

From: Functional Vertebrate Morphology
Milton Hildebrand, Dennis M. Bramble, Karen F. Liem,
and David B. Wake, eds.
The Belknap Press [Harvard University Press]
Cambridge, Massachusetts, 1985, pp. 210-229; 397-399.

Chapter 12



Aquatic feeding is the primitive mode of prey capture in vertebrates and is therefore of special interest in the study of vertebrate evolution and trophic biology. This fact has an especially important implication for the analysis of evolutionary patterns of structure and function in the feeding mechanism: the diversity of terrestrial methods of prey capture has been derived from a musculo-skeletal apparatus and neural control system that function in a medium 900 times as dense as air and 80 times as viscous. Accordingly, the hydrodynamic properties of water have played a fundamental role in shaping the basic mechanism of aquatic feeding and may have determined the nature of the feeding mechanism in a number of primitive tetrapods. Many underlying similarities within the diversity of aquatic feeding modes appear to result from hydrodynamic problems associated with the removal of small particles from a dense and viscous medium.

All the major groups of vertebrates contain species that feed aquatically. This chapter examines the two feeding processes that are used by more than 99% of all aquatic vertebrates, suspension feeding and suction feeding, with emphasis on the mechanics of feeding in selected lower vertebrates. Other taxa and modes of feeding will not be discussed here, specifically elasmobranchs (Springer, 1961; Moss, 1972, 1979); the Galapagos iguana *Amblyrhynchus*; adult lampreys and hagfishes (Reynolds, 1931; Gradwell, 1972; Hardisty, 1979); crocodiles and gavials; birds such as the penguin, loon, skimmer (*Rynchops*), and flamingo (Jenkin, 1957; Zweers, 1974); cetaceans,

Aquatic Feeding in Lower Vertebrates

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sirenians, and pinniped carnivores (Gordon, 1984).

The study of aquatic feeding in vertebrates has undergone a renaissance in recent years with the introduction of modern experimental techniques for the study of functional morphology. Many early studies on feeding mechanisms used manipulations of preserved specimens to deduce the sequence of movements occurring during feeding or employed macroscopic observations of filtering structures and surfaces. Within the last 20 years high-speed cinematography has allowed the accurate determination of bone movement during feeding and, coupled with simultaneous electromyographic recording of muscle activity, has permitted the quantitative study of musculoskeletal mechanics beyond what can be achieved by merely studying muscle origins, insertions, and lines of action. Other techniques that have vastly improved the description of feeding mechanics include strain gauges, which permit the direct recording of bone deformation patterns (Lanyon, 1976; Lauder and Lanyon, 1980), pressure transducers (Lauder, 1980a), and accurate particle density and size counters for the examination of the dynamics of suspension feeding (Wassersug, 1972). These new experimental approaches, coupled with theoretical analyses of feeding methods (Rubenstein and Koehl, 1977), have resulted in a more comprehensive understanding of the functions of head bones, muscles, and filtering systems than was previously possible. Many of the misconceptions and assumptions of earlier nonexperimental investigations have been revised.

Principles of Aquatic Prey Capture

The high density and viscosity of water relative to air has four important consequences for suspension and suction feeding in the aquatic environment. First, movement of the predator in approaching the prey affects the position of the prey because of the lateral deflection of flow streamlines anterior to the predator's head. Prey tend to be deflected to the side unless the flow streamlines are reoriented by expansion of the mouth cavity. Second, constraints are placed on the design of filters that remove small particles from the fluid. Small pore sizes in sieve filters greatly increase the drag experienced by predators during locomotion and increase the muscular effort and hence the use of available oxygen during feeding. This problem can be partially overcome by having a sieve with an adjustable pore size, as seen in the gill rakers of filter-feeding fishes. Third, the gravitational deposition of particles on a filter is regulated by the relative densities of the particles and of the fluid environment. Finally, inertial factors, such as kinetic energy at high flow velocities and the momentum of the flow (factors that can usually be neglected when analyzing feeding in air), must be taken into account.

Suspension feeding in vertebrates differs from suction feeding in that the selection of prey to be swallowed occurs primarily at the filter (gills, mucus net, and so on), usually after the prey has entered the mouth. In most cases the suspended particles are filtered out primarily by size, shape, and density, with little regard for the food value of the particles (Jorgensen, 1966). The filtered particles may then be sorted into those to be swallowed and those to be rejected. In suction feeding prey selection is usually performed prior to ingestion and the determination of food value is made before particle capture.

Rubenstein and Koehl (1977) have recently summarized the six possible mechanisms of suspension feeding available to aquatic organisms. The mechanism often assumed to be the most common is sieving, in which all particles captured are larger than the pores in the filter, and no items smaller than the pores are retained (Fig.

12-1A). This may actually be a rather rare mechanism of prey capture. Direct interception occurs when particles in the flow contact and stick to a filter surface (Fig. 12-1B). Inertial impaction on a filter results from particle inertia as flow is diverted through the open areas of the filter (Fig. 12-1C). Particles cross streamlines and adhere to the filter surface. Gravitational deposition (Fig. 12-1D) occurs as denser items settle out onto the filter surface. Motile particle deposition on a filter results from active movement of particles (for instance, locomotion by planktonic copepods) or other external influences that give potential food particles sufficient energy to deviate from the streamlines (Fig. 12-1E). Finally, electrostatic attraction between particles in the water and the filter may result in adherence to the filter surface. This mechanism may be quite important when mucus secretions cover the filter. LaBarbera (1978) has shown in invertebrates that both positively and negatively charged particles are preferentially attracted to a mucus filter over those neutrally charged. Even irregularly shaped filters may be very effective at removing particles from fluids when nonsieving mechanisms dominate.

Rubenstein and Koehl (1977) noted that as a consequence of these six possible filtration methods, the diet of suspension feeders may be varied significantly by several different mechanisms. First, the pore size of the filter may be actively changed. Second, the rate of filter cleaning governs the size of food captured because the accumulation of food on a filter surface greatly affects the size of particles removed from the water. Finally, increasing the diameter of fibers in a fibrous netlike filter modifies the size distribution of captured particles primarily by increasing the proportion of particles trapped by direct interception.

In sharp contrast to suspension feeding, which may be modeled by steady-state hydrodynamic equations, the salient feature of suction feeding is its nonsteady, dynamic nature. For example, prey capture by the gar *Lepisosteus* may take place in 0.025 sec. and anglerfish can completely engulf their prey in 0.015 sec (Grobecker and Pietsch, 1979). Flow velocities in the mouth cavity of

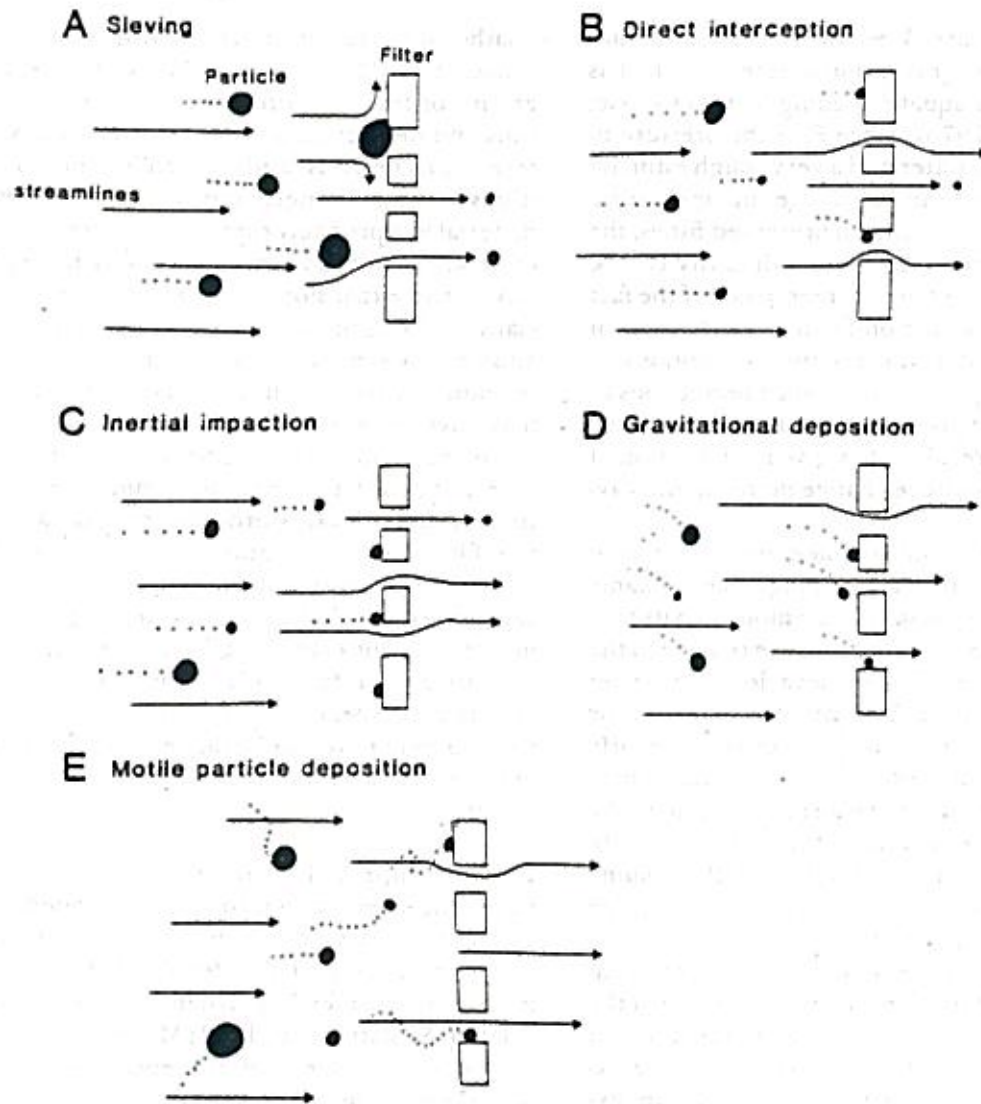


Figure 12-1 Five possible mechanisms of particle capture by a filter. Sieving appears to be the system used by ray-finned fishes, whereas direct interception and inertial impaction are used by most other suspension-feeding vertebrates. A sixth mechanism of particle capture, electrostatic attraction, may be important if mucus has a different electrical charge from the particles. Note that different predictions about the size distribution of particles on each side of the filter follow from the different mechanisms of particle capture. Dotted line represents particle path. (Modified from Rubenstein and Koehl, 1977.)

fishes often go from 0 to 12 m/sec in 0.03 sec (Osse and Muller, 1980). It is thus inappropriate to apply hydrodynamic models such as the Poiseuille relation and Bernoulli equation, which assume steady flows, to the analysis of suction feeding (Lauder, 1980b). Furthermore, the walls of the mouth cavity are compliant, and we have no

information to suggest that pressure-to-velocity relationships are linear for nonsteady flows.

As an example of a steady-state model, consider an application of the Bernoulli relation to the mouth cavity of a teleost fish. The equation

$$\frac{P_1}{\rho g} + \frac{1}{2} \frac{V^2}{g} = \frac{P_0}{\rho g}$$

where P = pressure, V = flow velocity, ρ = fluid density, and g = gravitational acceleration, has been applied to aquatic feeding in fishes (Osse, 1969; Pietsch, 1978). Since P_0 is the pressure in the surrounding water and a very rough estimate of flow velocity can be made by measuring changes in buccal volume in preserved fishes, the pressures generated in the mouth cavity can be estimated. However, one consequence of the fact that the dynamic suction-feeding mechanism of aquatic vertebrates violates the assumptions of the Bernoulli equation is that such predictions of change in buccal pressure are inaccurate by a factor of 10 or more; also, they give no indication of the pattern of pressure change in the mouth cavity.

Suction feeding (also called inertial suction feeding or gape-and-suck feeding) takes its name from the rapid expansion of the mouth cavity that causes a negative (suction) pressure relative to the surrounding water. This causes a flow that carries prey into the mouth. The jaws then close on or behind the prey while the water exits posteriorly between the gill arches (in fishes and aquatic urodeles). The inertia of the prey determines the flow velocity necessary to capture it (Gans, 1969). The greater the inertia, the higher the volume flow into the mouth cavity must be to draw the prey within reach of the jaws.

The dynamic nature of suction feeding has important implications for the understanding of the relationship between form and function in aquatic vertebrates that contrast with those extrapolated from steady-state situations. In dynamic events pressures within a single cavity need not be uniform. It is thus possible that pressures measured at different locations in the buccal cavity might be very different. Second, inertial effects (Streeter and Wylie, 1979), such as the momentum of water entering the mouth, may largely determine the dynamic characteristics of suction feeding. The role of inertial effects in the suction feeding of teleost fish is considered below.

Suspension Feeding

Suspension feeding was probably the primitive method of prey capture for both chordates and

gnathostomes (Denison, 1961; Moy-Thomas and Miles, 1971; Mallatt, 1981). Many of the earliest groups of fossil agnathans such as the osteostracans and heterostracans are believed to have filtered out detritus and suspended microorganisms with a pharyngeal mucus filter. Suspended material was probably captured by a combination of forward body motion, ciliary tracts in the pharynx, active expansion of parts of the head, especially of the floor of the mouth (Denison, 1961), and an active muscular velum inside the mouth opening. Active feeding on bottom sediments may have been common.

An important aspect of the suspension feeding of early chordates remains common in extant filter feeders: food is brought into contact with the filter by modifications of the respiratory pump. Respiratory movements in chordates result in a relatively steady flow of water into the mouth and out over the gills (Hughes and Shelton, 1958; Randall, 1971). This flow is used to transport suspended particles, and early agnathans may have used exaggerated movements of the respiratory pump to scoop up bottom sediments.

Larval Lamprey Larval lampreys (ammocoetes) have long been known to trap suspended algae and detritus on mucus within the pharynx, but it is only recently that the details of the trapping mechanism and feeding dynamics have been elucidated (Mallatt, 1979, 1981; Moore and Mallatt, 1980). Ammocoetes trap suspended particles by the mechanism of direct interception (Fig. 12-1B), not by sieving. In contrast to several previous hypotheses, Mallatt (1979) has shown that mucus is secreted in the lateral parabranchial chambers and on the lateral surface of the gill filaments. Mucus strands from the seven lateral chambers on each side move medially to join a central mucus food cord, which is propelled posteriorly into the esophagus by a central dorsal band of cilia. Food impacts directly onto mucus strands, lateral surfaces of gill filaments, and on the walls of the parabranchial chambers, but seldom on gill lamellae. The ventral endostyle adds digestive enzymes to the food cord and does not produce mucus.

Ammocoetes are partially selective feeders in

that they do not consume algae and detritus in the proportions present in the surrounding water. Selection is not based on particle size, although size does in part determine where particles are trapped in the pharynx. Ammocoetes are capable of capturing food in the size range of 5 to 340 μm with high efficiency (about 76%). The rate of water flow through the pharynx is slow (on the order of 40 ml/g/h) as compared with other suspension feeders, although ammocoetes gradually increase flow rates with increasing food concentration up to a critical concentration of 100 to 330 mg food/l (Mallatt, 1982).

Actinopterygian Fishes Surprisingly little research has been done on the mechanics of filter feeding in ray-finned fishes. Their mechanisms of filtration differ from the primitive direct interception of prey by mucus strands and thus provide examples of the other filter mechanisms listed earlier. Most discussions of the mechanics of particle filtration are highly speculative.

Filter feeding is accomplished with long gill rakers that extend anteriorly into the pharynx from the epibranchial and ceratobranchial gill arch elements. Mucus-producing cells are present on the gill arches at the base of the gill rakers and serve to coat the arches, and perhaps also the rakers, with mucus (Weisel, 1973). Experimental evidence suggests, however, that this mucus does not contribute significantly to particle entrapment by direct interception because the smallest particles filtered are generally much larger than the minimum mesh size — a circumstance consistent with a sieving filtration mechanism (Durbin and Durbin, 1975; Rosen and Hales, 1981). Particles enter the pharynx through the mouth, which is usually held widely open as the feeding fish swims through the water column. The particles then make contact with the gill rakers as the flow streamlines diverge laterally to pass over the gills. Filtration is primarily by sieving, and clogging of the filter may be prevented by water pressure that forces trapped particles along the gill rakers to the gill arch where they could become attached to mucus strands. There is no information on how the food-laden mucus is collected and ultimately swallowed. Perhaps the intermittent "coughing" movements observed during filter

feeding serve to agglutinate separate mucus strands from the gill arches into a larger mass, which is then swallowed.

Rosen and Hales (1981) have studied filter feeding in the paddlefish *Polyodon spathula* and have compared the size of spacings between gill rakers with the size of prey captured. *Polyodon* is an indiscriminate filter feeder and swallows all filtered particles including large amounts of detritus. The mean size of "pores" between the gill rakers is 0.07 mm, whereas the smallest prey filtered from the water averages about 0.12 mm in size. Very small prey items are not captured, even though available in the water column, and the smallest prey swallowed are generally twice as large as the filter pore size. Menhaden *Brevoortia tyrannus*, one of the most common filter-feeding fishes, can filter particles of 0.015 mm in size, although capture efficiency is then low (25%) as compared with that for larger particles (0.4 mm), where capture efficiencies of 60% to 80% are measured. Menhaden can filter an enormous quantity of water: each fish can filter 20 l/min at the mean swimming speed of 40 cm/sec (Durbin and Durbin, 1975). The mean size of "pores" in the gill raker filter of menhaden has been estimated at 0.08 mm, although the range is 0.01–0.10 mm.

Two mechanisms have been proposed for the selection of particles at the filter: active changes in size of filter pores by movements of the gill rakers or of the hyoid and gill arches, and changes in body velocity during filter feeding. The latter mechanism has been documented in the menhaden, which changes filtering velocity according to the size and availability of prey by adjusting the speed of locomotion. Changes in pore size may result from movements of the gill rakers by intrinsic muscles of the gill arches (as in *Polyodon*), but few fishes possess musculature attaching to the gill rakers. In menhaden the spacing between rakers or adjacent arches may be varied by relative movement of the arches as a result of dorsal and ventral branchial musculature (especially the transversi ventrales and dorsales muscles). The spacing between rakers on the same arch can be adjusted by dorsoventral movement of the arch that increases the angle between the epibranchial and ceratobranchial elements, thus fanning out

the gill rakers anteriorly. Both of these methods may result in a "dead space" between the gill rakers of adjacent arches through which water can flow without contacting the filter surface, thereby reducing both the drag and the efficiency of particle capture.

Most filter-feeding fishes are facultative feeders and can switch to picking individual prey items out of the water by inertial suction (Leong and O'Connell, 1969; Rosen and Hales, 1981). The menhaden is an exception, being an obligate filter feeder (Durbin and Durbin, 1975).

Anuran Larvae Anuran larvae, or tadpoles, are remarkable for their ability to filter extremely small particles from the water. The complexity of their suspension feeding apparatus provides an interesting comparison to the feeding of ammocoetes and ray-finned fishes. Particles enter the mouth cavity with the respiratory flow created by the buccal pump. The buccal pump consists of paired ceratohyal cartilages in the buccal floor that are moved dorsoventrally by the orbitohyoideus muscle extending between the palatoquadrate and the ceratohyal on each side (de Jongh, 1968; Wassersug and Hoff, 1979). Large particles may be rejected by the labial papillae; moderately sized particles pass directly back to the esophagus. Smaller suspended material is carried laterally with the flow of water to be trapped either on the gill filters or on mucus of the branchial food traps. Gradwell (1975) described cilia-driven food cords passing medially and caudally into the esophagus. The removal of food particles by the branchial food traps and gill filters has been proposed to occur by three methods: inertial impaction, direct interception, and possibly by electrostatic attraction between particles and mucus (Wassersug, 1980). The gill filters do not contain mucus-secreting cells; mucus is secreted initially on the ventral velum and branchial food traps in the pharynx before moving posteriorly to the esophagus.

The gill filters of tadpoles can have pore sizes of 5μ or less and, in contrast to the fish species discussed above, can filter suspended particles down to 0.13μ (Wassersug, 1972), a size considerably smaller than the pore size. This fact suggests that sieving is not an important mechanism of ultra-

planktonic food capture and that direct interception of food particles by mucus strands may be dominant. Tadpoles are not all obligate filter feeders; many create suspensions of food particles by biting off food from the bottom and drawing this suspension into the pharynx where filtering and trapping of the food pieces takes place. The feeding dynamics of tadpoles differ from those of fishes in that swimming velocity is not adjusted to change flow over the filter: either changes in the rate of buccal pumping or changes in stroke volume are used to vary filtration (Seale and Wassersug, 1979). Although no evidence has been obtained for clogging of the sieve filters of fishes, the ingestion rate declines and food may be ejected from the mouth when the concentration of food surpasses about $1.5 \times 10^3 \mu\text{m}^3/\text{ml}$. Both fishes and tadpoles exhibit a threshold in food concentration below which filter feeding does not occur.

Common to all three groups of filter feeders discussed is an intimate functional association between prey capture and relatively steady-state, low-velocity respiratory mechanisms and flows. By contrast, although the same basic muscular and skeletal elements are used for both respiration and suction feeding, the mechanisms underlying these two processes are significantly different. An understanding of suction feeding requires analysis in terms of rapidly varying kinematic parameters and dynamic flow.

Suction Feeding

Prey capture by suction feeding is primitive for the Osteichthyes and is common in all the major lineages of lower vertebrates, including ray-finned fishes (Actinopterygii), coelacanth (Lauder, 1980c), and lungfishes. Suction-feeding mechanisms are thus fundamental to considerations of the origin and evolution of tetrapod feeding mechanisms discussed in Chapters 13 and 14.

Actinopterygian Fishes The most comprehensive and detailed recent research on suction feeding has been done on ray-finned fishes, which allows us to consider the mechanics and hydrodynamics of feeding in this group in detail. Four

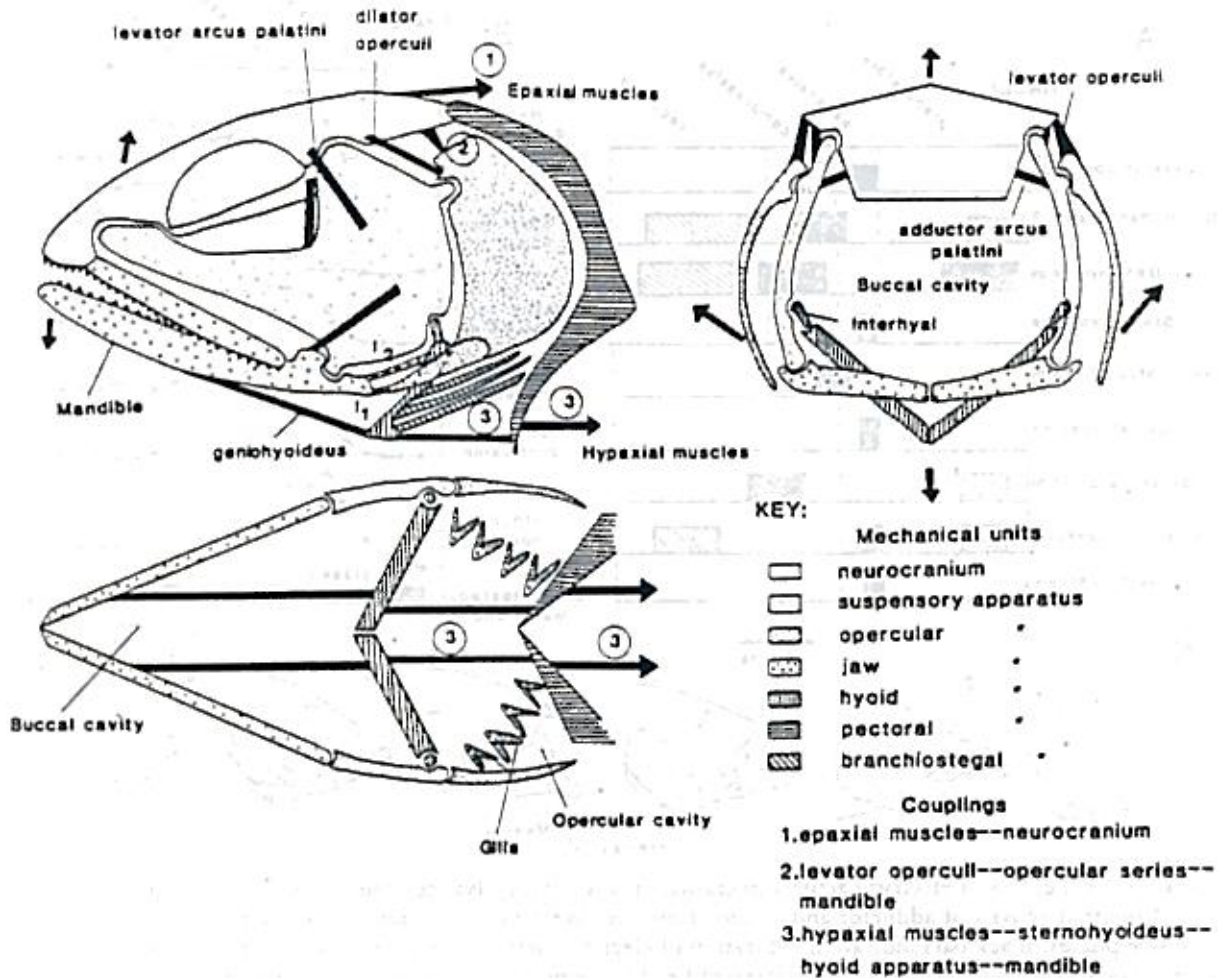


Figure 12-2 The major muscles and mechanical units in the head of a teleost fish. Three major musculoskeletal couplings are involved in the expansive phase of prey capture: (1) the epaxial muscles coupling, which causes cranial elevation; (2) the levator operculi coupling, which mediates mandibular depression via the opercular apparatus and interoperculomandibular ligament (ligament l_1); and (3) the hyoid coupling, which also governs mandibular depression via the mandibulohyoid ligament (l_2).

phases of prey capture may be defined by the timing of movements of cranial bones: a preparatory phase, an expansive phase, a compressive phase, and a recovery phase.

The preparatory phase (which has been found only in advanced percomorph teleosts) occurs as the prey item is being approached and before the mouth begins to open. The key feature of this phase is that the volume of the buccal cavity is decreased (Fig. 12-2), thus reducing the volume of water inside the mouth prior to rapid expansion as the mouth opens (Liem, 1978). Compres-

sion of the mouth cavity occurs by the action of the adductor mandibulae, adductor arcus palatini, adductor operculi, and geniopharyngeus muscles (Figs. 12-2, 12-3A). Buccal volume is thus reduced mainly by lateral compression of the head as the suspensory apparatus on each side moves medially and by elevation of the floor of the buccal cavity as the hyoid is protracted. Electrical activity in the adductor mandibulae stabilizes the lower jaw so that hyoid protraction by the geniopharyngeus can occur.

The expansive phase of the strike extends from

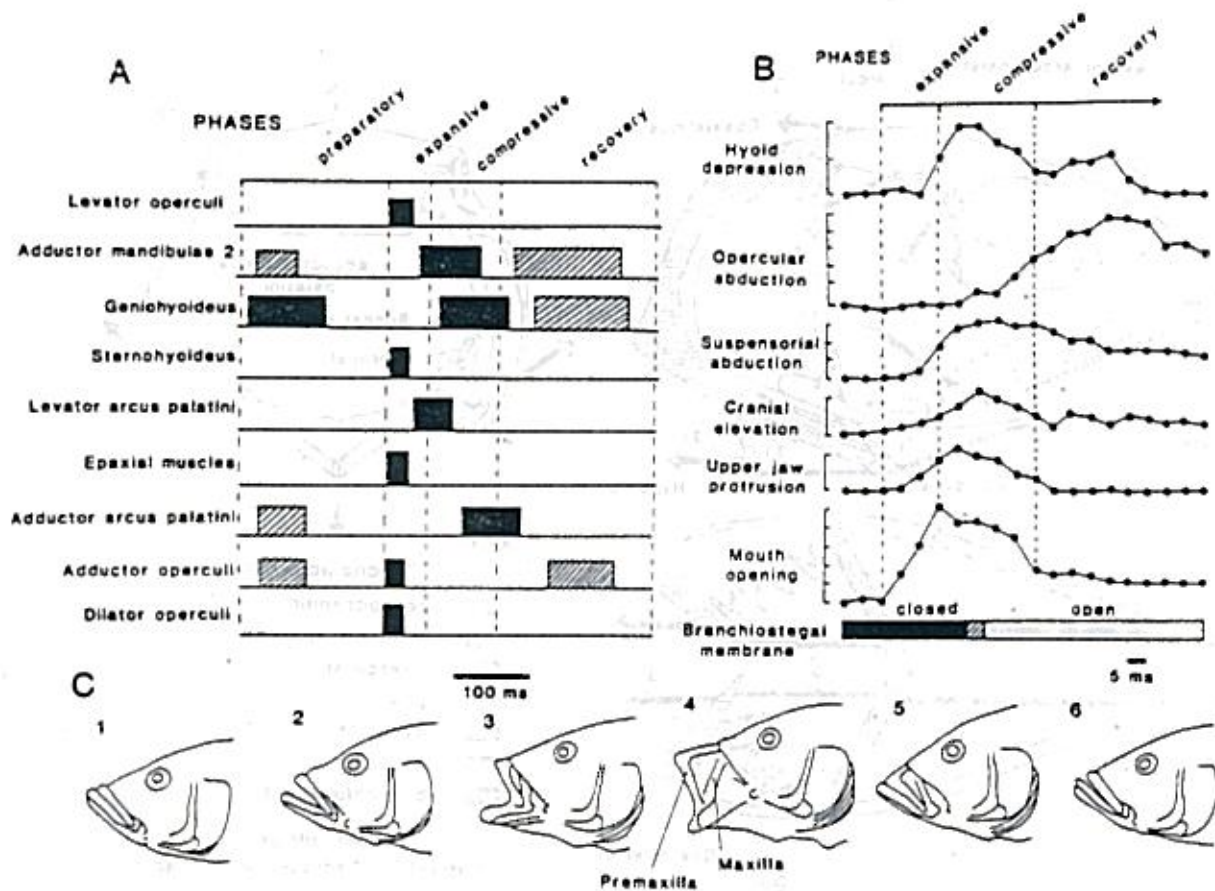


Figure 12-3 A: Periods of electrical activity in cranial muscles of an advanced teleost fish, *Lepomis*, during feeding. Note that activity of adductor and abductor muscles overlaps the boundaries of the expansive and compressive phases. Black bars indicate the duration of electrical activity common to all strikes; hatched bars indicate occasional activity. B: Kinematic pattern of head movements in *Lepomis* during capture of a goldfish. Note the delay in opercular abduction until the compressive phase, as well as the relative duration of the phases. C: Sequence of jaw movements in a cichlid fish, *Serranochromis*, showing protrusion and retraction of the upper jaw (modified from Liem, 1978).

the start of mouth opening to peak gape. Three musculoskeletal linkage systems function to increase the gape. (1) The epaxial muscles cause a dorsal rotation of the cranium on the vertebral column, thus expanding the roof of the mouth cavity. (2) The mandible is depressed ventrally by the action of the levator operculi muscle, which rotates the gill cover posterodorsally (Liem, 1970). This dorsal rotation is transmitted to the retroarticular process of the mandible by a ligament between the opercular series and the mandible (see Fig. 12-2, coupling 2; Fig. 12-4, *LOP*). (3) The mandible is also depressed ventrally by a

second musculoskeletal coupling involving the hyoid apparatus. Contraction of the sternohyoideus muscle causes an initial posterior retraction of the hyoid, and this movement produces depression of the mandible via a ligament from the hyoid to the opercular series or mandible (see Fig. 12-2, coupling 3; Fig. 12-4, *SH*). Shortly after the mouth begins to open, lateral expansion of the buccal cavity occurs as a result of lateral movement of the palatoquadrate, which is mediated by the levator arcus palatini (Figs. 12-2, 12-3), and the hyoid apparatus swings ventrally, greatly expanding mouth cavity volume. It is during this

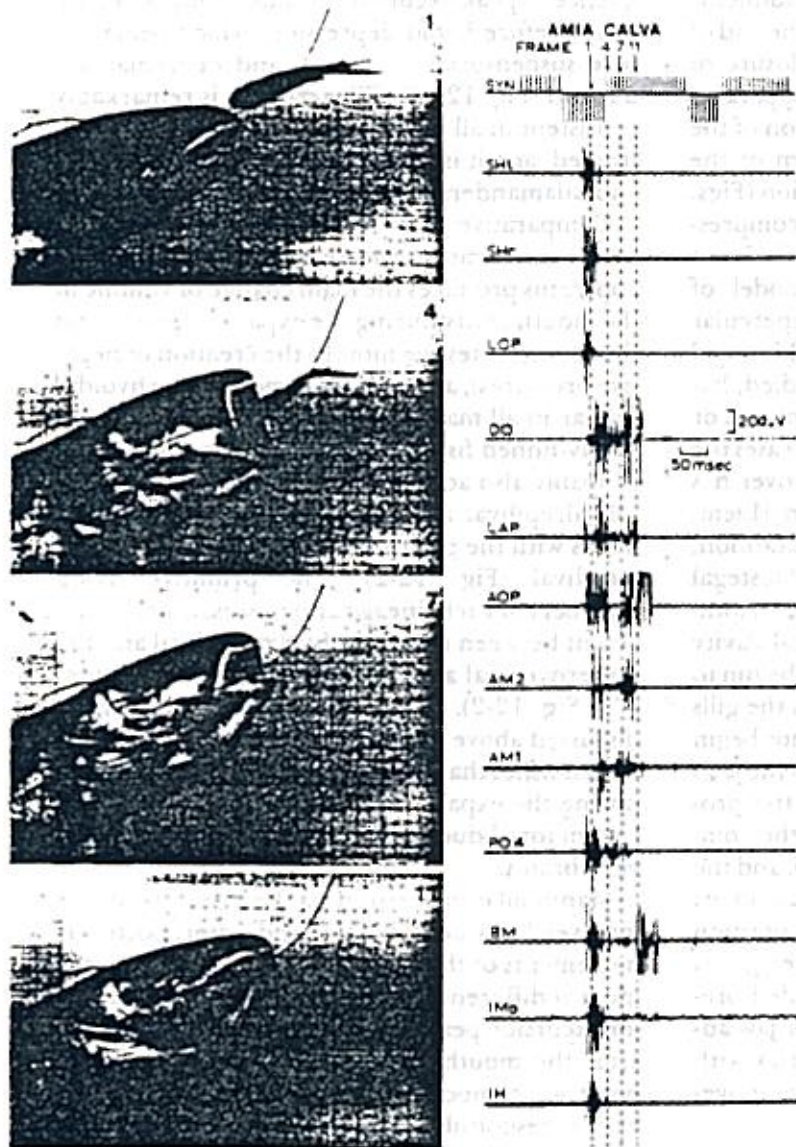


Figure 12-4 Prey capture in the bowfin *Amia calva*. The frames (left) are from a high-speed (200 frames/sec) film that is synchronized with electromyographic recordings of cranial muscles (right). The recordings are a summary of 45 feeding events. The wire leading from the head muscles to the recording apparatus can be seen in the photographs. Note that the maxilla swings anteriorly to produce a nearly circular mouth opening at peak gape (frame 4) as the prey enters the mouth. Both the levator operculi and sternohyoideus muscles are active at the start of the expansive phase and activate couplings 2 and 3 (Fig. 12-2) to cause mouth opening. Muscles: *SHL*, *SHR* = left and right sternohyoideus muscles; *LOP* = levator operculi; *DO* = dilator operculi; *LAP* = levator arcus palatini; *AOP* = adductor operculi; *AM2*, *AM1*, and *PO4* = divisions of the adductor mandibulae; *BM* = branchiomandibularis; *Imp* = intermandibularis posterior; *Ih* = interhyoideus. (From Lauder, 1980d.)

time that protrusion of the premaxillae toward the prey occurs in advanced teleost fishes (Fig. 12-3C, frame 3). The volume of the opercular cavity remains relatively constant throughout the expansive phase. Abduction of the gill cover usually begins after peak gape has been reached (Figs. 12-2; 12-3B), and the branchiostegal membrane and rays then tightly seal the posteroventral opening of the opercular cavity (Fig. 12-3B). The expansive phase is usually shorter than either the preparatory or compressive phases. In some

fishes, expansion of the mouth cavity is extremely rapid: in *Lepisosteus* peak gape is reached within 15 msec of the start of mouth opening (Lauder, 1980d), and Grobecker and Pietsch (1979) have described an expansive phase lasting only 5 msec in antennariid anglerfishes. In *Amia calva* the expansive phase lasts 20–40 msec (Fig. 12-4).

The compressive phase (the time from peak gape to closure of the jaws) lasts, on average, twice as long as the expansive phase (Figs. 12-3B, mouth opening; Fig. 12-4). The compressive

phase is characterized by activity in the adductor mandibulae (actually beginning during the end of the expansive phase), which initiates closure of the jaws; adduction of the suspensory apparatus by the adductor arcus palatini; protraction of the hyoid by the geniohyoideus; and return of the cranium nearly to its initial resting position (Figs. 12-2; 12-3A,B; 12-4). A feature of the compressive phase kinematic pattern that has significant implications for the hydrodynamic model of feeding discussed below is the timing of opercular abduction and opening of the branchiostegal valve. In nearly all ray-finned fishes studied, lateral movement of the operculum begins only at or near peak gape (Fig. 12-3B), and in some cases the mouth is nearly closed before the gill cover has undergone significant lateral excursion (Liem, 1970; Lauder, 1979; 1980a,d). In addition, opening of the opercular and branchiostegal valves occurs during the compressive phase, indicating that water sucked into the buccal cavity during the expansive phase has only just begun to exit to the outside after passing through the gills (Fig. 12-3B). In some cases water does not begin to emerge from the opercular cavity until the jaws have closed completely. Retraction of the protruded premaxillae also occurs during the compressive phase (Fig. 12-3C, frames 4,5,6), and the maxilla, which has rotated anteriorly about its dorsal palatal articulation, returns to its position during the preparatory phase. The lower jaw is often adducted against partially protruded premaxillae, but the relative timing of lower jaw adduction and premaxillary retraction varies with the type of prey and the velocity of jaw movement.

The recovery phase is defined as the time from the end of the compressive phase (zero gape) to return of the skull bones to their initial position before the preparatory phase. This phase may last 0.5 sec or longer if a large prey has been captured. Usually the gill cover is the last bone to return to the resting position (Fig. 12-3B), although hyoid depression, cranial elevation, and suspensory abduction all are present at the time the jaws close and are thus major movements also occurring during the recovery phase.

The pattern of bone movement during prey capture exhibits an anterior-to-posterior se-

quence of peak excursions. Thus, mouth opening peaks before hyoid depression, which peaks before suspensory abduction and opercular abduction (Fig. 12-3B). This pattern is remarkably consistent in all suction-feeding ray-finned fishes studied, and it is also found in the aquatic turtles and salamanders discussed below.

Comparative analyses of suction feeding in lower vertebrates have revealed that the hyoid apparatus produces the main change of volume in the mouth cavity during the expansive phase (and thus contributes the most to the creation of negative pressures), and that movement of the hyoid is similar in all major groups of lower vertebrates. In ray-finned fishes, coelacanth, lungfishes, and probably also acanthodians, the hyoid bar (ceratohyal, epihyal, and hypohyals) on each side articulates with the palatoquadrate by a small rodlike interhyal (Fig. 12-2). The primitive living members of each lineage also possess a strong ligament between the ceratohyal or epihyal and the posteroventral aspect of the mandible (ligament l_2 in Fig. 12-2). It thus appears that coupling 3, discussed above as one of the two mechanisms in teleost fishes that mediate mandibular depression during the expansive phase, is also the primitive system for abducting the lower jaw in teleostome vertebrates.

Mandibular depression via the hyoid apparatus involves both dorsoventral and anteroposterior movements of the hyoid, and these reach a maximum at different times (Fig. 12-5). Anteroposterior excursion peaks in the expansive phase shortly after the mouth begins to open and the initial posterior component of hyoid movement is primarily responsible for rapid depression of the lower jaw. Dorsoventral excursion of the hyoid peaks during the compressive phase and produces a large increase in buccal volume, which results in high flow velocities into the mouth. In lungfishes (Fig. 12-6), as in coelacanth, primitive ray-finned fishes, and probably acanthodians, the hyoid coupling is the only mechanism mediating mandibular depression. This pattern of hyoid movement is basic to lower vertebrates (Fig. 12-5) and was a fundamental feature of the early tetrapod feeding mechanism.

With this background on the pattern of muscle activity and bone movement during suction feed-

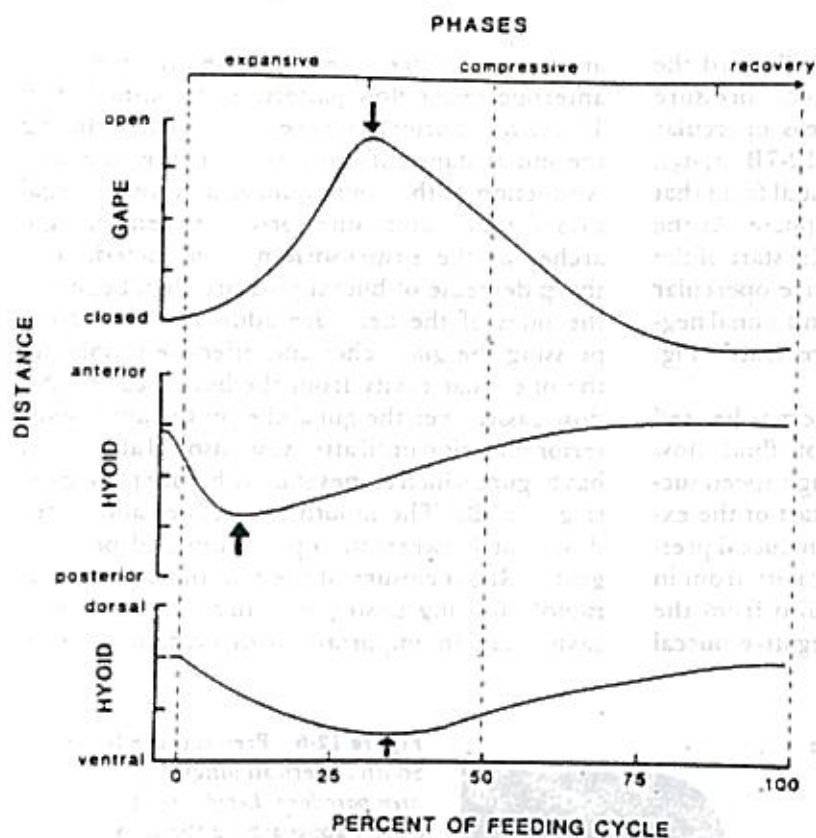


Figure 12-5 The relationship between hyoid movement and gape in primitive gnathostomes (lungfishes, coelacanths, and ray-finned fishes). Arrows indicate peak excursion. Note that anteroposterior excursion of the hyoid peaks during the expansive phase, whereas its dorsoventral movement peaks during the compressive phase. The initial posterior movement of the hyoid apparatus is related to mandibular depression via coupling 3 (Fig. 12-2).

ing, the pattern of pressure change in the mouth cavity can be examined and a general hydrodynamic model for suction feeding proposed. One experimental approach used to measure pressure in the buccal and opercular cavities during feeding is illustrated in Figure 12-7A. Cannulae are chronically implanted in the buccal and opercular cavities and attached to two transducers located above the aquarium. The cannulae and the pressure transducers are filled with a viscous fluid that allows pressure changes in the mouth cavity to be transmitted to the transducer diaphragm. High-speed FM tape records of pressure changes are played back at a greatly reduced speed through a chart recorder for analysis (Fig. 12-7B). Many technical problems are associated with measuring pressures with fluid-filled cannulae (summarized in Lauder, 1980b), the most serious of which is the low-frequency response (about 100 Hz) of the transducer. Newer techniques avoid these difficulties (Lauder, 1983a).

The pressure patterns recorded during suction feeding may be correlated with the four kinematic phases defined above by synchronizing a high-speed film with the pressure traces. When a preparatory phase is occurring, a sharp positive pressure pulse, caused primarily by hyoid protraction, is recorded in the buccal cavity (Fig. 12-7B, buccal pressure). During the start of the expansive phase, pressure in the buccal cavity drops precipitously, whereas pressure in the opercular cavity usually increases slightly. In a rapid and high-speed act of suction the pressure differential across the gills may reach 400 cm H_2O . At about the middle of the expansive phase, pressure in the opercular cavity begins to drop. It reaches a low value of -150 cm H_2O , which is considerably less than the -650 cm H_2O recorded in the buccal cavity (Fig. 12-7B). Buccal pressure reaches a minimum prior to opercular cavity pressure, and maximum negative values for both are reached in the compressive phase or

at the end of the expansive phase. Toward the end of the compressive phase, buccal pressure rapidly returns to ambient, whereas opercular pressure remains negative (Fig. 12-7B: t_4 - t_5), thus reversing the pressure differential from that of the beginning of the expansive phase. At the end of the compressive phase and the start of the recovery phase there occur a positive opercular pressure and both a short positive and a final negative pulse in the buccal pressure trace (Fig. 12-7B).

These patterns of pressure change may be used to formulate a general model of fluid flow through the mouth cavity during high-speed suction feeding (Fig. 12-7C). At the start of the expansive phase the rapid reduction in buccal pressure causes a flow into the buccal cavity from in front of the mouth and perhaps also from the opercular cavity posteriorly. As negative buccal

and opercular pressures decrease, the dominant anteroposterior flow pattern is established (Fig. 12-7C, t_5). A brief flow reversal may occur during the initial stages of high-speed suction feeding. Adduction of the operculum and branchiostegal rays forces water anteriorly between the gill arches as the suspensorium is adducted. The sharp decrease of buccal pressure then begins as the sides of the head are adducted, thus compressing the gill arches and effectively isolating the opercular cavity from the buccal cavity. No flow passes over the gill arches in the anteroposterior direction until after suspensorial abduction has begun, which comes shortly before peak gape (Fig. 12-3B). The mouth then closes and water flows out between the operculum and pectoral girdle. Rapid closure of the mouth while fluid is rapidly moving posteriorly through the mouth cavity has an important hydrodynamic conse-

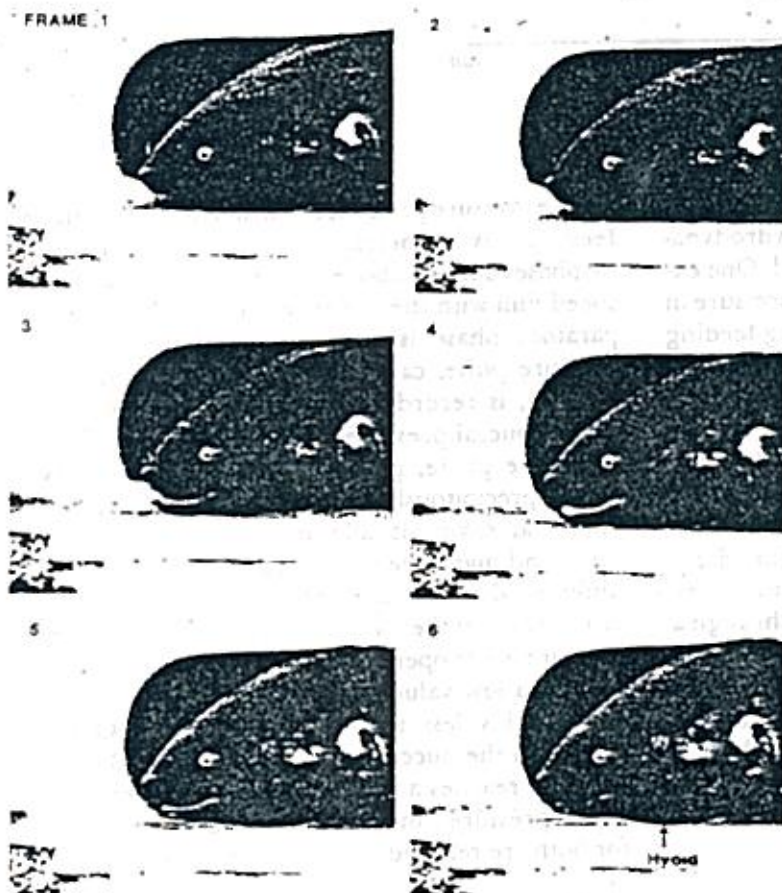


Figure 12-6. Prey capture by the South American lungfish *Lepidosiren paradoxa*. *Lepidosiren* feeds by closely approaching the prey, using a relatively narrow gape (with a consequent high velocity of flow) and rapid and extreme hyoid depression (arrow). The film was taken at 200 frames/sec; the time between sequential frames is 0.05 sec. The duration of the expansive phase in this sequence is 20 msec, and the total feeding sequence takes 35 msec.

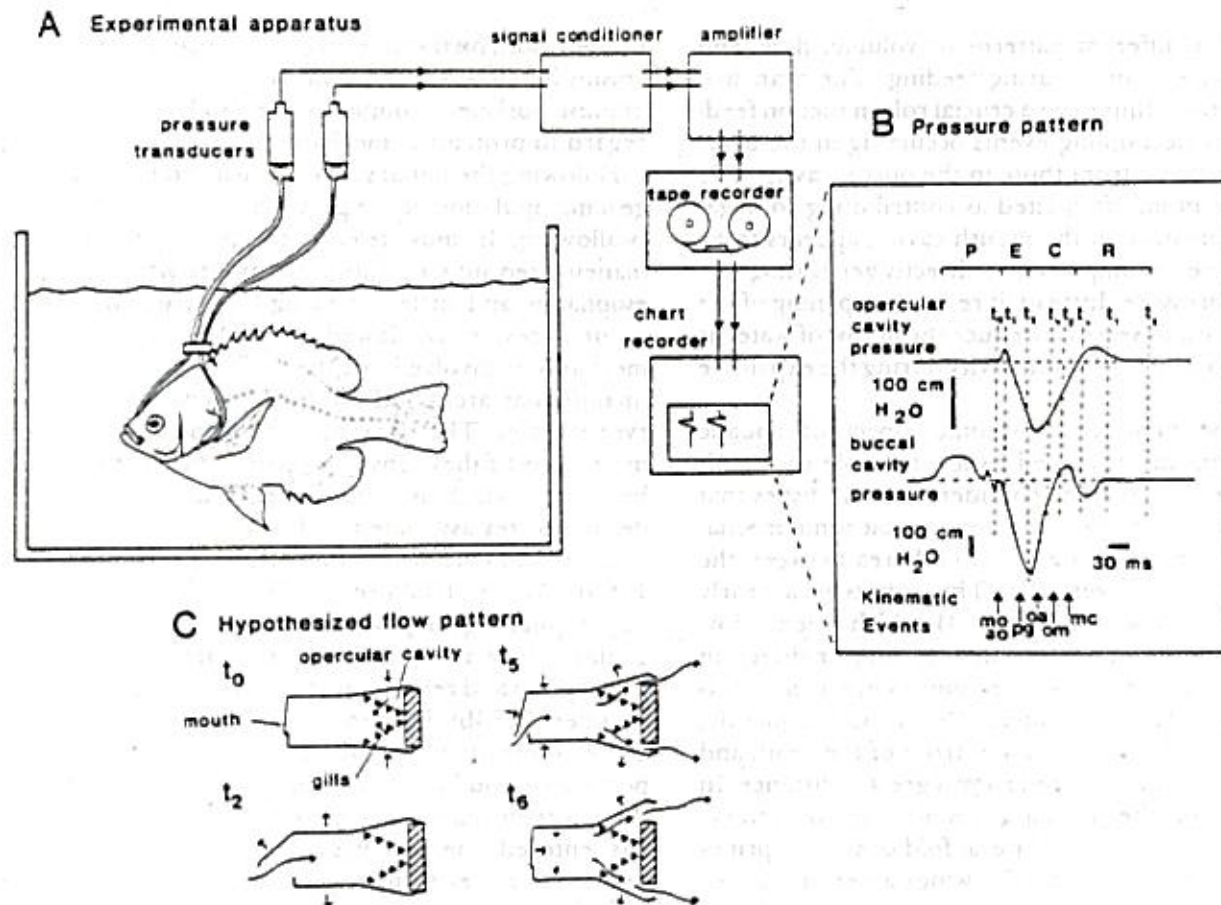


Figure 12-7 A: Experimental apparatus for recording pressures in the mouth cavity of fishes. Cannulae are implanted in the buccal and opercular cavities and are attached to transducers located above the aquarium. B: Representative traces from the buccal and opercular cavities of a bluegill sunfish *Lepomis macrochirus* feeding on a goldfish. The phases are: P = preparatory; E = expansive; C = compressive; and R = recovery. The preparatory phase is not found in all feeding events. Kinematic events are: mo = mouth opening; ao = opercular adduction; pg = peak gape; oa = opercular abduction; om = branchiostegal valve opens; mc = mouth closure. C: Proposed fluid flow through the mouth cavity during high-speed suction feeding over the period t_0 to t_6 . Large arrows indicate directions of flow; small arrows indicate movements of bones.

quence that is responsible for the second negative pressure pulse in the buccal cavity (Fig. 12-7B). This second pressure reduction is due to the "water hammer effect" — rapid closing of a valve in a pipeline having fluid flowing through it results in a sharp pressure decrease on the downstream side of the valve. This is exactly what happens when the mouth rapidly closes (in 15 msec) during feeding; a sharp pressure reduction occurs at the level of the vomer and anterior end

of the parasphenoid. During feeding on slowly moving prey, when the velocity of mandibular adduction is low, the second negative pressure phase is absent.

The key concept to emerge from the analysis of pressure records of suction feeding in ray-finned fishes is the role of the gills and gill arches as a resistant element in the mouth cavity; the branchial apparatus functionally segregates the mouth cavity into two distinct subsections that

exhibit different patterns of volume, flow, and pressure change during feeding. The branchial apparatus thus plays a crucial role in suction feeding by decoupling events occurring in the opercular cavity from those in the buccal cavity. The operculum, often cited as contributing to negative pressure in the mouth cavity, appears to be relatively unimportant in directly generating suction pressure. Instead, it regulates opening of the mouth and serves to reduce the inflow of water at the back of the mouth cavity during the expansive phase.

One final hydrodynamic aspect of aquatic feeding in ray-finned fishes, the role of mouth shape, merits some consideration. All fishes that feed by high-speed suction exhibit some mechanism for occluding the lateral area between the upper and lower jaws. This results in a nearly circular gape (see Fig. 12-4), which orients flow streamlines in a more anteroposterior direction than if the corners of the mouth were open (Alexander, 1967; Lauder, 1979). Consequently, water is drawn in from in front of the head, and prey may be captured from a greater distance. In *Polypterus* the jaw margin is occluded by a thickened and expanded lateral fold of skin; in primitive teleosts the maxilla swings anteriorly to occlude the corner of the mouth (Fig. 12-4); whereas in more advanced teleosts the premaxilla serves this function.

Protrusion of the upper jaw, or movement of the premaxilla and maxilla (relative to the neurocranium) toward the prey, has evolved independently in a number of teleost lineages. Protrusion is an especially important aspect of suction feeding in many advanced teleost fishes (Fig. 12-3C), yet the protrusion mechanisms remain poorly understood. Numerous hypotheses have been proposed to explain the "advantage" of protrusible jaws, but each suffers from many counterexamples (protrusion mechanisms are reviewed in Lauder and Liem, 1981). At least four separate mechanisms have been proposed, but although some kinematic and electromyographic data are consistent with each, no mechanism has been subjected to a controlled experimental analysis. In short, jaw protrusion has been the subject of considerable speculation, yet further work is badly

needed, both on the diversity of protrusion mechanisms in teleosts and on the detailed mechanics of musculoskeletal couplings (see also Fig. 18-2 in regard to protrusion mechanisms).

Following the initial strike, buccal and pharyngeal manipulation of the prey may occur prior to swallowing. In most teleosts the prey is simply maneuvered into a position for transport to the esophagus and little "chewing" or maceration occurs; prey are swallowed whole. Manipulatory mechanisms involve both the oral jaw apparatus (mandibular arch) and the hyoid arch and pharyngeal jaws. The pharyngeal jaw apparatus of most teleost fishes consists of paired fifth ceratobranchials, which usually bear teeth, and toothed dermal plates associated with the posterior epibranchial and pharyngobranchial bones (Nelson, 1969). These structures form the lower and upper pharyngeal jaws, respectively. Prey are swallowed by a regular, rhythmic simultaneous protraction and retraction of the pharyngeal jaws (Lauder, 1983b). Both the upper and lower jaws move anteriorly to grip the prey and then move posteriorly, pulling it into the esophagus. This cycle is then repeated until the entire prey item has entered the esophagus. This description probably applies to many teleostean fishes, but experimental analyses of more primitive ray-finned fishes are lacking.

Several clades of teleosts have modified the primitive pharyngeal transport mechanism, in which prey are swallowed whole, to perform masticatory and crushing functions. The most prominent lineage is the Pharyngognathi (Liem and Greenwood, 1981), which includes the cichlids, wrasses, parrotfishes, and damselfishes. In these fishes the two lower pharyngeal jaws are firmly attached in the midline and form a single unit. The upper pharyngeal jaws are hypertrophied and articulate with the base of the skull. Prey, or food-encrusted shells and rocks, are crushed by strong adduction of the pharyngeal jaws and may be subjected to extensive manipulation or shredding prior to swallowing (Liem, 1978).

Salamanders Prey capture by suction feeding is found in a variety of salamanders from different lineages. Presumably, aquatic feeding is primitive

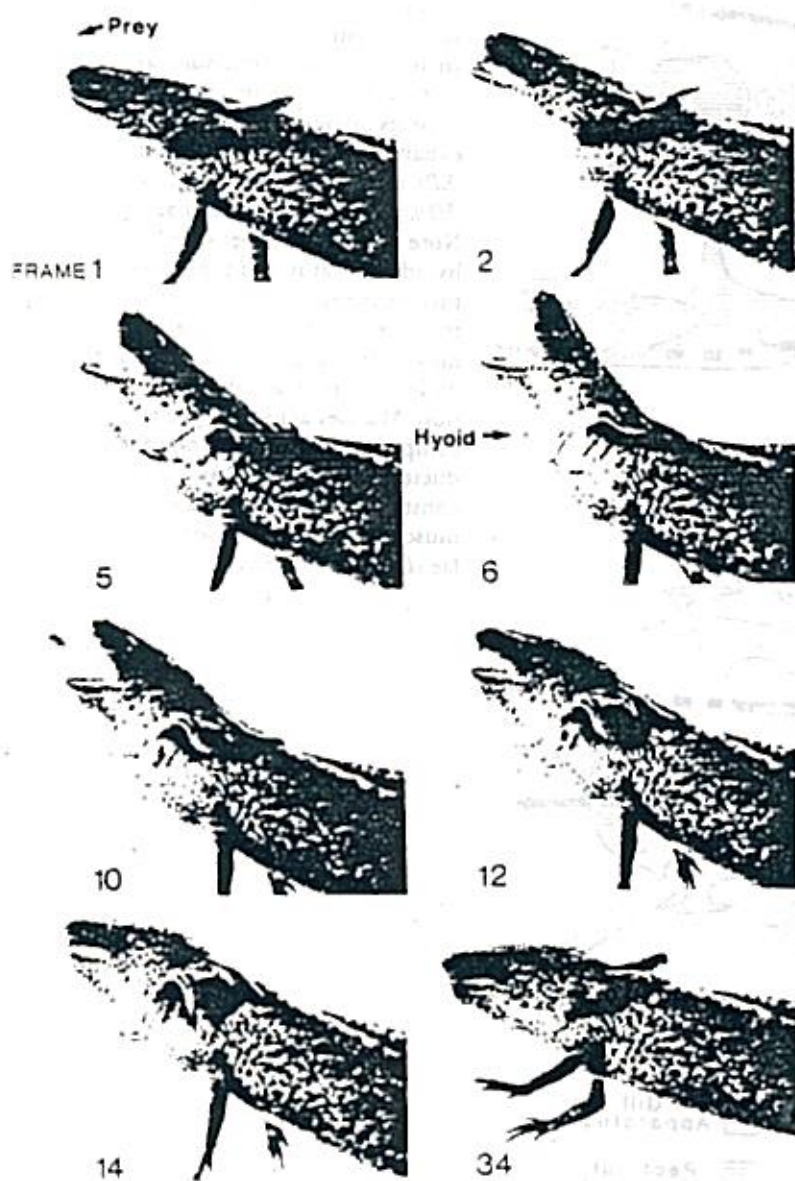


Figure 12-8 Frames from a high-speed film (200 frames/sec) of aquatic prey capture by *Ambystoma mexicanum*. The prey is a small piece of earthworm dropped down from above the head. Note the rapid expansive phase (frames 1-6), the extreme hyoid depression, and the dorsoventral extension of the gill arches.

for urodeles, and many living salamanders are either totally aquatic (*Pachytriton*), feed aquatically during larval periods (*Ambystoma*), or return to the water to feed during the breeding season (*Taricha*, *Notophthalmus*) (Ozetti and Wake, 1969).

The dynamics of aquatic feeding in salamanders has not been examined in detail since the early work by Matthes (1934), but high-speed films of feeding (Fig. 12-8) and an analysis of the

major muscles and mechanical units of the head (Fig. 12-9) strongly suggest a close similarity to ray-finned fishes (Shaffer and Lauder, in press,a,b). For the purposes of comparison the suction-feeding act in aquatic salamanders may be divided into the four phases used to describe ray-finned fishes above. A preparatory phase is difficult to demonstrate by kinematic data alone and thus the high-speed film frames shown in Figure 12-8 provide no evidence for a preparatory

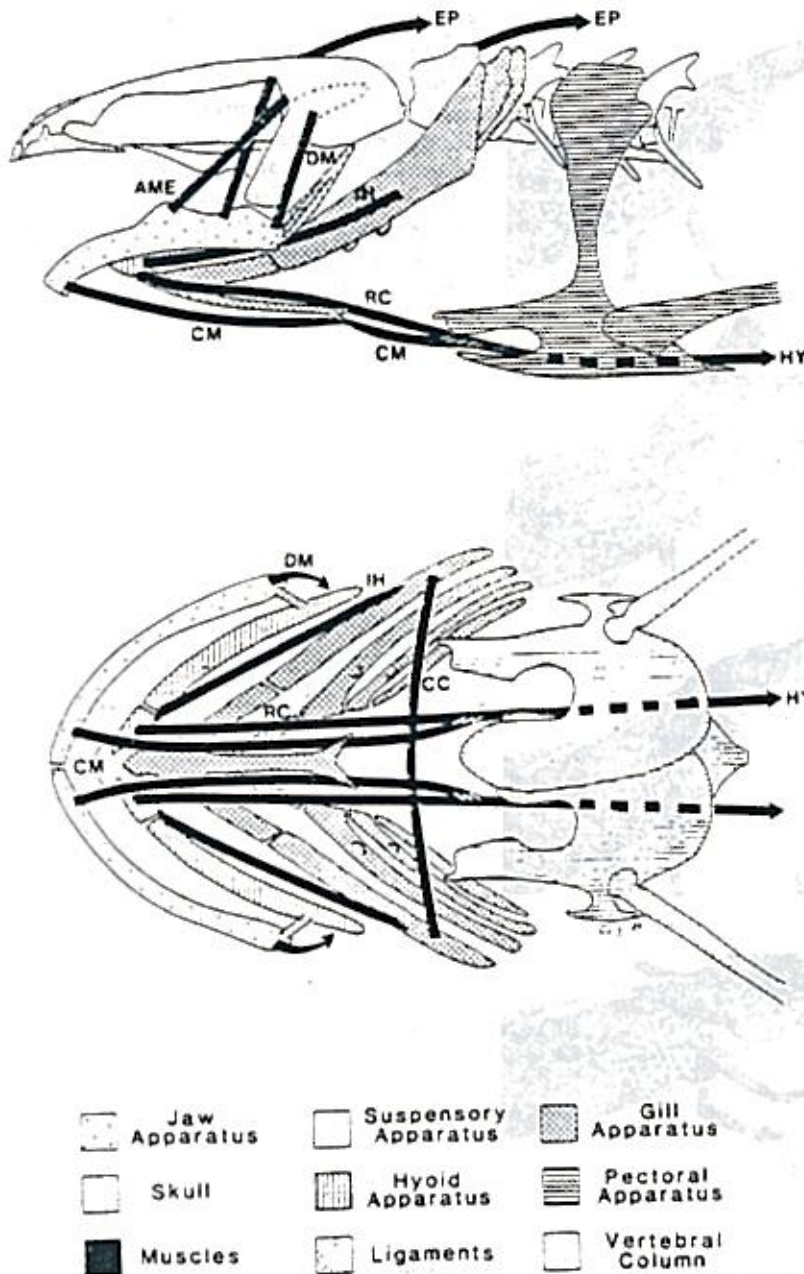


Figure 12-9 The major muscles and mechanical units in the head of an aquatic salamander such as *Ambystoma mexicanum*. The major muscles involved in the rapid expansive phase are the epaxialis (*EP*), rectus cervicis (*RC*), hypaxialis (*HY*), and coracomandibularis (*CM*). Note the ligament between the hyoid apparatus and the lower jaw: this ligament is important in transferring the posteroventral movement of the hyoid to the mandible and aids mandibular depression. Muscles active during the compressive phase include the adductor mandibulae (*AME*) and constrictor colli (*CC*). Other muscles are the depressor mandibulae (*DM*) and interhyoideus (*IH*).

reduction in buccal volume. However, a decrease in buccal volume could easily be achieved by synchronous activity of the adductor mandibulae and coracomandibularis (Fig. 12-9) prior to mouth opening (for instance, in Fig. 12-8, frame 1). Electromyographic evidence will be needed to demonstrate a preparatory phase. The expansive

phase (Fig. 12-8, frames 1–6) lasts only 25 msec, as maximum gape is achieved very rapidly. Hyoid depression begins early in the expansive phase as the result of electrical activity in the rectus cervicis and its intrabranchial muscle slips (Fig. 12-9). As in ray-finned fishes the pectoral girdle moves posteriorly during the expansive phase as a

result of strong activity in the hypaxial body musculature that attaches to it. The forelimbs also move posteriorly as the girdle is retracted.

Mandibular depression is the result of activity in the depressor mandibulae, but based on the kinematic pattern illustrated by Figure 12-8, the ventral body and throat muscles and the hyoid and branchial apparatus appear to play an equally important role. Posterior movement of the pectoral girdle and hyoid resulting from contraction of the hypaxial and rectus cervicis muscles could be transmitted to the mandible either through the geniohyoideus muscles, which may be synchronously active, or via ligamentous connections between the ceratohyal and mandible. Elevation of the neurocranium by the epaxial musculature is also a prominent feature of the expansive phase.

The compressive phase is slightly longer in duration than the expansive phase, lasting about 35 msec. Hyoid depression reaches its peak during the compressive phase, and by the end of this phase the ceratohyal cartilages have reached a nearly vertical position, which causes a small prominence in the throat region beneath the eye (Fig. 12-8, frame 10). The adductor mandibulae appears to be primarily responsible for adduction of the lower jaw. During the recovery phase the hyoid apparatus returns to its resting position, presumably as a result of activity in the coracomandibularis or geniohyoideus, and the pectoral girdle and forelimbs are protracted.

One point of great similarity in aquatic prey capture between fishes and *Ambystoma mexicanum* is that flow does not begin to emerge from between the gill arches until the very end of the expansive phase. In the salamander maximum dilation of the skin covering the gill bars laterally is not achieved until the end of the compressive phase (compare with the delay in opercular abduction shown in Fig. 12-3B).

Perhaps the salient feature that distinguishes the dynamics of aquatic feeding in salamanders from that of fishes is the lack of a well-defined opercular cavity bounded laterally by bony elements. This morphological difference may have relatively little effect on suction dynamics, however, if, as in fishes, the branchial apparatus constitutes an important barrier to flow. If this is

true, then the gills and gill arches of aquatic salamanders are analogous to the operculum of teleosts in preventing fluid inflow from the back of the buccopharyngeal cavity during the expansive phase and in delaying outflow until the compressive phase. Alternating gill rakers on adjacent arches, may, as in fishes, function to create a resistance to flow until the expansive phase is over.

Ozeti and Wake (1969) identified several anatomical features of aquatic or partially aquatic salamanders that seem to be related to specialization for suction feeding. A reduction in the size of the tongue and tongue pad is common, as is a relatively robust hyoid and branchial skeleton. Figure 12-8 demonstrates that the pattern of hyoid and branchial movement in at least some aquatic salamanders very closely resembles that of fishes, especially in the sharp posteroventral hyoid rotation near the start of the expansive phase. In an interesting parallel with fishes, salamanders that return to the water to breed develop labial "lobes" (Ozeti and Wake, 1969), which serve the same function as the various structures of actinopterygians that prevent water inflow lateral to the jaws.

Primitive salamanders exhibit many features of the cranial musculature that are common to other lower vertebrates, and the pattern of jaw movement during aquatic feeding is similar to that seen in fishes. Thus, despite several major differences in skull morphology, the primitive suction-feeding mechanism is clearly comparable with that of fishes and exhibits many of the jawbone movements that are primitive for teleostomes.

Turtles Many turtles feed aquatically, and several possess a high-speed suction-feeding mechanism capable of capturing prey in only 30–50 msec (Shafland, 1968; D. M. Bramble, personal communication). The snapping turtle *Chelydra* and the mata-mata (*Chelus*) are two of the best known turtles that feed by suction, but aquatic feeding has also evolved in several other lineages. From the preliminary data available in the Shafland and Bramble papers (see Fig. 12-10), suction feeding in turtles seems to show many similarities to that of aquatic salamanders and fishes, although, to be sure, there are also key differences. A preparatory phase has been ob-

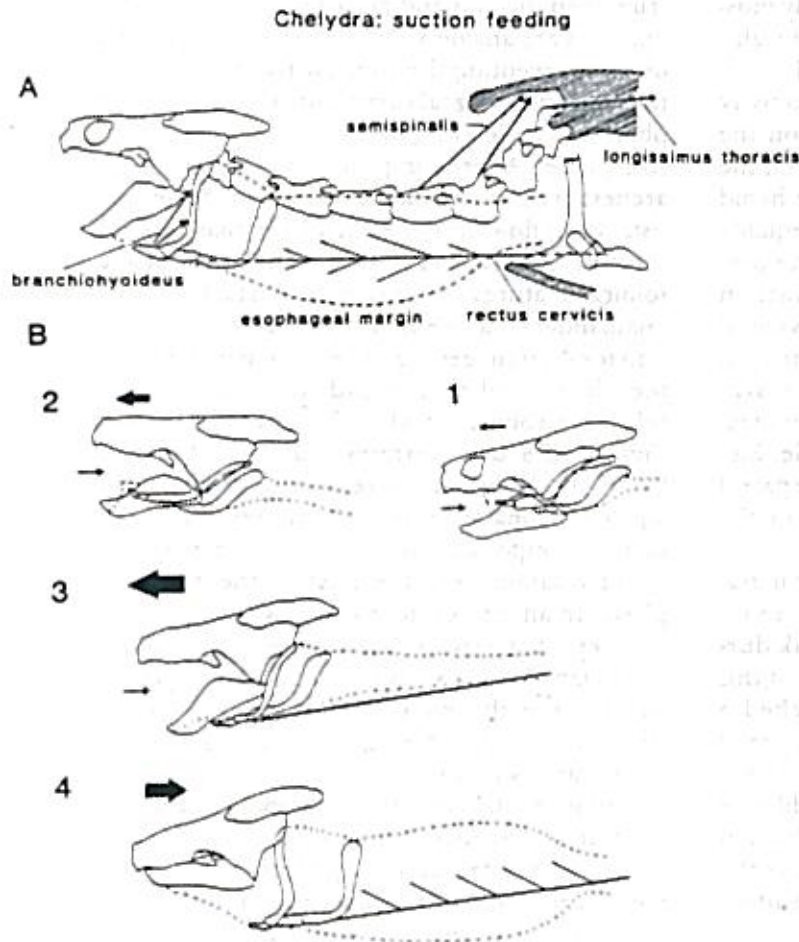


Figure 12-10 A: The major muscles and mechanical units involved during aquatic prey capture in turtles. B: Major movements occurring during prey capture in *Chelydra*. Large arrows indicate movement of the head, which is rapidly thrust at the prey during the expansive phase and part of the compressive phase; small arrows indicate fluid flow into the mouth. Stage 1: preparatory phase. Bramble (1982) has shown that this phase differs from that in teleost fishes in that the mandible is depressed while the hyoid is protracted, and water is forced anteriorly out of the esophagus. Stages 2 and 3: beginning and end of the expansive phase. Stage 4: end of the compressive phase. Head retraction is occurring at this time and water flow continues posteriorly within the esophageal bag. (Figure modified from Bramble, 1982.)

served by Bramble in which the mandible is partially depressed while the hyoid and tongue are protracted (presumably by the branchiohyoideus muscles, Fig. 12-10A), thus reducing buccal volume (Fig. 12-10B, drawing 1). Esophageal compression also occurs at this time to reduce intraoral water volume. During the expansive phase (Fig. 12-10B, drawing 2,3) the head and neck are rapidly accelerated toward the prey, and water begins to flow into the buccal cavity as depression of the hyoid begins. Mandibular depression may be partially due to activity in the rectus cervicis and geniohyoideus muscles, and the epaxial musculature is active to elevate the cranium. The expansive phase may be extremely rapid (50 msec or less). During the compressive phase jaw closure occurs as a result of activity in the adductor mandibulae, and the head and neck

begin to move posteriorly (Fig. 12-10B, drawing 4). The hyoid reaches maximum posteroventral rotation during this phase, and expansion of the esophagus occurs as a result of tendinous insertions from the rectus cervicis (D. M. Bramble, personal communication). Esophageal expansion reaches a maximum in the recovery phase (Shafland, 1968), although eventually the hyoid and esophagus return to their resting positions. Turtles thus show the two basic attributes of suction feeding mentioned earlier: posteroventral rotation of the hyoid apparatus, which makes a major contribution to expansion of the buccal cavity; and an anteroposterior sequence in peak excursion of successive movements of head elements. In turtles this sequence is mouth opening, hyoid depression, and esophageal expansion. Esophageal expansion, which starts late in the compressive

sive phase and reaches a peak in the recovery phase, appears to be analogous to expansion of the opercular cavity in fishes, serving to maintain unidirectional flow at the mouth opening until the jaws have closed on the prey.

One obvious difference between aquatic feeding in turtles and adult salamanders and feeding frogs on the one hand and most fishes on the other is the presence of bidirectional flow in most of the former. Water entering the mouth during the expansive phase must ultimately exit by the same path it entered, and this reverse flow must be timed so as not to greatly reduce the intake velocity and jeopardize the chances of prey capture.

The principles of the dynamics of aquatic feeding discussed earlier permit several predictions concerning comparative pressure and flow patterns in unidirectional and bidirectional feeding systems. First, because of the nonsteady flow pattern during suction and the dominance of inertial effects, almost no difference in either flow or pressure patterns will be observed during the expansive and early compressive phases. Second, flow velocities will peak in the expansive phase and as the jaws close, and a second negative pressure will be recorded just inside the jaws owing to the water hammer effect. Third, in bidirectional flow systems pharyngeal pressure will show either a single prolonged positive pressure pulse or a biphasic pattern with a negative phase occurring during the flow reversal.

The major difference between unidirectional and bidirectional flow systems concerns the patterns of pharyngeal and opercular pressure that occur late in the feeding cycle. The highly nonsteady flow dynamics of suction feeding ensures that the inability of water to escape posteriorly will have little effect, if any, on flow and pressure patterns in the expansive phase and most of the compressive phase.

Conclusions and Summary

A remarkably consistent pattern of head movements is found in aquatic vertebrates that feed by inertial suction. The hyoid apparatus in particular appears to represent a fundamental element in

aquatic feeding systems, at least since the appearance of the first teleostomes (the acanthodians) in the Silurian. In forms as diverse as sturgeons, perch, coelacanths, lungfishes, turtles, and salamanders, the hyoid apparatus retains its dominant role in producing large and rapid volume changes of the oral cavity by means of posteroventral rotation.

A second consistent aspect of suction feeding is the anteroposterior sequence of cranial expansion and the importance of this sequence in mediating nonsteady flow regimes during suction. The importance of distinguishing between nonsteady and steady flow regimes cannot be overemphasized, because the hydrodynamic models, fluid properties, and assumptions underlying cause-effect relationships between kinematics and pressures are radically different for the two flow patterns (Webb, 1978; Streeter and Wylie, 1979; Osse and Muller, 1980). Steady-state models (for instance, the Poiseuille relation) result in gross errors when applied to dynamic flows.

The dynamics of prey capture in fishes has been the subject of many investigations in the last decade, and the use of techniques such as high-speed cinematography, pressure transducers, and electromyography has resulted not only in a greater understanding of trophic mechanics in fishes, but also in an emerging set of general principles and concepts for aquatic prey capture. But in order to achieve a comprehensive understanding of the process, data comparable to that on fishes must be acquired for turtles, salamanders, and anurans. Comparative information will allow the testing of models of pressure change and fluid flow and will permit the assessment of differences between bidirectional and unidirectional feeding systems. It is important to realize that in any comparative study of functional morphology, the techniques applied to examine structure and function have a significant influence on the type of questions asked and the level of detail in which the system is analyzed. Unless pressure transducers and electromyography are used in the study of aquatic feeding in vertebrates other than fishes, it will be difficult to develop general concepts of aquatic prey capture. New techniques not only allow greater descriptive precision, but also

open up new questions and problems and expose inconsistencies in previous accounts. In fishes, for example, prior to the *in vivo* use of pressure transducers, steady-state models were the descriptive paradigm for suction feeding. It is now clear that this approach is inadequate and that descriptions of aquatic feeding will need to be framed in a dynamic context.

Research on the dynamics of filter feeding in fishes, by contrast, lags far behind studies on other vertebrates. The feeding dynamics and mechanics of particle capture are virtually unknown despite the importance of filter-feeding fishes in aquatic food chains. It remains to be seen if the properties of filter-feeding systems are as consistent as those of suction feeding appear to be. The existence of multiple theoretical mechanisms for entrapping particles, as well as the independent evolution of filter-feeding systems in several ver-

tebrate lineages, suggests, however, that a considerable diversity of approaches to filter feeding may occur. The extent to which this diversity is a consequence of the variation available in systems with steady-state flow regimes (in contrast to the apparently rigid constraints imposed by the use of nonsteady dynamic flows) will be of considerable interest and significance in determining the role of extrinsic, environmental factors in governing the design of vertebrate structure. Relatively steady, low-velocity flows may permit a wider range of functional and structural solutions to the problem of capturing prey than high-speed flows having nonsteady dynamic characteristics. The constraints imposed on jaw function by the use of high-velocity flows may be responsible for the remarkable uniformity in kinematic patterns observed during suction feeding in lower vertebrates.

I thank D. Bramble and J. Mallatt for making available unpublished information, B. Shaffer for his assistance in filming aquatic salamander feeding, and J. Hives for her assistance in preparing the manuscript. Reviews of this chapter by the editors of the volume are greatly appreciated. Preparation of this paper was supported by grants from the Andrew W. Mellon Foundation, the Block Fund of the University of Chicago, and NSF DEB 81-15048.

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