

Chapter 9 FOOD CAPTURE

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INTRODUCTION

The capture of energy is a process of fundamental importance to the growth, reproduction, and maintenance of physiological function in organisms. Energy is the focus of many physiological analyses that seek to determine how energy use is distributed among various body functions and the metabolic costs of locomotion, breathing, or reproduction. Energy is often the currency used to compare alternative life-history strategies, and it provides a common denominator for optimality models of behavior and ecology (see Chap. 11).

Despite the important role of energy use in discussions of fish mechanics and ecology, we are just beginning to understand the actual processes by which energy is acquired: the biomechanical pathways and mechanisms underlying the capture of prey items. The feeding apparatus provides an especially interesting problem in fish mechanics. The cranial musculoskeletal system is an extremely complex multilinkage system with over 30 movable bony elements controlled by more than 50 muscles. Furthermore, movements of this complex feeding apparatus may occur extremely quickly, and fishes are known to possess the most rapid feeding mechanisms in vertebrates: prey capture can occur in 0.012 sec (Grobeck and Pietsch, 1979).

The primitive method of prey capture in vertebrates was probably suspension feeding (Mallatt, 1981). Suspended matter in the water column of

organic material on the bottom were filtered by the branchial apparatus or mucus in the pharynx. Many extant fish species capture prey by combining a high-velocity attack with rapid mouth opening to trap prey in the oral cavity, and both predator body velocity and jaw movements are important components of feeding behavior. Sustained high-velocity attacks used to overtake prey is the capture method used by many elasmobranchs and appears to be primitive for ray-finned fishes.

In teleost fishes suction feeding is the dominant aspect of food capture. Body velocity during the strike may contribute less to the capture of prey than does rapid high-volume water flow entering the mouth cavity. Suction feeding (or inertial suction feeding) involves rapid mouth cavity expansion that causes an intraoral pressure reduction relative to the surrounding water. This results in water flowing rapidly into the mouth carrying in the prey. During suction feeding, prey tend to be drawn toward the predator by water entering the mouth cavity. The major structural modifications relating to high-speed suction feeding are found first in the halecomorph fishes (e.g., *Amia*) and have been retained in most teleost lineages. One key aspect of the teleost radiation is the structural and functional diversification in the feeding mechanism (Marshall, 1971), and the primitive suction mechanism of teleosts has been modified greatly in relation to different prey and habitat types.

This chapter analyzes the biomechanics of suction feeding in teleost fishes, the mechanics of intraoral prey manipulation and transport following initial capture, and certain evolutionary and ecologic aspects of feeding mechanics. Filter feeding has evolved independently in many teleost clades and will be discussed as a contrast to suction-feeding mechanisms.

MECHANICS OF SUCTION FEEDING

Suction feeding may be divided into a number of discrete phases each having distinct kinematic, electromyographic, and pressure attributes (Table 9-1). The preparatory phase occurs before mouth opening and involves buccal and opercular cavity compression that forces water out and reduces mouth volume. The expansive phase, defined for convenience by mouth opening movements, begins as the jaws first open and lasts until peak gape has been reached. The compressive phase extends from peak gape to closure of the jaws, while the recovery phase is the time after mouth closure in which skeletal elements return to their initial position. The expansive phase can be explosively rapid (from 10 to 50 msec in most high-speed suction feeding fishes) and is usually 20% to 50% shorter than the compressive phase.

The buccal cavity is defined as that portion of the mouth cavity lying anterior to the gill arches, medial to the suspensory apparatus, and posterior to the buccal valve. The opercular (gill) cavity is bounded laterally by the operculum, posteriorly by the pectoral girdle and body wall, anteriorly by the

Table 9-1
PHASES OF PREY CAPTURE IN GENERALIZED PERCOMORPH FISHES

PHASES	MAJOR ATTRIBUTES		
	Pressure	Electromyographic	Kinematic
Initial Strike			
Preparatory	Buccal cavity positive	Adductor arcus palatini, adductor mandibulae, geniohyoideus, pharyngohyoideus muscles active	Hyoid and suspensorium protracted
Expansive	Buccal and opercular cavities negative	Levator operculi, sternohyoideus active	Mouth opens; hyoid retracted
Compressive	Buccal cavity positive; opercular cavity negative	Adductor mandibulae, geniohyoideus muscles active	Mouth closes; opercular abduction
Recovery	Buccal cavity negative → ambient; opercular cavity positive → ambient	Adductor operculi, adductor mandibulae, geniohyoideus active	Opercular adduction; hyoid protraction
Buccal Manipulation	Similar to initial strike	Sternohyoideus, hypaxialis, levator operculi active; no preparatory phase	Similar to initial strike without the preparatory phase
Pharyngeal Manipulation	—	Sternohyoideus inactive; hypaxialis and branchial musculature active	Pectoral girdle retraction; abduction of pharyngeal jaws
Transport	—	Rhythmic activity in pharyngeal muscles; no activity in sternohyoideus, epaxialis, or hypaxialis	Alternate protraction and retraction of the upper and lower pharyngeal jaws

— No available data.

gill filaments and arches, and ventrally by the branchiostegal rays. It is extremely important to realize that the buccal and opercular chambers form functionally distinct units and cannot be treated as one in considering suction dynamics.

The anatomic basis of suction feeding will not be described in detail here, and the reader is referred to Liem (1970, 1978), Lauder and Liem (1980), Osse (1969), and Tchernavin (1953) for anatomic descriptions. Suffice it to note that buccal expansion is achieved by abduction of all four sides of the cavity: hyoid depression and cranial elevation in the ventral and dorsal aspects, lateral movement of the suspensory apparatus, and anterior extension of the upper jaw bones (maxilla or premaxilla). The opercular cavity is expanded primarily by lateral movement of the gill cover and ventral expansion (abduction) of the branchiostegal rays. Posterior rotation of the pectoral girdle on the skull may also contribute to opercular cavity volume increase.

Kinematics and Muscle Mechanics

During high-speed suction feeding there is extensive overlap in the timing of electrical activity between the different cranial muscles, particularly during the expansive phase (Fig. 9-1). The preparatory phase, usually of much longer duration than the expansive phase (up to 0.5 sec), shows less synchrony. The major preparatory phase muscles include the adductor mandibulae (part A2.3) and the geniohyoideus, which together cause hyoid protraction, and the adductor operculi and adductor arcus palatini, which compress the mouth cavity laterally. Interestingly, several branchial muscles are also active during the preparatory phase (Fig. 9-1). The pharyngohyoideus protracts the entire branchial basket, while the levatores externi (parts 3 and 4) draw the upper gill arch elements (pharyngobranchials and epibranchials) forward. Just as the expansive phase begins, the branchial apparatus may be moved posterioventrally by activity in the pharyngocleithralis internus and externus.

During the expansive phase, both buccal and pharyngeal muscles are active to rapidly expand the mouth cavity (Fig. 9-1). The expansive muscles of the buccal cavity have short duration bursts (<50 msec) and may only lead the compressive phase muscles by 5 minutes (Lauder, 1980b). Rapid mouth opening and closing results in increased synchrony of abductor and adductor muscle activity. In slower jaw movements, overlap in activity period is less marked.

Three musculoskeletal linkage systems are active during the expansive phase (see Figs. 9-2 and 9-3). The epaxial muscles cause upward rotation of the neurocranium on the vertebral column. A complex ventral coupling is active to mediate mandibular depression. This musculoskeletal coupling involves synchronous activity in the ventral body muscles (which retract the pectoral girdle) and in the sternohyoideus muscle, resulting in a posterioventral rotation of the hyoid apparatus (visible in Fig. 9-2) that causes mandibular depression via the mandibulohyoid ligament. The opercular series rotates posteriodorsally (Fig. 9-3), causing the mandible to abduct (Liem, 1970). These three mechanisms are critical elements of the expansive phase in all teleost fishes.

Just before the end of the expansive phase, electrical activity is observed in the adductor mandibulae, which initiates adduction of the lower jaw, and a second burst of activity occurs in the geniohyoideus muscle, initiating the return of the hyoid to its rest position, a movement not completed until well into the recovery phase (Figs. 9-1 and 9-3).

One important aspect of the kinematic profile that appears to be extremely consistent in teleosts is the delay in lateral expansion of the operculum. Although opercular abduction is often held to contribute to negative pressure generation in the mouth cavity (e.g., Osse, 1969; Osse and Muller, 1980), the kinematic data do not corroborate this assumption (see Fig. 9-3). Lateral movement of the gill cover does not begin until the compressive phase or late

Pomoxis: initial strike

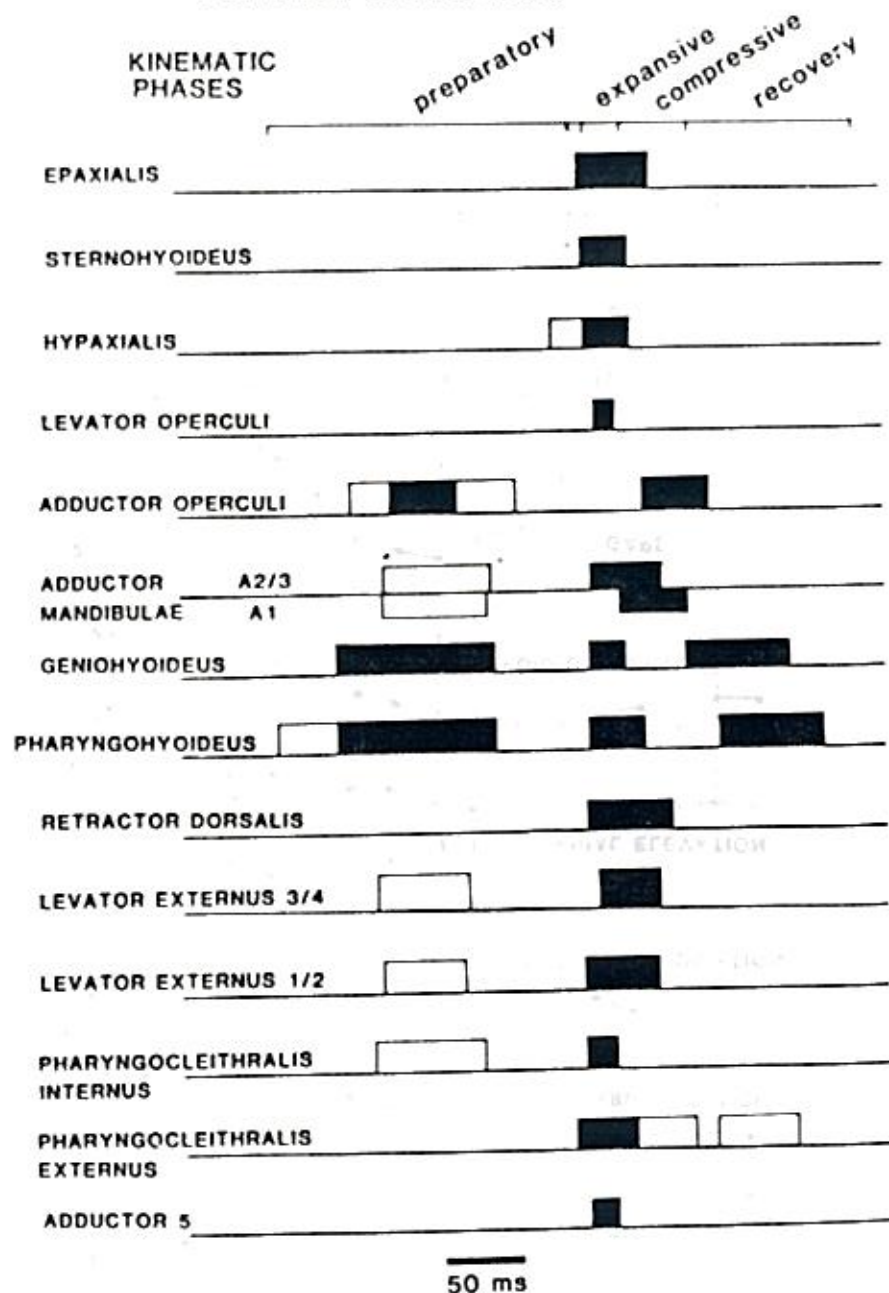


Figure 9-1
Summary of the electromyographic activity in the mandibular, hyoid, and pharyngeal muscles during the initial strike by *Pomoxis annularis* (Centrarchidae). Black bars indicate consistent muscle activity; white bars indicate that the muscles were active in fewer than 50% of the observations. A preparatory phase is not observed in all strikes. Note the occasional activity of three sets of branchial muscles during the preparatory phase (pharyngocleithralis internus and levatores externi muscles) and the consistent activity of a fourth, the pharyngohyoideus. For

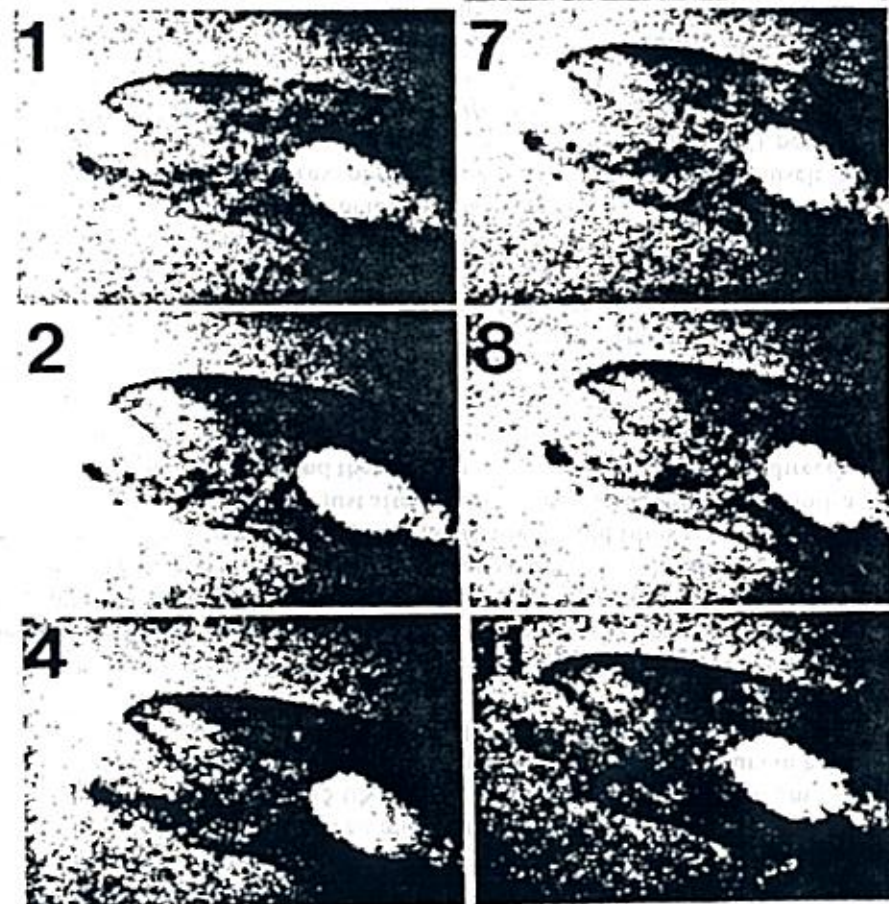
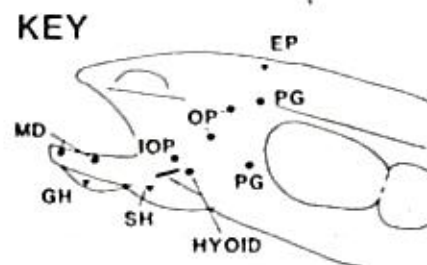


Figure 9-2
Frames 1, 2, 4, 6, 7, 8, and 11 from a high-speed x-ray film (180 frames per second, unretouched) of prey capture in *Hoplerythrinus* (Erythrinidae). Small metal markers have been implanted in the skull bones and muscles to permit direct visualization of bone movement as indicated in the key. Note the changing relationship between the sternohyoideus marker and the short wire implanted along the ceratohyal. (Dots indicate screws in bones; triangles indicate small lead pellets imbedded in heat musculature; EP, epaxial marker; GH, geniohyoid marker; hyoid, screw, and short wire located in the ceratohyal; IOP, screw in the interoperculum; MD, two screws in the dentary; OP, two screws in the operculum; PG, two screws in the cleithrum; SH, sternohyoideus marker.)

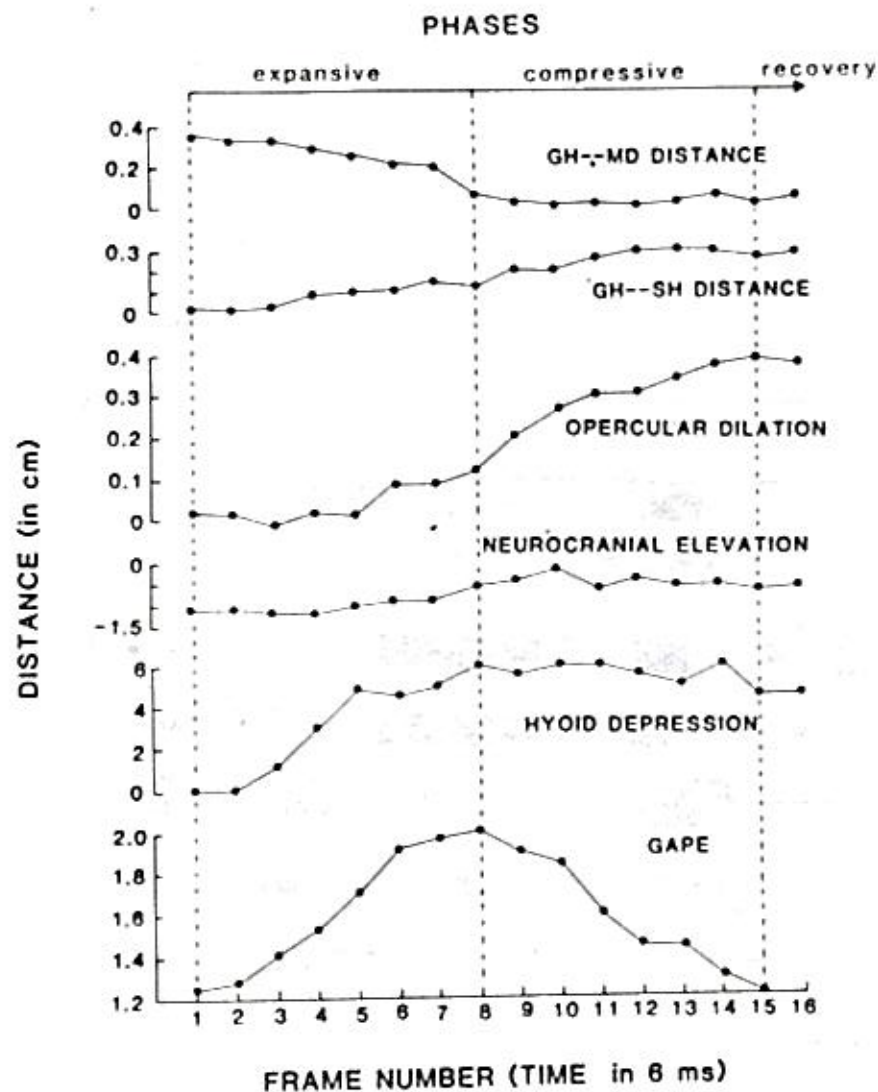


Figure 9-3

Kinematic events measured from a high-speed x-ray film of initial prey capture in *Hoplostethus*. Note the onset of hyoid depression synchronously with the increase in gape and the maintenance of hyoid depression into the recovery phase. Opercular dilation begins late in the expansive phase. GH, SH, and MD distances refer to the changing lengths between the markers shown in Figure 9-2.

expansive phase, often after the mouth has begun to close. Indeed, measurement of opercular abduction and branchiostegal expansion in sunfishes (Lauder, 1980a) showed that in many cases water does not begin to exit the opercular cavity to the exterior until the mouth has nearly closed.

Alexander (1969) calculated the tension that could be produced by the dilator operculi of the golden orfe (*Idus idus*) assuming that fish muscle at 20°C can generate 25 N/cm² cross-sectional area. He showed that the dilator operculi could generate a moment about the anterior opercular articulation of about 0.3 N/cm, sufficient to abduct the gill cover against a negative pressure of -7 cm of water. This negative pressure is far exceeded during the expansive phase and most of the compressive phase (see below), so it is not surprising that there is a delay in opercular abduction. The moments of other muscles were considerably higher: sternohyoideus—5.0 N/cm; levator arcus palatini—1.0 N/cm.

Branchial muscle activity during the initial strike usually occurs in both expansive and compressive phases (Fig. 9-1). The retractor dorsalis, levatores externi 3 and 4, and pharyngocleithralis internus and externus are all active to abduct the pharyngeal jaws as the mouth opens. This contributes to reducing the pressure within the buccal cavity and greatly expands the posterior portion of the mouth cavity. One consequence of branchial expansion is that small prey items may be sucked directly into the stomach. In *Hoplias* (Lauder, 1979) and *Antennarius* (Grobeck and Pietsch, 1979), high speed films reveal a significant distention of the stomach just after the prey has entered the mouth. Both a considerable mass of water and the prey item appear to be transported directly into the anterior portion of the stomach. Constriction of the esophageal sphincter then traps the prey, and the water is released over the next several seconds.

Three aspects of the mechanics of initial prey capture have received considerable attention in recent years: the function of the geniohyoideus muscle, the kinematics of the levator operculi mouth opening system, and the mechanisms governing premaxillary protrusion.

The geniohyoideus muscle of teleosts has been of special interest because it shows two different patterns of electrical activity. Either the muscle is electrically active during the expansive phase as in cichlids (Liem, 1978), percids (Elshoud-Oldenhave and Osse, 1976), and *Hoplias* (Lauder, 1981), or there is a considerable delay after mouth opening (up to 100 msec) as in *Salvelinus* and most centrarchids before the muscle is active. An important feature of the geniohyoideus is that in at least some fishes (*Hoplias*; *Gymnocephalus*) the mandible may either be adducted or abducted by the geniohyoideus depending on its line of action. If the line of action is above the quadratomandibular articulation, then contraction will adduct the mandible and protract the hyoid; if it is below, the mandible will be abducted. Complicating this picture further is the observation that in several species, the line of action changes during the feeding sequence. At present there is no clear understanding of the functional diversity in the geniohyoideus muscle (Lauder, 1981).

The mechanical roles of two mechanisms operating during the expansive phase, the hyoid apparatus and opercular series couplings, have been modeled as a four-bar linkage system by Anker (1974) and Barel and associates (1977).

The four bars of the opercular linkage system are the suspensorial bar, the opercular bar, the interopercular bar, and the mandibular bar (Liem, 1980a). A mathematical relationship between these elements can be derived that expresses the degree of mandibular depression as a function of the input rotation of the gill cover. A ratio, the kinematic transmission efficiency of opercular rotation (K) is given by q/r where q is the perpendicular distance from the operculo-hyomandibular articulation to a horizontal line drawn through the mandibular insertion of the interoperculo-mandibular ligament and the articulation between the suboperculum and interoperculum, and r is the perpendicular distance from the quadrato-mandibular joint to the same horizontal line. The reciprocal, $F = r/q$, indicates the force transmission efficiency. Barel and colleagues (1977) suggested that high-speed suction feeding fishes have K ranging from 2 to 4, while particle and small invertebrate eaters have K values of 10 or higher. Liem (1980a) tested this model and showed that while this rough pattern seemed to hold in some fishes, it seriously failed in others. The small invertebrate pickers *Eretmodus* and *Spathodus* (Liem, 1979) had K values of 2.5 to 4 while several piscivores had values of up to 17. The hyoid apparatus, when modeled in the same fashion, is revealed to have high K and low F values (Barel *et al.*, 1977), emphasizing the relative kinematic inefficiency of this coupling but its high force transmission capability.

JAW PROTRUSION

Jaw protrusion, extension of the premaxilla and maxilla toward the prey, is one of the most prominent features of prey capture mechanisms in acanthopterygian fishes, but there is relatively little understanding of the diversity of mechanisms by which protrusion occurs (Lauder and Liem, 1981). Jaw protrusion has evolved independently several times in teleosts, and there appear to be at least three major structural and functional systems governing this function. In cyprinids, protrusion of the premaxilla has been proposed to occur by contraction of the superficial divisions of the adductor mandibulae muscle, which pull the maxilla ventrally (Alexander, 1966). As the maxilla slides ventrally, it causes the kinethmoid bone to rotate anteriorly causing premaxillary protrusion (Ballintijn *et al.*, 1972). Protrusion can thus be accomplished independently from lower jaw depression.

In acanthopterygian fishes at least two protrusion mechanisms occur. One, first proposed by Alexander (1967a), depends on the presence of an articular process of the premaxilla that abuts a premaxillary process on the maxilla. As the mandible abducts, the maxilla is pulled ventrally and rotates about its long axis. This rotation causes the premaxillary process to move laterally and press against the articular process of the premaxilla; in a camlike action, the premaxilla is forced anteriorly. Protrusion of the upper jaw is closely linked to lower jaw depression. Alexander (1967a) demonstrated this mechanism in *Gasterosteus* and *Pterophyllum*, but many other acanthopterygian

fishes lack the requisite maxillary and premaxillary processes for the cam action.

Liem (1970) has shown experimentally in nandid fishes that the degree of upper jaw protrusion is closely coupled with mandibular depression. By surgically eliminating selected anatomic pathways by which protrusion could be effected, he showed that reducing the degree of mandibular depression consistently reduced the amount of upper jaw protrusion. More recently, Liem (1979) has suggested another system by which the jaws are protruded. This "decoupled model," originally proposed for cichlids, also appears to be true for centrarchids and may have wide applicability to advanced teleosts. If the mandible is held in a fixed, partially depressed position by activity in the geniohyoideus, levator operculi, and/or sternohyoideus, activity in the epaxial muscles would elevate the neurocranium causing the premaxilla to protrude. The degree of protrusion could be modulated by varying the amount of cranial elevation. Films and synchronous electromyograms reveal that protrusion does indeed occur by this mechanism, which seems to be particularly important during prey manipulation in the buccal cavity (Table 9-1).

The function of the protrusible upper jaw of teleost fishes has been the subject of more speculation than probably any other aspect of the feeding mechanism. Only one point is clear: no single explanation will serve for all species. Lauder and Liem (1981) reviewed the various proposed functions for jaw protrusion and noted that one species, *Luciocephalus pulcher*, refutes all hypotheses. *Luciocephalus* possesses one of the most protrusible jaws known to teleosts, the premaxilla extending anteriorly a distance of 33% of the head length; however, feeding occurs exclusively by surrounding the prey with an open mouth cavity and using the forward speed of the predator, not by suction. Peak gape and maximum jaw opening are reached well before the prey enters the buccal cavity.

The most commonly hypothesized function of jaw protrusion is that the "added velocity" obtained as the jaws move toward the prey increases the efficiency of suction (Nyberg, 1971; Gosline, 1971; Alexander, 1967b). This explanation receives indirect support in the recent model of suction feeding proposed by Weihs (1980), showing that forward movement by a fish can increase the distance from which prey can be sucked in by over 60%. Protrusion of the jaws may significantly contribute to this effect, especially when protrusion velocities may exceed body velocity during a strike by $50 \text{ cm} \cdot \text{sec}^{-1}$ or more.

JAW MUSCLES

One final aspect of the mechanics of the teleost musculoskeletal system concerns physiological properties of jaw muscles. Remarkably little work has been done, and even the most basic attributes of the jaw musculature, such as time to peak tension for twitch and tetanic stimuli and fusion frequencies have

yet to be published. Preliminary experiments on the adductor mandibulae of *Lepisosteus*, a fish in which mouth opening and closing can be accomplished in 20 msec, showed that time to peak tension for a twitch stimulus averaged 34 msec and that tetanic stimuli of 300 Hz resulted in peak tensions after about 150 msec, although 50% of peak tension was achieved in about 40 msec (the experiments were conducted at 20°C). These values compare favorably with those from locomotor muscle (Johnston, 1980), where the time to half peak tension at 15°C (t_{1/2}) for cod white myotomal muscle averaged 15.4 msec, with a peak twitch tension of 10.4 g/cm².

These values are of interest in the light of the rapid jaw movements occurring during feeding and are consistent with the "peripheral control" hypothesis of Thexton and associates (1977). It is not necessary for the central nervous system to precisely preprogram both the sequence of muscle activity and the force of contraction in order to generate a precision movement such as mouth opening and closing. Both opening and closing muscles may be maximally activated within 5 to 20 msec of each other, and the opening muscles may have a considerably greater mechanical advantage in the rest position than do the closing musculature. As the mandible is depressed, the mechanical advantage of the opening muscles steadily decreases, and shortening reduces the amount of force generated per unit length change. Continuing activation of the closing muscles during the expansive phase generates a lengthening contraction that can produce 15% more force in one-fifth the time, compared to a normal isotonic contraction (Hill, 1970). Thus, at some point toward the end of the expansive phase, jaw opening begins to slow as a result of the increasing mechanical advantage of the closing muscles. Jaw closure may occur considerably more rapidly than might be expected on the basis of *in vitro* twitch or tetanic shortening times because of the marked change in physiological response when a quick stretch precedes active shortening.

Complicating the analysis of physiological properties in fish muscles is the lack of comparative and quantitative information on jaw muscle-fiber types. The perch, (*Perca*) is the only species for which published information is available (Akster and Osse, 1978; Barends, 1979), and there appear to be a number of differences from myotomal fiber types. Akster and Osse (1978) distinguished four main types, two of which were "white" and two "red." While the physiological properties of these fibers are unknown, only the red-fiber component of the adductor operculi muscle (showing both high adenosine triphosphatase [ATPase] and lactate dehydrogenase [LDH] reactions) was electrically active during quiet respiration. In the adductor mandibulae, the most medial (A3) fibers are highly vascularized, have a small diameter ($\bar{x} = 0.002 \text{ mm}^2$), and show mainly oxidative metabolic properties (Barends, 1979); this portion of the muscle is active during respiration. In contrast, the lateral adductor divisions consist of large fibers ($\bar{x} = 0.015 \text{ mm}^2$) with fewer mitochondria, a reduced vascular supply, and high LDH activity and are not active during quiet respiration.

Hydrodynamics

The study of fluid flow through the mouth cavity of fishes during prey capture poses a considerable number of technical problems in that the process of prey capture is dynamic, and unsteady flows require measuring devices of high frequency response; the mouth cavity is not uniform throughout its length, rendering simplistic geometric models of the mouth cavity inaccurate; key resistances within the mouth cavity (such as the gills) vary during the feeding cycle; and feeding is noncyclical and can be considerably more difficult to elicit than repetitive locomotor movements.

BUCCAL AND OPERCULAR PRESSURE CHANGES

In part because of these difficulties, investigators (with one exception) have until recently attempted to deduce the patterns of pressure change in the buccal and opercular cavities from the pattern of bone movement and muscle activity. The one exception is the work of Alexander (1969, 1970), who trained fishes to suck small pieces of food from the end of a pressure transducer cannula suspended in an aquarium. Alexander found that pressures as low as $-400 \text{ cm H}_2\text{O}$ could be generated in the buccal cavity, but this technique did not allow opercular cavity pressures or buccal pressure waveforms to be determined.

Elshoud-Oldenhave and Osse (1976), on the basis of a kinematic analysis, proposed a model of suction feeding consisting of three phases: phase I, the buccal and opercular cavities are expanded with the mouth closed, generating an initial negative pressure; phase II, mouth opening occurs with rapid expansion of both cavities and a peak in negative pressure; phase III, mouth closure and compression of the buccal cavity create a positive pressure and force water out over the gills. While this proposed sequence of events is inconsistent with the kinematic data presented earlier, the hydrodynamic predictions have only recently been tested. Four key predictions about fluid flow and pressure may be derived from the work of Elshoud-Oldenhave and Osse (1976), Osse (1969), Liem (1970, 1978), Alexander (1969, 1970), Nyberg (1971), and Osse and Muller (1980):

1. The opercular and buccal cavities are not functionally distinct, and both can be treated as one large cavity.
2. Flow is unidirectional through the mouth cavity.
3. The buccal and opercular cavity pressure waveforms and magnitudes are similar.
4. The lateral expansion of the operculum contributes to the pressure drop in both the buccal and opercular cavities.

The most important implication of these statements is that the gill bars and filaments can be neglected as an element resistant to flow during feeding (*i.e.*, the "gill curtain" does not form an important resistance to flow).

Recently, experimental tests of these predictions have been conducted in bluegill sunfish (*Lepomis macrochirus*) by implanting pressure transducer cannulae in the buccal and opercular cavities and recording the pressures simultaneously with a film at 200 frames per second to record the pattern of bone movement (see Lauder, 1980a and c for procedures and results). The results from a similar set of experiments on *Ambloplites rupestris*, the rock bass, are shown in Figures 9-4 and 9-5A.

The expansive phase of prey capture is characterized by an immediate pressure drop in the buccal cavity as the mouth begins to open, whereas the pressure in the opercular cavity increases (Fig. 9-4). This pressure increase is caused by adduction of the gill cover against the side of the head. At the end of the expansive phase, there may be up to a 400-cm H₂O pressure differential across the gill arches. Pressures measured at the very back of the buccal cavity, as close to the anterior face of the gill arches as possible, confirm that the pressures here are equal to or slightly more negative than in the front of the buccal cavity (Lauder, 1980a, p. 56). Peak negative pressures are reached in the buccal cavity 5 to 15 msec before the opercular cavity, and the ratio of peak buccal to opercular pressure averages 6:1 in *Lepomis* and 2:1 in *Ambloplites*. The maximum negative pressure recorded to date is -790 cm H₂O in the buccal

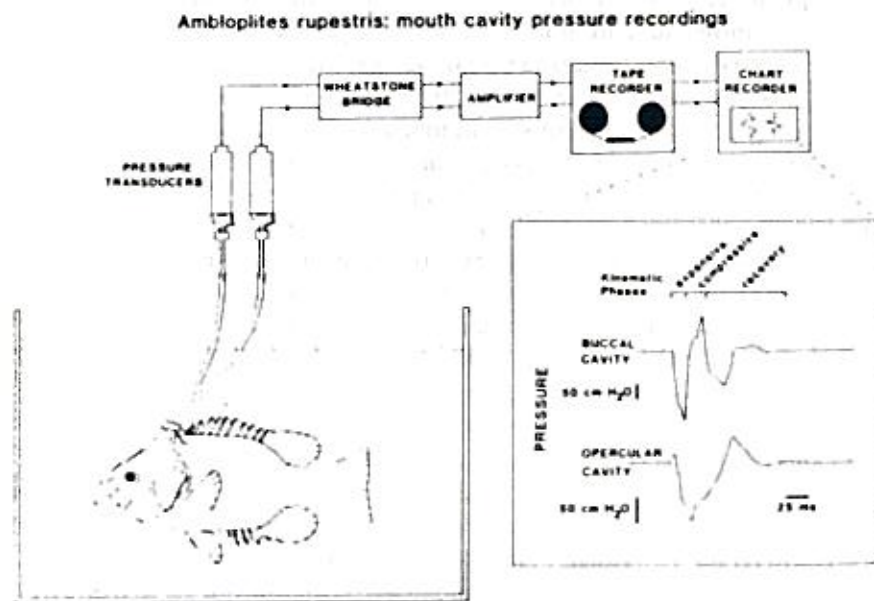


Figure 9-4
Pressure recordings from the mouth cavity of *Ambloplites rupestris* during high-speed suction feeding (on the right) and a diagrammatic view of the methods and apparatus used to obtain these traces (left and top). The pressure transducers are fluid-filled Statham P23 Gb units; calibration, cannula implantation procedures and difficulties with this method are discussed in Lauder (1980a). See text for discussion of pressure traces.

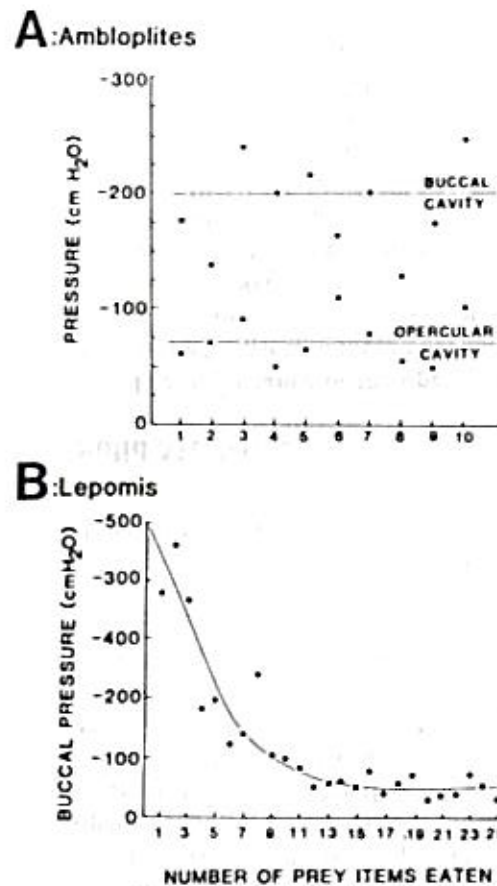


Figure 9-5
Satiation curves for *Ambloplites rupestris* (A) and *Lepomis macrochirus* (B). *Ambloplites* possesses a highly stereotyped feeding pattern, and suction pressure does not vary with the number of prey items eaten (increasing satiation). In contrast, as prey are fed to bluegill (*Lepomis*), suction pressure declines in a roughly exponential fashion, showing that the process of prey capture is modulated in response to satiation. The buccal and opercular pressures for each prey item in A were recorded simultaneously.

cavity of *Lepomis macrochirus*; and the peak opercular cavity pressure is -185 cm H₂O.

Buccal pressure rises rapidly to ambient pressure during the compressive phase (Fig. 9-4), and opercular pressure follows at a slower rate of pressure decrease. During high-speed suction, the buccal pressure trace then undergoes a characteristic second decrease after being above ambient pressure for 10 to 50 msec. Opercular pressure is usually positive during this stage and slowly returns to ambient pressure (Fig. 9-4).

An interesting difference occurs between the satiation curves for *Lepomis* and *Ambloplites* (Fig. 9-5). In *Lepomis*, as prey are sequentially fed to a hungry individual, the magnitude and velocity of buccal cavity pressure decrease in a roughly exponential fashion (Fig. 9-5B). In contrast, *Ambloplites* shows a highly stereotyped pattern of pressure change that does not vary with prey number (Fig. 9-5A). Prey are consumed with the same pattern and ratio of buccal-to-opercular cavity pressure regardless of the number previously eaten.

The difference between the modulated prey capture of *Lepomis*, in which the pattern of jaw movement can be varied in response to satiation, prey type, and prey location, and the stereotyped prey capture of *Ambloplites* is also present in the kinematic and electromyographic pattern. Highly stereotyped prey capture indicates a very consistent motor outflow from the central nervous system to the peripheral jaw structures and that this outflow is not modified by visual, lateral line, or other input from the prey. Each cycle of mouth opening and closing is the same. The implications of the modulated versus stereotyped methods of capturing prey for fish ecology and evolution are discussed below.

Based on the measurement of water pressure in the buccal and opercular cavities of fishes, a fluid flow pattern through the mouth cavity may be proposed that is testable by the direct measurement of velocity magnitude and direction with hot-wire anemometers. At the start of the expansive phase, the gill covers are adducted sharply, and water is forced both anteriorly between the gill bars into the buccal cavity and laterally between the pectoral girdle and the operculum; thus there may be a brief posterior-to-anterior flow. As the buccal cavity expands, water enters the mouth establishing the anterior-to-posterior flow pattern. Water does not begin to flow through the opercular cavity until the jaws have nearly closed. The rapid closure of the jaws (within 25 msec) and the high-velocity flows that can be created by rapid mouth cavity expansion (up to 12 m/sec; Osse and Muller, 1980) suggest an explanation of the second negative phase in the buccal pressure waveform (Fig. 9-4) in terms of the water-hammer effect.

Rapid closure of a valve on a stream of fluid moving through a pipe results in a sharp pressure decrease on the downstream side of the valve and a pressure increase on the upstream side. A high-pressure wave is propagated upstream, causing the banging in old pipes that gives this effect its name. During high-speed suction, the mouth may act like a valve. If the stream of water moving through the mouth cavity is analogous to flow through a pipe, when the mouth closes, the second negative phase of the buccal waveform is produced because of the downstream pressure decrease caused by fluid inertia.

CAVITATION

In addition to the water-hammer effect, a second phenomenon of fluid mechanical interest involved in suction feeding is cavitation. Cavitation of water occurs when the pressure is reduced sufficiently to cause water vapor to come rapidly out of solution in the form of small vapor-filled cavities (as behind a rapidly rotating propeller; Blake, 1949a). The pressure at which fluids cavitate depends on the size of minute air bubbles already suspended in the fluid (Blake, 1949b; Birkhoff and Zarantonello, 1957). Aquarium water normally contains many bubbles in the 0.01-mm size range, and the tensile strength of water is about 0.7 atm when bubbles of this size are present. Small cavitation bubbles collapse within 1 to 30 msec after formation (Strasberg, 1959), and a

characteristic sound spectrum is associated with the bubble collapse (Mellen, 1954; Haddle and Skudrzyk, 1969).

At least one fish, the bluegill (*Lepomis macrochirus*), seems to be capable of cavitating water during rapid suction-feeding. Pressures as low as 0.7 atm have been measured with pressure transducers, and this is likely to be a considerably smaller pressure difference than can be produced under unrestrained conditions. In addition, during high-speed suction a sharp sound can be heard as the mouth opens, possibly caused by the collapse of cavitation bubbles. Alexander's calculations (1969) of the tensile strength of fish muscles show that fish muscle is easily capable of generating forces in the range of 70 N/cm², a tension sufficient to cause cavitation in aquarium water. Cavitation of water during aquatic feeding appears to set a practical limit on the capture of prey by the use of suction. At least one species of fish appears to have reached this limit.

Finally, the gill cover appears to play little or no role in generating negative opercular and buccal pressures in fishes feeding by high-speed suction. Four pieces of evidence lead to this conclusion: the calculations of Alexander (1969) show that the dilator operculi muscle can generate only sufficient force to abduct the gill cover against a 10 cm H₂O pressure differential, considerably less than that present during feeding; the consistent delay in the onset of opercular abduction indicates that opercular cavity expansion does not even begin in many cases until the mouth is closing; the role of the gill arches as a resistance in the mouth cavity; and a strain-gauge analysis of opercular deformation patterns, which reveals that the operculum is being flattened laterally against the side of the head and twisted during the expansive phase.

Solid Mechanics

The importance of the operculum in controlling mouth opening and in preventing fluid inflow into the opercular cavity suggested that this bone might be a good subject for an analysis of bone strain and loading patterns (Lauder and Lanyon, 1980), and indeed the operculum is the only element of the feeding mechanism that has been analyzed within a solid mechanics framework.

By bonding a rosette strain-gauge to the operculum of the bluegill (*Lepomis macrochirus*), Lauder and Lanyon (1980) showed that this bone, during rapid-feeding, is deformed at a rate that far exceeds strain rates reported for normal functional activity in other vertebrates. A peak strain of $-615 \times 10^3 \mu\epsilon$ /sec and peak principal compression of $-1800 \mu\epsilon$ on the lateral surface of the operculum was recorded. These strains were viewed as the result of opercular deformation caused by the pressure decrease in the opercular cavity (of up to -145 cm H₂O). The rapid pressure decrease flattens the laterally convex gill cover against the side of the head, causing the center of the operculum to be subjected to predominantly compressive strains. A twisting

moment is also produced by contraction of the levator operculi and adductor operculi muscles and the resistance of the lower jaw to movement. This twisting causes the principal strain axis on the operculum to be displaced anteriodorsally from the purely vertical and horizontal planes. The gill cover is thus being twisted at a 45-degree angle to the two prominent orthogonal bony struts on the medial opercular surface.

Much of the interest in this data lies in the comparison of deformation patterns with other vertebrates and in the properties of fish bone as they relate to strain rates (see Chap. 3). The bone of advanced teleost fishes is acellular in structure—the osteoblasts are not surrounded and embedded in growing bone. The osteoblasts remain on the surface of the bone, and thus acellular teleost bone is not capable of undergoing internal remodeling to repair microfracture damage. This is of special interest in that the peak strain rates recorded on the operculum exceed by a factor of nearly ten the highest *in vivo* strain rates previously recorded in vertebrates ($-76 \times 10^1 \mu\text{e sec}$; Lanyon and Rubin, 1980). The high physiological strain rates on the operculum may, however, result in less potential disruption of the bone matrix than the same strain magnitude imposed at a lower rate. It is a general property of vertebrate bone that high strain rates increase the fracture strain and that higher absolute compressive strain magnitudes are thus possible (Robertson and Smith, 1978). It may be that the dynamic nature of the imposed loads during suction feeding considerably increases the maximum possible strain for a given permitted level of fracture damage to the head bones.

MECHANICS OF INTRAORAL MANIPULATION AND DEGLUTITION

Three major classes of kinematic and electromyographic patterns following initial prey capture are discernable in generalized teleosts (Table 9-1): buccal manipulation, pharyngeal manipulation, and pharyngeal transport. It is important to realize that these three processes are characterized by unique patterns of muscle activity and bone movement because failure to distinguish between them can lead to the conclusion that intraoral manipulatory patterns are highly modulated and variable, when in fact there are three distinct stereotyped patterns.

Buccal Manipulation

Buccal manipulation (Fig. 9-6) is similar to the electromyographic pattern during the initial strike (compare Fig. 9-6 to Fig. 9-1) except that a preparatory phase is lacking. Both pharyngeal, mandibular, and hyoid arch muscles are active to create suction and move the prey from the anterior buccal cavity (between the parasphenoid and basihyal) back to the pharyngeal jaws. A key

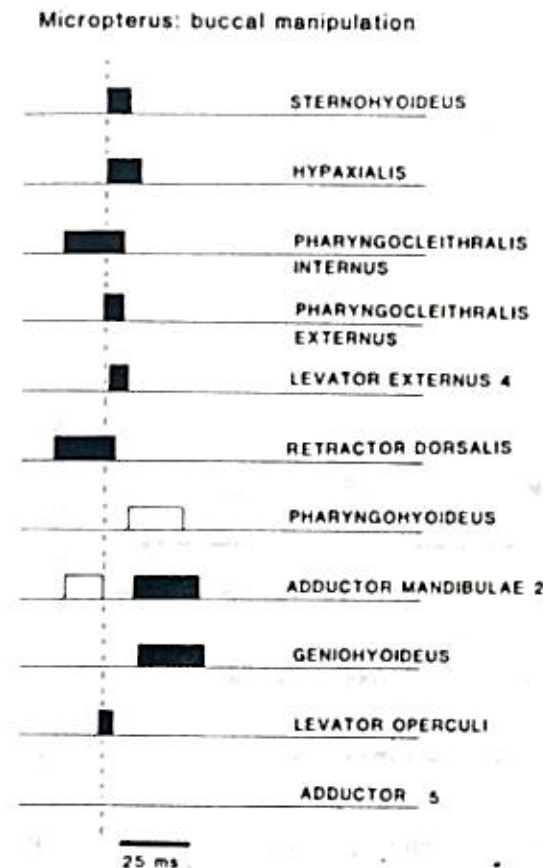


Figure 9-6
Summary of the pattern of electromyographic activity in branchial and selected hyoid arch muscles during buccal manipulation in *Micropterus salmoides*. Note the similarity to muscle activity patterns during the initial strike (Fig. 9-1; Table 9-1). A preparatory phase is never present. Black bars indicate consistent activity; white bars indicate activity in less than half of the observed cases. No activity is observed in the fifth branchial adductor. Dashed line indicates the onset of sternohyoideus activity.

feature by which buccal manipulation may be distinguished from pharyngeal manipulation (at least in centrarchids) is the nearly synchronous activity in the sternohyoideus and obliquus inferioris (hypaxial) muscles (Fig. 9-6). By causing a rapid depression of the hyoid, anterior-to-posterior water flow is created, which carries the prey back to the pharyngeal jaws. Repeated cycles of manipulatory movements may also be used to position irregularly shaped prey, such as crayfish, for swallowing.

Pharyngeal Manipulation

Pharyngeal manipulation (Table 9-1) is distinct from buccal manipulation in generalized percoids because the dominant mandibular and hyoid arch muscles used to create suction are not active. The ventral body muscles are active in conjunction with the pharyngocleithralis externus and internus (see Fig. 9-7 for a diagrammatic illustration of the major pharyngeal muscles and

PHARYNGEAL APPARATUS: MUSCULOSKELETAL COUPLINGS

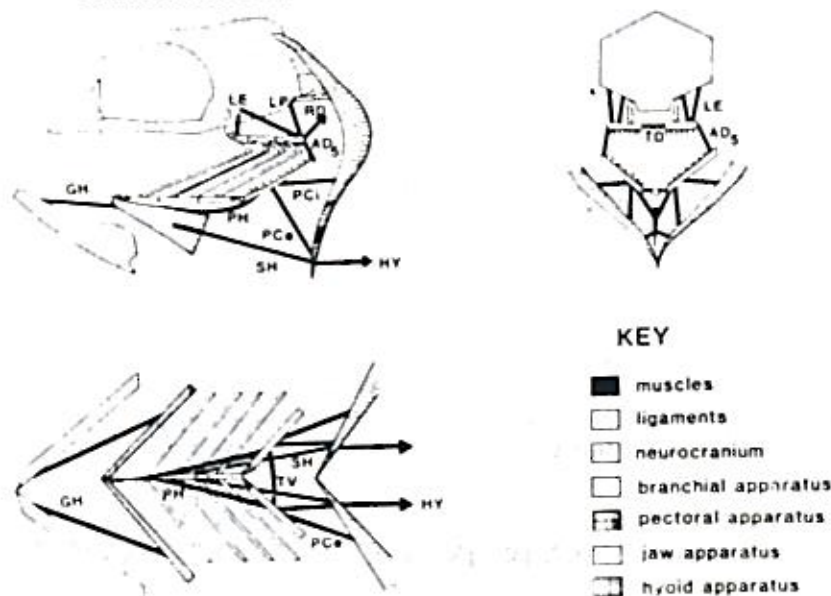


Figure 9-7

Diagrammatic view of the major musculoskeletal couplings in the pharyngeal apparatus involved in pharyngeal manipulation and transport of prey items. The structural pattern depicted is that of a generalized percomorph. Intrinsic gill arch muscles have been omitted. (AD5, adductor arcus branchialium 5; GH, geniohyoideus; HY, hypaxialis; LE, levatores externi muscles; LP, levator posterior; PCe, pharyngocleithralis externus; PCi, pharyngocleithralis internus; PH, pharyngohyoideus; RD, retractor dorsalis; SH, sternohyoideus; TD, transversus dorsalis; TV, transversus ventralis.) Origin of the retractor dorsalis is from the ventral surface of the first few vertebral bodies.

their lines of action) to move the lower pharyngeal jaw posteroventrally, and the sternohyoideus is inactive. At the same time, the retractor dorsalis and levatores externi (Fig. 9-7) elevate the upper pharyngeal jaw. Prey are thus positioned and manipulated in the pharynx before deglutition. If extensive intraoral manipulation of awkwardly shaped prey occurs, buccal manipulation will usually alternate with pharyngeal manipulation. In these cases, a reverse flow (posterior to anterior) may occur, and prey may be sucked anteriorly from between the pharyngeal jaws, repositioned in the buccal cavity, and then moved back between the pharyngeal jaws for swallowing.

Pharyngeal Transport

Transport of prey from the pharynx into the esophagus and stomach involves the coordinated action of the upper and lower pharyngeal jaws (Table 9-1). In teleosts with relatively generalized pharyngeal jaw structure, the movements occur primarily in the anteroposterior plane as the prey is raked into the esophagus (Fig. 9-7; Liem, 1970).

Five main musculoskeletal couplings are involved in pharyngeal transport (this is a considerable simplification). (1) Protraction of the lower pharyngeal jaw occurs by the combined action of the pharyngohyoideus, geniohyoideus, and occasionally the adductor mandibulae (Figs. 9-7 and 9-8). The actual protraction of the lower pharyngeal jaws relative to the branchial basket is rather small, and the pharyngohyoideus also pivots the lower pharyngeal jaws laterally because of its line of action (Fig. 9-7). (2) Retraction of the lower jaw occurs by contraction of the pharyngocleithralis internus (Figs. 9-7 and 9-8). During transport, the ventral body musculature and (usually) the pharyngocleithralis externus are inactive. (3) Retraction of the upper pharyngeal jaws occurs by activity in the retractor dorsalis muscle (Figs. 9-7 and 9-8), which also has a dorsal (elevating) component to its line of action. (4) Protraction of the upper pharyngeal jaws occurs by the levatores externi and levatores interni muscles (Fig. 9-7); usually, the levatores externi 3 and 4 have a significantly greater anteroposterior line of action than the levatores externi 1 and 2 or the anterior levatores interni. (5) Finally, the adductor arcus branchialium 5

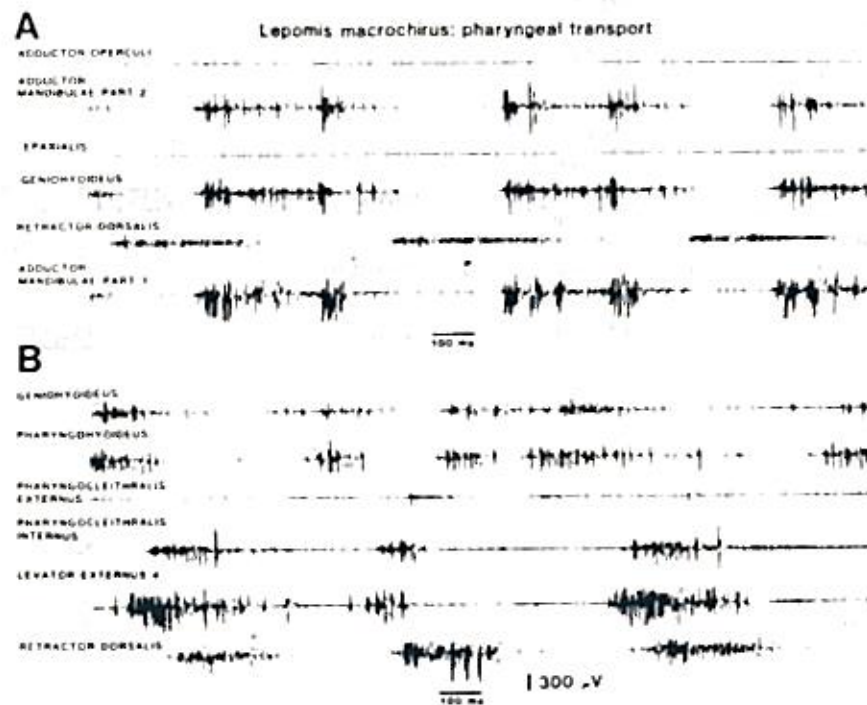


Figure 9-8 Pattern of muscle activity during the pharyngeal transport phase of feeding (see Table 9-1) in *Lepomis macrochirus*. Note the rhythmic pattern of activity and the greatly expanded time scale compared with either the initial strike or buccal manipulation. A and B. Two sets of six simultaneous recordings of pharyngeal muscle activity during transport of prey into the esophagus. (See text for discussion of activity patterns.)

adducts the lower pharyngeal jaw towards the upper (Fig. 9-7), squeezing the prey between the posterior portion of the toothed pharyngeal jaws.

The electromyographic pattern during pharyngeal transport in centrarchids shows that the upper and lower jaws move synchronously in raking the prey into the esophagus (Fig. 9-8; Lauder, 1982): the upper and lower pharyngeal jaws are protracted and retracted together. While there is considerable overlap between activity of the levator externus 4 and the retractor dorsalis, levatores externi 1 and 2 alternate cleanly with the retractor dorsalis. The lower jaw couplings show relatively little overlap between protractive and retractive muscle activity. The pharyngohyoideus and geniohyoideus are usually synchronously active and do not significantly overlap with the pharyngocleithralis internus (Fig. 9-8B). During transport, the sternohyoideus, ventral body musculature, epaxialis, and most of the mandibular and hyoid arch muscles show no activity. Not all electromyographic patterns during swallowing are symmetrical. Occasionally, asymmetrical activity between the right and left sides of the pharynx occurs to rotate the jaws around a sagittal axis. Presumably this orients the prey for transport.

At present there is very little data on the mechanics of the pharyngeal apparatus of teleosts, and the available comparisons are limited. Preliminary analysis reveals that the synchronous pattern of upper and lower pharyngeal jaw movement occurs in other acanthopterygian fishes also. Sponder and Lauder (1981) found in *Periophthalmus* that both the upper and lower jaws are protracted and retracted together, and Liem (1970) found this to be true of nandids. In both *Periophthalmus* and the centrarchids analyzed here, the upper pharyngeal jaw plays the dominant role in raking the prey into the esophagus. The lower jaw, while it does have some independent mobility, is constrained by its anterior attachment to the branchial basket. *Esox* and *Perca* also use synchronous movements of the upper and lower pharyngeal jaws during prey transport. In *Esox*, as in all non-neoteleostean fishes, a retractor dorsalis muscle is absent. Retraction of the upper pharyngeal jaws occurs by the levator externus 1 and levator internus 2, which have a posterodorsally inclined line of action (Lauder, 1982). This contrasts with the protractive effect of these muscles in neoteleostean fishes (e.g., Fig. 9-7). Retraction and posterior rotation of the lower pharyngeal jaw about its anterior attachment to the basibranchials occurs by the pharyngocleithralis internus as in neoteleostean fishes.

The only other experimental studies on pharyngeal jaw mechanics have been on the Cichlidae (Liem, 1973, 1978; Liem and Osse, 1975). Cichlids provide an interesting comparison with the morphologically generalized Centrarchidae. The cichlid upper pharyngeal jaw is relatively immobile in the anteroposterior direction because of its articulation with the base of the skull (Fig. 15 in Liem, 1978). The upper jaw pivots on the pharyngeal apophysis, and the lower jaw provides the primary transport movement. Cichlid fishes have an

extremely complex pharyngeal manipulation phase of intraoral food processing that involves prey maceration via two power strokes of the upper and lower pharyngeal jaws.

In power-stroke one, the upper jaw pivots anteriorly, and the lower jaw is adducted against it, crushing the prey. A transitional stroke follows as both jaws move posteriorly, and finally power-stroke two occurs with the jaws in the retracted position. Power-stroke one involves a "bite" between the anterior teeth of the pharyngeal jaws, while in power-stroke two the bite is between the posterior jaw teeth. The electromyographic pattern of chewing differs significantly from that of centrarchids in that the sternohyoideus is active during pharyngeal manipulation, and a protracted pharyngeal transport phase appears to be absent. A comparative experimental analysis of several taxa at different phylogenetic levels will be necessary before any more general conclusions about the evolutionary mechanics of the pharyngeal apparatus can be formulated; this is a key task for future research on the mechanics of food capture.

MECHANICS OF FILTER FEEDING

Filter feeding as a mode of food capture in fishes is distinct from suction feeding. In filtering small particles from the water column, the selection of prey to be swallowed occurs at the filter itself after the potential prey items have entered the mouth. Food value thus plays little role in determining which particles enter the mouth, and mechanical attributes of the particles such as size, shape, and density as well as mobility may regulate capture (Jorgensen, 1966). In suction feeding, prey selection usually occurs before the mouth is opened, and the visual system plays a major role in the initiation of feeding (Confer *et al.*, 1978; Durbin, 1979).

The theoretical mechanisms by which particles may be removed from a flowing fluid have been considered within the context of aerosol theory by Rubenstein and Koehl (1977), who identified seven possible mechanisms by which suspended particles can be filtered, one of which is sieving. Most vertebrate and invertebrate suspension feeders use other methods of particle capture such as direct interception by filter fibers and mucus or gravitational deposition onto the filter surface (Rubenstein and Koehl, 1977; Jorgensen, 1966), and sieving appears to occur relatively rarely.

In fishes, however, sieving is the dominant filtration mechanism. If a sieving mechanism is being used by suspension-feeding fishes to remove food particles from the water, then no particles on the downstream side of the filter should be larger than the pore size of the sieve. Conversely, the food particles found in fish stomachs should in theory be equal to or larger than the pore size of the filter. Because flow streamlines might bypass the filter pores (passing between the tips of adjacent gill rakers for example), one might expect to find a

few large particles downstream of the filter, but no particles smaller than the mesh size should be captured.

A number of studies have confirmed these expectations. Durbin and Durbin (1975) studied filter feeding in menhaden (*Brevoortia tyrannus*). They suggested that the gill rakers have a mean pore size of less than 80 μ and measured capture efficiencies of 20- μ particles at 2%, 80- μ particles at 21%, and 1200- μ particles at 68%. Magnuson and Heitz (1971), Galbraith (1967), and Leong and O'Connell (1969) have all noted that prey sizes in the stomachs of filter-feeding fishes invariably exceed the estimated mesh size of the gill raker filter.

Rosen and Hales (1981), in an excellent study of particle filtration in the paddlefish (*Polyodon spathula*), measured a mean mesh size of 0.06 mm to 0.09 mm in the gill filter. They showed that particles strained from the water were at least 0.2 mm long and 0.1 mm wide, and that while smaller particles did occur in the water column, they were not retained by the filter. These results confirm a sieving model of prey capture for filter-feeding fishes, as the particle size distribution in relation to filter pore size is not consistent with other filtration mechanisms (Rubenstein and Koehl, 1977). Rosen and Hales (1981) also showed that all particles of the appropriate size, regardless of food value, were filtered from the water. Detritus and sand particles constituted 50% of the stomach content volume.

The actual mechanism by which particles are held on the gill filters and subsequently swallowed has not been investigated. If food is trapped on the lateral surface of the gill rakers as water entering the mouth passes laterally into the opercular cavities, it may be forced by water pressure to the base of the gill rakers and entrapped in mucus covering the gill arches. Mucus strands from the separate arches may be swallowed when the mouth is closed between periods of filtering, and pharyngeal jaw movement probably aids deglutition.

The rate of filtration is varied in fishes by two mechanisms: altering swimming speed and thus the volume flow over the filter and active alterations in the filter mesh size. Changing body velocity in response to food particle concentration is a well-documented phenomenon. Durbin and associates (1981) showed that swimming speed in menhaden increases approximately hyperbolically with increasing particle density, and feeding usually stops below a certain prey-density threshold. Active changes in gill raker spacing are less well documented, but branchial arch musculature could adjust the spacing between adjacent arches and thus influence the flow pattern through the gill rakers.

Most filter feeding fishes can switch to a particulate or suction feeding mode for larger prey, and the process of prey capture occurs by the musculo-skeletal couplings discussed above under Suction Mechanics. Leong and O'Connell (1969) analyzed feeding in the anchovy (*Engraulis mordax*) and found that suction feeding was used for *Artemia* adults from 5 to 10 mm long,

but that anchovies switched to filter feeding to capture the 0.6-mm sized nauplii. Filter-feeding individuals usually swim actively and hold the mouth widely open for 2 to 3 seconds. The mouth then closes, locomotion ceases, and a brief glide ensues before the mouth is opened and forward progress resumed; 30 to 50 feeding cycles of this type can occur per minute in an actively filtering fish.

From this brief review of filter feeding dynamics, it is apparent that the hydrodynamics of flow over the gill arches and rakers is poorly understood (see also Chap. 4). Flow patterns over the gill rakers could be examined in a horizontally sectioned head of a freshly dead menhaden, for example, in a flow tank with small hydrogen bubble tracers or even live *Artemia* as prey. This would allow the direct observation of particle entrapment and flow pattern, and the gill rakers and arches could be manipulated to examine the effect on particle capture efficiency at different prey size classes. A second puzzling feature of filter feeding concerns swallowing of the prey. It is not at all clear how prey trapped on gill rakers are ultimately swallowed. Perhaps only pulse feedings with dyed particles will allow determination of the route captured particles take on their way to the esophagus.

FOOD CAPTURE: ECOLOGY, BEHAVIOR, EVOLUTION

Kinematic Modulation

From an ecologic viewpoint, one of the most interesting concepts to emerge from recent investigations on fish feeding mechanics is the distinction between modulating and highly stereotyped feeding behavior in different species (e.g., Liem, 1978, 1979, 1980b). Modulation of feeding is the alteration of kinematic, electromyographic, and pressure patterns during feeding in response to different prey types and locations (Lauder, 1981). Highly stereotyped feeders show very little variability between feeding sequences even when eating prey of widely differing escape capacity. Of special interest is the fact that modulating and stereotyped feeders can be closely related.

Ambloplites and *Lepomis*, as noted earlier, show radically different satiation curves but are very similar in anatomic design; *Hoplias* and *Lebiasina*, two characoid species studied by Lauder (1981), share many structural features in common but differ greatly in the jaw movement pattern elicited in response to different prey. *Lebiasina*, for example, uses a different pattern of muscle activity and jaw movement in feeding on the bottom than is used in eating the same prey type on the surface. The differences between stereotyped and modulated trophic types can be expressed in terms of the neural control of motor output to the jaw muscles (Fig. 9-9). Both *Lebiasina* and *Hoplias* share the same structural network, but *Lebiasina* possesses a greater number of independent functional units that can be altered to produce any one of three

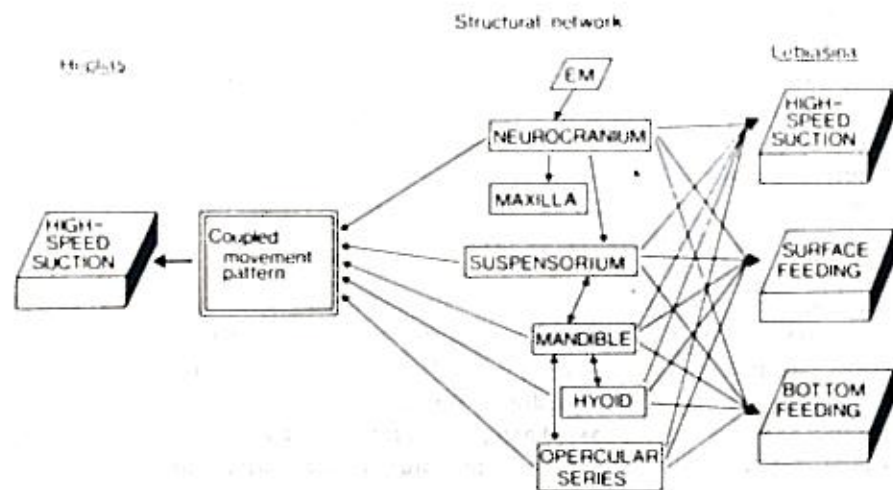


Figure 9-9

Diagrammatic illustration of modulated (*Lebiasina*) and stereotyped (*Hoplias*) feeding patterns in two fishes with a very similar structural network in the head. Based on data presented in Lauder (1981). In *Lebiasina*, the various components of the structural network can be linked in a number of patterns and with different temporal relations to produce varying kinematic outputs during feeding. This results in at least three statistically definable outputs (three-dimensional boxes). In *Hoplias*, movement of the structural network is governed by a "coupled-movement pattern" that only allows one kinematic sequence of jaw movement regardless of the type or position of the prey.

motor output patterns (Fig. 9-9). *Hoplias* possesses a "coupled movement pattern" in that the various functional units of feeding behavior are tightly associated into a single fixed pattern of motor output (Fig. 9-9).

These findings have major implications for ecologic models of prey capture (Keast and Webb, 1966; Werner and Hall, 1979). Diversity in the functional repertoire (i.e., species with an increased number of modulated patterns) may show a greater breadth of trophic resource utilization than do highly stereotyped species. Modulated functional patterns are predicted for species that use a wide range of food resources. In addition, the versatility and plasticity inherent in nonstereotyped feeders may permit greater adaptability to varying trophic conditions (Liem, 1980b), while at the same time confounding optimality models of prey capture behavior.

The concept of ecologic specialization takes on new meaning in the light of differences in fish functional repertoires (Liem, 1980b). Piscivorous species and "generalized predators" are often considered to represent ancestral unspecialized types (e.g., Schaeffer and Rosen, 1961), but if these species are highly stereotyped suction feeders with a single pattern of motor output to the jaw muscles, they must be considered as specialized when compared to modulating forms. *Lepomis*, for example, possesses a broad functional repertoire and is generalized in comparison with the more predaceous but

highly specialized *Ambloplites*. Nonmodulating, high-speed suction feeding is a specialized mode of prey capture that has evolved independently numerous times in ray-finned fishes. Through this type of analysis, the study of fish mechanics can contribute to ecologic investigation and suggest hypotheses for future exploration.

Evolutionary Mechanics of Food Capture

The major feature of the evolution of the feeding mechanism in ray-finned fishes (Actinopterygii) is the increase through time (in a series of discrete stages) of the complexity of the biomechanical pathways governing jaw movement (Lauder, 1982). This increase in complexity is correlated with an increase in the diversity of structural and functional patterns shown in derived actinopterygian clades.

As an example, consider the primitive musculoskeletal apparatus involved in prey capture. The earliest ray-finned fishes retained the mechanism of mandibular depression that is primitive for gnathostomes: posteroventral rotation of the hyoid apparatus mediated by the sternohyoideus and ventral body musculature. The structure of the skull was such that relatively little lateral mobility of the cheek occurred, and ventral depression of the hyoid was limited by the extensive series of closely articulated branchiostegal plates (Jessen, 1968). The buccal volume change that could occur during feeding was thus small, and it is unlikely that negative pressures of less than -100 cm H₂O below ambient pressure could have been generated. The process of prey capture, as inferred from morphology, appears to have been relatively conservative throughout primitive actinopterygians, and this may be reflected in the conservatism of muscle activity patterns in primitive, living actinopterygians (Lauder, 1980b).

The halecostome fishes, including *Amia* and the Teleostei as extant clades plus a number of extinct taxa, are characterized by two mouth-opening couplings. Halecostomes retain the primitive hyoid system for mediating mandibular depression, and an additional system is present: rotation of the operculum causes depression of the mandible via a ventral connection through the interopercular bone and interoperculomandibular ligament. This provides two independent mechanical systems that both control mouth opening; the mechanical relationships of these two systems are such that the opercular coupling is more efficient at translating a small muscular contraction into mandibular depression, while the hyoid apparatus is a more force-efficient system.

The major consequence of this duality in mouth opening mechanisms is an enormous increase in constructional and functional flexibility of the skull, and primitive teleost clades exemplify this by exhibiting a considerable diversity in trophic apparatus. The osteoglossomorph fishes have modified

the primitive hyoid coupling into a third set of jaws, the basihyal-parasphenoid bite, and prey are macerated and crushed between the tongue and the base of the skull. This type of structural modification is not possible within the structurally rigid skull framework of primitive ray-finned fishes. Clupeomorph fishes have repeatedly evolved microphagous habits and the concomitant structural and functional modifications in the trophic apparatus.

Within the acanthopterygian fishes, similar evolutionary consequences of biomechanical changes are observable in the mechanism of upper jaw protrusion (Liem, 1980b). Cichlid fishes, for example, have five different mechanical pathways that can be used to produce protrusion of the premaxilla. More primitive acanthopterygians (such as *Perca*) possess four or fewer pathways, and there are tight functional and mechanical linkages between the protrusion systems that constrain directions of evolutionary change in structure and function.

The basic concept underlying this discussion is that independent biomechanical pathways in a structural and functional system promote constructional flexibility in the evolutionary sense, and permit new morphologies and a greater diversity of functional patterns. Clades with fewer pathways of structural control are limited in the direction and amount of evolutionary modification of functional design. The analysis of fish trophic mechanics has thus furnished an excellent example of general properties of biological design and the pathways by which it is transformed.

One final aspect of the evolutionary mechanics of ray-finned fishes that has received relatively little attention is the branchiostegal apparatus. The interopercular bone, noted above as being a key element in the chain of elements transmitting contraction of the levator operculi muscle to the mandible, is generally considered to be homologous to a branchiostegal ray. In *Amia*, the uppermost branchiostegal ray is expanded and has ligamentous connections both with the mandible and hyoid apparatus (Allis, 1897). The dorsal branchiostegal elements may thus have played an important role in the early evolution of the levator operculi coupling by forming a functional linkage between the hyoid, operculum, and mandible. Halecostome fishes possess a branchiostegal apparatus that is considerably reduced in comparison to that of primitive, ray-finned fishes. The individual plates have become more slender, anteroventral elements have been consolidated into gular plates, and there has been a reduction in the number of plates. These modifications may relate to increased mobility of the hyoid in the dorsoventral plane and to the increased role of the branchiostegal apparatus in the halecostome suction-feeding mechanism. The hyohyoideus adductores and abductores muscles (Winterbottom, 1974) that adduct and abduct the branchiostegal rays are hypothesized to be derived from the primitive actinopterygian interhyoideus (Lauder, 1982). These muscles, in permitting finer control over branchiostegal ray movement, may have had an important impact on the nature of respiratory patterns and suction feeding in the early halecostome

fishes, but we still lack basic functional data on the branchiostegal apparatus in living forms, and until this badly needed information is obtained, the role of the branchiostegal apparatus in actinopterygian evolution will remain obscure.

CONCLUSIONS AND PROSPECTUS

The last decade has witnessed enormous progress in our understanding of the dynamics of aquatic prey capture in fishes. New experimental techniques have revealed details of the feeding mechanism, and general concepts relevant to fish ecology and the evolutionary biology of complex systems have emerged. Two main topics are in need of considerable future work before a comprehensive understanding of the regulatory processes governing food capture in fishes can emerge. First, the physiological properties of the jaw muscles must be determined. Length-tension curves for opening and closing muscles and the response of these muscles to a quick stretch will aid in interpreting high-speed films and electromyographic data. Second, detailed empirical analysis of feeding hydrodynamics must be extended beyond the current research on mouth-cavity pressures to include the measurement of flow velocities, pressure-velocity relationships for modulated and stereotyped trophic categories, and the effect different patterns of pressure and velocity in the mouth cavity of the predator have on the prey.

Perhaps the area with the greatest potential for experimental and conceptual advance is the relationship between locomotor patterns and feeding behavior. Over the last 10 years, research on the functional morphology of feeding and locomotion has proceeded along separate lines; yet in order to analyze predator-prey interactions and to elucidate patterns of evolution in fishes, the mutual relationships between structure and function in feeding and locomotion need to be considered. Is there a functional relationship between prey capture by high-speed suction and pectoral fin placement? How is the timing of jaw movement modified in ambush predators, and are different locomotor patterns at the strike (Webb and Skadsen, 1980) correlated with differences in jaw movement (Rand and Lauder, 1981)?

Armed with new techniques and a considerable background of experimental data, we now have to consider more general questions and begin to integrate concepts and approaches from feeding and locomotor functional morphology into a synthetic evolutionary framework.

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