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Functional and Morphological Bases of Trophic Specialization in Sunfishes (Teleostei, Centrarchidae)

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ABSTRACT The gross morphology and electrical activity of the muscles of the pharyngeal apparatus of centrarchid sunfishes *(Lepomis)* are analyzed within a monophyletic clade containing species specialized for snail-eating. Outgroup comparisons of both structure and activity patterns of muscles permit examination of the relationship between specialized diet and function of the trophic apparatus. In most sunfish species, electrical activity in the pharyngocleithralis internus muscle significantly overlaps that in the retractor dorsalis muscle during pharyngeal transport, indicating that the upper and lower pharyngeal jaws retract together. Activity in the pharyngohyoideus, levatores externi, and levator posterior also significantly overlaps activity of the retractor dorsalis.

Snail-eating is associated with derived morphological, behavioral, and functional features. The shell is crushed before pharyngeal transport, correlated with extensive overlap in activity periods of muscles. One species, *Lepomis microlophus,* possesses a highly stereotyped neuromuscular repertoire that does not vary with prey type. All prey, even fish and worms, are subjected to crushing. *Lepomis gibbosus* exhibits the crushing pattern of muscle activity only when feeding on snails. *L. microlophus* has a hypertrophied levator posterior muscle, but the lines of action of the pharyngeal muscles are similar to the primitive condition. Pharyngeal transport in this species is unique in that activity of the pharyngocleithralis internus alternates with that of the retractor dorsalis.

In sunfishes, alterations in the central control of peripheral structures have produced major changes in the sequence in which homologous components of the structural network are activated.

The evolution of feeding specializations and the diversity of morphological features used to obtain energy from the environment have long been of interest to biologists. The concept of resource partitioning is basic to many ecological models and analyses, and the interactions of individuals and species in relation to environmental nutrients is an area of active research. Knowledge about the availability of energy and the ability of organisms to capture and utilize energy-giving substances is of critical importance to our understanding of evolutionary patterns and processes (Van Valen, '76).

Recent interest in the trophic biology of organisms has centered on the application (and applicability) of optimal foraging models and on the comparison of resources actually used by organisms to those available in the environment. Teleost fishes have been especially important in the study of trophic biology, and several analyses have provided new field data on feeding ecology or reassessed the conceptual basis for models of foraging behavior (Keast, '78a,b; Goulding, '80; Liem, in press; Lobel, '81; Hobson, '74; Hobson and Chess, '76, '78; Savitz, '81; Stein et al., '75; Werner, '74; Werner and Mittelbach, '81). Despite this progress in understanding trophic biology, we still lack detailed studies of the morphological and physiological patterns associated with trophic diversification within a clade.

In this paper I present an analysis of both morphological and functional patterns associated with the acquisition of a specialized

feeding function (snail-eating) within a monophyletic lineage of sunfishes; snail-crushing is rare among higher teleosts (Lauder, '83b). Species-level comparisons are conducted in order to provide an appropriate scale for reconstructing the history of change in the trophic apparatus (see Cracraft, '81). The morphology and function of the feeding mechanism in the snail-crushing species is compared to patterns exhibited by phylogenetic outgroups. Specifically, four species within the genus *Lepomis* are compared with each other as well as with the other centrarchid species studied previously in another context (*Pomoxis, Micropterus,* and *Amblo-plites;* Lauder, '83a). Two of these species, *L. microlophus* and *L. gibbosus,* feed on snails in addition to a wide variety of other aquatic invertebrates (Keast, '78a,b; Savitz, '81).

The overall goals of this investigation are 1) to provide an analysis of patterns of interspecific variation in structure and function of the feeding apparatus (especially patterns of muscle activity), 2) to compare patterns of trophic biology associated with feeding on molluscs to previous analyses of other sunfish species, 3) to relate these results to the extensive information now available on ecological relations and diets of sunfishes, and 4) to examine functional and morphological patterns associated with the origin of trophic specializations.

MATERIALS AND METHODS

Morphology

Gross morphological features of the pharyngeal jaw apparatus in sunfishes were studied by dissection using a Zeiss IVb dissecting microscope. A camera lucida attachment was used to prepare the figures. Osteological descriptions were based on specimens that had been cleared and stained following the procedure of Taylor ('67).

Muscle architecture was analysed by digesting away much of the intramuscular connective tissue in acid digestion when preparing muscles for fascicle length measurements (see below). The orientation of fascicles within each muscle was noted and the length of 25 fascicles throughout the muscle measured. In several cases, the mean fascicle length was much shorter than the length of the muscle belly. In none of the muscles examined were the fascicles at an angle of more than 10° to the long axis of the whole muscle. Thus none of the muscles in the pharyngeal region is significantly pinnate, although several do exhibit a fairly complex pattern of fascicular length variation within the muscle belly.

The physiological cross section of a muscle provides a method of comparing muscles of different architecture with respect to the expected maximal force-gathering capacity (Gans and Bock, '65). Physiological cross sections of eight pharyngeal muscles were determined for four species, *Lepomis cyanellus, L. microlophus, L. gibbosus,* and *L. macrochirus* (one individual each, all of nearly the same size; see Table 1). The appropriate muscles from one side of the head were dissected out, blotted, and weighed three times (the weight reported in Table 1 is the mean of these three weights), and placed in a solution of 25% nitric acid at 30°C for as much as a week until the muscle fascicles could be easily teased apart. The muscles were then placed in 50% glycerol in a small petri dish and the fascicles separated under the dissecting microscope (Williams and Goldspink, '71; Gorniak et al., '82) and measured using an ocular micrometer. The physiological cross-sectional area of each muscle was calculated from the weights and fascicular lengths (mean of 25 measurements from representative parts of the muscle), using a muscle density of 1.05 mg/mm^3 (Alexander, '68; Lowndes, '55). Fish muscle is slightly denser than mammalian muscle, for which the value of 1.00 mg/mm^3 is used for similar calculations (e.g., Weijs and Dantuma, '81).

In order to assess variation in physiological cross section due to body size or interindividual variation of similarly sized specimens, two tests were conducted on the pharyngocleithralis internus muscle in *Lepomis macrochirus.* First, muscles from ten individuals of similar size (mean standard length, $\bar{x}$ = 13.7 cm, SE = 0.23) were measured and found to have a mean cross section of 3.9 mm^2 (SE = 0.18). Second, muscles from five individuals varying in size from 5.0 cm standard length to 16.9 cm standard length were measured. Muscle cross section was positively correlated with body length (r = 0.97) and the least squares regression had a slope of 0.6. The smallest individual had a physiological cross section of 0.26 mm^2 for the pharyngocleithralis internus muscle; the largest had a cross section of 7.65 mm^2.

Experimental techniques and data analysis

The sunfish species studied experimentally were *Lepomis macrochirus, L. gibbosus, L. auritus, L. cyanellus,* and *L. microlophus.* Voucher specimens for each of these species

have been deposited in the Field Museum of Natural History, Chicago.

Electromyographic recordings were obtained using the techniques and equipment described previously (Lauder, '83a). Briefly, electromyograms were recorded through fine wire (0.051-mm-diameter) steel alloy electrodes implanted in the pharyngeal muscles. Muscular activity was amplified by Grass P511J preamplifiers with either a 30-Hz or 100-Hz high-pass filter and 3,000 Hz as the low-pass cutoff. After amplification, signals were recorded on a Bell and Howell 4020A FM tape recorder at 37.5 cm/second. Six channels were usually recorded simultaneously. Data were played back on a Gould 260 chart recorder at a tape speed of 4.7 cm/second, giving an effective frequency response of nearly 1,000 Hz. Electrodes were implanted in the branchial musculature of fish anesthetized with tricaine methane sulfonate. Using a fiber-optic illuminator, each muscle (with the exception of the retractor dorsalis) could be seen through the mucous membrane medial to the gills. Electrode placement in the levatores externi 3 and 4 and levatores externi 1 and 2 could not be reliably distinguished and data from these pairs of muscles were pooled (e.g., Fig. 5). The method of constructing the summary block diagrams of muscle electrical activity (Figs. 5, 6, 8, 10, 11) is also described in Lauder ('83a). Briefly, the retractor dorsalis muscle was chosen as a reference on the basis of its well-defined action, overall consistency in its activity period, and its predominant bilaterally symmetrical activity pattern. The onset of activity in this muscle was taken as the "zero point" and both the onset and offset of activity in the other muscles measured relative to this time. This procedure also was used for times reported in the tables. The interval encompassing two bursts of activity in the retractor dorsalis was used to assess activity patterns in the pharyngeal muscles. Summary diagrams were also constructed by scaling all muscle activity periods using the duration of two retractor bursts as 100%. An example is shown in Figure 7. This compensates for differences in burst duration among feeding events and gives a clear differentiation in the relative timing of muscle activity. Although this approach did not change the relative sequence of muscle activity, it did reduce the variability in muscle onset and offset times (an important parameter). Therefore, only one figure is presented in this style; all others illustrate unscaled data, and all statistical analyses were performed on unscaled data. Each summary diagram represents data from at least 40 separate feeding events from which over 100 different transport sequences were measured. The number of individuals included varies from three *(L. microlophus)* to 11 *(L. macrochirus)*.

One pharyngeal muscle, the levator posterior, was large enough to permit accurate placement of more than one electrode into the belly. In one experiment, two electrodes were located approximately 1 mm deep to the surface at the anterior and posterior borders of the muscle. The tips of the electrodes were approximately 3 mm apart. No significant differences in onset or offset of electrical activity were found between the two sets of electrodes.

Several different types and sizes of prey were used to assess the dependence of muscle activity pattern on prey morphology. All species consumed live minnows *(Notropis, Pimephales)* from 3 to 6 cm in total length, and earthworms *(Lumbricus)* cut into pieces varying in length from 1 to 6 cm. In addition, *Lepomis microlophus* and *L. gibbosus* accepted and crushed snails *(Helisoma)* ranging from 0.2 mm to 1.5 mm in diameter. *L. cyanellus* could occasionally also be induced to crush snails, but *L. macrochirus* never exhibited crushing behavior.

The most extensive intraspecific analysis of muscle activity patterns was conducted for *L. macrochirus* (see Table 2): The effect of prey type and size on the duration of electrical activity, the interburst period, and total transport time were analyzed. Differences between muscle activity durations and onset and offset times (Tables 2–4) were examined using two-sample t-tests. Because multiple pairwise comparisons were conducted (e.g., Table 4), the Bonferroni t-test (Glantz, '81) was used with a significance level of 0.001 to ensure that the likelihood of accepting the hypothesis of no difference between muscle activity times when a difference actually exists did not exceed 5%. When large numbers (> 30) of comparisons are performed, the Bonferroni correction provides a conservative estimate of the error rate, so that the pairs indicated as significant in Table 4 are likely to be significant at a higher level than 5%.

Three other techniques were used to study the mechanics of food acquisition and transport. Only the first two were conducted simultaneously with muscular activity recordings. 1) Light cinematography using a

Photosonics 16-mm-1PL camera at 200 frames per second and Kodak 4X Reversal film provided information on jaw, hyoid, and pectoral girdle movement. 2) Hydrophone recordings within the experimental aquarium indicated when fracture of the snail shell occurred during crushing (see Lauder, '83b). The hydrophone was attached to a DC power supply and the output was amplified through a Grass P511J preamplifier and recorded on a Bell and Howell FM tape recorder. Sound was recorded simultaneously with electrical activity of four pharyngeal muscles. 3) x-ray films at 100 frames per second of feeding in *L. microlophus* were obtained through the courtesy of Dr. K. Liem (Harvard University) using Siemens radiographic equipment, a Sirecon image intensifier, and Plus-X Reversal film at the Museum of Comparative Zoology, Harvard University. The technique used was similar to that described in Lauder and Liem ('80) and Liem ('78).

RESULTS

Morphological patterns

General features of the morphology of the pharyngeal jaw apparatus in acanthopterygian fishes have been discussed elsewhere (Johnson, '80; Lauder, in press; Liem, '70; Liem and Greenwood, '81; Nelson, '67, '69; Rosen, '73; Stiassny, '81; Winterbottom, '74), and a summary of the lines of action of pharyngeal muscles and descriptions of the generalized centrarchid morphology is presented in Lauder ('83a). Here only those aspects of pharyngeal structure that bear directly on jaw function in the species examined in this paper or features unique to these taxa are emphasized.

The lines of action of the pharyngeal muscles in all the *Lepomis* species examined are similar. All levatores externi and interni arise anteriorly from the ventrolateral surface of the skull near the otic capsule and insert posteroventrally on the upper pharyngeal elements (Fig. 1). The levatores externi three and four are often difficult to distinguish along most of their length as the muscle bellies lie in close approximation (Fig. 1: LE3, LE4). The insertions of these two muscles do differ: Levator externus 3 inserts primarily on the posterodorsally directed uncinate process of epibranchial three, but levator externus 4 inserts on the uncinate process of epibranchial four. In *Lepomis* as well as in most other centrarchids, the uncinate processes from epibranchials 3 and 4 meet dorsally, and a ligament is usually present connecting epibranchials 3 and 4. In *L. microlophus* the levator posterior is hypertrophied when compared to the primitive condition (Figs. 1, 2: LP). The fifth branchial adductor muscle has a thickened tendinous strap on its lateral face connecting epibranchial four with ceratobranchial five (Fig. 1B); *L. cyanellus* exhibits the primitive condition in having only a thin lateral fascia covering the muscle.

All species show two obliqui dorsales muscles (Fig. 2), but the arrangement of the insertions varies considerably. In the primitive condition (also exhibited by *Micropterus,* see Lauder, '83a: Fig. 4B), a large obliquus dorsalis 4 extends anteromedially to pass beneath the posterior transversus dorsalis anterior fibers (as in *L. cyanellus,* Fig. 2A). In *L. macrochirus* and *L. gibbosus,* a large thickened fibrous pharyngeal pad interrupts the dorsal pharyngeal musculature so that the left and right obliquus dorsalis 2 and transversus dorsalis anterior no longer meet in the midline to form a continuous sheet of muscle (PP in Fig. 2C, D). This pad appears to be derived from a thickening of the dorsal intermuscular aponeurosis. In *L. cyanellus,* the obliquus dorsalis 4 extends ventral to the pharyngeal pad to insert anteriorly on the third and fourth pharyngobranchials. In *L. microlophus* and *macrochirus,* the pharyngeal pad is thickened posteriorly and the fibers of the obliquus dorsalis 4 insert laterally on pharyngobranchial 4 and do not extend anteriorly (OD4 in Fig. 2B). In *Lepomis microlophus* the transversus dorsalis posterior

Abbreviations

AD5, Adductor arcus branchialum five muscle
AM2, Adductor mandibulae muscle, part two
EP, Epaxial muscles
GH, Geniohyoideus muscle
LAP, Levator arcus palatini muscle
LE 1, 2, 3, 4, and LE3/4, Levatores externi muscles for branchial arches I–IV
LI 2, 3, and LI1/2, Levatores interni muscles for branchial arches I–IV
LOP, Levator operculi muscle
LP, Levator posterior muscle
OBI, Obliquus inferioris muscle, a division of the hypaxialis
OD 2, 4, Obliquui dorsales muscles for branchial arches II and IV
PCe, Pharyngocleithralis externus muscle
PCi, Pharyngocleithralis internus muscle
PH, Pharyngohyoideus muscle
PP, Pharyngeal pad
RD, Retractor dorsalis muscle
SH, Sternohyoideus muscle

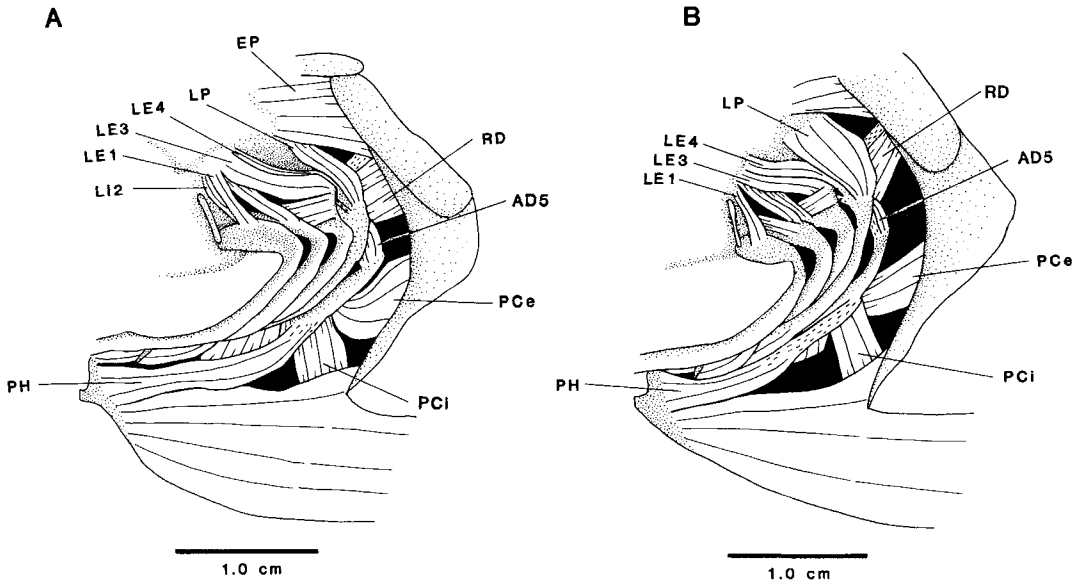

Fig. 1. A. *Lepomis cyanellus.* Lateral view of the branchial musculature. The gills and mucous membranes lining the opercular cavity have been removed. Note the close apposition of levatores externi 3 and 4 throughout their lengths and the general orientation of muscle lines of action. B. *Lepomis microlophus.* Similar view of branchial musculature to show the hypertrophied levator posterior muscle and the otherwise very similar organization of the pharyngeal region to other *Lepomis* in this mollusc-crushing species.

muscle is not well developed and a small unique differentiated strap of transverse esophageal muscle just posterior to each pharyngobranchial 4 exists (Fig. 2B).

Skeletal specializations for snail-crushing in *Lepomis* include modifications of both the upper and lower pharyngeal jaws; both jaws have teeth that are more molariform than those of more primitive species (compare Fig. 3A,B with Fig. 3C,D). In both *L. gibbosus* and *L. microlophus,* the endoskeletal portion of ceratobranchial 5 supports a large toothplate that extends both medially and laterally beyond the ventral endoskeletal supports.

The areas of physiological cross section for eight pharyngeal muscles are presented in Table 1. (These data may be compared between and within individuals, keeping in mind the estimated variation noted above in Materials and Methods.) *Lepomis gibbosus* and *microlophus* differ from *cyanellus* and *macrochirus* in several important aspects. The most dramatic difference lies in the hypertrophy of the levator posterior muscle. *L. microlophus* shows a greatly increased physiological cross section of this muscle that derives both from an increase in mass and from a decrease in mean fascicle lengths in comparison to the other species. The pharyngohyoideus and pharyngocleithralis internus both have greater cross sections in *L. gibbosus* and *microlophus* than in the other two species. The fifth branchial adductor and levatores externi 3 and 4 of *L. gibbosus* and *microlophus* have significantly shorter fibers but greater cross-sectional areas than *L. cyanellus* and *macrochirus* (Table 1). The other two notable differences are the reduced area of the retractor dorsalis in *L. microlophus* and the increased cross sectional area of the pharyngocleithralis externus in *L. gibbosus.*

Functional patterns

Only the results of electromyographic analyses of the pharyngeal transport and crushing phases of feeding are presented here. All four *Lepomis* species also show buccal manipulation and pharyngeal manipulation but these do not differ substantially from previous descriptions in other centrarchid species (Lauder, '83a).

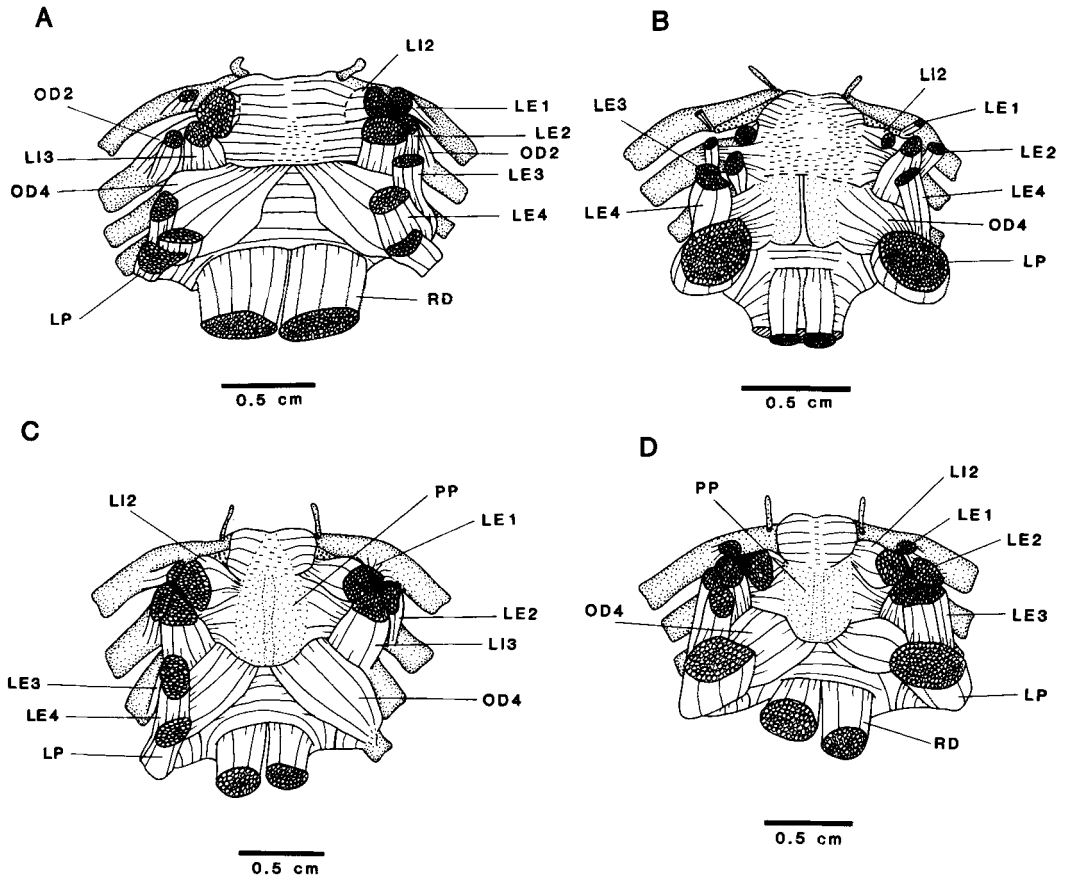

Fig. 2. Dorsal views of the branchial musculature in *Lepomis cyanellus* (A), *L. microlophus* (B), *L. macrochirus* (C), and *L. gibbosus* (D). In B the posterior portion of the pharyngeal pad has been removed to show the insertion of the obliquus dorsalis four on pharyngobranchials 3 and 4, and in C the levatores externi 3 and 4 have been removed on the right side. Compare the relative development of the pharyngeal pad in A (where it is limited to a small fibrous intersection in the transversus dorsalis), to the condition shown in C and D, and note the overall similarity in organization of the dorsal pharyngeal region.

Lepomis cyanellus and macrochirus

The pattern of muscular activity during pharyngeal transport in *L. cyanellus* is characterized by extensive overlap in the activity periods of dorsal pharyngeal muscles. The major burst of activity in the levatores externi 1 and 2 alternates with these times of overlap. For example, the pharyngocleithralis internus, pharyngohyoideus, fifth branchial adductor, levatores externi 3 and 4, and the levator posterior activity all overlap significantly activity of the retractor dorsalis muscle (Figs. 4, 5). The muscles that typically show activity between bursts of the retractor dorsalis are the pharyngohyoideus, pharyngocleithralis externus, and the levatores externi 1 and 2. Only when large prey (5–6 cm long) are being transported into the esophagus is activity observed in the adductor mandibulae and obliquus inferioris (Fig. 5: OBI, AM2). The sternohyoideus is never active during pharyngeal transport.

The type and size of prey influence both the duration of muscle activity periods and the relative timing of activity in the branchial musculature. Of the four muscles examined in detail (Table 3), two exhibited shorter burst durations during the transport of fish than they showed during transport of

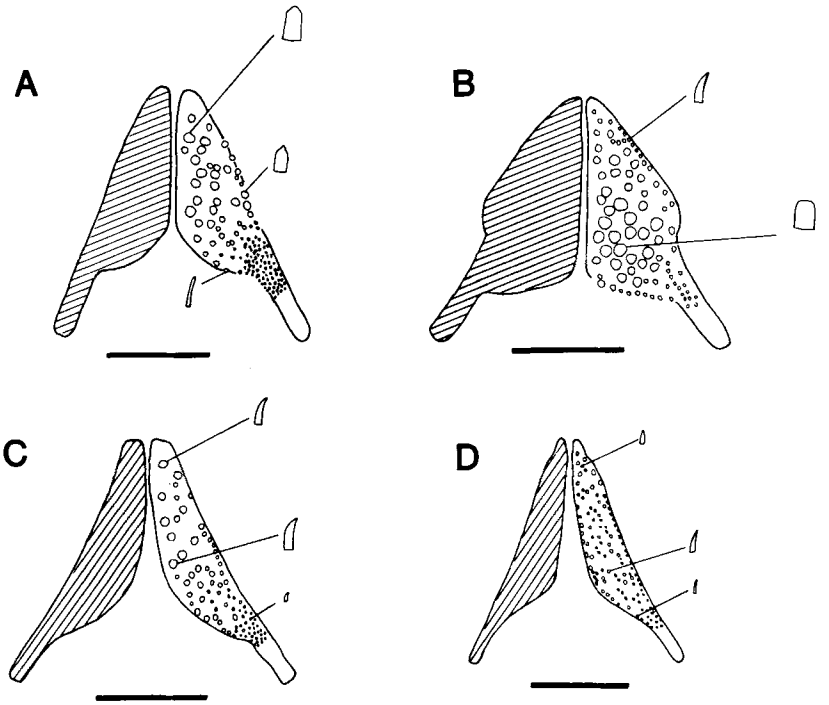

Fig. 3. Dorsal views of the lower pharyngeal jaws (fifth ceratobranchials) in *Lepomis gibbosus* (A), *L. microlophus* (B), *L. macrochirus* (C), and *Micropterus salmoides* (D). Scale = 2.0 mm. The left ceratobranchial (shaded) is shown in outline to emphasize shape differences between the species while the right bone is illustrated with tooth circumferences drawn from dorsal view to emphasize the distribution of tooth size. Selected teeth are shown in lateral view to show shape differences. Note that small-diameter pointed teeth are present on the lateral and posterior aspects of the lower pharyngeal jaws in all species.

similarly sized worms. The retractor dorsalis and pharyngocleithralis internus were active for a longer time when fish were used as prey than when worms were eaten. No differences in onset or offset times for fish versus worm prey (compared for three muscles with respect to the retractor dorsalis, see Table 4) are significant for any muscles.

Lepomis cyanellus occasionally accepts snails as prey in the laboratory. After the snail has been sucked into the buccal cavity, it is moved posteriorly to the pharyngeal region where the shell is crushed before swallowing. Shell pieces are often ejected from the mouth after pharyngeal transport, but many shell pieces adhere to the snail body and are swallowed. Transport of snails occurs by a pattern of muscular activity that closely resembles the rhythmic transport pattern illustrated in Figures 4 and 5. However, muscular activity during shell crushing is very different. Bursts of activity are not staggered, and extensive overlap occurs in all pharyngeal muscles (Fig. 4). Durations of muscle activity are significantly shorter during crushing than during the transport of nonmolluscan prey (Table 3), although the coefficients of variation for activity durations are similar in crushing and transport (about 12%). Differences between onset and offset times for branchial muscle activity are much less during snail crushing than worm or fish transport (Table 4), indicating a greater overlap in activity periods.

Lepomis macrochirus would not crush snail shells in these laboratory experiments and so data are presented for fish and worm prey only. The overall pattern of muscle activity during pharyngeal transport is very similar to that of *L. cyanellus* (Fig. 6). Activities of the pharyngocleithralis internus, adductor arcus branchialum 5, levatores externi 3 and 4, and the levator posterior all overlap activity in the retractor dorsalis and all begin

TABLE 1. Branchial muscle characteristics in four sunfish species[1]

Species	Specimen size (standard length)	Muscle characteristics	Branchial muscle							
			RD	AD5	PH	PCi	PCe	LE1	LE3/4	LP
Lepomis macrochirus	13.2 cm	Mean fiber length (mm) ± 1 SE	7.6 ± .12	0.9 ± .02	4.9 ± .13	5.7 ± .13	6.1 ± .03	1.1 ± .07	5.3 ± .17	4.5 ± .15
		Wet weight (mg)	41.1	1.7	10.2	21.0	37.3	1.2	14.8	4.9
		Physiological cross section (mm^2)	5.2	1.8	2.0	3.5	5.8	1.0	2.8	1.0
Lepomis cyanellus	12.7 cm	Mean fiber length (mm) ± 1 SE	5.2 ± .21	1.3 ± .08	6.9 ± .15	5.0 ± .10	7.5 ± .16	2.3 ± .06	6.6 ± .11	6.2 ± .08
		Wet weight (mg)	50.1	5.8	13.9	18.5	33.4	2.3	23.8	11.4
		Physiological cross section (mm^2)	9.3	4.1	1.9	3.5	4.3	0.9	3.4	1.7
Lepomis microlophus	13.5 cm	Mean fiber length (mm) ± 1 SE	5.7 ± .14	0.4 ± .02	2.7 ± .10	3.7 ± .10	6.8 ± .21	1.3 ± .05	3.8 ± .06	3.3 ± .11
		Wet weight (mg)	19.1	1.6	20.8	19.6	38.9	1.7	15.3	57.9
		Physiological cross section (mm^2)	3.2	3.5	7.3	5.1	5.5	1.2	3.9	16.7
Lepomis gibbosus	13.3 cm	Mean fiber length (mm) ± 1 SE	7.2 ± .22	0.6 ± .03	3.5 ± .08	4.5 ± .14	4.3 ± .11	1.4 ± .03	4.6 ± .13	4.9 ± .07
		Wet weight (mg)	52.9	3.9	24.8	32.2	48.8	3.0	17.5	58.5
		Physiological cross section (mm^2)	6.9	6.3	6.7	6.7	10.7	2.1	3.6	11.3

[1]Abbreviations here and in following tables are identified in list preceding Figure 1.

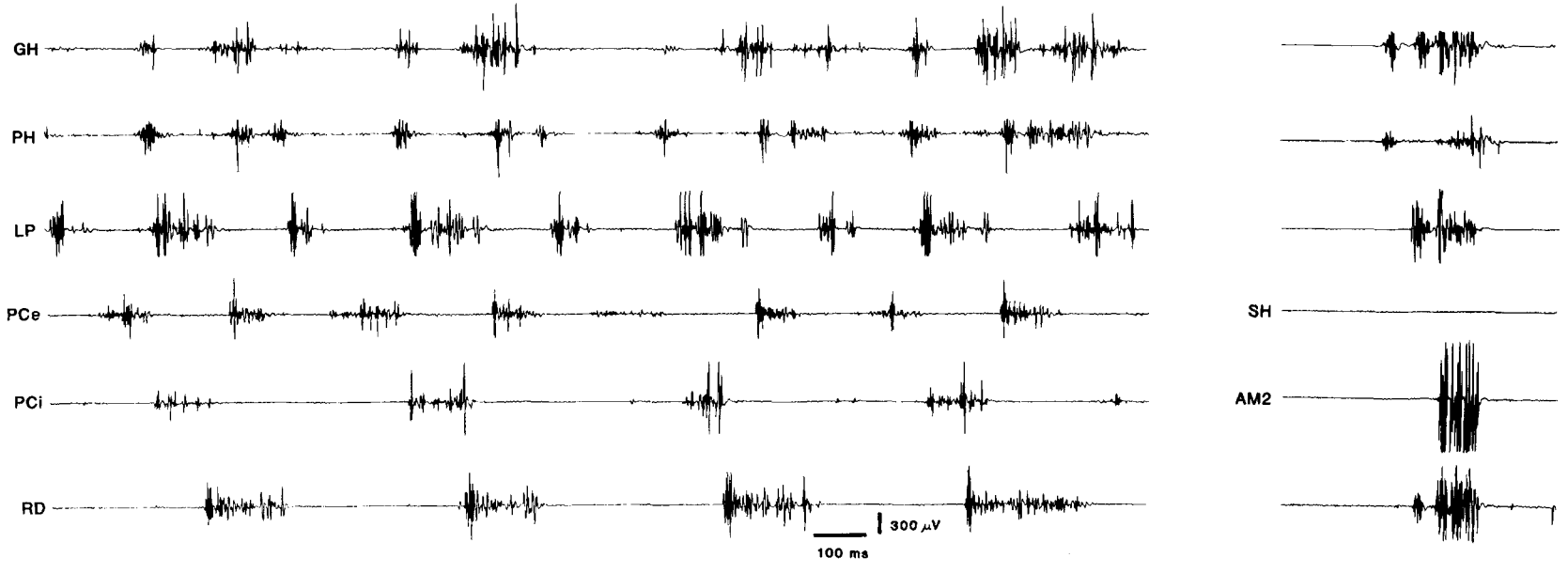

Fig. 4. *Lepomis cyanellus.* Electromyographic pattern during pharyngeal transport (of a 5.0-cm-long earthworm) on the left, and during crushing of a 1.0-cm-diameter snail on the right. All muscles in each panel were recorded simultaneously. Unlabeled muscles on the right are the same as those in the left panel.

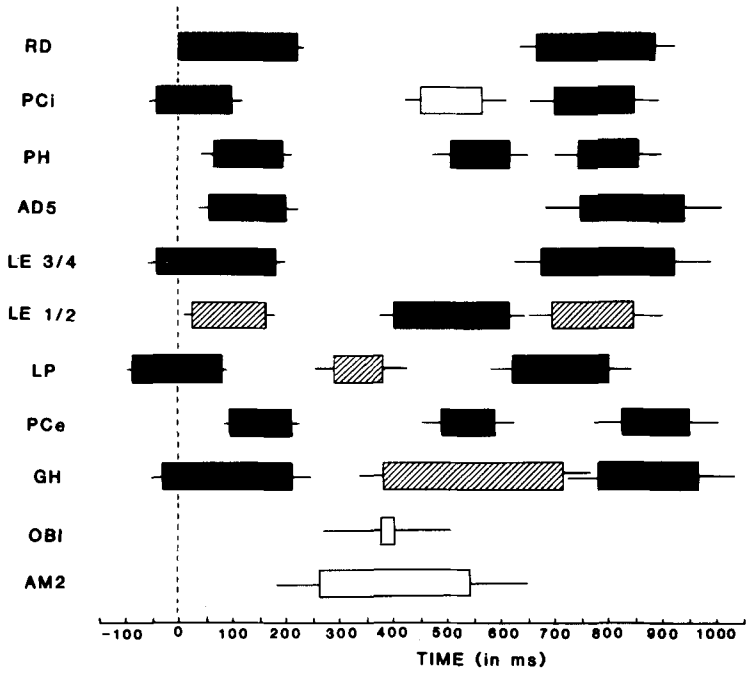

Fig. 5. *Lepomis cyanellus*. Summary "block diagram" of muscle activity during pharyngeal transport. See Materials and Methods for details on how this and subsequent similar figures were constructed. Data from all prey sizes and types are included in this figure. Tables 3 and 4 segregate muscle activity by prey type. The left and right edges of the bars mark the mean onset and offset of muscle activity and the thin line indicates one standard error of this mean. Black bars indicate activity in 67–100% of all experiments, shaded bars indicate activity in 34–66% of all experiments, and white bars indicate activity in 1–33% of all experiments.

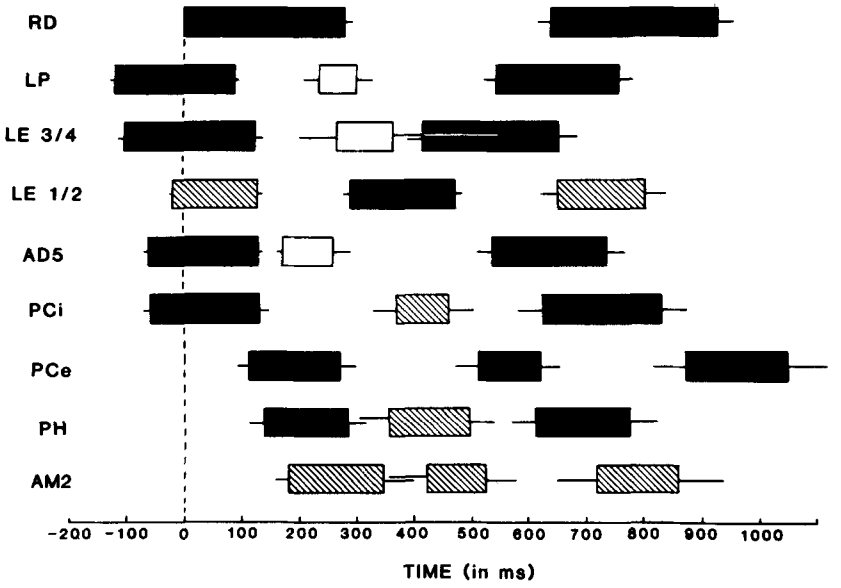

Fig. 6. *Lepomis macrochirus*. Summary "block diagram" of muscle activity during pharyngeal transport. Conventions as in Figure 5. This summary includes data from all prey types and sizes. Tables 2 and 4 provide a breakdown of muscle activity durations and relative activity times by prey type, size, and position in the chewing cycle.

activity significantly before the retractor (Fig. 6). The onset of activity in these muscles occurs earlier in the transport cycle in *L. macrochirus* than in *L. cyanellus* (compare Fig. 6 to Fig. 5), and the external levators show more variability during the time between the retractor dorsalis bursts. The levatores externi 1 and 2 display very similar activities in these two species, as does the pharyngocleithralis externus. The pharyngohyoideus shows three bursts of activity, two mostly overlapping activity in the retractor dorsalis and a middle one between retractor bursts (in *L. macrochirus* the middle burst is not consistently present). The adductor mandibulae was active in 66% of the transport sequences recorded, but no activity was observed in the sternohyoideus.

The effect of size and type of prey on muscular activity was assessed by comparing patterns of electrical activity elicited by three prey classes (fish and two sizes of worms; see Table 2). Transport was divided into thirds. Burst durations and interburst intervals were measured separately in each third to study the influence of transport duration on muscle activity patterns (Table 2). Large prey resulted in long mean activity periods in all three of the muscles measured, although not significantly so in the pharyngocleithralis internus (Table 2). Fish and large earthworms (4–5 cm long) produced burst durations that increase with time during the transport cycle, but for earthworm prey 1–2 cm long this trend did not occur. No trend toward increasing duration with prey size was found in the pharyngocleithralis internus muscle. For all three muscles, fish elicited significantly longer mean activity durations than earthworms. The total duration of transport was not significantly different between fish and large earthworm prey (Table 2), but transport was significantly longer for large prey than for small earthworms. Interburst intervals did not show any tendency to increase or decrease in any consistent fashion during transport, although the mean interburst time for pharyngeal transport was (with one exception, the retractor dorsalis) greater for large than for small prey.

When the onset times for branchial muscles in *Lepomis macrochirus* are compared for fish versus earthworm prey, only the fifth branchial adductor shows a significant difference (Table 4). The offset times are significantly different for the two prey types in all three muscles, and in all cases the offset

TABLE 2. Branchial muscle activity characteristics in Lepomis macrochirus during pharyngeal transport

Muscle	Size and type of prey	Mean muscle burst duration[1] (msec) ± 1 SE				Mean muscle interburst interval[1] (msec) ± 1 SE				Mean duration of transport phase (second ± 1 SE)
		First 1/3	Second 1/3	Third 1/3	Total	First 1/3	Second 1/3	Third 1/3	Total	
RD	Fish (3–5 cm)	231 ± 32	300 ± 41	315 ± 39	282 ± 22	247 ± 24	407 ± 46	446 ± 53	367 ± 29	13 ± 1
	Earthworm (1–2 cm)	194 ± 32	163 ± 16	136 ± 17	164 ± 14	361 ± 53	375 ± 55	400 ± 110	379 ± 43	6 ± 1
	Earthworm (4–5 cm)	197 ± 19	241 ± 35	251 ± 47	236 ± 20	417 ± 92	528 ± 103	494 ± 77	480 ± 52	14 ± 4
LE 3/4	Fish (3–5 cm)	210 ± 37	285 ± 26	314 ± 31	270 ± 19	317 ± 46	474 ± 35	429 ± 46	406 ± 27	11 ± 2
	Earthworm (1–2 cm)	158 ± 24	127 ± 11	156 ± 16	147 ± 10	208 ± 20	267 ± 16	266 ± 22	247 ± 12	7 ± 1
	Earthworm (4–5 cm)	205 ± 25	206 ± 26	231 ± 21	214 ± 14	277 ± 22	309 ± 21	368 ± 44	301 ± 20	11 ± 2
PCi	Fish (3–5 cm)	118 ± 17	269 ± 36	204 ± 30	197 ± 20	426 ± 91	506 ± 79	621 ± 40	518 ± 44	13 ± 2
	Earthworm (1–2 cm)	95 ± 9	102 ± 11	132 ± 14	117 ± 7	222 ± 22	298 ± 54	254 ± 21	258 ± 20	5 ± 1
	Earthworm (4–5 cm)	152 ± 12	125 ± 19	66 ± 11	114 ± 11	199 ± 22	421 ± 29	527 ± 40	382 ± 31	11 ± 3

[1]The pharyngeal transport phase was divided into thirds and muscle activity characteristics measured separately for each interval. The sample size (N) was ten for each interval, with each N being the mean of three burst durations for fish and large earthworms. For small earthworm pieces (1–2 cm) individual Ns represent one burst duration because of the short duration of transport.

TABLE 3. Muscle activity characteristics in relation to prey type for three centrarchid species

Species	Muscle	Mean burst duration (msec) ± 1 SE during pharyngeal transport and snail crushing (sample size)		
		Worms (3 cm)	Fish (3–5 cm)	Snails (1 cm)
Lepomis cyanellus	RD	225 ± 25 (25)	285 ± 25 (28)	85 ± 12 (15)
	LE 1/2	181 ± 17 (25)	144 ± 16 (20)	67 ± 9 (15)
	LE 3/4	270 ± 21 (15)	239 ± 21 (20)	102 ± 14 (15)
	PCi	123 ± 10 (25)	211 ± 31 (20)	72 ± 10 (15)
Lepomis gibbosus	RD	257 ± 11 (32)	464 ± 26 (28)	139 ± 11 (42)
	LE 1/2[1]	151 ± 20 (15)	141 ± 12 (15)	132 ± 10 (51)
	LE 3/4	206 ± 24 (20)	276 ± 44 (15)	142 ± 11 (42)
	PCi	141 ± 12 (18)	157 ± 23 (8)	124 ± 10 (38)
Lepomis microlophus	RD	235 ± 17 (24)	239 ± 16 (18)	278 ± 25 (53)
	LE 1/2	293 ± 16 (19)	366 ± 21 (7)	321 ± 27 (19)
	LE 3/4	275 ± 18 (19)	273 ± 20 (10)	271 ± 25 (29)
	PCi	289 ± 11 (13)	221 ± 27 (7)	275 ± 23 (29)

[1]Burst occurring between activity of retractor dorsalis.

times are longer for fish than earthworm prey (Table 4). This activity pattern indicates less overlap in activity of the pharyngocleithralis internus, levatores externi 3 and 4, and the fifth adductor, with the retractor dorsalis.

Lepomis gibbosus

Muscular activity during pharyngeal transport is generally similar to that described above for *L. macrochirus* and *cyanellus* and only the major differences will be mentioned. The transport summary presented in Figure 7 is scaled with the time from the start of one retractor dorsalis burst to the offset of activity in the next burst equal to 100%. This does not change the relative timing of muscle activity, and unscaled data are analyzed in Tables 3 and 4. All of the dorsal pharyngeal muscles that exhibit overlapping activity with the retractor dorsalis in the other *Lepomis* species also do so in *L. gibbosus* (Fig. 7). The levatores externi 1 and 2 are active predominantly between bursts in the retractor, but occasionally some activity was observed synchronously with the retractor dorsalis. It is important to emphasize that the pattern of muscular activity during transport was observed for all prey: fish, worms, and snails (following crushing of the shell).

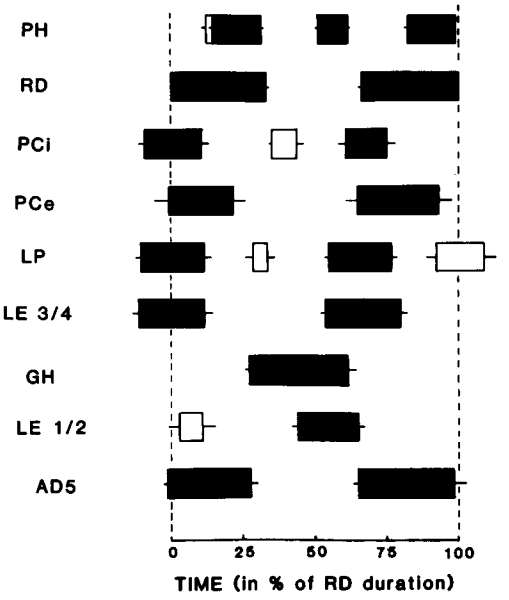

Fig. 7. *Lepomis gibbosus.* Summary "block diagram" of muscle activity during pharyngeal transport. Conventions as in Figure 5. In this figure muscle activity times are scaled with the time from the beginning to end of two bursts of the retractor dorsalis equal to 100% (see Materials and Methods for a discussion and rationale). Data from all prey types and sizes are included; Tables 3 and 4 provide muscle burst durations and unscaled relative timings for the different prey types.

The durations of activity in the retractor dorsalis and levatores externi 3 and 4 were significantly longer when feeding on fish than on earthworms (Table 3), but no significant differences in activity duration were found for the pharyngocleithralis internus and levatores externi 1 and 2. Differences in onset and offset timing were not significant for any muscle (Table 4).

The pattern of muscular activity during snail crushing was radically different from

TABLE 4. Differences in onset and offset of muscle activity compared for four species of Lepomis

Species	Muscle pairs	Mean onset time difference (msec) ± 1 SE			Significance of onset time differences (degrees of freedom)[1]			Mean offset time difference (msec) ± 1 SE			Significance of offset time differences (degrees of freedom)[1]		
		Worms (W)	Fish (F)	Snails (S)	WvsF	FvsS	WvsS	Worms (W)	Fish (F)	Snails (S)	WvsF	FvsS	WvsS
Lepomis macrochirus	PCi-RD	81 ± 7	78 ± 6	—	NS(58)	—	—	121 ± 8	222 ± 18	—	S(58)	—	—
	LE 3/4-RD	101 ± 10	117 ± 18	—	NS(45)	—	—	71 ± 9	201 ± 25	—	S(45)	—	—
	AD5-RD	20 ± 3	63 ± 7	—	S(58)	—	—	26 ± 6	141 ± 12	—	S(58)	—	—
Lepomis cyanellus	PCi-RD	75 ± 12	72 ± 20	16 ± 6	NS(43)	NS(33)	S(38)	174 ± 19	98 ± 30	16 ± 5	NS(43)	NS(33)	S(38)
	LE 3/4-RD	29 ± 9	84 ± 12	9 ± 2	NS(33)	S(33)	NS(28)	56 ± 17	143 ± 34	16 ± 4	NS(33)	NS(33)	NS(28)
	AD5-RD	74 ± 14	78 ± 19	13 ± 4	NS(33)	NS(33)	S(28)	64 ± 17	142 ± 22	24 ± 4	NS(33)	S(33)	NS(28)
Lepomis gibbosus	PCi-RD	105 ± 16	63 ± 15	25 ± 3	NS(31)	S(45)	S(44)	236 ± 18	265 ± 38	19 ± 3	NS(31)	S(45)	S(44)
	LE 3/4-RD	58 ± 14	123 ± 19	21 ± 4	NS(32)	S(43)	NS(48)	161 ± 24	231 ± 36	21 ± 3	NS(33)	S(43)	S(48)
	AD5-RD	7 ± 2	35 ± 8	10 ± 3	NS(31)	S(40)	NS(37)	81 ± 9	195 ± 28	11 ± 3	NS(31)	S(40)	S(37)
Lepomis microlophus	PCi-RD	107 ± 14	25 ± 5	32 ± 6	S(28)	NS(40)	S(40)	42 ± 5	18 ± 5	14 ± 4	NS(28)	NS(40)	S(40)
	LE 3/4-RD	28 ± 10	51 ± 13	35 ± 9	NS(32)	NS(41)	NS(46)	26 ± 6	28 ± 9	22 ± 6	NS(32)	NS(42)	NS(46)
	AD5-RD	35 ± 16	48 ± 10	45 ± 11	NS(28)	NS(42)	NS(42)	33 ± 6	25 ± 7	26 ± 6	NS(28)	NS(42)	NS(42)

[1]See Materials and Methods for procedures used to establish significance levels. NS = not significant, S = significant.

Fig. 8. *Lepomis gibbosus.* Summary "block diagram" showing the pattern of muscle activity during snail crushing. Conventions as in Figure 5. Note that all muscles except the pharyngocleithralis externus and internus start activity within a short time of the retractor dorsalis. There is no activity in the obliquus inferioris, sternohyoideus, and epaxial muscles.

that seen during pharyngeal transport (Fig. 8). Considerable overlap in activity period is seen in all branchial muscles, and no activity is found in the obliquus inferioris, sternohyoideus, and epaxial muscles. More variability is observed in offset than onset times where differences are small. The only muscle showing a slightly different pattern is the pharyngocleithralis externus, which is active significantly later than any other muscles (Fig. 8). Variation in burst duration between muscles during snail-crushing is much less than it is during transport of fish and worms (Table 3). Significant differences in branchial muscle onset and offset times are observed for fish and worm prey compared to snails, but not when worms are compared with fish prey (Table 4).

Lepomis microlophus

In *Lepomis microlophus,* relatively little variability is seen between pharyngeal transport of different prey types. The most complete kinematic data are available for feedings on snails; thus, buccal manipulation, crushing, and transport of this prey type are considered first. Both x-ray cinematogra-

phy (Fig. 9) and behavioral observations reveal that extensive manipulation of the prey may occur within the buccal cavity before attempts to crush the shell. Prey located in the buccal cavity are moved back to the pharyngeal region by movements of the mandibular and hyoid arches that create a flow of water through the mouth cavity (Fig. 9: frame 12). This flow carries the prey posteriorly to the pharyngeal jaws (Fig. 9: frame 18). As the mouth opens, the pectoral girdle is retracted and the pharyngeal jaws abducted. The anteroventral margins of the lower pharyngeal jaws move ventrally because of buccal floor depression, producing a space between the jaws for the prey. Once the snail is located in this position it is usually sucked anteriorly into the buccal cavity again and the entire positioning sequence is repeated several times before crushing of the prey occurs. The prey appears to be moved roughly the same distance during each positioning sequence. Buccal expansion during prey manipulation creates a flow of water from the opercular cavity into the buccal cavity that moves the prey anteriorly.

When the snail shell is crushed, the pharyngeal jaws move very little. The jaws approach each other in the midline but do not make contact. As in *L. gibbosus,* there is extensive overlap in branchial muscle activity during crushing (Fig. 10A). In contrast to crushing in *L. gibbosus* (Fig. 8), the pharyngocleithralis externus muscle is not active. During crushing of large snails activity occurs in the adductor mandibulae part 2 and the sternohyoideus. The levator arcus palatini is active at the end of crushing, beginning after activity in most of the other muscles has ended. No activity is observed in the epaxial muscles, obliquus inferioris, or levator operculi during crushing (Fig. 10A). The crushing pattern of muscle activity is repeated several times (up to 20 for large shells) with periods of either no activity, or of buccal and pharyngeal manipulation between crushing phases. Activity of the sternohyoideus and obliquus inferioris is often observed between attempts to crush the prey. These muscles may be involved in repositioning the lower pharyngeal jaw for the next crushing sequence. Large snails (up to 1.4 cm in diameter) take much longer to position and crush than small snails, which may be crushed immediately. After shell fracture, small pieces of the snail shell fall out of the opercular cavities on each side as well as out of the mouth anteriorly.

The onset of pharyngeal transport immediately after crushing is marked by a distinct and rapid posterior movement of the upper pharyngeal jaw produced by the retractor dorsalis muscle (Figs. 11, 12). Pharyngeal transport in *L. microlophus* involves a different sequence of muscular activity than in any of the other *Lepomis* species studied. Activity in the pharyngocleithralis internus alternates with that of the retractor dorsalis (Fig. 11), whereas the pharyngohyoideus, fifth branchial adductor, and levatores externi 3 and 4 all begin activity before the retractor dorsalis. The variability of muscle activity onset and offset in the adductor is much greater in *L. microlophus* than in any of the other *Lepomis* species, and the levatores externi 3 and 4 begin activity well before the retractor (compare LE3/4 activity in Fig. 11 and Fig. 5). The pharyngocleithralis externus is not active during transport, and the levatores externi 1 and 2 are only sporadically active (Fig. 11). As in the other species, the sternohyoideus and obliquus inferioris do not contribute to the transport phase.

The upper and lower pharyngeal jaws alternate retraction strokes during transport, and the upper pharyngeal jaw moves posteriorly while the lower one travels anteriorly (Fig. 12). The upper jaw has a greater anteroposterior excursion than the lower, moving a distance roughly equal to its own length. The lower jaw only moves anteriorly about one-third of its length, but it also rotates dorsoventrally during the transport cycle (Fig. 12). Although synchronous electromyograms and x-ray films were not obtained, the alternating pattern of pharyngeal jaw movement appears to be generated by an alternating pattern of activity in the retractor dorsalis (RD) and pharyngocleithralis internus (PCi). Both of these patterns are unique to *L. microlophus,* and the muscle lines of action are well suited to produce the observed movement. In all other centrarchids studied, the PCi and RD overlap considerably in activity, and the pharyngeal jaws are retracted together (although subsequent movements are slightly out of phase; see Lauder, '83a). During transport, small pieces of shell continue to emerge from the opercular cavities. After transport of the snail into the esophagus has been completed, a large quantity of shell fragments are then ejected from the mouth in a spitting movement.

Prey other than snails are also subjected to crushing by the pharyngeal jaws and the patterns of muscular activity are similar to those

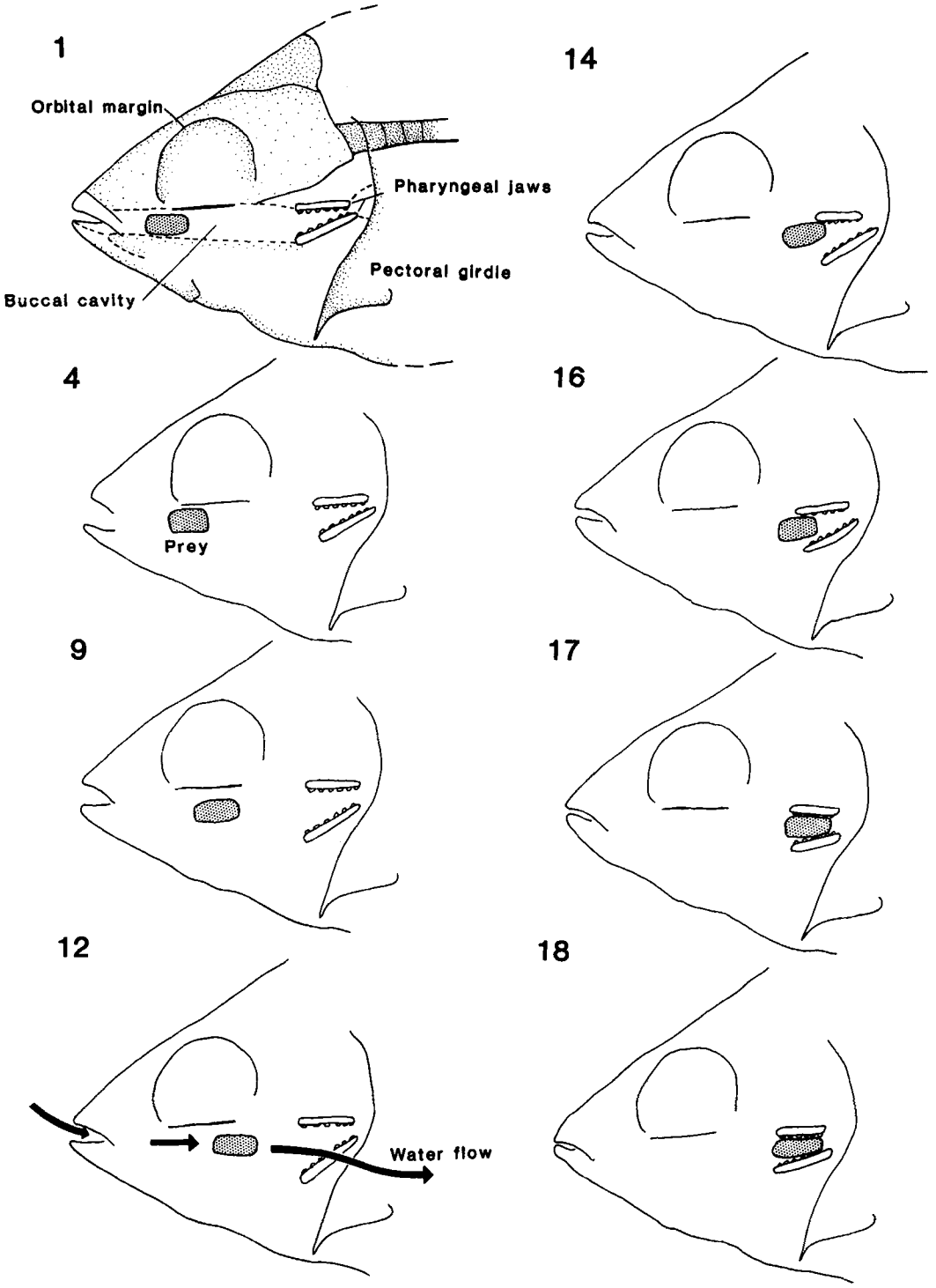

Fig. 9. *Lepomis microlophus.* Tracings from an x-ray film taken at 100 frames per second to show movement of a snail in the buccal cavity (shaded) posteriorly to the pharyngeal jaws during buccal manipulation prior to crushing. Numbers indicate the frame number in the sequence. The snail is crushed in the position shown in frame 18.

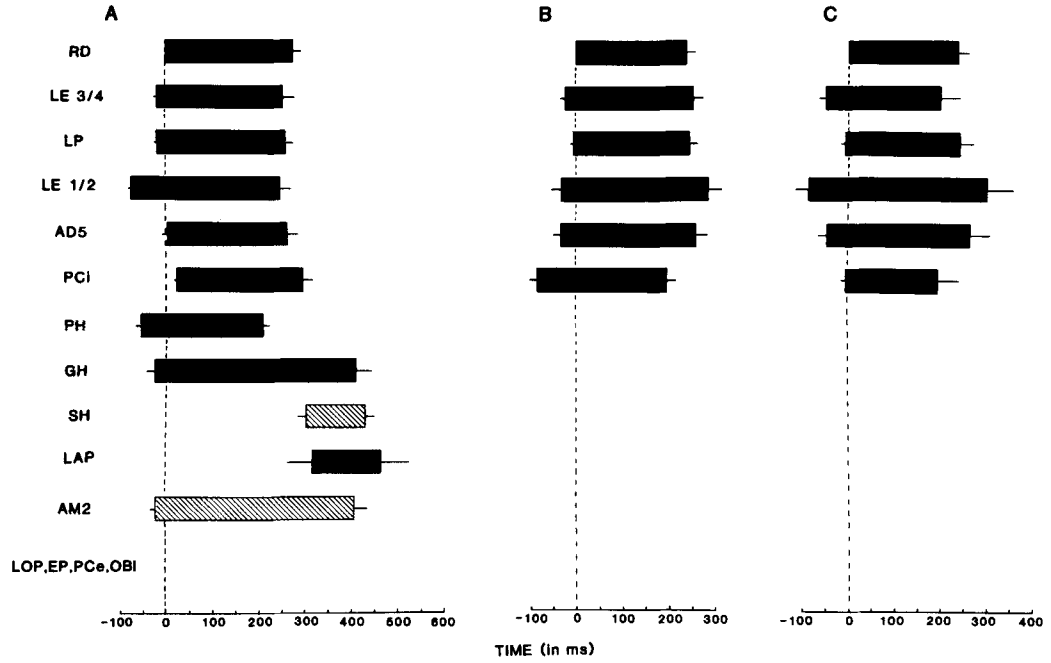

Fig. 10. *Lepomis microlophus.* Pattern of muscle electrical activity summarized in a "block diagram" (conventions as in Fig. 5) for crushing (A) snails, (B) earthworms, and (C) fish. Note the extensive overlap in muscle electrical activity during pharyngeal crushing and that this pattern is used for *all* prey types, not just snails. Tables 3 and 4 provide additional information on muscle burst duration and relative timing during crushing different types of prey. The sternohyoideus is occasionally active during snail crushing. Cracking of the snail shell occurs at the very end of muscle activity (see Lauder, '83b: Fig. 1).

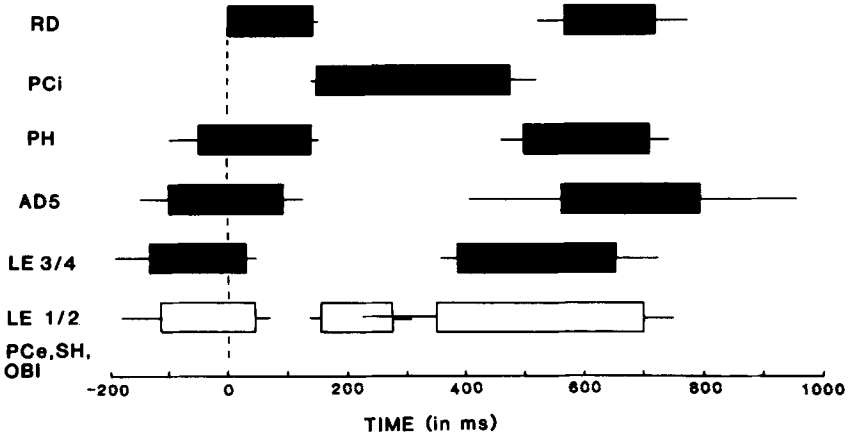

Fig. 11. *Lepomis microlophus.* Summary pattern of muscle electrical activity (conventions as in Fig. 5) during pharyngeal transport. Note that neither the obliquus inferioris nor the sternohyoideus are active as in other species, but the pharyngocleithralis externus is also inactive. A unique feature of pharyngeal transport is the alternation of the pharyngocleithralis internus and retractor dorsalis muscles, which indicates that the upper and lower pharyngeal jaws are not moving posteriorly at the same time (see Fig. 12 and the text for discussion). During pharyngeal transport in *L. microlophus* much of the cracked snail shell is removed from the body.

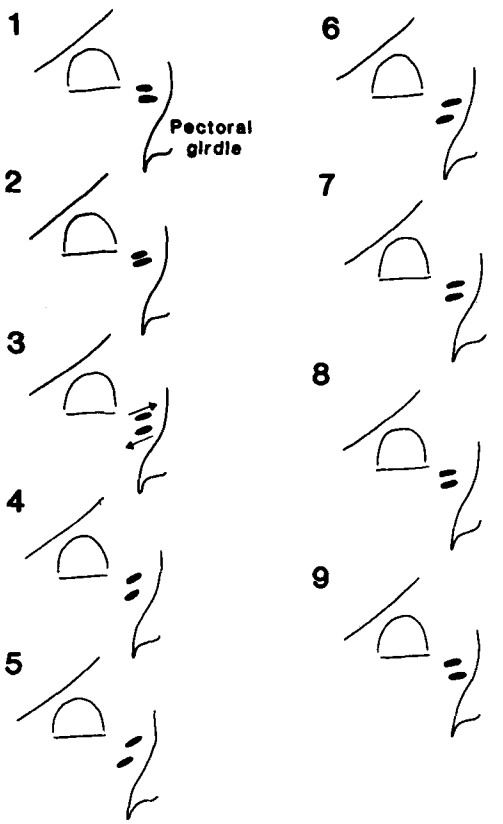

Fig. 12. *Lepomis microlophus.* Nine sequential stages showing movement of the pharyngeal jaws during pharyngeal transport of a crushed snail as traced from an x-ray film. The upper and lower jaws are shown as black ovals relative to the pectoral girdle, orbital margin, and the dorsal outline of the skull. Note the alternating pattern of anteroposterior movement: As the upper pharyngeal jaw moves posteriorly, the lower travels anteriorly. Arrows in frame 3 indicate the relative directions of upper and lower pharyngeal jaw movement.

used for snails. Both worms and fish elicit strong, nearly synchronous activity in the branchial musculature (Fig. 10B,C). Little or no activity is seen in the mandibular and hyoid muscles. Slight differences in burst duration are found in branchial muscles used during transport of different prey (Table 3), but the variation due to prey type is less than for other species. Onset and offset times relative to the retractor dorsalis are typically not significantly dependent on prey type (Table 4), with the only exception being the pharyngocleithralis internus.

Transport of nonsnail prey usually involves a pattern of muscle activity similar to that illustrated for snails in Figure 11. However, several variations on this pattern do occur: 1) The retractor dorsalis may be only weakly active during pharyngeal transport; 2) the pharyngocleithralis internus may occasionally display a pattern that is similar to that of other *Lepomis* species; i.e., overlapping activity in the retractor dorsalis; 3) finally, the crushing phase may be omitted and fish or worms transplanted directly into the esophagus by branchial muscles activated in the sequence illustrated in Figure 11.

DISCUSSION

Functional morphology

The mechanisms by which teleost fishes with relatively generalized pharyngeal morphologies process prey in the oral cavity and transport prey into the esophagus and stomach have received only limited attention (Liem, '70; Lauder, '83a). In this previous work I established that fishes in several euteleostean clades exhibit a pattern of pharyngeal jaw movement that involves synchronous retraction of both the upper and lower pharyngeal jaws, and that the orbit of movement of the lower jaw is smaller than that of the upper. Although the retraction stroke is postulated to take place at the same time in both jaws, this does not mean that all movements of the lower jaw exactly mirror those of the upper. In fact, the pattern of muscular activity suggests that the lower pharyngeal jaw begins to move posteriorly during pharyngeal transport before the upper jaw. Pharyngeal muscular activity found in *Perca, Pomoxis, Ambloplites, Micropterus* (species that can be considered outgroups to *Lepomis*), and to some extent also in *Esox* (Lauder, '83a) is similar to that reported here for *Lepomis cyanellus, L. gibbosus,* and *L. macrochirus.* In all species the sternohyoideus, obliquus inferioris, and epaxial muscles are inactive during pharyngeal transport. In all species the pharyngocleithralis internus, adductor arcus branchialum 5, levator posterior, and levatores externi 3 and 4 begin activity significantly before the retractor dorsalis and significantly overlap its activity. One last aspect common to all the muscular activity patterns is the alternation of activity in the retractor dorsalis and levatores externi 1 and 2. These features are hypothesized to be primitive for the Centrarchidae

based on the phylogenetic distribution of these characteristics within both the family Centrarchidae and the Euteleostei.

Lepomis microlophus is the only species exhibiting a markedly divergent pattern. In contrast to all other species, the lower pharyngeal jaws protract as the upper jaws retract during pharyngeal transport (Fig. 12). In addition, the pharyngocleithralis internus, the dominant retractor of the fifth ceratobranchial, alternates in activity with the retractor dorsalis (Fig. 11). When this species is swallowing crushed snails, this alternation appears to promote separation of the shell from the body of the snail after it has been crushed. The pharyngeal jaws, moving in opposite directions while applying pressure to the prey, may scrape off adherent pieces of shell. However, the same alternating pattern is observed when *L. microlophus* is fed worms and fish, and the basic pattern of muscular activity is thus not altered by changing prey type (Table 4). Although the other centrarchid species do show variability in burst duration and relative timing based on the type and size of prey, none change the basic pattern.

Crushing of snails in the pharyngeal apparatus involves an entirely different sequence of muscle activity than in pharyngeal transport (described above). In all three *Lepomis* species studied that crush snails, extensive overlap of muscle activity occurs during crushing. Both *L. cyanellus* and *gibbosus* display the crushing pattern only when feeding on snails, and omit this aspect of intraoral prey manipulation when feeding on worms or fish. In the latter cases, after positioning the prey within the pharynx, the characteristic pharyngeal transport pattern is immediately initiated to move prey into the esophagus and stomach. Only in *L. microlophus* is the crushing pattern of muscle activity used for prey other than snails (Fig. 10), and the differences between muscle burst durations associated with prey types are less than for interprey differences in the other species studied during the transport phase.

These data indicate that all species which crush shells coactivate the pharyngeal muscles to generate force by adducting the pharyngeal jaws. This pattern is an addition to the primitive repertoire of pharyngeal muscular activity patterns. The ability to separate most of the shell from the body of the snail is dependent on first crushing the shell and then separating the shell fragments from the body by differential movement of the upper and lower pharyngeal jaws. Compared with the hypothesized primitive condition, *L. microlophus* shows two salient specializations in the neuromuscular pattern controlling the pharyngeal apparatus. First, the crushing pattern used by other species only for molluscan prey is employed for all prey types, including soft-bodied organisms. Second, *L. microlophus* shows an alternating pattern of pharyngeal jaw movement and alternation of activity in the pharyngocleithralis internus and retractor dorsalis during pharyngeal transport in contrast to all other nonpharyngognath teleosts (the numerous structural and functional specializations in the pharyngeal apparatus of pharyngognath teleosts have been described in Liem and Greenwood, '81; Liem, '78; Kaufman and Liem, '82).

The gross morphological changes associated with snail crushing in the pharyngeal apparatus of sunfishes are limited to hypertrophy of the lower and upper pharyngeal jaws, teeth, and selected pharyngeal muscles (Table 1). Many of the physiological cross sections of pharyngeal muscles are smaller in *L. microlophus* than in other *Lepomis* species having a more varied diet. Previous work has suggested that mollusc-eating teleosts have more massive pharyngeal musculature than trophic generalists so that large forces can be generated in the pharyngeal region (Hoogerhoud and Barel, '78). *L. microlophus* crushes snail shells by apposing the upper and lower pharyngeal jaws and activating all the branchial muscles simultaneously to generate compressive forces that exceed the strength of the snail shell. No data are available on the mechanism of shell failure or on the area of the shell that cracks first. However, it is expected that the pharyngeal musculature of snail-eaters will generate greater compressive forces on the prey than will the musculature of species that do not crush snails and display only the transport pattern of muscle activity (provided prey of the same hardness and size are compared). In *L. microlophus* only the levator posterior muscle and to a lesser extent the pharyngohyoideus display increased area in comparison to the other sunfish species studied. Although molariform teeth are more common on the fifth ceratobranchials of species that eat larger numbers of molluscs (Fig. 3; Ono and Kaufman, '83), few consistent differences exist in lines of pharyngeal muscle action or architec-

ture in the snail-eating species: No muscle in any of the four species studied had fiber angles greater than 10°, and no new muscles or changes in muscle number occur. *L. microlophus* does have shorter muscle fibers in the levator posterior and fifth branchial adductor than do the other species, and this may be related to the length of these muscles when they are active during shell crushing.

The hypertrophy of the levator posterior and pharyngohyoideus may provide a clue to the mechanism by which the shell is cracked. The levator posterior, by elevating the upper pharyngeal jaw as well as the posterior portion of the lower jaw, could hold the snail shell rigidly between the posterior pharyngeal jaw teeth. The pharyngohyoideus could then produce a shearing movement of the lower pharyngeal jaw relative to the upper. *L. gibbosus* and *L. microlophus* thus may crack the shell by differential anteroposterior pharyngeal jaw movements, rather than by direct dorsoventral apposition, but this proposal needs detailed experimental examination. It is of considerable interest that only minor alterations in line of muscle action occur in mollusc-crushing species and that no major structural changes in the pharyngeal region have occurred (such as new muscles or the loss of muscles). This is in distinct contrast to the major alterations in muscular activity patterns, which have changed to such an extent that the most trophically specialized species, *L. microlophus,* has neuromuscular patterns of crushing and pharyngeal transport not found in *any* outgroup taxon (e.g., *Esox, Perca, Micropterus, Ambloplites, Pomoxis*).

Structural and functional specialization

A classical problem in comparative biology is the relationship between behavioral and morphological patterns of evolutionary change and the role that changes in behavior may play in governing the evolution of new structural features (Atz, '70; Greene and Burghardt, '78; Lorenz, '50; Mayr, '58). One method of approaching this question from an historical perspective is to consider the phylogenetic distributions of both structural and functional novelties in a clade in which a specialized behavior has evolved. If homologous muscles in different species retain their primitive pattern of motor output to the trophic apparatus, for example, then one would expect considerable congruence between the distribution of functional and structural novelties within a clade. At a different level of analysis, one could compare patterns of neural organization to those of muscular activity to examine the morphological basis for peripheral motor patterns.

The patterns of structural and functional novelties within the sunfish family Centrarchidae, as elucidated in this study and in Lauder ('83a), reveal that major changes may occur in the pattern of motor output to homologous jaw muscles between closely related species. *Lepomis microlophus,* for example, has a pattern of muscular activity during pharyngeal transport that is not found in any of the outgroup species studied. Yet, the number of muscles and their origins and insertions are similar for those outgroup taxa within the family. Furthermore, *L. microlophus* uses the crushing pattern of muscular activity for all prey types, not just molluscs—a behavior unique to this species. It is thus clear from the alteration in muscle activity patterns in *L. microlophus* that, even at the species level, alterations in the central nervous control of peripheral structures can produce major changes in the sequence in which homologous components of a structural network are activated. These data provide no support for the concept of conservatism in the activity periods of homologous muscles during the evolution of new behavioral patterns, and they suggest that intraspecific variability in the motor output to jaw musculature may be of considerable significance in the evolution of specialized behavioral patterns. At least for the species studied here, the critical evolutionary novelties involved in the acquisition of a specialized feeding mode appear to be functional; i.e., those related to controlling movement of the trophic apparatus.

This study has documented the structural and functional patterns associated with the evolution of trophic specialization in the North American teleost family Centrarchidae. By trophic specialist I mean (following Liem, in press) that a species has acquired either morphological and/or functional novelties enabling it to obtain prey that cannot be captured by suction feeding (the dominant mode of prey capture in teleosts), or novel mechanisms to process prey once it has been captured.

The results emphasize the extent to which changes in the control of peripheral structures by the central nervous system are involved in evolutionary modifications of

complex morphological designs. At some level, the changes in patterns of muscle activity observed here probably do have a structural basis (as in neural connections in those portions of the brain providing motor output to the pharyngeal musculature). But this does not alter the basic result that homologous pharyngeal muscles in ecologically and functionally specialized species have significantly altered activity patterns from the primitive condition. In addition, these data suggest that in conjunction with transformations in the overall pattern of muscular activity involved in the evolution of mollusc-crushing behavior, there has been a change in the degree of variability of the motor pattern. Of the three species that ate snails in these experiments, *Lepomis gibbosus* showed the largest number of significant differences (ten) in muscle activity times for feeding on different prey items (Table 4). The sister species of *L. gibbosus, L. microlophus,* showed the least variability with only three of the 18 paired comparisons between food types significantly different. The outgroup species to this pair, *L. cyanellus,* showed only five significant differences out of 18 possible comparisons linked to prey type. More comparative data are needed to indicate if *L. gibbosus* is uniquely specialized in possessing an increased ability to modulate muscle activity pattern with prey type, or if this condition is part of a transformational sequence resulting in the extreme trophic specialization shown by *L. microlophus.*

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