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CRUSHING MOTOR PATTERNS IN DRUM (TELEOSTEI: SCIAENIDAE): FUNCTIONAL NOVELTIES ASSOCIATED WITH MOLLUSCIVORY

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Summary

This study explores the evolution of molluscivory in the marine teleost family Sciaenidae by comparing the motor activity patterns of the pharyngeal muscles of two closely related taxa, the molluscivorous black drum (*Pogonias cromis*) and the generalist red drum (*Sciaenops ocellatus*). Muscle activity patterns were recorded simultaneously from eight pharyngeal muscles. Electromyographic (EMG) activity was recorded during feeding on three prey types that varied in shell hardness. Canonical variate and discriminant function analyses were used to describe the distinctness of drum pharyngeal processing behaviors. Discriminant functions built of EMG timing variables were more accurate than muscle activity intensity at identifying cycles by prey type and species. Both drum species demonstrated the ability to modulate pharyngeal motor patterns in response to prey hardness. The mean motor patterns and the canonical variate space of crushing behavior indicated that black drum employed a novel motor pattern during molluscivory. The mollusc-crushing motor pattern of black drum is different from other neoteleost pharyngeal behaviors in lacking upper jaw retraction by the retractor dorsalis muscle. This functional modification suggests that crushing hard-shelled marine bivalves requires a 'vice-like' compression bite in contrast to the shearing forces that are applied to weaker-shelled fiddler crabs by red drum and to freshwater snails by redear sunfish.

Key words: durophagy, feeding, crushing, motor pattern, pharyngeal jaw, mollusc, function, electromyography, prey processing, Sciaenidae, black drum, *Pogonias cromis*, red drum, *Sciaenops ocellatus*.

Introduction

Durophagy in fish feeding systems, the ability to consume armored invertebrate prey, has been studied extensively in numerous bony and cartilaginous fish families: Cyprinidae (Sibbing, 1982), Centrarchidae (Lauder, 1983b; Osenberg and Mittlebach, 1989; Wainwright et al., 1991; Huckins, 1997), Cichlidae (Greenwood, 1965; Liem, 1974; Hoogerhoud and Barel, 1978; Liem and Kaufman, 1984; Hoogerhoud, 1986, 1987), Labridae (Liem and Sanderson, 1986; Wainwright, 1987, 1988; Clifton and Motta, 1998), Embiotocidae (Liem, 1986), Tetraodontidae (Turingan and Wainwright, 1993; Ralston and Wainwright 1997), Sparidae (Hernandez and Motta, 1997) and stingrays of the Myliobatidae (Summers, 2000). While many of these studies sought correlative links between the morphology of feeding structures and a durophagous diet, fewer of them investigated functional aspects of the crushing behavior inherent in durophagy (see Lauder, 1983b; Liem and Sanderson, 1986; Liem, 1986; Turingan and Wainwright, 1993; Ralston and Wainwright, 1997; Wainwright et al., 1991). Obviously, the mechanical destruction of hard-shelled prey requires the generation of large biting forces. Thus, the evolution of a durophagous diet is expected to be associated with morphological and/or behavioral modifications that increase the ability of the predator to impart effective crushing forces on the prey. There are clear predictions regarding the ways in which the functional morphology of durophagous taxa should diverge from that of related taxa that do not consume hard-shelled prey.

In teleost fishes, mollusc crushing is the most extreme form of durophagy. The strongly mineralized shells of gastropods and bivalves are among the hardest armored prey encountered in either marine or freshwater habitats. Molluscivorous fishes have evolved crushing ability by modifications either to the oral jaws, as in the pufferfishes (Ralston and Wainwright, 1997; Friel and Wainwright, 1999) and porgies (Hernandez and Motta, 1997), or to the pharyngeal jaws, as in the wrasses (Wainwright, 1987), cichlids (Liem and Kaufman, 1984), sunfishes (Lauder, 1983b) and several other teleost families. The latter functional system is an integrated system of modified gill arches that produces the biting actions used to process engulfed prey. Pharyngeal molluscivores have repeatedly met the challenge of force production through hypertrophy of the musculoskeletal architecture (i.e. larger, stronger muscles that increase force generation and heavier denser bones and toothplates that enhance force transmission). While these morphological specializations of the pharyngeal jaws have been documented in several molluscivorous taxa (Lauder, 1983b; Liem and Kaufman, 1984; Hoogerhoud, 1986; Liem and Sanderson, 1986; Wainwright, 1987), only the North American freshwater sunfishes of the Family Centrarchidae have been investigated comparatively to identify the behavioral modifications associated with pharyngeal molluscivory (Lauder, 1983b; Wainwright et al., 1991). For example, the snail-crushing behavior of redear (*Lepomis microlophus*) and pumpkinseed (*Lepomis gibbosus*) sunfishes has been linked to the evolution of robust pharyngeal jaws and a novel neuromuscular motor pattern that is used during prey processing (Lauder, 1983b).

One approach to determining whether modifications of pharyngeal behavior are adaptive is to explore the convergence of crushing activity in other taxa (Leroi et al., 1994; Lauder et al., 1993; Ricklefs and Miles, 1994; Futuyma, 1986). Such an opportunity presents itself within the Family Sciaenidae, in which two closely related monotypic genera, the generalist predator red drum (*Sciaenops ocellatus*) and the molluscivorous black drum (*Pogonias cromis*), possess robust pharyngeal jaws used for prey processing. Considerable morphological differences exist between the pharyngeal jaws of these two species, which appear to be associated with their dietary habits. Red drum possess large pointed canine pharyngeal teeth that are used in the shredding of shrimp, fish and other soft-bodied prey, while black drum have mollariform teeth and heavy toothplates that transmit large forces to hard-shelled bivalve prey. A review of Sasaki's (1989) phylogeny of the Sciaenidae suggests that such morphological modifications for molluscivory are derived in the clade containing black drum. Yet, the presence or absence of underlying differences in motor pattern between these two species has never been investigated. The ability of this two-species comparison to identify whether motor pattern changes associated with molluscivory are derived will be elaborated upon in the Discussion.

Structural novelties associated with ecological performance need not co-evolve with behavioral novelties (Lauder, 1996). Indeed, Wainwright et al. (1991) demonstrated the independent nature of structural and functional modifications in an intraspecific comparison of snail-crushing performance in pumpkinseed sunfish. The functional task that the increased hardness of mollusc shells presents to the musculature in the pharyngeal jaws can be met either by changes in the intensity of muscular contractions of a common behavior or by changes in the sequence and duration of pharyngeal muscle recruitment. Changes in the timing aspects of motor patterns could lead to the acquisition of unique pharyngeal movements and, hence, become an addition to the behavioral repertoire of pharyngeal processing.

Electromyographic (EMG) comparisons of pharyngeal processing behaviors in red and black drum can be used to address the motor basis of durophagy in these taxa to determine whether any functional differentiation has occurred and whether these changes are associated with the evolution of a mollusc-crushing bite in black drum. Furthermore, recordings of pharyngeal EMG activity in black drum will provide another independent example of mollusc-crushing behavior that, when compared with that of centrarchid sunfishes, may shed light on potential constraints that the evolution of a molluscivorous diet has imposed on the functional characteristics of the generalized perciform pharyngeal bite. The main goals of this study are threefold: (i) to determine the distinctness of pharyngeal processing behaviors in red and black drum feeding on similar prey types; (ii) to measure the effects of prey hardness on pharyngeal motor patterns in both red and black drum; and (iii) to identify the motor basis of mollusc-crushing behavior in black drum.

Materials and methods

Experimental animals

Specimens of black drum (*Pogonias cromis* L.) and red drum (*Sciaenops ocellatus* L.) of the Family Sciaenidae were collected from the northern Gulf of Mexico near the Florida State University Marine Laboratory, Turkey Point, Florida, USA. Black drum (N=3) ranged in size from 175 mm to 335 mm standard length (SL). Red drum (N=5) ranged from 265 mm to 335 mm SL. Individuals were housed in 100 l laboratory aquaria at 24±2 °C and were fed a mixed diet of shrimp and crab pieces for at least 1 week prior to EMG feeding experiments. Black drum were also fed hard-shelled mollusc prey.

Phylogenetic relationships and ecology

In the most comprehensive phylogenetic hypothesis of the family, red drum are the monotypic sister genera to black drum plus freshwater drum (*Aplodinotus grunniens*) (Sasaki, 1989). Black drum and red drum are sympatric along the eastern seaboard of North America and the Gulf of Mexico. Dietary studies indicate distinct feeding habits in these two species. Red drum are documented generalist species with an apparent ontogenetic dietary shift. Juvenile and subadult fishes (<500 mm SL) feed primarily on small benthic invertebrates such as penaeid shrimps and various crab species; as they become larger and sexually mature, they include more elusive fish prey in their diet (Pearson, 1929; Boothby and Avault, 1971; Overstreet and Heard, 1978). In contrast, black drum are molluscivorous throughout most of their ontogeny, feeding on several types of hard shelled prey such as gastropods, bivalves, barnacles, echinoderms and various crustaceans (Welsh and Breder, 1924; Simmons and Breuer, 1962; Overstreet and Heard, 1982; J. R. Grubich, personal observation). Furthermore, captive black drum have been shown to feed preferentially on the dominant bivalve species of their local habitat (Case, 1978).

Identification of muscle function and behavior

To identify variation in pharyngeal motor patterns between species, eight homologous muscles, which vary in their effects on jaw movements during prey processing, were analyzed. The proposed muscle functions refer to actions identified by Lauder (1983a,b) and Wainwright (1989b) (Fig. 1). The lower jaw

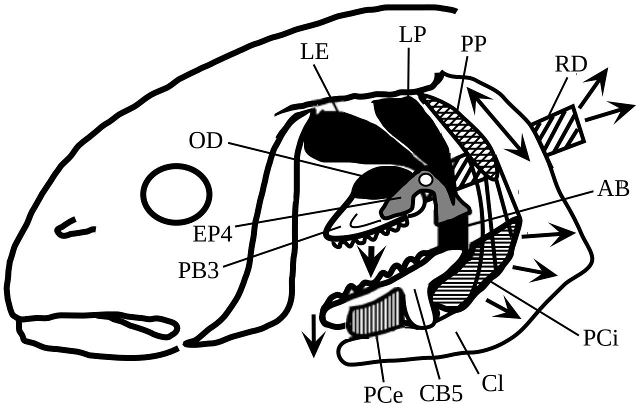

Fig. 1. Generalized anatomy of the drum pharyngeal jaw apparatus. Muscles are coded according to their functions (denoted by arrows) as described by Lauder (1983a,b), Wainwright (1989b) and Galis (1997). Black muscles (LE, LP, OD, AB) occlude the jaws through ventral depression of the third pharyngobranchial (PB3) by the fourth epibranchial (EP4)/PB3 (stippled) joint mechanism (Wainwright, 1989b). Diagonally hatched muscle (RD) retracts and raises the upper pharyngeal jaw towards the esophagus. Horizontally hatched muscle (PCi) retracts and stabilizes the lower pharyngeal jaw (fifth ceratobranchial toothplate, CB5) against the cleithrum (Cl). Vertically hatched muscle (PCe) depresses and stabilizes the lower pharyngeal jaw. Cross-hatched muscle (PP) apparently stabilizes the pectoral girdle to the neurocranium in red drum. In black drum, this muscle is hypertrophied (black lines) and acts to squeeze the head together by pulling the neurocranium down and elevating the cleithrum. For muscle and bone names, refer to Table 1.

muscles, the pharyngocleithralis externus (PCe) and the pharyngocleithralis internus (PCi), originate on the cleithrum and insert on the lateral anterior and posterior margins of the fifth ceratobranchial toothplate (CB5), respectively. The main function of PCe is to abduct the lower jaw from the dorsal elements, resulting in ventral depression of the toothplate. PCi acts to retract the lower jaw in a posterior and slightly dorsal fashion, secondarily stabilizing CB5 against the cleithrum (Lauder, 1983a). The protractor pectoralis (PP) functions as a stabilizing muscle between the neurocranium and pectoral girdle (Winterbottom, 1974). This muscle originates on the intercalar–exoccipital–pterotic region of the neurocranium and fans out to the dorsal anterior region of the pectoral girdle *via* tendinous connective tissue. This muscle is not directly associated with moving any pharyngeal elements. The retractor dorsalis (RD) originates on the anterior region of the vertebral column and runs rostrally to insert on the posterior margins of the third and fourth pharyngobranchials (PB3 and PB4) of the upper jaw. As its name suggests, this muscle functions primarily to move the upper jaws posteriorly towards the esophagus (Lauder, 1983a). The four upper jaw muscles, levator externus 3/4 (LE), levator posterior (LP), obliquus dorsalis 3 (OD) and adductor branchialis 5 (AB), all have different osteological origins (LE and LP from the neurocranium, OD from PB3 and PB4, and AB from CB5), but insert on different regions of the fourth epibranchial (EP4). In Wainwright's (1989b) model of pharyngeal jaw function, synergistic contractions of these muscles cause EP4 to pivot ventromedially, depressing the lateral margins of PB3 and resulting in a ventrally directed biting movement of the upper toothplates.

Analysis of pharyngeal motor patterns was restricted to processing bouts during which the prey item was being chewed and structurally broken down. The majority of these bouts fall into the range of behaviors defined as 'pharyngeal transport' (Lauder, 1983a; Fig. 2). Although these cycles possessed the traits of generalized acanthopterygiian pharyngeal transport (i.e. overlapping activity in RD and PCi alternating with activity in PCe), Wainwright (1989b) noted, as was reconfirmed here, that concurrent activity in the upper jaw muscles (LE, LP, OD and AB) results in mastication of the prey item to varying extents. In the light of this evidence, the working stroke of pharyngeal transport behavior can be thought of as a 'raking' motion of the pharyngeal jaws and will be referred to as such throughout the manuscript. This functional interpretation of Lauder's (1983a) original pharyngeal transport behavior more accurately describes the effects of the motor pattern on the prey item: not only is the prey moved posteriorly, it is also chewed and macerated between the jaws. Although pharyngeal movements were not directly visible, variation in motor pattern was linked to characteristic external head movements that were described simultaneously with muscle activity on a voice track. Pharyngeal crushing cycles were identified by audible cracks of bivalve shells and crab pieces, which were also noted on the voice track. In addition, mastication of prey items was confirmed by inspection of the stomach contents following each experiment.

Pharyngeal EMG experiments

Neuromuscular activity during prey processing was recorded simultaneously in eight pharyngeal muscles. Electromyographic recordings of muscle activity were made through 2 m long polyinsulated bipolar electrodes 0.051 mm in diameter (California Fine Wire). The wire was threaded through 26 gauge needles that varied in length from 1.3 to 3.8 cm. Longer needles were used for electrode insertion into the deep medial pharyngeal muscles, OD and RD. At the insertion tip, 0.5 mm of insulation was scraped away with a razor blade under a dissecting microscope, and the two exposed metal tips were separated to approximately 45 ° with a pair of fine forceps. The resulting forked tips were then bent back over the shaft of the needle to form a hook that anchored the electrode in the muscle belly upon insertion. Eight electrodes were implanted into the muscles of the left side, led out through the operculum, tied to a suture on the dorsum of the fish (anterior to the opercular opening) and glued into a common cable. Electrodes were implanted while the fish was under anesthesia (approximately $0.7\,\mathrm{g\,l^{-1}}$ tricaine methanesulfonate). During recording sessions, electrodes were connected to Grass P511 high-impedance signal amplifiers. Muscle electrical activities were amplified 10 000 times, and a bandpass of 100–1000 Hz was employed with a 60 Hz notch filter activated. During feeding experiments, a simultaneous voice track was recorded along with the eight EMG implants

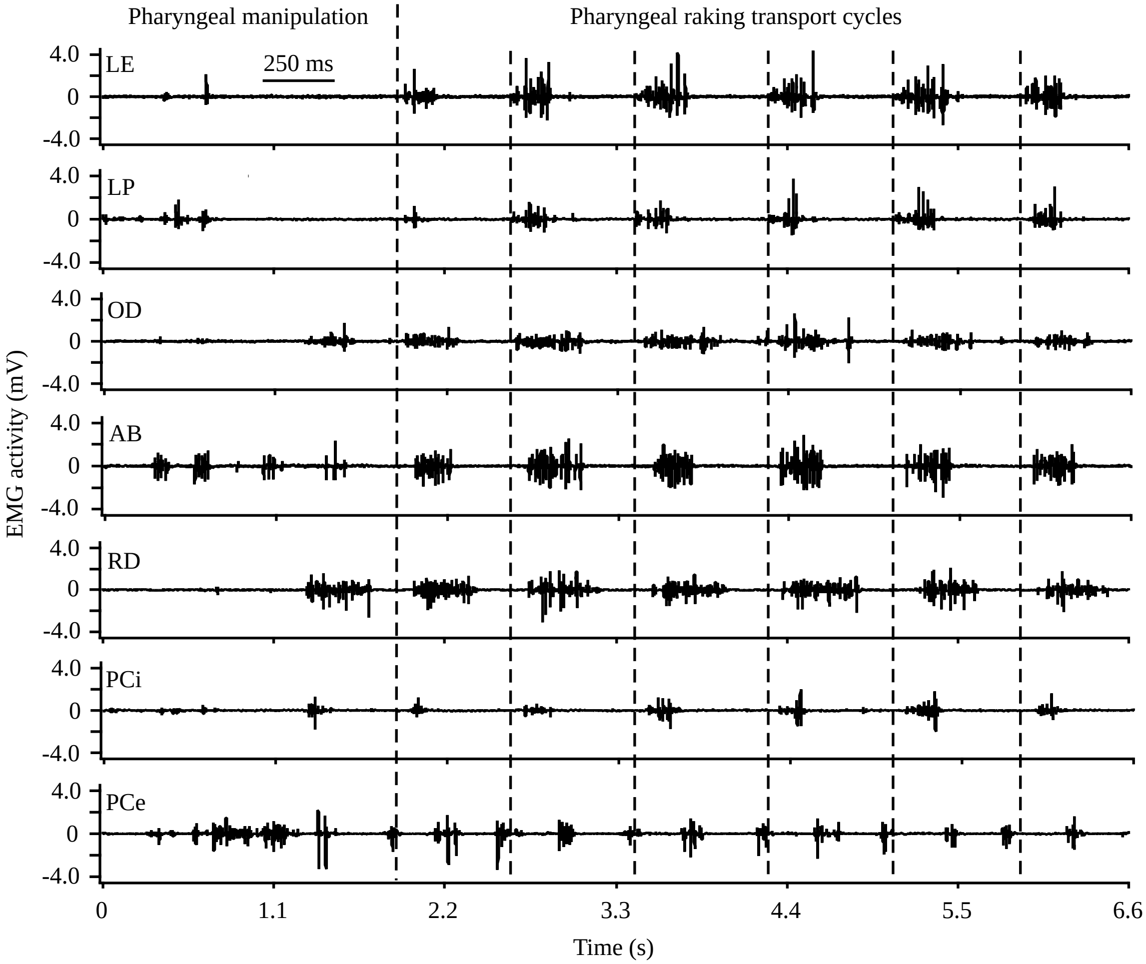

Fig. 2. Electromyographic (EMG) activity of seven pharyngeal muscles during pharyngeal transport of shrimp by a red drum. Strong activity in the upper jaw muscles (LE, LP, OD, AB) overlapping with strong RD activity show that upper jaw depression is coincident with retraction, indicating a raking motion of the upper pharyngeal jaws. PCi is active at the beginning of transport, stabilizing the lower jaw and providing resistance to the raking motions of the upper jaw. PCe becomes active towards the end of the cycle, depressing the lower jaw and presumably facilitating posterior movement of the prey. Dashed lines delineate cycles of processing activity. Muscle abbreviations are explained in Table 1.

on a 14-channel TEAC XR-5000 FM recorder. Pharyngeal processing sequences were later played back to produce a hard copy on a Graphtec thermal array recorder for visual inspection of the EMG events recorded.

Because of the close anatomical proximity of the eight pharyngeal muscles and the possibility of regional activity, special care was taken to standardized electrode placement among all individuals. From pharyngeal dissections of preserved specimens, a list of skeletal landmarks and muscle angle orientations was compiled for each species and used as a guide during EMG implantation. At the end of the feeding experiments, drum were killed with an overdose of tricaine methanesulfonate, and electrode placement was verified by dissection of the fresh specimen.

Prior to feeding experiments, individuals were starved for 1–2 days to increase hunger level. After electrode implantation, fish were returned to their aquaria and allowed to recover from anesthesia. Recording sessions of pharyngeal processing began as early as 30 min and as late as 4 h after surgical implantation. To investigate crushing ability in drum, individuals were fed three prey types that covered a range of structural hardness. The hard prey category items were different for red and black drum. Red drum were fed pieces of blue crab appendages that they readily consumed, while black drum were fed live bivalve and gastropod molluscs: *Cardita floridana*, *Donax variabilis*, *Cerithium floridana* and *Moidylus* sp. Initially, efforts were made to record activity from all fish feeding on the same hard prey species, but red drum consistently rejected bivalves. Similarly, black drum could not be enticed to consume blue crab pieces. However, the blue crab pieces used were similar in size and were estimated to have similar hardness to the bivalve species through force gauge crushing trials (J. R. Grubich, unpublished data).

For crushing events in black drum, the mollusc species and size was noted. Live fiddler crabs (*Uca* sp.), similar in size to the hard prey items, were the intermediate prey type for both drum species. The soft prey category was shrimp pieces, *Penaeus* sp., cut to be similar in size to the other prey items (approximately 1 cm^2). Prey size was carefully controlled to minimize possible effects of prey size on gape and pharyngeal motor patterns. Pharyngeal muscle activity was recorded from the beginning of the strike, at which point the prey was taken into the buccal cavity, until the cessation of head and jaw movements indicated that the prey had been swallowed.

Analysis of EMG activity

Analog recorded electromyographic data were digitized with a Keithley 500A system using a sampling rate of 8 kHz. A custom-designed computer program was used to measure three variables of EMG activity for each muscle during each cycle of activity (see Table 1): the relative onset of activity, the duration of the burst and the relative intensity of activity. The onset of activity in the LE muscle was used as the reference time against which the recruitment of the remaining seven muscles was measured. A cycle of pharyngeal processing was identified as beginning at the onset of activity in the LE muscle and lasted until the onset of next LE burst (Fig. 2). The intensity of muscle activity was calculated by dividing the integrated area of the rectified EMG burst by the duration. In this way, intensity defines the mean amplitude of EMG spikes during a burst of muscle activation. To correct for potential variation in electrode recording properties between muscles and to create a time-independent measure of EMG activity, muscle intensity was standardized by dividing the intensity of the individual cycles by the mean intensity recorded across all prey types for that electrode during the experiment. This methodology creates a standardized voltage ratio variable within a muscle, relative intensity, that allows one to compare the relative contributions of contraction force among muscles during a specific behavior (Friel and Wainwright, 1999). Variation in EMG amplitude (i.e. intensity) and duration variables among bouts of activity have been shown to be directly proportional to the force being generated in a muscle (Bigland and Lippold, 1954; Lawrence and De Luca, 1983; Basmajian and De Luca, 1985; Wainwright and Turingan, 1996).

Statistical analysis of pharyngeal behaviors

By comparing pharyngeal muscle activity for prey types of different hardness, it was possible to determine (i) whether motor patterns were altered in response to prey, and (ii) whether crushing activity occurred as a result of an increase in the intensity of a common pharyngeal transport behavior or whether increasing prey hardness elicited a different temporal pattern of muscle recruitment. To determine whether the pharyngeal behaviors employed by red and black drum feeding on prey types of different hardness were statistically distinct, canonical variates and discriminant functions were generated. Canonical variate analyses reduced the dimensionality of the multivariate data by creating new variables (canonical axes) that are linear combinations of the original variables (Johnson, 1999). In the context of classifying pharyngeal processing behaviors, this method is analogous to creating a series of multiple regressions in which the new canonical axes are made up of specific combinations of muscle variables that provide the strongest discrimination between the sample mean vectors of each prey type. To determine the extent of variation in prey type mean vectors, multivariate analysis of variance (MANOVA) models were constructed using identity matrices of the pooled hard and soft prey type cycles for both species. The dependent variable was prey type, resulting in four categories of pharyngeal processing cycle: mollusc, black drum shrimp, blue crab and red drum shrimp. The EMG parameters of the eight pharyngeal muscles were the independent variables.

To determine whether crushing in drum was achieved primarily by increasing the strength of raking motions in a common pharyngeal transport behavior or by using a novel pharyngeal bite, separate models were produced for relative intensity and timing EMG variables using all eight muscles as the independent variables. However, because relative onset of activity is undefined if the muscle is never active, the onset of activity in the RD muscle for all prey types was omitted from the model because it was inactive in over 50 % of the hard prey cycles in black drum. Each model included 65 blue crab and 65 shrimp cycles from five red drum and 61 mollusc and 34 shrimp cycles from three black drum for a total of 225 pharyngeal processing cycles.

χ^2 analyses of discriminant scores were produced that tested the null hypothesis of no discrimination among prey types by estimating each model's ability to accurately classify (by prey type and species) individual processing cycles. Plots of the canonical axes were produced to visualize the dispersion of cycles from different prey types in the reduced dimensional space of each model. Finally, a third canonical model was generated that compared only crushing cycles between species. The identity matrix consisted of hard-shelled mollusc and fiddler crab cycles for black and red drum, respectively. The data included only black drum mollusc cycles that were recorded with an audible cracking of the shell and all cycles of red drum processing fiddler crab (total number of cycles 113: 33 black drum mollusc and 80 red drum fiddler crab). To enable comparisons with previously reported motor pattern data from mollusc-crushing sunfish, the timing variables of this model included only those muscles that had been previously reported in the redear sunfish *Lepomis microlophus* (LE, LP, AB, RD, PCi, PCe) (Lauder, 1983b).

All descriptive statistics and multivariate analyses were generated using JMP statistical software version 3.1 for Macintosh from SAS Institute. Canonical variates and discriminant functions were generated using $\log_{10}$-transformed data of EMG variables to approximate better the normalized distributions required of parametric statistics.

Results

Pharyngeal muscle mean intensities and motor patterns

Histograms of relative intensities for the eight pharyngeal jaw muscles revealed some trends between species and prey types (Table 1; Fig. 3). All eight muscles in the red drum showed greater intensity of activity for hard prey (mean blue crab 1.13, mean shrimp 0.87). For black drum, the intensity of the LE, LP, OD and PCi muscles varied less across prey types. There was a trend in the black drum AB and PP muscles for molluscs to elicit a greater relative intensity than shrimp (mean mollusc 1.19; mean shrimp 0.86).

Muscle timing variables differed markedly between species and prey types (Table 1; Fig. 4). Red drum shrimp cycles showed nearly simultaneous onset of activity in the LE, LP, OD and PCe muscles, while the relative onset of activity in the other four muscles was delayed (AB 25 ms, RD 49 ms, PCi 29 ms and PP 63 ms). In addition, a secondary burst of PCe activity, characteristic of processing shrimp, began 195 ms after the onset of activity in LE and overlapped with the last half of activity in the RD.

No muscles were activated simultaneously with LE in black drum shrimp cycles (Table 1; Fig. 4). All muscles showed a noticeable staggering of recruitment. For instance, LP was commonly recruited before LE (relative onset –21 ms), and the remaining six muscles showed progressively delayed onsets ranging from 24 ms for OD to 161 ms for PCe (Table 1; Fig. 4). Unlike red drum, black drum generally exhibited only a single burst of PCe activity during shrimp processing. Further, black drum generally showed much longer burst durations in the

Table 1. *Descriptive statistics of muscle activity for prey processing in red and black drum*

	Red drum (five individuals)		Black drum (three individuals)	
Muscle variable	Blue crab (*N*=65)	Shrimp (*N*=65)	Mollusc (*N*=33)*	Shrimp (*N*=34)
Relative onset (ms)				
LP	9±6	0±3	–31±10	–21±6
OD	–2±12	–5±20	–12±7	24±44
AB	49±22	25±2	–16±21	98±91
RD	53±13	49±11	ND	153±67
PCi	35±12	29±12	33±6	102±67
PP	52±18	63±19	18±13	89±77
PCe	26±30	3±65	63±10	161±107
Duration (ms)				
LE	151±31	164±28	111±20	293±93
LP	132±33	114±22	134±16	264±100
OD	171±45	226±35	115±9	213±82
AB	96±47	172±35	135±32	362±141
RD	205±29	244±20	0±0	137±22
PCi	103±10	76±10	84±20	114±26
PP	112±9	34±21	97±17	172±6
PCe	145±28	94±35	167±91	108±25
Relative intensity				
LE	1.15±0.16	0.93±0.17	1.52±0.17	1.40±0.07
LP	1.33±0.20	0.87±0.07	1.17±0.09	1.02±0.16
OD	1.16±0.34	0.82±0.23	1.08±0.15	1.08±0.33
AB	0.83±0.19	0.99±0.09	1.23±0.16	0.80±0.14
RD	1.09±0.12	0.97±0.09	0±0	0.70±0.08
PCi	1.17±0.14	0.83±0.15	0.95±0.05	0.93±0.11
PP	1.17±0.10	0.64±0.10	1.14±0.02	0.92±0.11
PCe	1.14±0.18	0.92±0.13	0.95±0.02	1.15±0.17

Values are means ± S.E.M. across individuals; prey (*N*) = number of EMG cycles.

ND, not defined because of inactivity.

*Crushing cycles identified by audible cracking of the shell.

AB, adductor branchialis; LE levator externus; LP, levator posterior; OD, obliquus dorsalis; PCe, pharyngocleithralis externus; PCi, pharyngocleithralis internus; PP, protractor pectoralis; RD, retractor dorsalis.

The onset of activity is given relative to the onset of activity in LE.

See text for details of how relative intensity was calculated.

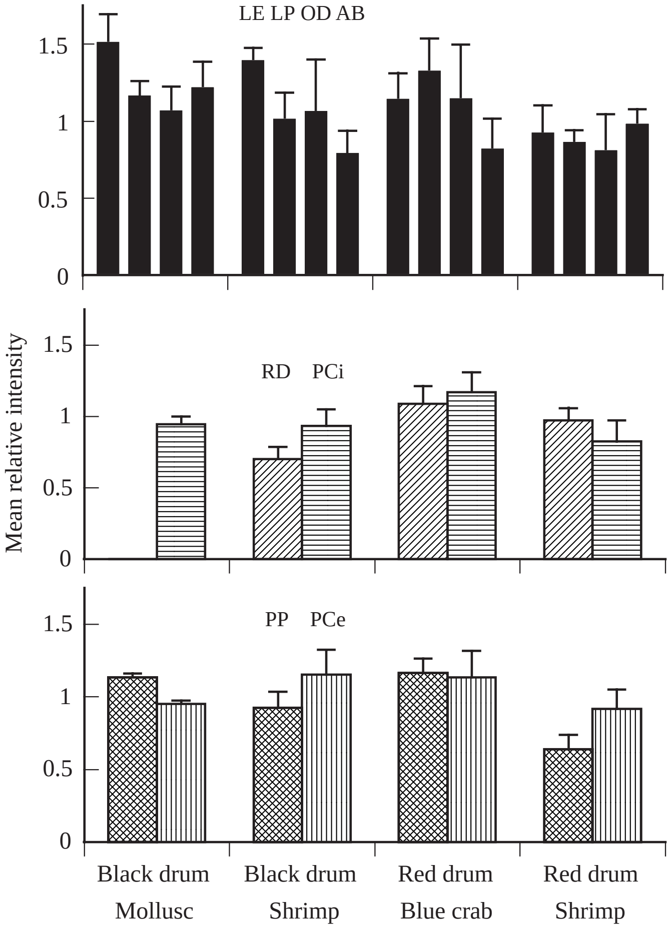

Fig. 3. Mean relative intensities of eight pharyngeal muscles during prey processing. Histograms show hard and soft prey types for each species. Error bars represent standard errors among individuals (*N*=3 for black drum; *N*=5 for red drum). Intensities were greater during blue crab cycles than during shrimp cycles for seven pharyngeal muscles in red drum. Black drum showed little difference in intensity between hard and soft prey types across most pharyngeal muscles. Muscle shading is coded as in Fig. 1. Muscle abbreviations are explained in Table 1.

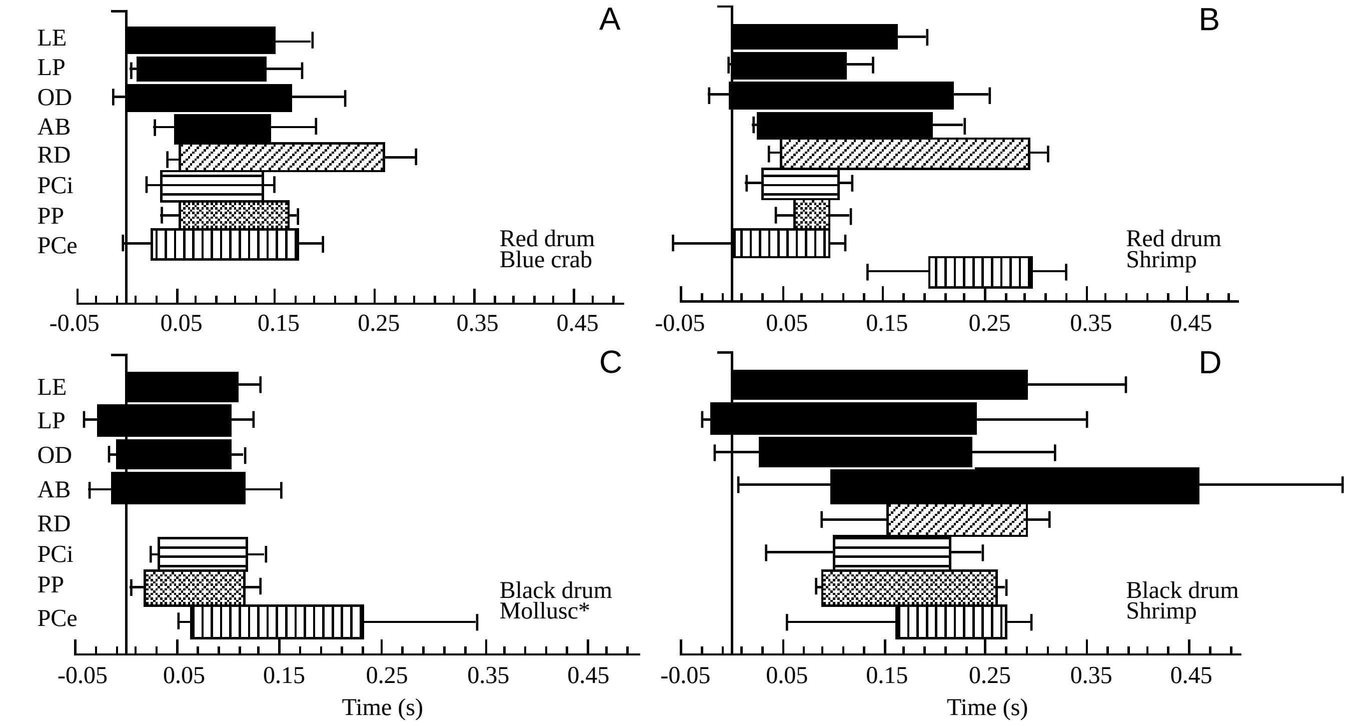

Fig. 4. Mean motor patterns of eight pharyngeal muscles during prey processing of hard (A,C) and soft (B,D) prey in red drum (A,B) and black drum (C,D). Bars represent mean burst durations and muscle onsets relative to activity in LE. Lines represent standard errors among individuals (*N*=3 for black drum; *N*=5 for red drum). Motor patterns in both species show modifications in response to prey hardness. Between-species comparisons show distinct changes in recruitment and duration among homologous pharyngeal muscles. Note the absence of activity in the RD muscle during mollusc crushes in black drum. Muscle shading is coded as in Fig. 1. Muscle abbreviations are explained in Table 1. *, mean motor pattern of audible shell cracks in black drum.

pharyngeal muscles (Fig. 4). One noteworthy exception to this trend was RD duration, which was an average of 107 ms longer in red drum cycles than in black drum cycles.

Species also appeared to differ in pharyngeal motor patterns when feeding on hard prey items. Red drum processing blue crab showed extensive overlap of activity in all eight pharyngeal muscles. As in shrimp processing, LE, LP and OD began activity nearly simultaneously, while the remaining five muscles showed a marked delay in recruitment ranging from 26 ms in PCe to more than 50 ms in RD and PP (Table 1; Fig. 4). The duration of muscle activity in LE, LP, OD and RD was similar to that in shrimp cycles; however, unlike shrimp cycles, blue crab elicited longer contractions in the PCi and PP (mean duration 103 ms and 112 ms, respectively). Further, blue crab motor patterns were characterized by a single PCe burst that was mostly in phase with activity in the other seven muscles.

Black drum mollusc-crushing motor patterns revealed distinct differences from red drum hard prey processing. Recruitment of activity in LP, OD and AB began prior to activity in LE (mean relative onset −19 ms; Table 1; Fig. 4). In addition, PCe was recruited much later than in red drum blue crab cycles (mean relative onset difference >35 ms). As in blue crab, there was extensive overlap in activity of most pharyngeal muscles during mollusc crushing. However, in comparison with shrimp cycles, mollusc-crushing cycles had much shorter bursts in the upper jaw muscles, LE, LP, OD and AB (Fig. 4). Finally, the most distinct trait of black drum mollusc-crushing was the absence of activity in RD.

Discriminant models of pharyngeal EMGs

The intensity and timing models using canonical functions differed substantially in their ability to discriminate among prey processing cycles. Although the overall intensity model was significant (*F*=21.7; *P*<0.0001; Table 2), neither of the

Table 2. *Canonical details of muscle intensity model*

	Canonical axis 1	Canonical axis 2
Eigenvalue	0.80	0.31
Canonical correlation	0.67	0.49
Muscle intensity	Canon 1 eigenvector	Canon 2 eigenvector
LE	−0.53	0.01
LP	−0.01	0.77
OD	0.12	0.19
AB	0.17	−0.60
RD	0.45	0.20
PCi	0.23	−0.07
PP	−0.20	0.22
PCe	0.03	0.05

MANOVA approximate *F*=21.7 (Roy’s maximum root); d.f. 8, 216; *P*<0.0001.

Muscle abbreviations are explained in Table 1.

Table 3. *Classification of prey cycles by discriminant function analysis of muscle intensity variables*

	Red drum		Black drum		Total classified
	Blue crab	Shrimp	Mollusc	Shrimp	
Red drum					
Blue crab	45 (69)	12	8	6	71
Shrimp	13	49 (75)	8	2	72
Black drum					
Mollusc	1	0	33 (54)	11	45
Shrimp	6	4	12	15 (44)	37
Total observed	65	65	61	34	225

χ^2=177.8 (likelihood ratio); P<0.0001

Source	d.f.	–log(likelihood)	r^2
Model	9	88.9	0.29
Error	213	214.3	
Total	222	303.1	

Cells, number of EMG cycles (% correctly classified); columns, observed prey; rows, classified prey.

Table 4. *Canonical details of timing model*

	Canonical axis 1	Canonical axis 2
Eigenvalue	3.15	0.70
Canonical correlation	0.87	0.64
Centroid value blue crab	1.98	0.61
Centroid value red drum/shrimp	3.09	1.86
Centroid value mollusc	–1.14	0.89
Centroid value black drum/shrimp	–0.45	2.97
Muscle duration	Canon 1 eigenvector	Canon 2 eigenvector
LE	0.76	1.79
LP	–2.63	–2.90
OD	1.15	–0.13
AB	–0.08	2.06
RD	1.72	–0.39
PCi	–1.67	–0.63
PP	0.50	2.34
PCe	–0.05	–1.22
Muscle onset		
LP	0.04	–2.54
OD	–0.49	–2.16
AB	–0.10	1.51
PCi	–1.51	–0.83
PP	3.17	1.02
PCe	–0.15	0.12

MANOVA approximate F=47.2 (Roy's maximum root); d.f. 14, 210; P<0.0001.

Muscle abbreviations are explained in Table 1.

Table 5. *Classification of prey cycles by discriminant function of motor pattern timing variables*

	Red drum		Black drum		Total classified
	Blue crab	Shrimp	Mollusc	Shrimp	
Red drum					
Blue crab	50 (79)	5	1	1	57
Shrimp	11	60 (92)	1	0	72
Black drum					
Mollusc	3	0	54 (90)	10	67
Shrimp	1	0	5	23 (71)	29
Total observed	65	65	61	34	225

χ^2=370.3 (likelihood ratio); P<0.0001

Source	d.f.	–log(likelihood)	r^2
Model	9	185.1	0.62
Error	213	115.8	
Total	222	300.9	

Cells, number of EMG cycles (% correctly classified); columns, observed prey; rows, classified prey.

first two canonical axes generated eigenvalues greater than 1.0, indicating a weak ability to identify major axes of differentiation between prey type means. The χ^2 analysis testing the null hypothesis of no difference in relative intensities among prey types was significant (χ^2=177.8; P<0.0001, Table 3). However, the intensity model (r^2=0.29) was only moderately successful at correctly classifying pharyngeal EMG cycles according to prey and species (Table 3). Of the 130 individual cycles of red drum blue crab and shrimp processing, the model could only accurately classify 69 % and 75 % of the cycles, respectively. The intensity model was even less successful at classifying black drum cycles (54 % for molluscs and 44 % for shrimp).

The canonical model of timing variables (F=47.2; P<0.0001) discriminated prey types more effectively than did the intensity model (Tables 4, 5). The large eigenvalue (3.15) of the first canonical axis accounted for 87 % of the variance, and the χ^2 analysis for the timing model was highly significant (r^2=0.62, Table 5). This model substantially improved resolution among prey cycles. Classification of red drum blue crab and shrimp cycles improved to 79 % and 92 %, respectively, while classification of black drum prey cycles revealed even greater improvement: 90 % for mollusc and 71 % for shrimp.

Plots of individual processing cycles among the canonical axes of the two models visually illustrate their different abilities to discriminate among prey types (Fig. 5A,B). It should be noted that black drum mollusc cycles of both models are composed of both 'crushing' actions that occurred with shell failures (indicated by cracking sounds and noted on the voice recorder) and the later processing cycles that employed 'raking' type motor patterns during which RD activity was observed.

The intensity model plot revealed considerable overlap among the four categories (Fig. 5A). Extensive overlap

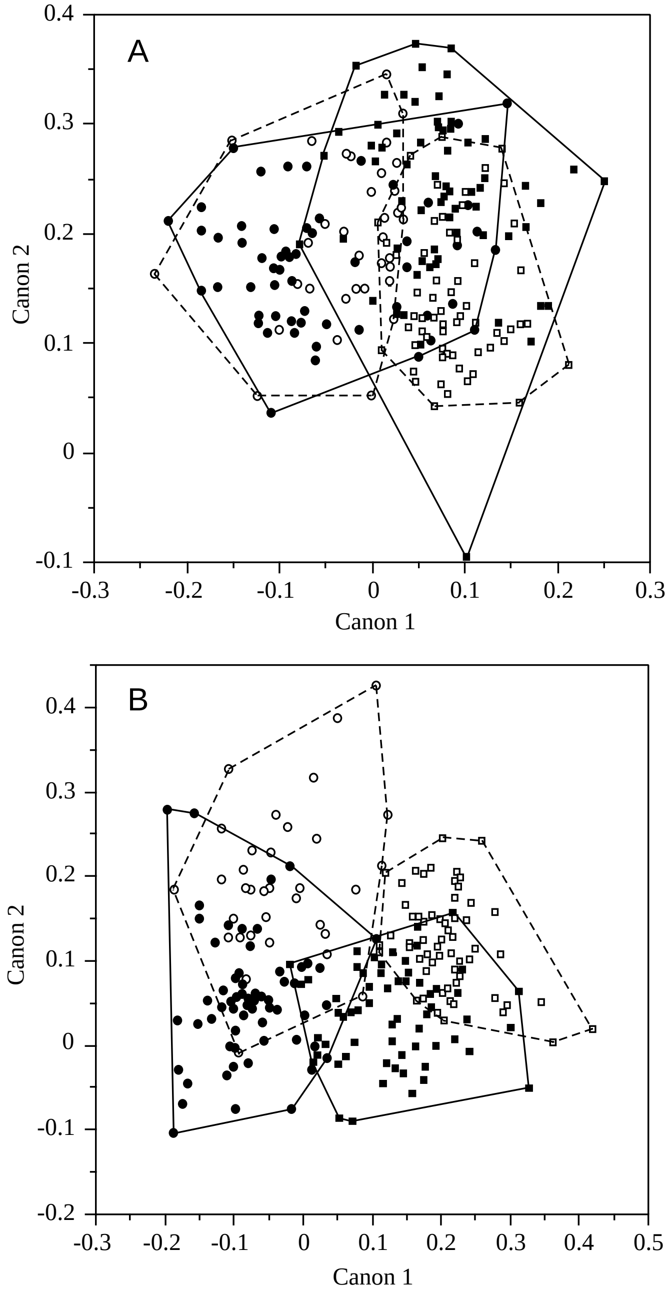

Fig. 5. Canonical variate plots of pharyngeal muscle intensity (A) and motor patterns (timing) (B). Data points represent individual prey processing cycles: black drum feeding on mollusc (●); black drum feeding on shrimp (○); red drum feeding on blue crab (■); red drum feeding on shrimp (□). Polygons represent the range of activity cycles by prey type (solid lines are for hard prey; dashed lines are for soft prey) for both drum species. The muscle intensity model showed extensive overlap between prey types, while the timing variable model strongly separated species along canonical axis 1 and to a lesser extent prey types within species along canonical axis 2. Canon 1 (B) distinguishes species by differences in timing aspects of retracting muscles, RD and PCi, the head-stabilizing muscle, PP, and the main upper jaw depressor, LP (see Table 4). Canon 2 (B) distinguishes hard and soft prey types primarily by the timing aspects of different sets of upper jaw depressing muscles (see Table 4). Muscle abbreviations are explained in Table 1.

Table 6. *Canonical details of crushing comparison model*

	Canonical axis 1	Canonical axis 2
Eigenvalue	4.06	0.51
Canonical correlation	0.90	0.58
Muscle duration	Canon 1 eigenvector	Canon 2 eigenvector
LE	–2.00	1.16
LP	–0.49	–1.04
AB	0.35	1.57
RD	5.08	–0.91
PCi	–0.69	0.28
PCe	–0.82	2.51
Muscle onset		
LP	3.86	3.06
AB	–2.59	0.16
PCi	2.43	4.99
PCe	–0.59	–0.80

MANOVA approximate F=41.8 (Roy’s maximum root); d.f. 10, 103; P<0.0001.

Muscle abbreviations are explained in Table 1.

between blue crab and mollusc polygons indicates that the model was ineffective at discriminating hard prey cycles between species. However, the intensity plot illustrates moderate separation of soft prey cycles between species. Most importantly, this plot reveals the inability of the intensity model to separate hard and soft prey types within species.

The timing model plot more clearly resolves differences among prey categories in canonical space (Fig. 5B). Canonical axis 1 produced almost complete separation of species, with only a slight overlap occurring between red drum blue crab and black drum prey cycles. The discriminant function of this axis separated cycles that had late recruitment of PP and long bouts of activity in RD (characteristic of red drum) from cycles that elicited early recruitment and short durations in the PCi muscle (characteristic of black drum) (Table 4). There was also some separation of prey types within species along canonical axis 2. Shrimp cycles in both species tended to occupy the upper half of canonical space, while hard prey cycles were primarily positioned in the bottom half. Muscle variable eigenvectors of this axis indicate that soft prey cycles were characterized by late recruitment in AB and by long durations of activity in AB, PP and LE (Table 4). In contrast, hard prey cycles were characterized by early recruitments of LP and OD and by short bouts of activity in LP and PCe (Table 4).

Comparing crushing motor patterns

Black drum crack hard-shelled molluscs with short bursts of activity in their jaw adducting and stabilizing muscles. The first three cracks of an 11 mm *Cardita floridana* bivalve illustrate this pattern (Fig. 6). Prior to the first crush, strong lower jaw PCe activity suggests prey manipulation in which the fish oriented the bivalve between the pharyngeal tooth plates. The first crush cycle was marked by simultaneous short bursts of activity in LE, LP, OD, AB, PP and PCi. Also, PCe activity decreased during this crush and,

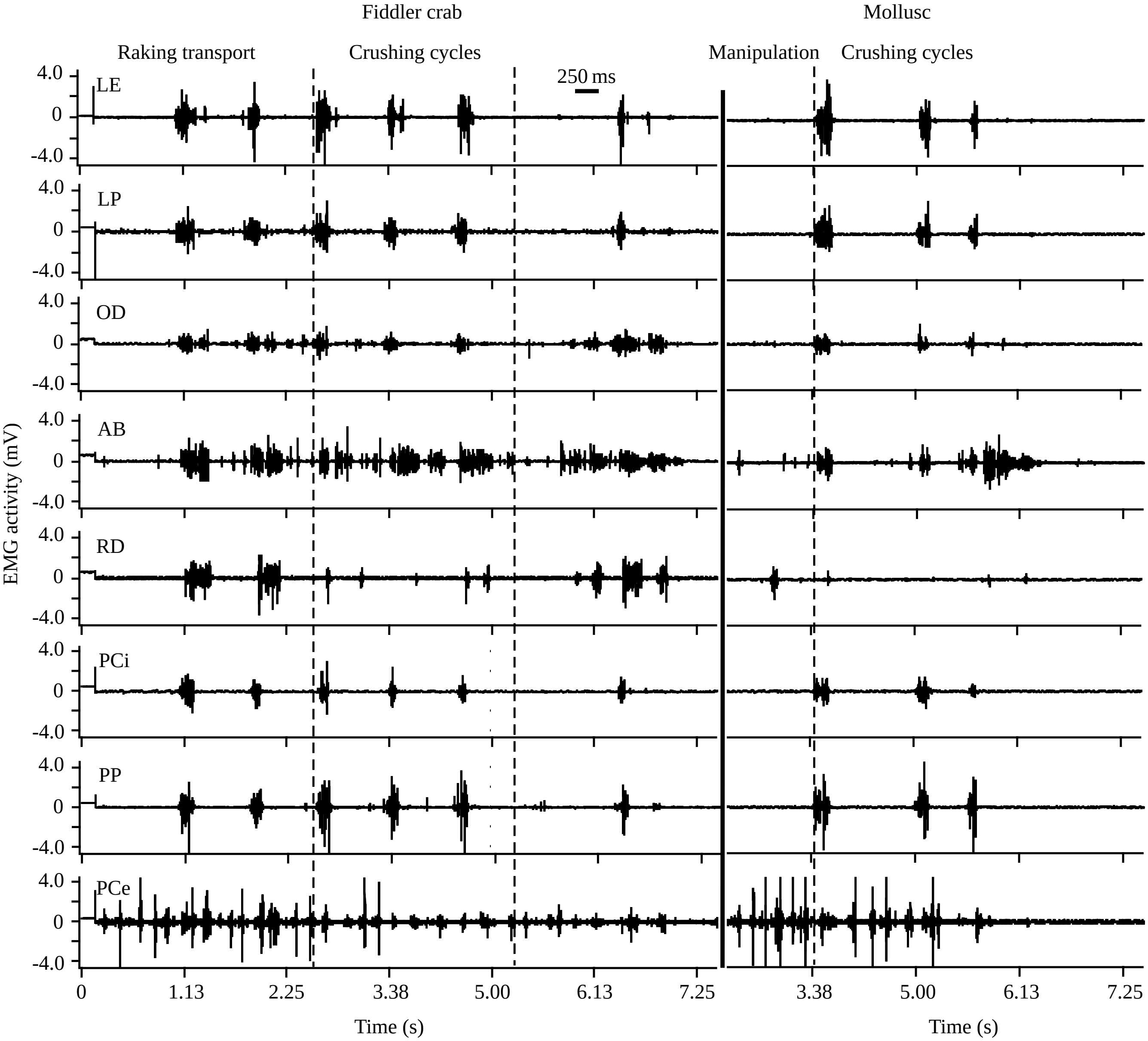

Fig. 6. Black drum crushing electromyographic (EMG) activity in eight pharyngeal muscles identified by audible cracks of the prey. The first six cycles represent mastication of a fiddler crab, demonstrating the use by this black drum of variable motor patterns on weaker, intermediate prey. Cracking sounds were noted among cycles with and without RD activity (bordered by dashed lines). The last three cycles depict the EMG activity of the first three cracks during crushing of an 11 mm *Cardita floridana* bivalve (approximately 82.7 N of shell resistance; J. R. Grubich, unpublished data). Note the similarities between this forceful crushing event and the middle fiddler crab cycles: (i) the total absence of activity in RD and (ii) the decreased PCe activity during the first crush. The lack of RD activity during mollusc crushing suggests that extremely hard-shelled prey require a vice-like compression bite. Muscle abbreviations are explained in Table 1.

most notably, RD was inactive during all three crushing bites. By the third crush, after initial shell failure had occurred, the intensity of most muscle contractions was attenuated, with the exception of those of AB, which increased in duration and amplitude.

When the same black drum crushed a much weaker fiddler crab, it utilized a more varied motor pattern (Fig. 6). The first two cycles demonstrated a raking motor pattern similar to pharyngeal transport (Fig. 2; Lauder, 1983a) with overlapping RD and PCi contractions and high-amplitude, long-duration bursts in RD and AB. Mastication of the prey item was probably occurring during these cycles. The next three crushes were very much like the third crushing cycle of the bivalve, with the virtual cessation of activity in RD and PCe in association with strong contractions in AB.

Red drum crushed fiddler crabs with motor patterns that had generally lower amplitudes and longer burst durations than in black drum (Fig. 7). Red drum crushes recruited simultaneous,

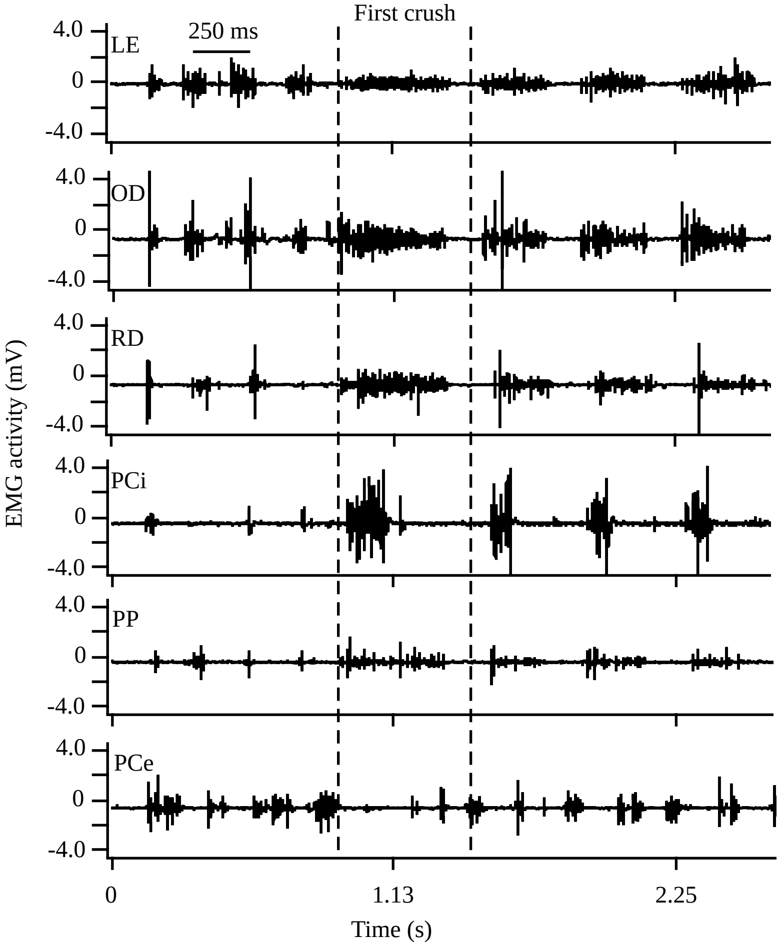

Fig. 7. Red drum crushing electromyographic (EMG) activity of six pharyngeal muscles during feeding on fiddler crab. The first audible crack of the carapace was identified as the cycle bordered by dashed lines. Note the simultaneous low amplitudes and long durations of activity in most pharyngeal muscles compared with black drum muscles (see Fig. 6). Most notably, activity in RD was in phase with upper jaw depression during the crush, suggesting the application of raking motions to the carapace. Muscle abbreviations are explained in Table 1.

low-amplitude, long-duration bursts of activity in LE, OD, PP and RD (Fig. 7). In contrast, the PCi muscle showed high-amplitude, shorter bursts of activity during crushing. Like black drum, there was minimal activity in the lower jaw PCe muscle. In red drum, the sequence of muscle recruitment during fiddler crab crushing was similar to the pharyngeal transport of shrimp prey (Fig. 2).

Canonical variate analysis of drum crushing cycles produced a large eigenvalue for the first axis (4.06) and accounted for a high percentage of the variation among species (90 %) (Table 6). The model discriminated completely between black drum mollusc-crushing cycles and red drum fiddler crab-crushing cycles (Fig. 8). Canonical axis 1 discriminated cycles with late recruitment of LP and PCi and long contractions in RD from cycles that primarily demonstrated early recruitment of AB and, to a lesser extent, shorter durations of activity in LE (Table 6). Interestingly, when black drum fiddler crab-crushing cycles (black dashed polygon) are placed in this model *via post-hoc* substitution, they span canonical space along axis 1, overlapping both red drum fiddler crab-crushing cycles and black drum mollusc-crushing cycles (Fig. 8). In another *post-hoc* substitution, the redear snail-crushing motor pattern falls among the red drum fiddler crab-crushing cycles and is near the centroid of red drum crushing cycles.

Discussion

Three main conclusions can be drawn from this comparative investigation of drum pharyngeal processing. First, prey processing behavior in red and black drum was distinguished primarily by the temporal features of pharyngeal motor patterns. Differences in the onsets and burst durations of pharyngeal muscle activity clearly separated crushing and transport behaviors between species. Second, both drum species demonstrated the ability to modulate pharyngeal motor patterns in response to prey hardness; however, greater motor pattern modulation was observed in the molluscivorous black drum. Finally, mollusc crushing in black drum demonstrated a previously undocumented motor pattern in which the absence of activity in the retractor dorsalis and the onset of activity in the protractor pectoralis indicate the use of a novel vice-like bite mechanism.

Drum motor patterns and prey type modulation

Red and black drum consume prey that differ in hardness. During pharyngeal processing, these two closely related species use their formidable pharyngeal jaws not only to transport prey items from the buccal cavity to the esophagus but also to macerate and break down the prey prior to swallowing. It is within this latter context that prey hardness may (i) affect motor patterns within each species to varying

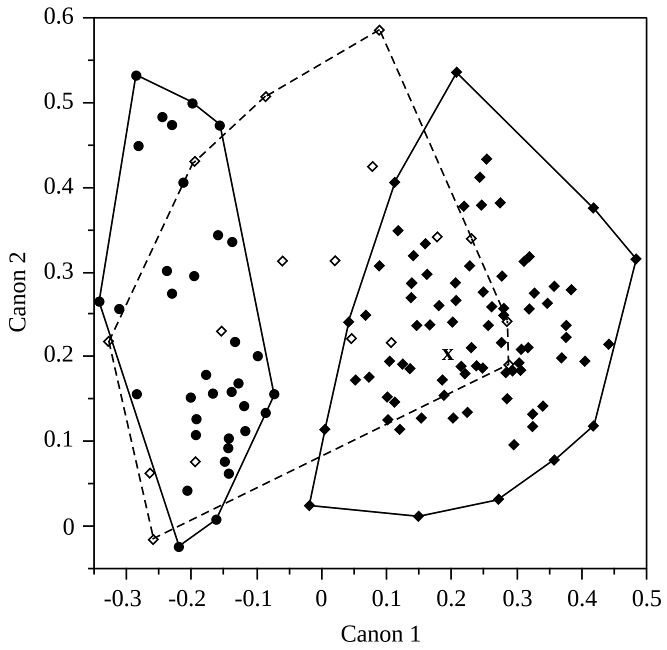

Fig. 8. Canonical variate plot comparing only crushing cycles between red and black drum. Red drum cycles (◆) represent fiddler crab processing activity among five individuals. Black drum cycles (●) are mollusc crushes that were audibly recorded among three individuals. The dashed polygon represents the range of all fiddler crab crushes (◇) recorded from the black drum individual in Fig. 6 (note that fiddler crab crushes from another individual showed the same pattern). For comparisons with sunfish motor patterns, the model used only muscle variables reported in Lauder (1983b). Note the total separation of red drum fiddler crab and black drum mollusc crushing cycles in canonical space. Black drum fiddler crab cycles span both regions, indicating the use of variable crushing motor patterns on this weaker prey. In a *post-hoc* substitution, the mean snail-crushing motor pattern (**X**) of redear sunfish (*Lepomis microlophus*) occurs near the centroid of red drum fiddler crab crushes.

extents, and (ii) be linked to functional divergence in motor patterns of such trophically dissimilar species.

As the discriminant function indicates, muscle activity intensity was similar for all prey types (Table 3; Fig. 5A). The inability of the intensity model to discriminate among prey types suggests that the relative force contributions of individual muscles were similar among hard and soft prey types for both species (Fig. 3). In contrast to this generally weak effect of prey hardness on muscle activity intensity, previous comparative studies of prey processing in oral-processing tetraodontid species (Friel and Wainwright, 1999) and pharyngeal-processing haemulid species (Wainwright, 1989b) have shown significant modulation of muscle intensity across functionally different prey types. These slight increases in relative intensity between hard and soft prey types (on average 27 % for red drum and 11 % for black drum within individual muscles; Table 1) are consistent with relative amplitude increases among crushing and noncrushing bites measured in the snail-crushing shingle-backed lizard *Trachydosaurus rugosus* (Gans and De Vree, 1986). So, while red drum modulated muscle intensity slightly in response to prey hardness, which may have moderately increased the strength of the pharyngeal bite, black drum applied remarkably similar muscle intensities during prey processing irrespective of prey hardness. Comparisons of prey type relative intensities across species are uninformative because measures of intensity have been standardized within individuals and are not representative of absolute differences in contraction strength.

In comparison with muscle intensity, timing variables showed a stronger prey-type effect within each species. While there was moderate overlap of hard and soft prey cycles in canonical space for both species (Fig. 5B), black drum cycles were more variable and covered a larger portion of overall space than red drum cycles. This trend, coupled with the fact that the prey type mean centroids of black drum are farther apart along canonical axis 2, suggests that black drum exhibited greater motor pattern modulation than red drum (Table 4; Fig. 5B). Here, changes in motor pattern associated with prey type in red drum were manifest primarily by slight variations in the mean burst durations of seven pharyngeal muscles, while the relative recruitment pattern of these pharyngeal muscles was altered in less than four muscles (Table 1; Fig. 4). In contrast, prey-type effects on black drum motor patterns were manifest by extensive modulation of both the recruitment times and burst durations of all pharyngeal muscles (Table 1; Fig. 4).

The results for both drum species are consistent with a frequently tested generality of fish feeding systems: the modulation of motor patterns in response to functionally variable prey types (Liem, 1978, 1979; Lauder, 1983b; Sibbing et al., 1986; Wainwright, 1989a; Ralston and Wainwright, 1997; Friel and Wainwright, 1999). Interestingly, the molluscivorous black drum demonstrated a greater capacity for motor pattern modulation than the red drum, a dietary generalist. When the functional attributes of prey are considered (i.e. hard-shelled *versus* semi-hard and soft), this finding is counter to ecological predictions of a positive correlation between functional flexibility and trophic breadth (Liem, 1984; Futuyma and Moreno, 1988). It may be that the evolution of a molluscivorous diet necessitates the enhancement of pharyngeal motor patterns that can crush, transport and effectively manipulate crushed prey to remove fractured shell pieces. Indeed, laboratory observations of black drum show that the initial crushing bout was typically followed by several cycles of pharyngeal manipulation and raking that resulted in shell fragments being expelled through the buccal and opercular cavities. Pharyngeal behavior in molluscivorous sunfishes lends support to this hypothesis. In addition to a novel crushing behavior, Lauder (1983b) identified a novel pharyngeal transport behavior in snail-crushing redear (*Lepomis microlophus*) that was associated with the removal of shell fragments. Hoogerhoud (1987) provided explanations for the derivation of such behavior by suggesting that the removal of shell fragments can be advantageous for increasing the volume available for flesh storage in the gut and in maintaining neutral bouyancy.

The timing variables of pharyngeal motor patterns almost completely separated drum species in canonical space for both hard and soft prey types, suggesting that processing behaviors have diverged since the red and black drum lineages separated (Fig. 5B). In a similar study of pharyngeal processing in haemulid fishes, Wainwright (1989a) made motor pattern comparisons among four closely related species feeding on prey ranging in hardness. The haemulids showed a strong tendency, across taxa, towards conservation of motor patterns in pharyngeal transport behavior. However, the results for the timing variables in the present study indicate that processing motor patterns on both hard and soft prey types have diverged in drum evolution. Muscle eigenvectors (greater than ±1.0) along the first canonical axis reveal that motor pattern divergence occurred in 43 % (6/14) of the timing variables (Table 4). These timing modifications are similar to the types of changes described in the pharyngeal motor patterns of molluscivorous sunfishes (Lauder, 1983b).

However, a limitation inherent to two-species comparisons is the inability to attribute differences between two taxa to changes along one or the other lineage. Without reference to other closely related sciaenids, it is equally likely that it is the red drum motor patterns that are specialized and contain derived modifications. Another comparative EMG analysis of the sister taxa to black drum, the durophagous freshwater drum (*Aplodinotus grunniens*), with an outgroup species to the clade containing red and black drum (i.e. *Sciaena umbra*) (Sasaki, 1989) might help resolve the origin of the mollusc-crushing motor pattern. If the freshwater drum crushes hard-shelled prey with a similar motor pattern to black drum and the outgroup does not, then it would support the hypothesis that the mollusc-crushing pattern was derived in the common ancestor of the *Pogonias*/*Aplodinotus* clade and coincided with the evolution of molluscivory in this clade.

With this limitation noted, it is evident that both the raw data of mean muscle activity and the results of the two canonical discriminant functions lend support to the hypothesis that the evolution of a molluscivorous diet in black drum is associated with the acquisition of novel pharyngeal motor patterns (Fig. 8). Molluscivory appears to have arisen in conjunction with changes in the timing aspects of behavior and the recruitment of muscles and not simply as a result of an increase in the intensity of muscular contractions of a shared behavior with red drum.

Pharyngeal muscle activity and functional consequences for mollusc crushing

Muscle activity during drum pharyngeal transport behavior indicates that the motions of the jaws are similar to the pharyngeal bite mechanism of haemulids and other generalized perciform fishes. The raking action of the pharyngeal bite is caused by simultaneous upper jaw depression and retraction against an elevated and stabilized lower jaw (Wainwright, 1989b; Galis and Drucker, 1996). While the pharyngeal raking mechanism is the predominant musculoskeletal motion used on soft shrimp prey, muscle activity during processing of hard-shelled bivalve prey in black drum suggests that different pharyngeal jaw movements are employed for crushing.

Three mechanical interpretations of the black drum crushing bite can be derived from EMGs. Upper jaw depression, as in pharyngeal transport, is signified by extensive overlap of activity in LE, LP, OD and AB, which transmit dorsal crushing forces downwards through contact with the pharyngobranchial toothplates and the top of the mollusc shell (Figs 1, 6). Observations of pharyngobranchial movements in anesthetized individuals (J. R. Grubich, unpublished data) indicate that depression occurs by the same force-coupling mechanism between the third and fourth epibranchial and the third pharyngobranchials as seen in haemulids (Wainwright, 1989b).

Strong lower jaw elevation during mollusc-crushing in black drum appears to be caused by the protractor pectoralis muscle. In red drum, the PP is a thin muscle that has no direct insertion onto the pectoral girdle. Yet in black drum, this muscle has undergone tremendous functional modification. The PP is hugely hypertrophied and extends *via* a strong anterior tendon from the intercalar–exoccipital–pterotic region of the skull (Winterbottom, 1974) to the ventral region of the cleithrum, masking PCi along its path (Fig. 1). In black drum, the fibers of this robust muscle are covered in a thick tendinous fascia and run in postero-ventral fashion, attaching over a wide area along the length of the anterior face of the pectoral girdle. During strong crushing bites, this muscle showed high-amplitude activity (Fig. 6, mollusc), which coincided with observations of ‘head squeezing’ when the neurocranium and pectoral girdle were compressed together through a ventral depression of the neurocranium and a dorsally directed protraction of the cleithrum (J. R. Grubich, personal observation). Twitch contractions of the PP initiated by manually probing the muscle of anesthetized individuals caused similar elevations of the cleithrum and depressions of the neurocranium (J. R. Grubich, unpublished data).

Morphological observations of the junction between the cleithrum and fifth ceratobranchial in black drum suggest that such cleithral elevation by the PP may be transmitted to the lower jaw during crushing. The fifth ceratobranchial has a large lateral process that separates the ventrally directed fibers of the anterior PCe from the horizontally running fibers of the posterior origin of the PCi (Fig. 1). In fact, this large ceratobranchial process was identified as a synapomorphic character uniting the black drum (*Pogonias cromis*) with the durophagous freshwater drum (*Aplodinotus grunniens*) (Sasaki, 1989). This process lies dorsally, juxtaposed to a medial flange that runs the ventral length of the cleithrum. Therefore, strong PP contractions may generate forceful dorsal movements not only of the cleithrum but also of the lower jaw during crushing.

This modification of the protractor pectoralis in black drum is the first evidence in generalized perciform fishes of this muscle evolving an active crushing role in association with molluscivory. Indeed, the onset of activity in this muscle was the highest loading variable in canonical space that discriminated between the two drum species (Table 4), and this muscle tended to display a higher mean intensity during mollusc crushing (Fig. 3). Galis (1997) described similar pectoral girdle movements as an important aspect of transmitting dorsally oriented forces in the pharyngeal bite of pomacentrids. The protractor pectoralis has undergone a similar functional modification in the Haemulidae without a causal link to a strict diet of hard-shelled molluscan prey. In generalized and presumably molluscivorous haemulids, lower jaw elevation occurs by the action of a novel connection of the PP to the posterior margin of the fifth ceratobranchial *via* a derived tendon (Wainwright, 1989b). Similarly, morphological investigations of a molluscivorous carangid, *Trachinotus* sp., indicate that pharyngeal crushing involves a protractor pectoralis that functions to raise the lower jaw (J. R. Grubich, personal observation). The apparent mechanical convergence of PP architecture across two and possibly three families of generalized perciform fishes (Sciaenidae, Carangidae and Haemulidae) suggests that effective crushing of hard prey may require powerful lower jaw elevation.

Finally, the most significant functional aspect of black drum crushing is the absence of upper jaw retraction. Crushing cycles during feeding on hard-shelled bivalve prey were devoid of activity in RD, the main effector of upper jaw retraction (Figs 4, 6, mollusc). This lack of RD activity in black drum crushes contributed strongly to the separation of biting cycles in the two drum species (Table 4; Fig. 5). The fiber orientation of this muscle leads to contractions that not only retract the toothplates posteriorly but also raise them along a dorsal trajectory (Lauder, 1983a). Simultaneous activity of this muscle with the levator muscles would mechanically decrease the ventral forces of upper jaw depression (Fig. 1). Therefore, the absence of RD activity may contribute to maximization of force transmission and focus the direction of upper jaw depression into a single downward vector.

Thus, unlike raking motions, during which shearing forces apparently dominate processing in red drum, haemulids and centrarchids, mollusc-crushing motor patterns in black drum indicate that upper and lower jaw movements produce a unique vice-like compressive bite in which the mollusc is squeezed between opposing forces to crack the shell.

Evolution of crushing motor patterns

Both drum species investigated here demonstrated the ability to crush prey. Red drum, however, were only capable of crushing the semi-hard carapaces of fiddler crabs (*Uca* sp.). High levels of activity in PCi, decreased levels of activity in PCe and simultaneous, long contractions in the upper jaw muscles and RD indicate that fiddler crab crushing involves modified raking motions of the generalized pharyngeal transport behavior (Figs 2, 7). This motor pattern is very similar to snail crushing by the redear sunfish *Lepomis microlophus* (Lauder, 1983b) (Fig. 8). This similarity in motor pattern implies that freshwater snails and fiddler crabs can be crushed by shearing forces generated through analogous raking movements of the pharyngeal jaws in redear and red drum.

Cycles of fiddler crab crushing by a single black drum revealed the utilization of two motor patterns. In breaking down the carapace of fiddler crabs, the black drum employed motor patterns that used raking actions similar to the red drum pattern and the vice-like compressions of mollusc crushing (Figs 6, 8). This evidence shows that black drum are able to modulate action of the pharyngeal jaws during crushing of semi-hard prey, such as fiddler crabs, and further supports enhanced modulatory capacity in black drum. The fact that red and black drum share a crushing motor pattern for semi-hard prey, itself a modification of pharyngeal transport in drum, suggests a possible predecessor to mollusc-crushing behavior.

In achieving a molluscivorous diet, black drum acquired a novel crushing motor pattern that has not been described in generalized perciform pharyngeal jaws. Yet, within the context of pharyngeal molluscivory, the only other specialized molluscivorous taxa from which crushing EMGs have been recorded, the redear and pumpkinseed sunfish (Lauder, 1983b), use a motor pattern to crush freshwater snails that is surprisingly similar to the crushing pattern of the red drum. Why then do black drum use a novel motor pattern to crush marine bivalves? The answer may lie in the physically stronger shells of marine molluscs. Vermeij and Covich (1978) attributed the differences in shell strength between marine and freshwater molluscs to the physiochemical nature of most freshwater systems, which have much lower levels of dissolved calcium and thereby provide a poorer resource for shell calcification. Therefore, if inherently stronger forces are required to crack marine bivalves, then selection would favor motor patterns that are modulated to maximize the crushing capacity of the pharyngeal jaws. In support of this hypothesis, the mollusc-crushing behavior of black drum appears mechanically to maximize dorsal and ventral forces applied to the shell of the prey. Estimations of black drum crushing performance and the strength of the marine bivalves they feed upon will ascertain whether black drum generate greater forces during molluscivory than reported among redear sunfish and may support a mechanical link to this novel motor pattern.

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