# Morphological and Functional Bases of Durophagy in the Queen Triggerfish, *Balistes vetula* (Pisces, Tetraodontiformes)

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**ABSTRACT**  Tetraodontiform fishes are characterized by jaws specialized for powerful biting and a diet dominated by hard-shelled prey. Strong biting by the oral jaws is an unusual feature among teleosts. We present a functional morphological analysis of the feeding mechanism of a representative tetraodontiform, *Balistes vetula*. As is typical for the order, long, sharp, strong teeth are mounted on the short, robust jaw bones of *B. vetula*. The neurocranium and suspensorium are enlarged and strengthened to serve as sites of attachment for the greatly hypertrophied adductor mandibulae muscles. Electromyographic recordings made from 11 cranial muscles during feeding revealed four distinct behaviors in the feeding repertoire of *B. vetula*. Suction is used effectively to capture soft prey and is associated with a motor pattern similar to that reported for many other teleosts. However, when feeding on hard prey, *B. vetula* directly bit the prey, exhibiting a motor pattern very different from that of suction feeding. During buccal manipulation, repeated cycles of jaw opening and closing (biting) were coupled with rapid movement of the prey in and out of the mouth. Muscle activity during buccal manipulation was similar to that seen during bite-captures. A blowing behavior was periodically employed during prey handling, as prey were forcefully "spit out" from the mouth, either to reposition them or to separate unwanted material from flesh. The motor pattern used during blowing was distinct from similar behaviors described for other fishes, indicating that this behavior may be unique to tetraodontiforms. Thus *B. vetula* combines primitive behaviors and motor patterns (suction feeding and buccal manipulation) with specialized morphology (strong teeth, robust jaws, and hypertrophied adductor muscles) and a novel behavior (blowing) to exploit armored prey such as sea urchins, molluscs, and crabs. © 1993 Wiley-Liss, Inc.

The biomechanics of prey capture in fishes have been the subject of extensive study by functional morphologists during the past two decades (Liem, '70, '79; Lauder, '80, '83a; Muller and Osse, '84; Muller et al., '82). Experimental investigations, especially on the mechanics of upper jaw protrusion, have presented evidence that the design of teleost feeding systems reflects the common usage of suction feeding (Osse, '69; Liem, '78, '79; Lauder and Lanyon, '80; Lauder, '80, '83a, '85; Lauder and Clark, '84; van Leeuwen, '84; van Leeuwen and Muller, '83, '84; Sibbing et al., '86; Sanderson, '88; Westneat and Wainwright, '89). However, because prey capture is only the initial step in feeding behavior, the mechanisms of intraoral and pharyn-geal-jaw prey processing have also attracted the attention of functional anatomists (Liem, '78; Lauder, '83b,c; Liem and Sanderson, '86; Sibbing et al., '86; Sibbing, '88; Wainwright, '89a,b; Sanford and Lauder, '89). Most of these experimental studies have benefitted from the use of sophisticated procedures such as electromyography, high-speed cinematography, cineradiography, and pressure recordings. These techniques have allowed the acquisition of an enormous data base through which has emerged a solid understanding of the functional morphology of

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the musculoskeletal components of the teleostean feeding machinery.

Two major trends that have been noted during the evolution of feeding systems in teleost fishes are 1) the great majority of fishes retain suction feeding, the phylogenetically primitive means of prey capture in vertebrates, as the principal means of capturing and ingesting food (Lauder, '83a, '85) and 2) associated with this emphasis on suction feeding, many lineages of teleosts possess a highly mobile and protrusible upper jaw (Schaeffer and Rosen, '61; Lauder, '85; Motta, '84). The majority of teleost species use suction to capture mobile, unattached animal prey. In relatively few lineages is this trend reversed. In this paper we present an analysis of the feeding mechanism in the queen triggerfish, *Balistes vetula*, a representative of a major clade of percomorph teleost fishes (the Tetraodontiformes) that exhibits a reversal of both of these trends.

As with most members of the order, *B. vetula* feeds principally on nonelusive, heavily armored prey types that are apparently captured by biting the prey directly (Randall, '67; Reinthal et al., '84) without the use of suction. Numerous major modifications of the cranial skeleton, musculature, and teeth (including a complete loss of upper jaw protrusion) are associated with this durophagous feeding habit and characterize the two lineages of derived tetraodontiforms, the Balistoidei and the Tetraodontoidea (Winterbottom, '74a). The primary goal of this study is to describe the feeding mechanism of a representative tetraodontiform fish and to explore the morphological and functional specializations for a durophagous feeding habit. We document the first electromyographic recordings made during feeding in a free-swimming tetraodontiform. Functional data on the feeding mechanisms of tetraodontiform fishes are almost completely lacking in the literature (Sarkar, '60; Winterbottom, '74a; Tyler, '80; Gosline, '87), so a second goal of this paper is to lay the foundations for future research on the evolution of the feeding system within this diverse clade. Phylogenetic hypotheses exist for the major lineages of tetraodontiforms (Winterbottom, '74a; Tyler, '80; Lauder and Liem, '83; Winterbottom and Tyler, '83; Mok and Shen, '83; Leis, '84), and the extensive differences seen among these taxa in skull anatomy indicate a potentially rich system for studies of the evolution of the complex feeding mechanism.

## MATERIALS AND METHODS
### Specimens and anatomy

Four freshly frozen specimens and five formalin preserved specimens (95–210 mm standard length; SL) of *B. vetula* were dissected for osteological and myological analyses. In addition, seven dry skeletons (130–280 mm SL; prepared using dermestid beetles) were also examined. All specimens examined for this study were sexually mature. Freehand drawings were made from these specimens (Figs. 1, 2). Osteological terminology follows Matsuura ('79) and Tyler ('80), and myological terminology follows Winterbottom ('74a,b).

For electromyographic experiments, four live individuals of *B. vetula* (145–174 mm SL) were collected by hand from fringing coral reefs off the southwestern coast of Puerto Rico. The fish were maintained in free-flowing saltwater aquaria at the Marine Sciences Laboratory of the University of Puerto Rico for 2 weeks prior to shipment to the Department of Biological Science, Florida State University. Each fish was maintained separately in 100 liter aquaria at room temperature (24°C) and fed pieces of squid, live earthworms, live fish, and thawed frozen crabs for up to 4 weeks prior to the experiments. These same food types were also used for all feeding experiments.

### Electromyography

The activity patterns of 11 muscles were documented using electromyography to examine the functional role of these muscles during feeding in *B. vetula*. The electromyographic procedures followed Wainwright ('89a,b) and Westneat and Wainwright ('89). Briefly, steel alloy bipolar fine wire (0.002 gauge) electrodes were threaded through a 26-gauge hypodermic needle. To ensure that the paired electrode wires did not spread apart during the experiment, the first 15 cm of wire were glued together using a thin coat of cyanoacrylate adhesive. Approximately 0.5 mm of the plastic coating that insulated the wire was scraped off each electrode tip using a blade under a dissecting microscope. The exposed tips were then bent back against the needle barrel until they were almost parallel to one another and ~1 mm apart. The bent wire tips also served as hooks that anchored the electrode into the belly of the muscle during the experiments.

Each experimental fish was anesthetized using a seawater solution of tricaine methane-

sulfonate (MS-222; 1.0 g/liter) for ~10 min and then transferred to a shallow dissecting tray containing 50% fresh seawater and 50% anesthetizing solution. Up to 10 color coded electrodes were used during each experiment, and each electrode was implanted directly into the belly of the target muscle. The electrode wires were glued together to form a single cable that was secured to a suture looped through the skin posterior to the fish's head just lateral to the first dorsal spine. Muscle activity was recorded from the left members of the levator operculi (LOP), dilator operculi (DO), epaxialis (EP), obliquus inferioris (OBI), sternohyoideus (SH), protractor hyoidei (PH) (=geniohyoideus), retractor arcus palatini (RAP), and four sections of the adductor mandibulae muscle ($A_1\alpha$, $A_2\alpha$, $A_2\beta$, $A_2\gamma$) (see Figs. 1 and 2). These muscles were chosen because they have been shown to play major roles in moving the cranial elements of other teleosts during feeding or because they were anticipated to be of particular interest regarding *B. vetula*. The symmetrical and asymmetrical firing of morphologically symmetrical cranial muscles during feeding in fishes may be a possible source of motor pattern variation (Liem, '79; Lauder and Norton, '80). Because simultaneous bilateral recordings of the cranial muscles of *B. vetula* were not conducted in this study, the contribution of this source of variation to the modulation of the oral jaw mechanism in this fish could not be determined.

To ensure that the electrodes were properly implanted into the target muscles, several trial electrode implantations were made on formalin preserved and thawed, frozen specimens of *B. vetula* prior to the actual electromyographic recordings. We also relied on the relative positions of specific skeletal landmarks to guide electrode placement. After each electromyographic recording session, the fish was sacrificed using an overdose of the anesthetizing solution and then dissected to confirm electrode placement. We found no electrode that was improperly positioned.

After implanting the electrodes, experimental fish were returned to their aquarium, where, upon recovery from anesthesia, they were offered a variety of prey: 3–5-cm pieces of squid mantle, 6–10-cm-long live earthworms (*Lumbricus*), 3–5-cm (SL) live fish (*Poecelia latipinna*), and 1–2 cm (carapace diameter) fresh/thawed majid crabs (*Mithrax sculptus*). Electrical signals from up to eight muscles were simultaneously amplified 10,000 times using Grass P511J preamplifiers. A bandpass of 100–3,000 Hz was used, and the 60 Hz notch filter was always employed. Analog recording of electrical signals from the muscles were recorded on a Teac XR-5000 tape recorder at a tape speed of 19 cm/sec. The electromyographic recordings were later played back at one-fourth the recording speed and printed using a Western Graphtec Mark-11 thermal array recorder. All experiments were conducted at room temperature (24°C ± 0.5°C).

To summarize the temporal pattern of muscle activities, a total of 21 variables (11 duration of activity variables and 10 relative onset of activity variables) were measured from the electromyograms. Average values (with standard errors; S.E.) for each EMG duration and onset variable were calculated. The duration of activity of each of the 11 muscles (see above) was measured directly from the chart recordings for each feeding (e.g., LOP-DUR). To examine the sequence of firing of each muscle, the onset of activity of th levator operculi (LOP) was designated as time zero, and, from this point, the relative onset of activity of each of the other 10 muscles was determined (e.g., LOP-RAP). The LOP was chosen as the reference muscle because it was consistently active in all cycles of muscle activity and to facilitate comparisons with other studies that have used this muscle as a reference (Wainwright and Lauder, '86; Westneat and Wainwright, '89). All measurements were made manually using a digital caliper (Mitutuyo Series 500) and are expressed in milliseconds.

Only some of the 11 muscles were active during each cycle of motor activity for each of the four feeding behaviors observed (see below). Thus the frequency of activation of each muscle was calculated as a percentage of the maximum number of cycles analyzed for the behavior. An overall frequency of activity was computed by averaging the values across all four fish.

## RESULTS
### Anatomy of the feeding apparatus
Osteology

In the anatomical descriptions of the queen triggerfish that follow, emphasis is given to areas of the head that are of particular functional interest. Additional osteological and myological descriptions of this species and other tetraodontiform fishes are found in Gregory ('33), Sarkar ('60), Tyler ('68, '80),

Matsuura ('79), and Winterbottom ('74a). The musculoskeletal linkages that play significant roles in the feeding repertoire of *B. vetula* include the oral jaws (upper and lower jaws), the neurocranium, the suspensorial apparatus, the hyoid apparatus, the opercular apparatus, and the pectoral girdle (Fig. 1).

The neurocranium of *B. vetula* is elongated rostrocaudally and serves as the dorsal mechanical element of the feeding apparatus (Figs. 1, 2). The anterior portion of the skull is dominated by an elongated ethmoid (Fig. 2A; EM) that interdigitates laterally with the prefrontals (Fig. 2A; PF) and dorsally with the frontals (Fig. 2A; FR). The other skull bones include the laterally flattened parasphenoid (Fig. 2A; PA) that runs ventral to the ethmoid and the orbit, the relatively small vomer (Fig. 2A; VO), the sphenotic (Fig. 2A; SN), and the pterotic (Fig. 2A; PT). The anterior region of the neurocranium, particularly the anteroventral tip of the ethmoid and the vomer, provides points of articulation with the upper jaw and the anterodorsal leg of the suspensorium. Just below its orbital region, the neurocranium articulates via the pterotic and the sphenotic with the posterodorsal leg of the suspensory apparatus, the pectoral girdle, and the opercular series.

The suspensorium is divided into two major regions. The anterior end of the T-shaped palatines (Fig. 2A; PL) represents the anterodorsal leg of the roughly U-shaped suspensory apparatus. The palatines articulate, anteriorly, through a ligamentous connective tissue with the ethmoid, vomer, premaxilla (Fig. 2A; PM) and the maxilla (Fig. 2A; MX) and, posteriorly, with the ectopterygoid (Fig. 2A; ET). The ectopterygoid, the mesopterygoid (Fig. 2A; MS), the metapterygoid (Fig. 2A; MT), the quadrate (Fig. 2A; QD), and the symplectic (Fig. 2A; SM) interdigitate either completely or slightly with one another. The posterodorsal leg of the suspensorium is dominated by the dorsoventrally elongated hyomandibular bone (Fig. 2A; HM) that articulates primarily with the pterotic and the sphenotic. The broad preoperculum (Fig. 2A; PO) articulates anteriorly with the quadrate and symplectic and posteriorly with the hyomandibula. Both anterodorsal and posterodorsal joints between the suspensory apparatus and the neurocranium (Figs. 1, 2A) allow for slight mediolateral swinging of the suspensorium relative to the skull.

Structural deviations from the generalized percomorph design are particularly evident in the upper and lower jaws. One novel feature is the almost complete fusion of the premaxilla (Fig. 2A; PM) to the maxilla (Fig.

2A; MX), allowing these bones to function as a single unit on each side of the upper jaw. The primary articulation of the upper jaw to the neurocranium is through a strong ligamentous joint between the concave posterodorsal edge of the premaxilla and the anterior tips of the ethmoid and the vomer. The dorsal edge of the maxilla and the dorsolateral edge of the premaxilla are connected to the anterior and anteroventral portions of the palatine. The short and thick lower jaw consists of the dentaries (Fig. 2A; DN), the articulars (Fig. 2A; AR), and the angulars (Fig. 2A; AN). These bones are articulated to each other by interdigitation. Each articular is concave posterolaterally to accommodate the thickened knob of the anterior tip of the quadrate. Each angular is ventrolaterally concave to serve as a joint between the lower jaw and the interopercular bone (Fig. 2A; IO). Each premaxilla and dentary support an outer row of four long, stout teeth that are notched at their edges and are held closely to one another.

The greatly reduced opercular apparatus of *B. vetula* is modified from the condition seen in most teleosts. The hyomandibula has an expanded and thickened posterodorsal arm that articulates with the opercular bone. The small, flattened, and leaf-like opercular bone (Fig. 2A; OP) firmly articulates with the dorsal aspect of the thin subopercular bone (Fig. 2A; SO) by way of a ligamentous connective tissue. An obvious modification of the opercular apparatus is that the interopercular bone (Fig. 2A; IO) has been reduced into a tiny bony rod. A tough ligament connects the anterior tip of this tiny rod shaped bone to the ventrolateral concavity in the angular. Posteriorly, the IO has two ligamentous articulations: One ligament connects it to the dorsal aspect of the epihyal, and the other ligament (Figs. 1A, 2B, 2D; IOL) extends posterodorsally to connect this bone to the ventromedial edge of the opercular bone. This arrangement represents a retention of the phylogenetically primitive mechanical coupling between this bone and the hyoid bar on one hand and the opercular series on the other. This arrangement permits depression of the lower jaw in two ways: 1) by the depression of the hyoid bar (see below) and 2) by the posterior rotation of the operculo-subopercular bone complex on its articulation with the hyomandibula.

The hypohyal (Fig. 2A; HH), the urohyal (Fig. 2A; UH), the ceratohyal (Fig. 2A; CH), the epihyal (Fig. 2A; EH), and the interhyal (Fig. 2A; IH) are articulated with one an-
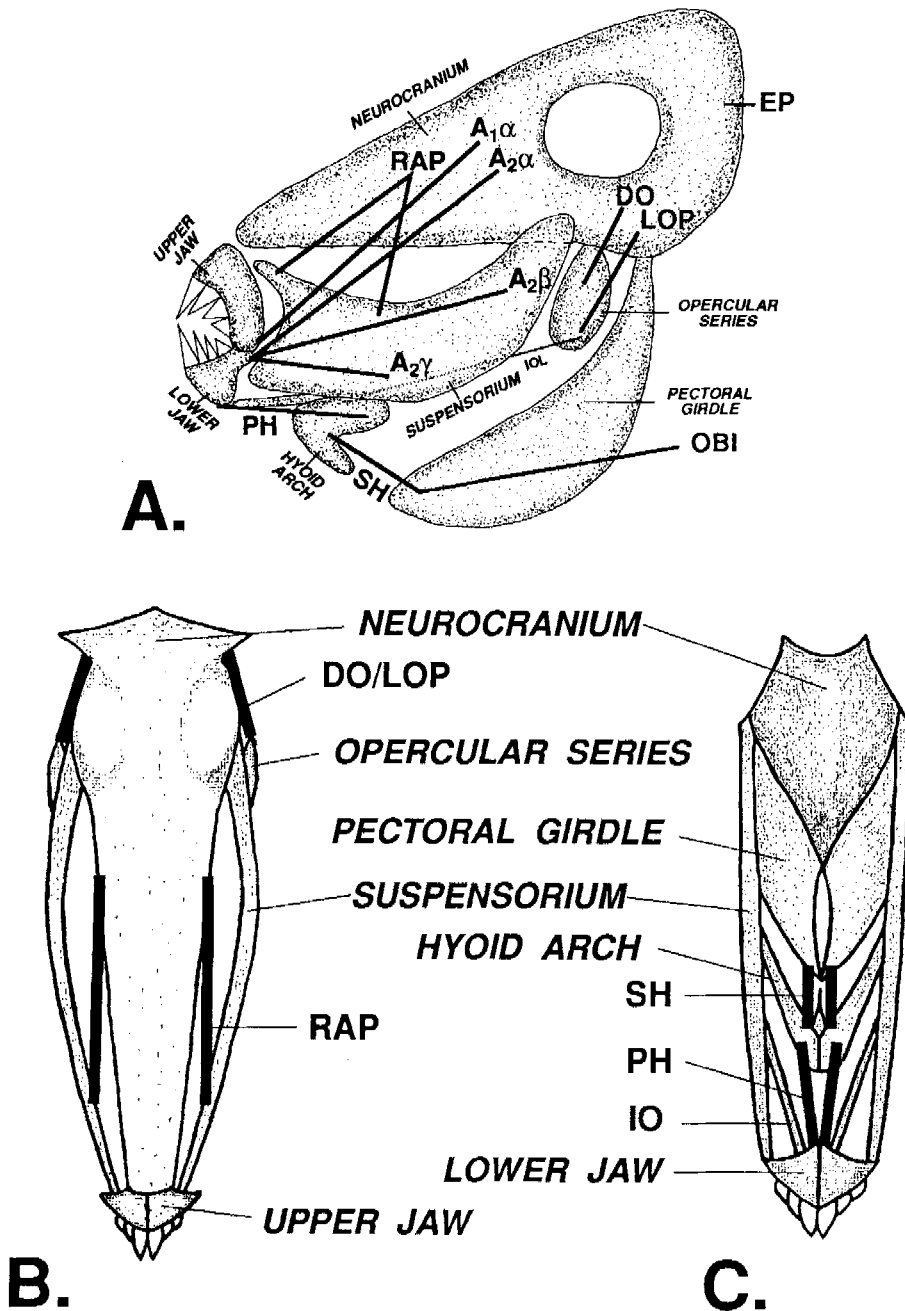
Fig. 1. *Balistes vetula.* Schematic diagram of the skull illustrating the major functional units of the feeding mechanism in lateral (**A**), dorsal (**B**), and ventral (**C**) views. Thick lines indicate the attachments of major muscles of the feeding mechanism discussed in this paper. In the dorsal view diagram (B), the superficial adductor mandibulae muscles are not illustrated in order to show the position of the retractor arcus palatini. Contraction of this muscle possibly generates the force that produces mediolateral movement of the suspensorium. Abbreviations as in Figure 2.

Fig. 2. *Balistes vetula*. **A**: Detailed drawing of the bones comprising the functional units diagrammed in Figure 1. Note the reduced size of the opercular series bones and the expanded rostral region of the neurocranium and the suspensorium that serve as sites of attachment for the adductor mandibulae muscles. **B**: Lateral view diagram of the superficial muscles of the head. Note the distinct sections of the adductor mandibulae complex. **C** : Deeper view of the adductor mandibulae muscles. The musculoskeletal components of the suspensorium, hyoid apparatus, opercular series, and the pectoral girdle were removed to expose the deeper structures. **D**: An even deeper dissection of the palatal region is illustrated to show the position of the retractor arcus palatini. Also illustrated is the opercular coupling to the jaw via the interopercle, and the sternohyoideus muscle. AN, angular; AR, articular; $A_1\alpha$, $A_2\alpha$, $A_2\beta$, $A_2\gamma$ sections of the adductor mandibulae; CC, coracoid; CH, ceratohyal; CT, cleithrum; DN, dentary; DO, dilator operculi; EH, epihyal; EP, epaxialis; EM, ethmoid; ET, ectopterygoid; FR, frontal; HH, hypohyal; HM, hyomandibula; IH, interhyal; IO, interopercle; IOL, interopercle-opercle ligament; LOP, levator operculi; MS, mesopterygoid; MT, metapterygoid; MX, maxilla; OBI, obliquus inferioris; OP, opercle; PA, parasphenoid; PF, prefrontal; PH, protractor hyoidei; PL, palatine; PM, premaxilla; PO, preopercle; PT, pterotic; QD, quadrate; RAP, retractor arcus palatini; SC, supracleithrum; SH, sternohyoideus; SM, symplectic; SN, sphenotic; SO, subopercle; UH, urohyal; VO, vomer.

other by way of cartilagenous and ligamentous tissues or through interdigitation to form the hyoid apparatus of *B. vetula*. The hyoid bar is linked to the suspensorium by way of a ligamentous joint between the interhyal and the symplectic. Movement of the hyoid apparatus is translated to the lower jaw or to the opercular bones via the interopercular bone, which is ligamentously articulated to the epihyal.

The pectoral apparatus is notably enlarged. It is dominated by the coracoid (Fig. 2A; CC) and the cleithrum (Fig. 2A; CT). These are broad, elongate bones, attached by fibrous connective tissue. The major contribution of the pectoral girdle to the feeding machinery of *B. vetula* appears to be its role as a site of attachment for important muscles such as the sternohyoideus and the obliquus inferioris.

## Myology

The adductor mandibulae muscle complex is enlarged and subdivided in *B. vetula* (and in other tetraodontiforms) relative to the phylogenetically primitive condition. There are six subdivisions of the almost completely parallel-fibered adductor mandibulae muscle of *B. vetula* (Winterbottom, '74a): $A_1\alpha$, $A_1\beta$, $A_2\alpha$, $A_2\beta$, $A_2\gamma$, and $A_3$. Both $A_1\beta$ and $A_3$ are very small and completely covered by the other subdivisions of the adductor mandibulae. Except for the small anterior portion that is superficially visible in lateral view, $A_1\alpha$ is overlain by $A_2\alpha$ (Fig. 2B). The lateroventral edges of the ethmoid and prefrontals, the infraorbital ligament, and the anterodorsal surface of the hyomandibula serve as sites of origin for the fibers of $A_1\alpha$, which insert by a tendon mainly on the ventromedial edge of the maxilla (Fig. 2C). Contraction of the $A_1$ sections of the adductor mandibulae would be expected to cause the upper jaw to rotate posterodorsally around its point of articulation with the neurocranium. The fibers of $A_2\alpha$ originate from the lateroventral portions of the ethmoid, the prefrontals, the infraorbital ligament, and portions of the lateral surface of the hyomandibula. Section $A_2\beta$ originates from portions of the hyomandibular, preopercular, and metapterygoid bones. The smallest of the $A_2$ subsections, $A_2\gamma$, originates mostly from the lateral surfaces of the ventral arm of the preopercular bone ventral to the prominent ridge that separates this muscle from the adductors dorsally. All three sections of $A_2$ converge anteriorly to insert by a common tendon on the posterodorsomedial edge of the dentary (Fig. 2B). When these muscles contract, they pull directly on the dentary, presumably causing the lower jaw to rotate posterodorsally around the joint between the articular and the quadrate. Because some fibers of $A_2\alpha$ and $A_2\beta$ insert on the tendon that connects the maxilla to the dentary, contraction of these muscles may also cause slight movement of the upper jaw.

The retractor arcus palatini (Fig. 2; RAP) is massive in *B. vetula*. The fibers of the RAP run parallel to one another and originate primarily from the lateral faces of the ethmoid and parasphenoid. The muscle is subdivided by a tendon that runs posterodorsally between the ectopterygoid and the prefrontal (Fig. 2D). The RAP inserts on the anterodorsal surfaces of the bones that compose the anterodorsal leg of the suspensory apparatus (see Results, Osteology).

The levator operculi (Fig. 2B; LOP) is a small muscle originating from the pterotic and supracleithrum and inserting on the posterodorsal surface of the opercular bone. The fibers of the dilator operculi (Fig. 2B; DO) originate from the sphenotic and insert on the dorsolateral surface of the opercular bone. The posterodorsal force of the LOP primarily causes the opercular bone to rotate posterodorsally about its articulation to the hyomandibula. Contraction of the DO is predicted to produce a similar action.

The fibers of the protractor hyoidei (Fig. 2B; PH) originate from the skin, the branchiostegal rays, and the hypohyal and insert on the ventral edge of the lower jaw. The superficial posterolateral fibers of the sternohyoideus (Fig. 2B; SH) run continuously with the obliquus inferioris (Fig. 2B; OBI). The more interior portion of the SH (Fig. 2D) is small relative to the condition seen in most teleosts. This interior section originates from the anterodorsal edge of the cleithrum, with some of the fibers forming a small bundle that originates from the anterior tip of the cleithrum and insert on the posterior tip of the urohyal (Fig. 2D; SH). The entire SH inserts on the urohyal with some fibers inserting on the hypohyal. Contraction of the SH muscle fibers depresses the hyoid bar in generalized teleosts, and, although this muscle and the hyoid bar are both reduced in *B. vetula,* the same function is expected for this species. Additional force to depress the hyoid apparatus is apparently generated by the posterior rotation of the pectoral girdle produced by the contraction of the OBI muscle fibers.

As in other teleosts, the epaxialis (Fig. 2B; EP) is the dominant component of the dorsal one-half of the lateral body musculature in *B. vetula* (Osse, '69; Liem, '70, '78, '79; Lauder, '80, '83b,c; Lauder and Clark, '84; Lauder and Liem, '83; Sibbing et al., '86).

### Patterns of muscle activity

Recordings of motor activity were made during four distinct feeding behaviors: 1) capture of soft and elusive prey, 2) capture of hard prey, 3) buccal manipulation, and 4) blowing (or "spitting out") (Figs. 3–8). Here we describe the basic motor patterns that were observed during these behaviors. In spite of the morphological specializations related to durophagy, *B. vetula* usually employed suction feeding to capture elusive (fish) and soft (earthworm and pieces of squid) prey items during our experiments. However,
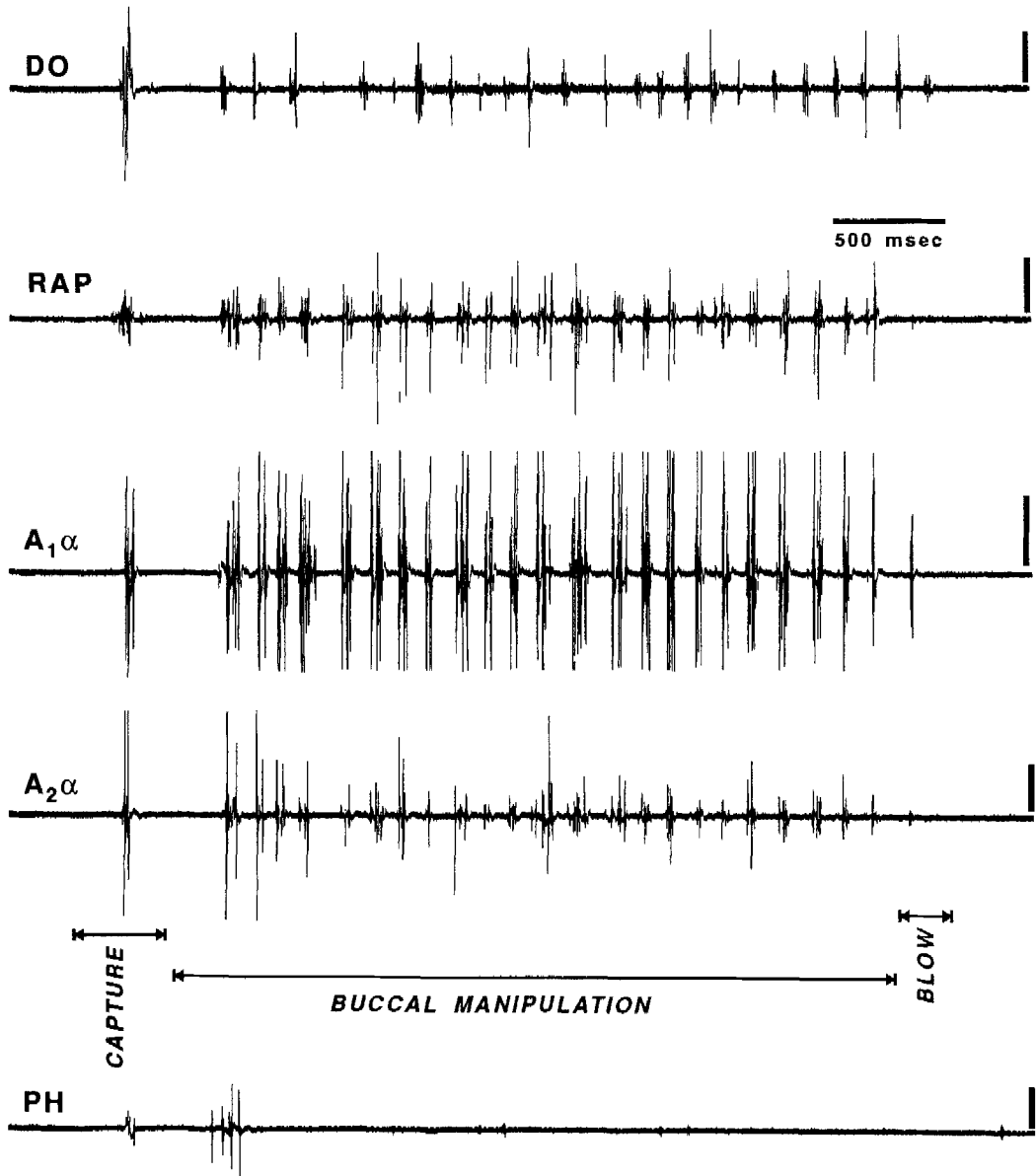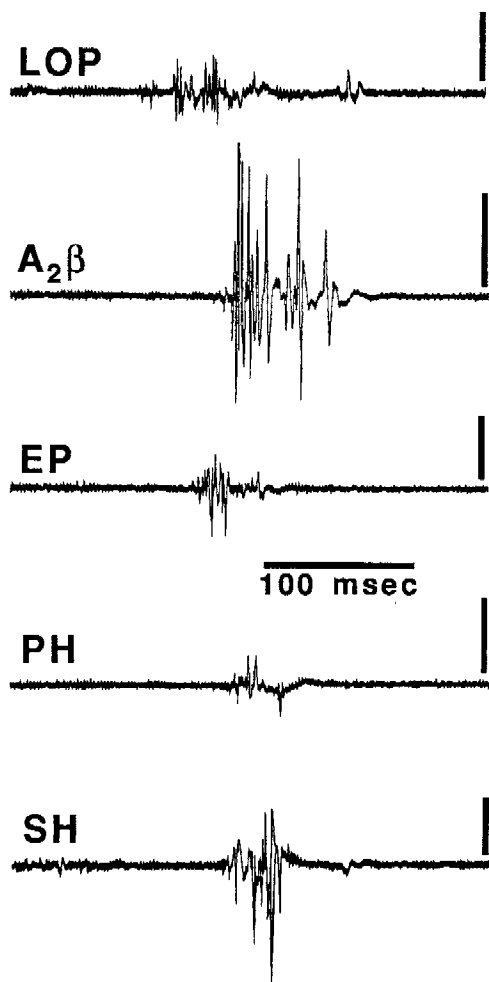
Fig. 3. *Balistes vetula*. Simultaneous electromyographic recordings from five cranial muscles during feeding on a live fish. This sequence illustrates the sequence of behaviors typical of feeding on soft and elusive prey. Prey capture is followed by > 20 cycles of buccal manipulation, during which the prey is repeatedly bitten and triturated. This sequence concluded with a single blowing event as the fish discarded unwanted material immediately before swallowing the prey. Vertical scale bar at the end of each EMG represents 100 microvolts. Abbreviations as in Figure 2.

when feeding on crab a different behavior was elicited.

The motor pattern observed during suction-type prey capture was characterized by a single, short burst of activity in all of the muscles examined (Figs. 3, 4, 7A). The activity periods of all muscles overlapped extensively. The cycle of muscular activity during this phase of the feeding repertoire of *B. vetula* lasted for an average of 150.69 msec

**LOP**

**A₂β**

**EP**

$\overline{\textbf{100 msec}}$

**PH**

**SH**

Fig. 4. *Balistes vetula.* Simultaneous electromyographic recordings from five cranial muscles during suction feeding on a fish prey. Note that this behavior is characterized by overlapping activity in all muscles. Vertical scale bar at the end of each EMG represents 100 microvolts. Abbreviations as in Figure 2.

($\pm$21.14 S.E., N = 14). The retractor arcus palatini was active in all suction-type prey capture cycles examined (Fig. 8) and was the only muscle to show activity prior to the onset of the levator operculi (LOP) activity (Fig. 7A). The LOP and dilator operculi (DO) began activity simultaneously, and the DO continued contraction for slightly longer than the LOP (Fig. 7A). Activity in the other muscles began ~20 msec following the onset of LOP activity. The sternohyoideus and protractor hyoidei muscles exhibited the most infrequent and variable activities during suc-

tion feeding sequences even involving the most mobile fish prey (Fig. 8). In contrast, all four adductor mandibulae muscles showed a long, high-amplitude burst of activity in 100% of the suction-type prey capture sequences analyzed (Figs. 7A, 8). Activity in the A₁α and A₂α muscles began ~30 msec following the onset of LOP activity, followed by A₂β and A₂γ which began firing around 40 msec after the onset of LOP activity (Fig. 7A).

The motor pattern associated with the capture of crabs was qualitatively different from that observed during suction feeding. *B. vetula* did not usually appear to employ suction feeding when capturing crab prey but instead directly bit the prey, usually removing an appendage or a piece of the carapace. This behavior was characterized by nonoverlapping activity of the mouth opening muscles (i.e., LOP and DO) and the other nine muscles (Fig. 7B). Activities in the jaw closing muscles (i.e., adductor mandibulae) did not begin until ~90 msec after the onset of LOP activity. Only the A₁α, A₂β, and LOP were consistently active during all crab prey capture events (Fig. 8). Very short activities were typical of the epaxialis and obliquus inferioris muscles. The cycle of muscular activity during this phase of the feeding repertoire of *B. vetula* lasted for an average of 313.40 msec ($\pm$21.14 S.E., N = 47).

Processing began immediately after prey were captured and held between the teeth of the upper and lower jaws. Reduction of large prey occurred by repeated sequences of biting the food between the oral jaws, coupled with rapid movements of the prey in and out of the mouth. We follow Lauder ('83a) in terming this behavior as "buccal manipulation." In *B. vetula*, buccal manipulation involved a continuous series of up to 23 cycles of alternating activity in the major mouth opening muscles (i.e., LOP and DO) and the major mouth closing muscles (i.e., adductor mandibulae sections A₁α, A₂β, A₂β, and A₂γ) (Figs. 3, 5). Each cycle of muscular activity (Fig. 7C) lasted for an average of 215.65 msec ($\pm$8.73 S.E., N = 113) and was characterized by short bursts of activity in the LOP and DO muscles (~50 msec), followed by longer bursts in the jaw adductors (>100 msec), and low level activity in the lateral body musculature (i.e., epaxialis [EP] and obliquus inferioris [OBI]). The four adductor mandibulae muscles were active in virtually all buccal manipulation cycles, while the sternohyoideus, protractor
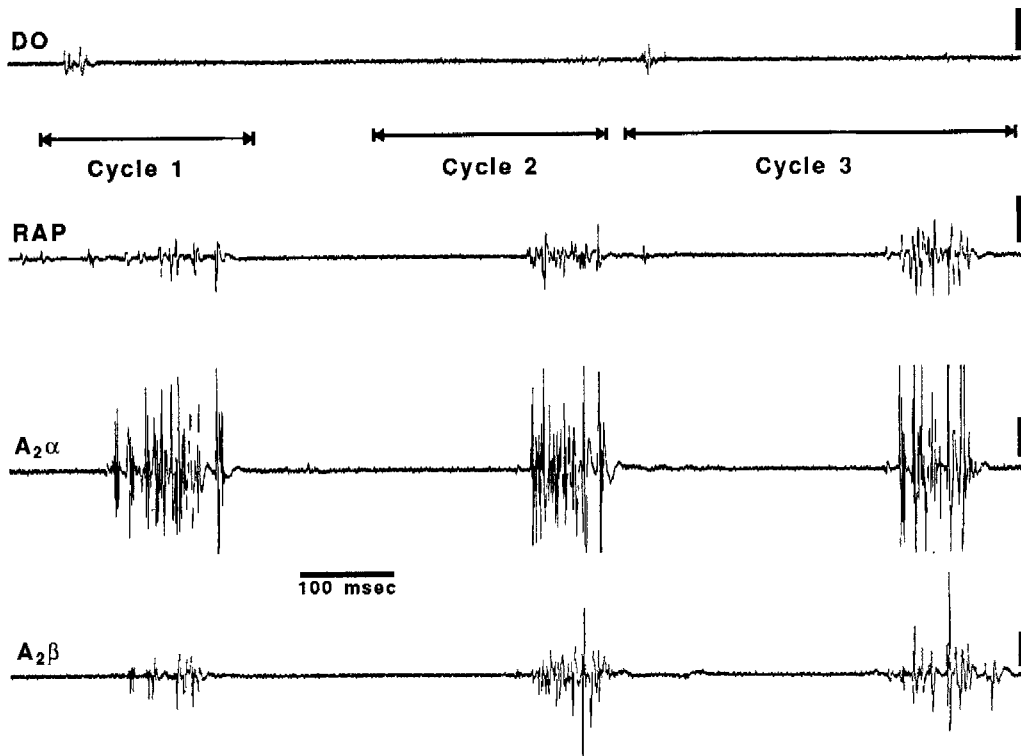
Fig. 5. *Balistes vetula.* Simultaneous electromyographic recordings of four cranial muscles showing three cycles of muscular activity during buccal manipulation of a crab prey. Note that, while the adductor mandibulae and retractor arcus palatini muscles are almost entirely overlapping, their activity occurs between burst of activity of the dilator operculi. Vertical scale bar at the end of each EMG represents 100 microvolts. Abbreviations as in Figure 2.

hyoidei, EP, and OBI were infrequently active (Fig. 8).

The blowing behavior occurred under two types of circumstances. In the first type, blowing was used to manipulate prey before capture, while, in the second and more common type, blowing was used after prey capture during the prey manipulation phase to forcefully expel the prey from the mouth. This activity often was preceded and followed by bouts of buccal manipulation.

The motor pattern during blowing was characterized by a very long burst of activity in the LOP (Figs. 6, 7D). This prolonged burst of activity of the LOP was accompanied by extended mouth opening observed while the fish exhibited the blowing behavior. Most of the other muscles fired toward the end of the activity period of the LOP, except for the DO, which fired at the same time as the LOP, and the epaxialis, which fired a little later (Fig. 7D). Several of the muscles that tended

to exhibit long activity bursts during both prey capture and buccal manipulation (e.g., adductor mandibulae and retractor arcus palatini muscles) exhibited shorter, less regular bursts of activity during blowing (Fig. 7). The cycles of muscular activity during this phase of the feeding process lasted for an average of 219.4 msec ($\pm$49.6 S.E., N = 18).

### DISCUSSION

The diet of *B. vetula* is dominated by hard-shelled and spiny benthic invertebrates such as sea urchins, decapod crabs, pelecypods, gastropods, and chitons (Randall, '67; Fricke, '71, '75; Reinthal et al., '84). This diet is typical of both tropical and temperate members of the genus as well as of other balistids (Hiatt and Strasburg, '60; Randall, '67; Fricke, '71, '75; Hobson, '74; Frazer et al., '91). Armored prey are not normally quick or otherwise elusive but require extensive handling and manipulation to break apart the
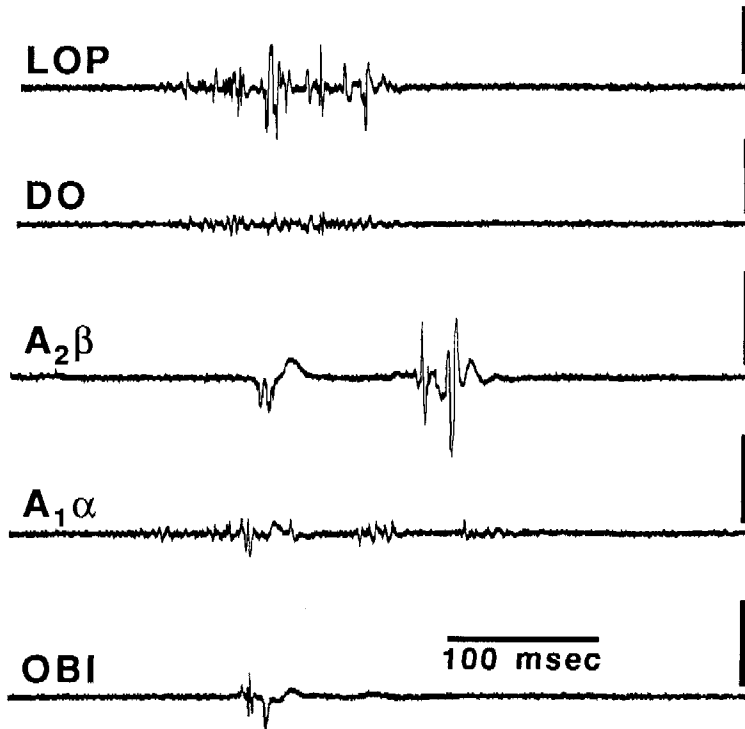
Fig. 6. *Balistes vetula*. Simultaneous electromyographic recordings of five cranial muscles made during a single blowing behavior. This behavior is dominated by activity in the levator operculi muscle, which is activated for long periods while material is expelled from the mouth by water currents. Vertical scale bar at the end of each EMG represents 100 microvolts. Abbreviations as in Figure 2.

protective coverings. This study has identified several morphological and functional (motor pattern) specializations of the feeding mechanism in *B. vetula* that diverge from the more generalized percomorph feeding condition and, in conjunction with numerous retained primitive features, are employed during prey capture and handling of diverse prey types. Key specializations related to durophagy include 1) complete loss of jaw protrusion and the development of a firm connection between the neurocranium and the fused upper jaw bones; 2) hypertrophy of the adductor mandibulae muscles and their sites of attachment; 3) presence of stout, anteriorly oriented teeth; 4) ability to capture prey either by using suction or by biting and presence of distinct motor patterns for these two behaviors; and 5) extensive use of blowing during prey handling and a novel motor pattern associated with this behavior. Below we discuss these, and other specializations related to the durophagous feeding habits of *B. vetula*.

## Structural design of the feeding apparatus

The head of *B. vetula* shows a mixture of derived and primitive features related to the durophagous habit of the species. Both the upper and lower jaw bones are equipped with very strong teeth that are tightly arranged together and have notched edges (Fig. 2). Fusion of the premaxilla with the maxilla accompanied by loss of upper jaw protrusion provides a jaw system that is braced firmly against the neurocranium for support when the adductor mandibulae muscles close the mouth (Barel, '83; Otten, '83). Both the lower and upper jaws are shortened, such that the outlevers resisting the adductor mandibulae muscles (i.e., the distance from the site of rotation of each jaw and the toothed surface) are extremely small relative to the size of the fish. This arrangement tends to maximize the resultant force experienced at the contact point between the teeth and prey.

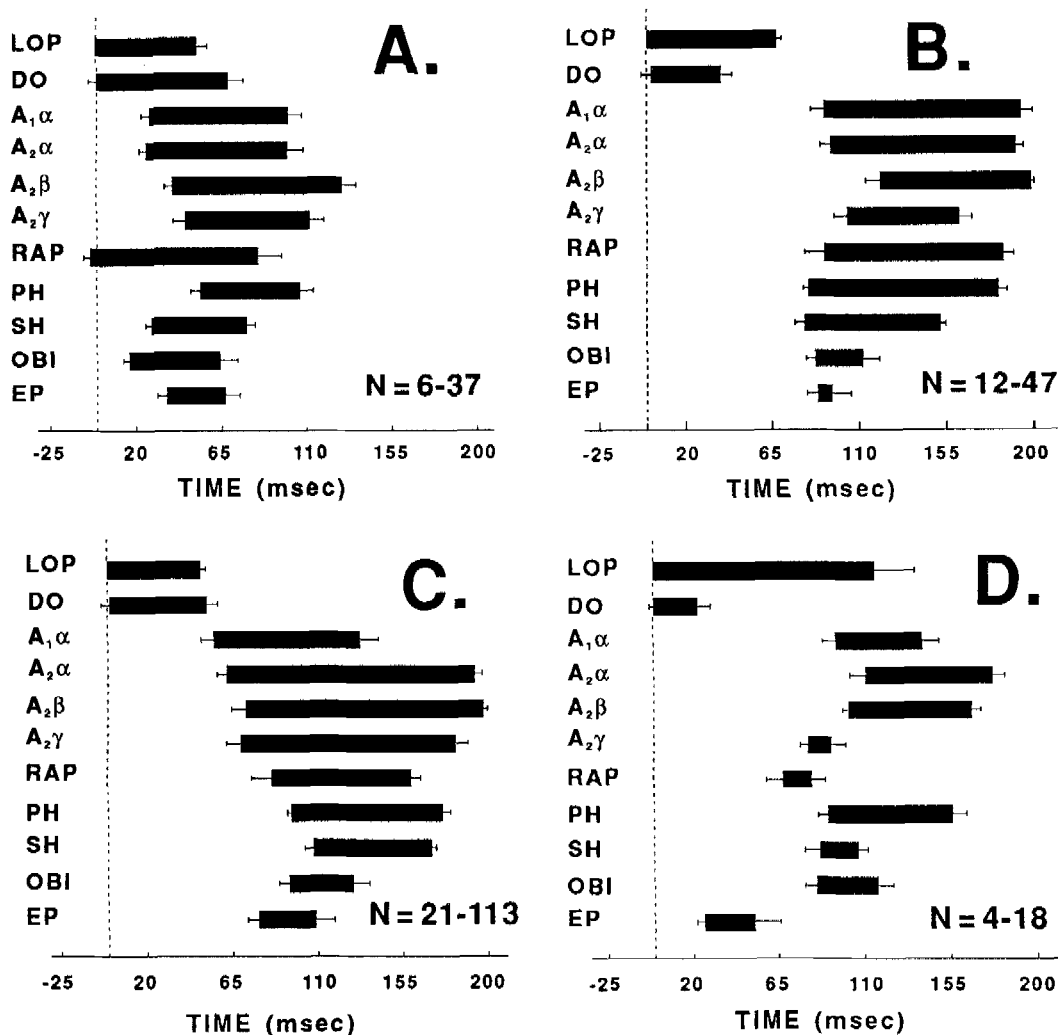The musculature of the skull is dominated by the adductor mandibulae complex, which

Fig. 7. *Balistes vetula.* Bar diagrams summarizing the temporal pattern of muscle activity in 11 cranial muscles during capture of live earthworm and pieces of squid prey by suction feeding (A), capture of crab prey by biting (B), buccal manipulation of crab prey (C), and blowing of crab prey (D). The length of each bar indicates the mean duration of activity of each muscle, with the S.E. of duration indicated at the right end of each bar and the S.E. of the onset time indicated at the left end of each bar. These bar diagrams summarize data collected from four individual fish. The range of the sample sizes (N) for each muscle analyzed for each behavior is given. Note the difference in muscle activity patterns between suction feeding (A) and biting (B) types of prey capture. Biting involves less overlap of activity between the mouth opening muscles (LOP and DO) and the mouth closing muscles (adductor mandibulae) than is seen during suction feeding. Capture by biting is very similar to the motor pattern seen during buccal manipulation (C). The motor pattern exhibited during blowing (D) is qualitatively different from that reported to occur in other fish taxa during similar behaviors. Abbreviations as in Figure 2.

is both hypertrophied and subdivided relative to more generalized fishes. Two subdivisions insert on the upper jaw ($A_1\alpha$ and $A_1\beta$), and four subdivisions insert on the lower jaw ($A_2\alpha$, $A_2\beta$, $A_2\gamma$, and $A_3$). The modifications of the adductor mandibulae and the distribution of the other muscles of the head have apparently influenced the construction of the bony elements of the feeding apparatus. There is an elongate ethmoid region of the skull, a ventral expansion of the parasphenoid, a laterally concave shape of the pterygoid bones (especially the metapterygoid), a broad preoperculum, and an enlargement of
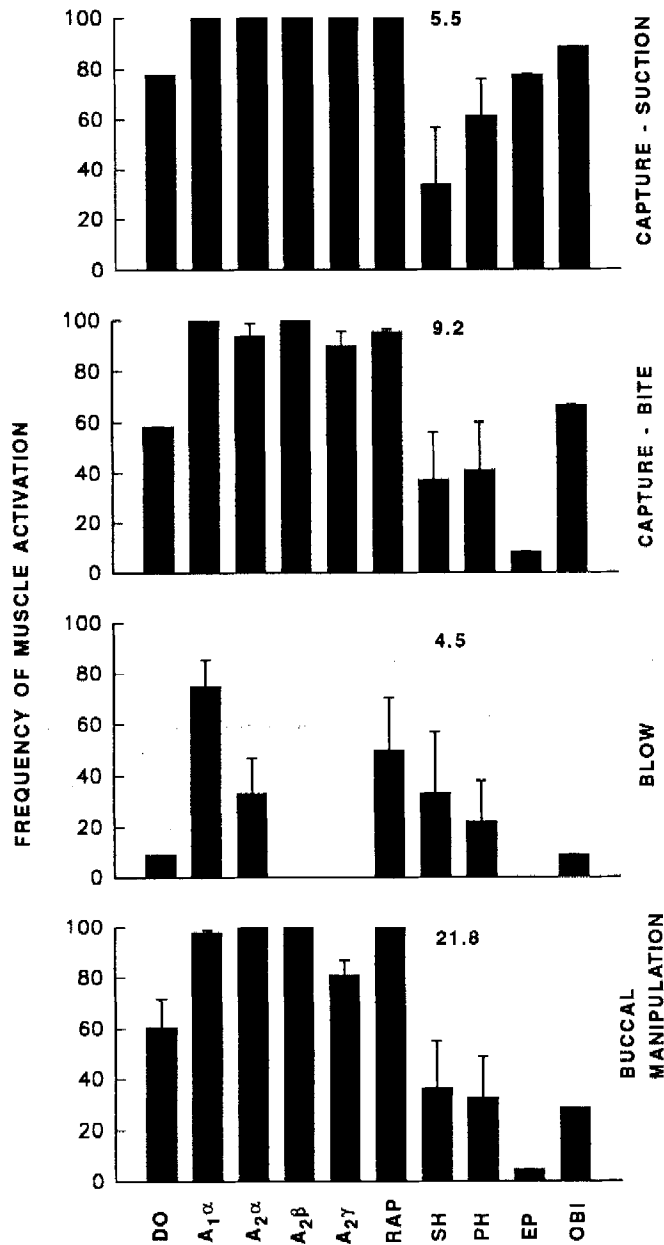
Fig. 8. *Balistes vetula.* Summary diagram showing the frequency of activation of each muscle expressed as a percentage of the maximum number of cycles exhibited during each behavior in the feeding repertoire. Each bar of the graph shows the average value for all four fish. Error bars represent standard error of the mean. The average number of cycles for each behavior is given. Note that the levator operculi (LOP) was consistently active (i.e., 100% activation) during all cycles of muscle activities analyzed for each behavior, so its bar is not included in each graph. Abbreviations as in Figure 2.

the hyomandibula (Fig. 2A). These enlarged structures serve as sites of attachment for the adductor mandibulae sections. The rigidity and the structural strength of the bony elements are apparently enhanced by the tough ligamentous and sutural joints between them, such as those connecting the bones of the suspensorium, oral jaws, neurocranium, and hyoid apparatus.

The sternohyoideus is reduced in size, as is the hyoid apparatus. It has a novel medial subdivision that runs dorsally to attach the tip of the cleithrum to the posterior tip of the urohyal, rather than to its keel.

Another important modification in the feeding apparatus of *B. vetula* is the presence of the retractor arcus palatini (RAP) muscle, which apparently develops as an anterior subdivision of the levator arcus palatini (Winterbottom, '74a). Among the Tetraodontiformes, the RAP is present only in the Balistoidei [and apparently convergently in the Acanthuridae (Winterbottom, '74a)]. This large, parallel-fibered muscle runs anteroventrally from the lateral surface of the ethmoid and the parasphenoid to insert on the palatine and the ectopterygoid (Fig. 2D). It replaces the levator arcus palatini as the prime adductor of the palatal arch. In most teleosts, lateral movement of the palatal arch is produced by the contraction of the levator arcus palatini (Osse, '69; Liem, '70, '78, '79; Lauder, '79, '83b; Lauder and Lanyon, '80).

Among the retained primitive characteristics of *B. vetula* (and other tetraodontiforms), the most striking is the presence of a very small, undeveloped pharyngeal jaw apparatus (Tyler, '80; Winterbottom, '74a). Many of the other groups of percomorph fishes that have diets of primarily hard-shelled prey have greatly hypertrophied pharyngeal jaw bones, teeth, and muscles (e.g., Liem and Greenwood, '81; Wainwright, '87, '88). It is clear that *B. vetula* is able to handle armored prey without the aid of a powerful crushing apparatus in the pharyngeal jaws and that virtually all of the functions involved in capture and reduction of prey are accomplished by the oral jaws.

### Motor patterns and feeding behavior

The queen triggerfish appears to rely on a combination of four distinct behaviors to capture and process a broad range of prey types: 1) inertial suction to capture soft and elusive prey, 2) direct biting to capture hard shelled prey or those attached to the substrate, 3) buccal manipulation, and 4) blowing. Interest-ingly, all of these behaviors have been reported in other fish taxa, although their phylogenetic distribution is not clear in every case. Here we contrast these behaviors and the motor patterns associated with them, and discuss the relative evolutionary novelty of each.

In spite of the apparent reduction in emphasis on suction feeding in *B. vetula,* this species retains the ability to capture soft and elusive prey (e.g., pieces of squid, live earthworm, and live fish) using strong suction. The motor pattern exhibited during capture of prey by suction in *B. vetula,* which is characterized by overlapping activity in all of the muscles recorded, is similar to the motor pattern exhibited during suction feeding by other percomorph teleosts (Liem, '78, '79; Lauder, '83b; Westneat and Wainwright, '89). When the force generated by the firing of the sternohyoideus and obliquus inferioris muscles is unopposed by any activity in the protractor hyoidei, a posteroventral movement of the hyoid apparatus probably occurs. This downward movement not only lowers the floor of the buccal cavity but also enhances the opening of the mouth by further depression of the lower jaw.

A particularly interesting feature of the motor pattern exhibited by *B. vetula* at the beginning of the suction feeding cycle (Fig. 7A) is the firing of the RAP ~5 msec prior to jaw opening and continuing well beyond the initiation of upper and lower jaw adduction (i.e., closing of the mouth). This was the only muscle examined that was active during the initial stages of the strike, with the levator operculi and dilator operculi. This unusual pattern is similar to the activity of the levator arcus palatini during suction feeding in other teleosts (Lauder, '79, '81; Liem, '70, '78, '79; Lauder and Lanyon, '80). In spite of the novelty of the separate RAP, these two muscles appear to function in much the same fashion during suction feeding. Contraction of the RAP in *B. vetula* applies a posterodorsal force on the palatal arch, causing it to rotate outward. This slight lateral movement of the suspensory apparatus has two possible functions: 1) it contributes to early expansion of the buccal cavity, thus reducing the pressure inside the oral cavity, or 2) it stabilizes the joint between the palatal arch and the neurocranium. In *B. vetula,* the latter may be important in conjunction with the action of the adductor muscles during buccal manipulation (see below), particularly those

adductor mandibulae sections that arise partly from the neurocranium.

Another noteworthy feature of the suction feeding motor pattern was the low level activity in the epaxialis (EP). Strong activity of EP is associated with the strike in other teleosts (e.g., Liem, '79, '80; Wainwright and Lauder, '86; Wainwright et al., '89) as part of the mechanism involved in elevating the cranium. Kinematic analysis of suction feeding in *B. vetula* will be necessary to determine if cranial elevation is a significant component of cranial movements during the strike. Because of the low level of activity in the EP, cranial elevation may not be significant during the strike.

Activity of the mouth closing muscles overlaps substantially with activity in many of the muscles that apparently expand the mouth cavity (Fig. 7A). This feature is also typical of other percomorphs (Lauder, '85). The contraction of the upper and lower jaw adductors immediately after mouth opening results in a biting action as both jaws move against each other to forcefully grasp the prey between the teeth. The antagonistic action of the protractor hyoidei (contraction of this muscle apparently pulls the hyoid apparatus anterodorsally, thus elevating the floor of the buccal cavity) and the combined forces of the sternohyoideus and obliquus inferioris (contraction of these muscles pulls on the hyoid apparatus posteroventrally) after the mouth is fully closed apparently stabilizes the hyoid bar in preparation for buccal manipulation of prey.

Prey capture by biting has been studied electromyographically only in some cichlid taxa (Liem, '79, '80) and has not been described in a strong durophage crushing prey in the oral jaws. It is not surprising that this behavior involved a motor pattern distinct from that seen during suction feeding, because the behavior is different. However, the biting motor pattern used during capture of prey is indistinguishable from the activity pattern seen in buccal manipulation of crab prey. A quantitative analysis of these data also showed that, although the biting motor pattern is different from that employed during suction feeding, it is not different from that observed during buccal manipulation (Wainwright and Turingan, unpublished manuscript).

Buccal manipulation of prey by *B. vetula* following capture involves a pattern of muscular activity that is distinct from the motor patterns exhibited during suction feeding and blowing. At least two features clearly distinguish this motor pattern from that seen during suction feeding: 1) activities of the levator operculi (LOP) and the dilator operculi (DO) do not overlap with activity in any other muscles and 2) retractor arcus palatini (RAP) activity does not commence until ~30–40 msec following the offset of the LOP and DO. During buccal manipulation, the jaws are opened and closed cyclically as the prey is moved in and out of the dentigerous area by water motion. The repetitious cycle of muscle activity involving mouth opening (caused by the short burst of activity of the LOP and DO) followed by the prolonged bursts of activities of the adductor mandibulae muscles (i.e., $A_1\alpha$, $A_2\alpha$, $A_2\beta$, $A_2\gamma$) apparently functions to reduce the prey, ultimately into smaller pieces that can be swallowed. Activity in the RAP during the jaw adduction phase may stabilize the suspensorium anteriorly, providing a more solid framework against which the $A_1\alpha$, $A_2\alpha$, $A_2\beta$, and $A_2\gamma$ may act. The almost simultaneous firing of the protractor hyoidei, sternohyoideus, and obliquus inferioris muscles following adduction of the oral jaws may contribute to the stabilization of the floor of the buccal cavity as the jaws close forcefully against the prey. Activity of the ventral musculature may also aid in creating a water flow that moves the prey posteriorly during mouth closing.

Although this behavior appears to conform to "buccal manipulation" as defined by Lauder ('83a), there are few comparative data for oral jaw muscles during buccal manipulation in other percomorphs. It is therefore not possible to determine the relative novelty of the motor pattern seen in *B. vetula* during this behavior. Data from the Cichlidae during manipulation of prey attached to the substrate (Liem, '79) indicate a motor pattern quite different from the one reported here, but the differences in function between the two behaviors may make comparisons inappropriate.

Blowing behavior in *B. vetula* was usually associated with the forceful expulsion of prey from the buccal cavity. This behavior was associated with a motor pattern that could be distinguished from suction feeding, bite-capture, and buccal manipulation by two features: 1) the LOP was strongly active for >100 msec (or about twice as long as those observed during the other three behaviors) and 2) the epaxialis was the only muscle

other than the dilator operculi that was active during the first half of the LOP activity. In general, blowing was characterized by reduced activity of most muscles, except the protractor hyoidei, LOP, and $A_2$ adductor mandibulae subdivisions that dominated the behavior (Fig. 7D). With the exception of the LOP, none of the cranial muscles examined in this study was active in all cycles of muscular activity during the blowing behavior (Fig. 8).

Blowing in *B. vetula* appears to be significantly different from similar behaviors reported in other fishes. The motor pattern exhibited during "spitting out" of undesirable materials ingested with the food item has been documented for the carp, *Cyprinus carpio* (Sibbing et al., '86), and by Lauder and Lanyon ('80) for the bluegill sunfish, *Lepomis macrochirus*. In the carp, the spitting cycle starts with the mouth closed and subsequent expansion of the oral cavity by lowering and protruding the jaws (Sibbing et al., '86). This rostral expansion of the oral cavity causes water to flow anteriorly through the gill slits. Opening of the mouth following adduction of the opercular series and compression of the oral cavity expels water and unwanted materials. No muscle activity data were presented for spitting by the carp (Sibbing et al., '86). In the bluegill sunfish, compression of the buccal cavity also occurred prior to mouth opening (Lauder and Lanyon, '80). This behavior is associated with a motor pattern in which strong activity in the adductor mandibulae, geniohyoideus (=protractor hyoidei), and sternohyoideus all occur at the beginning of activity in the LOP muscle. This pattern is different from that observed in *B. vetula* during spitting and blowing; here all muscles except the epaxialis are active only in the latest stages of the LOP activity. Thus, spitting in *B. vetula* appears to be associated with long periods of mouth opening followed by oral compression. In contrast, the bluegill sunfish compresses the oral cavity before opening its mouth.

In summary, the ability of *B. vetula* to reduce large, hard-shelled prey and to extract prey that firmly adhere to the substrate (e.g., chitons) is reflected in a suite of morphological and functional features of the feeding mechanism that enhance oral biting relative to less specialized percomorph taxa. Stout, anteriorly oriented teeth are mounted on reduced but sturdy jaw bones. The suspensorium and neurocranium are greatly modified, largely as the sites of attachment for the hypertrophied and subdivided adductor mandibulae muscles. *B. vetula* is fully capable of effective suction feeding on soft and elusive prey but employs direct biting when capturing large, hard, and substrate-attached organisms. During buccal manipulation, prey are repeatedly bitten between the jaws while rapidly being moved in and out of the oral cavity. A blowing behavior is periodically employed to move prey or "spit" them out during processing. The motor patterns associated with biting prey capture and blowing are distinct from the motor patterns reported for other percomorph fishes and are among the phylogenetically novel components of the feeding mechanism in *B. vetula*.

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