile of expansion, were also used to predict fluid speed using the early model. Ultimately, the predicted values of fluid speed exceed those measured under *in vivo* conditions. Reasons that the model could not fully explain the actual fluid speeds may include complex patterns of expansion within the mouth cavity and/or unsteady flow normal to the long axis of the fish. However, more work is needed to understand the dynamics of water flow inside the mouth of a fish.

Another technique for modeling fluid flow during suction feeding is computational fluid dynamics - a branch of fluid dynamics that utilizes the incompressible Navier–Stokes equations, which govern the flow of water during suction feeding. An interesting conclusion from a recent study is that prey size is a very important factor when considering the timing and magnitude of peak forces exerted on prey. Based on modeling, it is apparent that peak force can be reached most quickly for prey items that are approximately 33% of mouth diameter. This has important implications for prey selection by fishes.

Ecomorphology of Feeding

The relationships between morphology and ecology, and ultimately performance, have been well studied in fishes. In particular, several studies have focused on the

relationship between diet and structural aspects of the mouth. Recent work has provided a functional foundation for such studies, making the link between morphology and ecology more evident. For example, mouth size is strongly correlated with prey size such that species with larger mouths are able to ingest larger prey items.

Jaw lever mechanics are commonly studied in relation to ecology. One can measure the closing and opening in- and out-levers of the jaw, and then relate that to the diet or feeding style of the predator. In coral reef fishes of the Caribbean, species that use their oral jaws to grip, manipulate, bite, shred, or crush prey have very high jaw closing lever ratios. In contrast, those species that exhibit ram- or suction-based strike tactics exhibit much lower jaw closing ratios. Higher closing ratios indicate the ability to more efficiently transmit the force generated by the muscles to the tooth surface. Jaw opening ratios do not show an obvious pattern like the jaw closing ratios.

The ecomorphology of feeding in cottid fishes (sculpins) has also been examined in detail. The focus has primarily been on the species of the Northeastern Pacific. In these studies, a larger mouth was linked to feeding on more elusive prey (i.e., fishes, shrimp, mysids, and octopods). In addition to the general ecomorphological approach, functional studies have also been used to test whether the morphology exhibited by some species enhances their performance in an ecological context. Larger-mouthed species of sculpins exhibit significantly higher capture success on evasive shrimp than did smaller-mouthed species. This functional link is critical for providing a mechanism underlying the correlation between morphology and ecology.

Jaw Protrusion

As mentioned above, the flow of water generated by suction is limited to a narrow range outside of the fish's mouth. Thus, being able to get extremely close to a prey item is necessary for effective suction feeding. Jaw protrusion is one way in which the mouth can be extended

closer to the prey without having to move the entire body (Figure 1). Taken another way, the predator could initiate a strike at a farther distance from the prey.

The ability of fishes to protrude their upper jaw has been cited as a key innovation that facilitated the trophic diversity among fishes. The premaxilla is rotated or pushed into an extended position, and multiple paths to jaw protrusion have evolved. The upper jaw movement can involve anterior, anterodorsal, or anteroventral aspects, and the lower jaw or mandible can pivot around a ball and socket articulation.

Recent work has revealed that jaw protrusion enhances forces exerted on a prey item. Although this had been suggested for quite some time, empirical data exploring the functional ramifications of jaw protrusion are limited. Utilizing a framework based on data from bluegill sunfish, a recent study utilized empirical data and simulations to calculate the contribution of jaw protrusion to the forces exerted on prey. The observed speed of jaw protrusion was positively correlated with the peak measured force on the prey. Ultimately, the independent source of acceleration provided by jaw protrusion can increase the total force on the prey by up to 35%.

The Integration of Locomotion and Feeding

For several reasons, locomotion is critical for most fishes to successfully capture prey. Locomotor performance (e.g., maximum swimming speed and maximum acceleration) will be important for overtaking an evasive or elusive prey item. In addition, controlling the locomotor system (e.g., stability and positioning) will play a significant role in the timing and accuracy of a strike, which will ultimately determine capture success.

Ram Speed

Although ram is often a component of a feeding event, the relative contribution can vary considerably. One ramification of increased ram speed is a decreased capture success. Among other things, swimming fast during prey capture decreases the time that the predator has to adjust its position relative to the prey. This can result in poor aiming and/or incorrect timing of mouth opening. One critical aspect of suction feeding that is altered with ram speed is the shape of the IVW (Figure 4). As a fish swims faster during feeding, the resulting IVW will be increasingly elongate and narrow. This is important with respect to positioning of the prey in front of the predator's mouth. If the prey item is located farther away from the predator, an elongated IVW will facilitate prey capture.

Pectoral Fins

As outlined earlier in this article, strike accuracy is necessary for successful prey capture in fishes, especially those species that rely heavily on suction. In acanthomorph fishes, the pectoral fins are well suited for braking without inducing any unsteady maneuvers because of their location relative to the fish's center of mass (see also **Buoyancy, Locomotion, and Movement in Fishes: Paired Fin Swimming**). For these fishes, the reaction force generated by the pectoral fins during braking goes through the center of mass, thus maintaining the fish's position. Many fishes brake during prey capture, but why they do this is still in question. One explanation is that braking reduces the approach speed, which will allow the predator to adjust its position relative to the prey. Thus, braking may increase capture success. Another possible benefit to braking during prey capture is that it puts the predator in a position to quickly maneuver and follow the prey if it escapes. Finally, braking might prevent a collision with the substrate (if the prey is located close to structure), which will ultimately prevent injury.

Future Directions

Where is the field of feeding mechanics in fishes headed? With an increased understanding of the hydrodynamics and mechanics of suction feeding, we are now poised to explore the incredible diversity that is evident in the many thousands of extant species of fishes. In addition, few studies have attempted to understand the evolution of feeding mechanics, in part due to the incomplete understanding of the mechanics and also a lack of well-resolved phylogenies. This will be a fruitful area of research in the future. Finally, although we know much about the feeding and locomotor systems, our understanding of how multiple complex systems are integrated is poor. How do fishes move and rapidly expand their mouths with coordinated timing? What underlying neural control mechanisms permit the simultaneous actions of the systems?

See also: **Buoyancy, Locomotion, and Movement in Fishes:** Experimental Hydrodynamics; Maneuverability; Paired Fin Swimming. **Hagfishes and Lamprey:** Hagfishes; Lampreys: Energetics and Development; Lampreys: Environmental Physiology. **The Muscles:** Bony Fish Cranial Muscles; Cartilaginous Fishes Cranial Muscles. **The Skeleton:** Bony Fish Skeleton.

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- <http://www.youtube.com/watch?v=MSzEGg-6wWo> – You Tube; Particle image velocimetry video of suction feeding by a bluegill sunfish, *Lepomis macrochi*.
- <http://www.youtube.com/watch?v=OHivHHmYSDc> – You Tube; Particle image velocimetry video of suction feeding by a largemouth bass, *Micropterus salmoides*.

For supplementary material please also visit the companion site:
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