Intraspecific Functional Repertoires in the Feeding Mechanism of the Characoid Fishes *Lebiasina, Hoplias* and *Chalceus*

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The jaw movement pattern and the timing of cranial muscle activity were studied during feeding on a variety of prey types in three characoid fishes: *Lebiasina boruca, Hoplias malabaricus* and *Chalceus macrolepidotus*.

In *Hoplias*, the kinematic and electromyographic profiles do not vary with prey type or location. Mouth opening invariably occurs by synchronous activity in the levator operculi, sternohyoideus, geniohyoideus, epaxial and obliquus superioris muscles.

Jaw movement and muscle activity patterns in *Lebiasina* vary dramatically and consistently with prey type and location. Elusive prey elicit an electromyographic pattern similar to that in *Hoplias* except that the geniohyoideus is inactive. During capture of less elusive prey (insect larvae), three distinct feeding patterns are seen depending on whether prey are located on the surface, in the midwater or on the bottom. The epaxial muscles are always active during surface feeding whereas they are silent during feeding from the bottom. Midwater strikes were highly variable, and asymmetrical activity between right- and left-side muscles was observed.

Prey capture by *Chalceus* was highly variable and no particular muscle activity pattern could be correlated with a specific prey type or location. Asymmetrical activity between certain right- and left-side muscles was also found.

The functional repertoire of *Hoplias* represents a subset of the broader repertoires seen in *Lebiasina* and *Chalceus*. Prey capture by high-speed inertial suction is of limited versatility and is correlated with a nearly invarient movement and electromyographic pattern.

STUDIES of the functional anatomy and mechanics of feeding in teleost fishes have for the most part assumed that the process of prey capture represents a cyclical, oscillatory series of events that is uniform in duration and pattern (Alexander, 1969, 1970; Lauder, 1979; Liem, 1970; Osse, 1969). This assumption appears to be valid for those teleosts using a high-speed inertial suction strategy of prey capture, and for certain non-teleost actinopterygian fishes which possess a highly stereotyped pattern of jaw movement during feeding (Lauder, 1980; Lauder and Norton, 1980).

However, recent studies on fishes that feed on a wide variety of prey types have indicated that within a species the functional repertoire may consist of a number of components; i.e., each feeding sequence is not necessarily accomplished by the same pattern of jaw movement and muscle activity (Ballintijn et al., 1972; Elshoud-Oldenhave and Osse, 1976; Lauder and Liem, 1980; Liem, 1978). Liem (1978) showed that piscivorous cichlid fishes possess a reper-toire of two feeding patterns. Highly agile and elusive prey elicit a high-speed strike that is characterized by greater overlap in electrical activity between antagonistic muscles, greater velocity of mandibular depression, and greater suction pressure velocity than strikes at relatively stationary prey. Elshoud-Oldenhave and Osse (1976) and Lauder and Liem (1980) found consistent differences between electromyographic patterns in cranial muscles during feeding on the bottom and in the midwater by ruff (*Gymnocephalus*) and brook trout (*Salvelinus*) respectively.

Liem (1979, 1980) has described the functional repertoire of *Petrotilapia tridentiger*, a rock-scraping cichlid, and the invertebrate picking cichlids (*Eretmodus* and *Spathodus*) of Lake Tanganyika. These fishes possess extremely versatile feeding mechanisms with possibly as many as eight distinct kinematic and electromyographic feeding patterns. This diversity in feeding behavior has been observed only in cichlids.

Previous analyses of intraspecific functional repertoires, however, have not examined the range of variation within each presumed pattern. What have been proposed as discrete action patterns may thus simply represent different non-overlapping subsets chosen from a single highly variable action pattern and may not reflect distinct feeding modes.

The goal of this paper is to examine the functional repertoires of three characoid fishes, *Lebiasina, Hoplias* and *Chalceus,* to determine if the variability in feeding patterns is comparable to that found previously in advanced teleost fishes, and to quantify the number and variability of discrete components in the repertoire.

By comparing species utilizing high-speed inertial suction as the only mode of prey capture (*Hoplias*) with species possessing a wide range of feeding strategies (*Lebiasina* and *Chalceus*), it will be possible to compare the repertoires of these characoids with those of other fishes and to generate hypotheses relating the diversity of functional repertoires to trophic ecology.

MATERIALS AND METHODS

Two live *Lebiasina boruca* (Bussing) (Lebiasinidae; 14 and 13.2 cm SL), collected from the type locality (Bussing, 1976), were studied through the courtesy of S. H. Weitzman. These specimens will be deposited in the U.S. National Museum. One *Hoplias malabaricus* (Bloch) (Erythrinidae, 12 cm SL), and one *Chalceus macrolepidotus* Cuvier (13.2 cm SL) were obtained commercially.

Anatomical observations were made on the following specimens: *Lebiasina bimaculata* Valenciennes (MCZ 21446; USNM uncatalogued), *Hoplias malabaricus* (MCZ 54304) and *Chalceus macrolepidotus* (MCZ 54932).

High-speed films (200 frames per sec) and electromyographic recordings of cranial muscle activity were obtained following the procedure described by Lauder (1980), Lauder and Lanyon (1980) and Liem (1978). Briefly, fine-wire bipolar electrodes (Basmajian and Stecko, 1962) were implanted in up to 10 cranial muscles and attached to a small plastic clamp located behind the head. Electrodes were allowed to trail freely behind the subject until recordings were made, at which time the electrode leads were attached to a revolving connector located above the tank. Signals were recorded on magnetic tape and played back at ⅛ normal speed through a Gould 260 chart recorder for anal-

ysis. Synchronization of the high-speed films with the electromyograms was achieved by a digital pulse synchronizer that placed a coded pulse on the electromyographic record as each film frame was exposed. More than 200 feeding sequences were analyzed for *Lebiasina,* 30 feedings for *Chalceus* and 25 for *Hoplias.*

All fishes were fed a variety of prey types in order to elicit a range of feeding behaviors. The *Hoplias* was fed goldfish (*Carassius auratus*) and earthworms (*Lumbricus*). The *Chalceus* specimen was fed mealworms (*Tenebrio*) and earthworms. *Lebiasina* was fed goldfish, *Gambusia,* earthworms, mealworms and variously sized pieces of smelt (*Osmerus*), as well as commercially obtained "flake food." All prey were offered on the surface, in the midwater and on the bottom of the aquarium.

All prey types were offered during each series of muscle electrode implantations. The pattern of electrical activity elicited for each prey type was then compared to other recordings with the same electrode set and to recordings made from other implantations. The timing of onset and offset of muscle activity was extremely similar both within and between implantations. Multiple electrodes in the same muscle mass also showed highly similar activity patterns although spike patterns did differ. Five muscles were recorded synchronously in all experiments.

Kinematic data were compared using a two sample Student's *t*-test, one tailed.

LEBIASINA BORUCA

Because of the number of discrete feeding patterns observed in *Lebiasina,* the data are discussed by prey type. The feeding sequence may be divided into three phases: the initial strike, manipulation of the prey and deglutition.

Key anatomical features relevant to understanding the subsequent functional analysis are depicted in Fig. 1.

Fish

Initial strike.—The expansive phase, the time from the start of mouth opening to peak gape, has a mean duration of 30 msec (Fig. 2). The entire strike averages 55 msec in length and is significantly more rapid than strikes on any other prey type (Table 1; $P < .001$).

The increase in gape during the expansive phase is correlated with nearly simultaneous
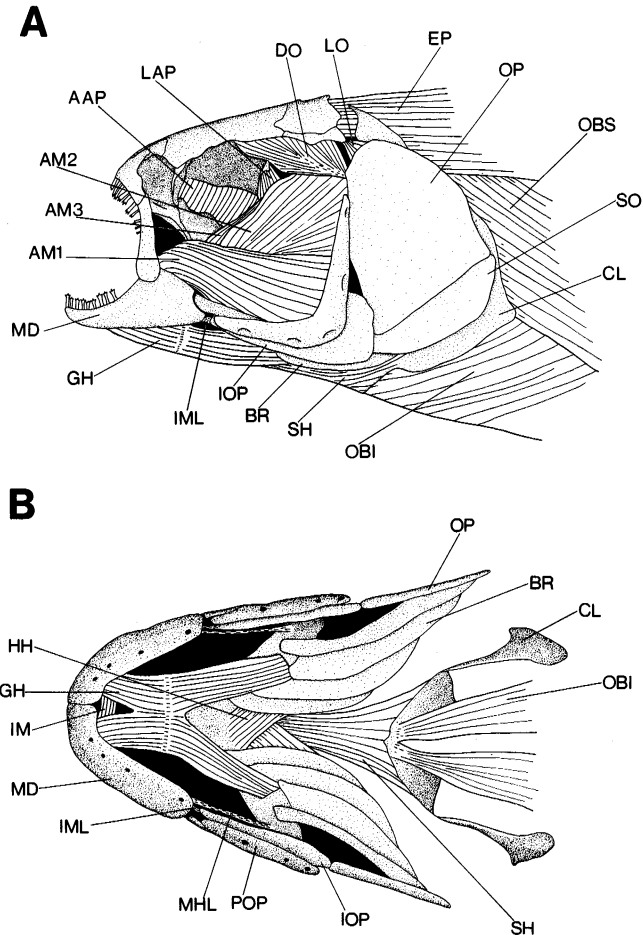
Fig. 1. Lateral view (A) and ventral view (B) of the head of *Lebiasina bimaculata* after removal of the eye, suborbital bones and skin. Abbreviations: AAP, adductor arcus palatini; AM1, 2, 3, parts one, two and three respectively of the adductor mandibulae complex; BR, branchiostegal ray; CL, cleithrum; DO, dilator operculi; EP, epaxial muscles; GH, geniohyoideus muscle; HH, hyohyoideus inferioris; IM, intermandibularis anterior; IML, interoperculomandibular ligament; IOP, interoperculum; LAP, levator arcus palatini; LO, levator operculi; MD, mandible; MHL, mandibulohyoid ligament; OBI, obliquus inferioris; OBS, obliquus superioris; OP, operculum; POP, preoperculum; SH, sternohyoideus; SO, suboperculum.

activity in the levator operculi, sternohyoideus and epaxial muscles (Figs. 1, 4: LO, SH, EP). The levator operculi and sternohyoideus mediate mandibular depression by exerting a posterodorsal force on the interoperculomandibular and mandibulohyoid ligaments respectively (Fig. 1: IML, MHL). Epaxial muscle activity causes an immediate lifting of the neurocranium (Figs. 2, 3) which continues until 15–20 msec after peak gape is reached. Cranial elevation is significantly greater than in feeding on any other prey type ($P < .001$), with the ex-

ception of mealworms taken on the surface ($P = .2$; Table 1).

The dilator operculi becomes active with the levator operculi (Figs. 1, 4: DO) while activity in the levator arcus palatini is delayed for up to 10 msec after the start of levator operculi activity (Figs. 1, 4: LAP).

The two divisions of the hypaxialis, the obliquus superioris and inferioris (Fig. 1; see Winterbottom [1974] for a discussion of muscle nomenclature) show differential expansive phase activity. The obliquus superioris becomes active

with the onset of activity in the levator operculi, while the obliquus inferioris shows a consistent delay of 5 to 10 msec behind the sternohyoideus and levator operculi (Fig. 4: OBS, OBI, SH). Because of this delay, hyoid depression lags behind the increase in gape (Figs. 2, 3). Hyoid depression is significantly greater ($P <$ .023) than in feeding on any other prey type. During the expansive phase the maxilla swings anteriorly and may achieve more than a 90° angle with the longitudinal axis of the body (Figs. 2, 3).

The compressive phase is equal in length to the expansive phase and is characterized by high-amplitude activity in the adductor mandibulae (Figs. 1, 4: AM1, 2, 3). The first and second adductor divisions are both active between 0 and 40 msec ($\bar{x} = 25$ msec) after the onset of levator operculi activity. The third adductor division may not be active until 75–100 msec after the start of mouth opening.

The adductor arcus palatini is active at a low level during the compressive phase but frequently exhibits high-amplitude activity following jaw closure (Figs. 1, 4: AAP). The geniohyoideus is never active during the initial strike at the prey (Figs. 1, 4: GH). First activity may occur just as the jaws close or may be delayed for 100–200 msec following completion of the compressive phase.

The delay between the first detectable activity in the jaw opening muscles and the onset of mandibular depression ranges from 10 to 15 msec.

Manipulation and deglutition.—Manipulation of the prey following capture is accomplished by the front jaws exclusively. If the prey is captured head-first then relatively little activity is seen in the jaw musculature during the swallowing phase which begins immediately. A common pattern of cranial muscle activity during deglutition is shown in Fig. 6C. The levator operculi is initially active followed within 50 msec by the geniohyoideus muscle. The sternohyoideus and adductor mandibulae are only occasionally active. Jaw closure during deglutition appears to occur primarily by elastic recoil in the adductor musculature and adduction occurs slowly. During "crushing" of the prey between the front jaws, however, high-level activity in the adductor mandibulae is seen.

When the prey is caught tail-first (Fig. 5), a complex diphasic manipulatory sequence occurs. During the first phase, the prey is ejected
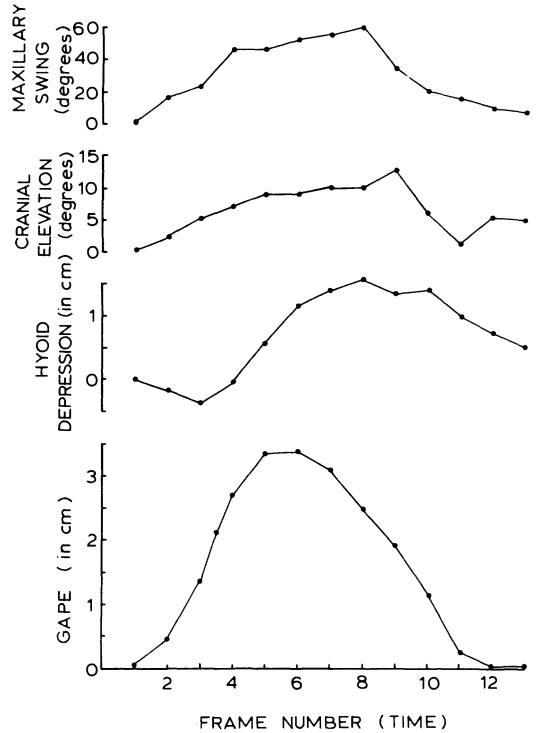

Fig. 2. *Lebiasina boruca.* Maxillary swing, cranial elevation, hyoid depression, and gape versus time during the initial strike at a fish. Note the steady increase in neurocranial elevation which peaks after gape. Filming speed was 200 frames per second and thus successive frames are 5 msec apart.

from the buccal cavity and rotated 90° so that it is held perpendicular to the head (Fig. 5: frames 1–40). As the mouth opens, the head is swung laterally by asymmetrical activity in the epaxial muscles and obliquus superioris (Figs. 5, 6A). This lateral head swing causes the prey to rotate through 90°. The geniohyoideus is generally active during this initial mouth opening phase.

Just after the prey has left the buccal cavity the head of *Lebiasina* swings back towards the midline (Fig. 5: frames 20–40), and the prey is grasped in the midbody region. This movement involves a second burst of activity in the levator operculi (Fig. 6A), activity in the sternohyoideus and epaxial muscles, and closure of the jaws by the adductor mandibulae. This sequence of events is repeated again during the second phase of manipulation (Fig. 5: frames 88–298). The mouth opens as a result of activity in the levator operculi and sternohyoideus (Fig.

TABLE 1.   MODULATION OF THE KINEMATIC PATTERN DURING FEEDING ON DIFFERENT PREY TYPES BY *Lebiasina boruca*.

Kinematic element	Prey type[1]				
			Mealworms		
	Fish[2]	Smelt[2]	Surface	Midwater	Bottom
1) Peak gape (cm)	3.0 (11, .39)	2.7 (12, .60)	3.2 (8, .44)	2.6 (17, .37)	3.0 (23, .57)
2) Peak cranial elevation (°)	15.2 (11, 3.99)	7.1 (12, 2.84)	13.6 (8, 3.58)	8.3 (12, 4.16)	2.2 (18, 2.45)
3) Peak hyoid depression (cm)	4.5 (11, .39)	3.9 (12, .70)	4.1 (8, .41)	3.9 (11, .85)	3.5 (13, .61)
4) Duration of strike (ms)	55.5 (11, 14.4)	78.8 (12, 15.97)	76.3 (8, 11.26)	95.3 (17, 18.1)	117.6 (25, 21.75)

[1] The mean value is given followed by the number of observations and standard deviation.
[2] Differences between prey caught at the surface, midwater, and bottom were not significant.

6B), and a small lateral movement of the head during jaw opening moves the prey head into a position anterior to the opening into the buccal cavity (Fig. 5: frame 103). The prey is then swallowed headfirst by inertial suction as a result of activity in the levator operculi and adductor mandibulae. Elongate prey are swallowed slowly as the pharyngeal jaws rake the prey into the esophagus (Fig. 5: frames 116–298).

The electromyographic patterns during manipulation are consistent between experiments.

Smelt Cubes

A wide size range of smelt cubes (approximately .2 cm^3 to 1.5 cm^3) was offered as food to test the effect of prey size on the kinematic and electromyographic pattern. No significant differences were found that could be correlated with the size or position of the food.

Peak gape for strikes at smelt cubes is significantly different only from surface strikes at mealworms (Table 1; $P = .03$), and does not increase with increasing prey size. Cranial elevation is significantly less than occurs during feeding on fish or on surface mealworms (Table 1; $P < .001$), significantly greater than elevation during feeding on bottom mealworms ($P = .001$), and not significantly different from midwater mealworm strikes. Hyoid depression during feeding on pieces of smelt is significantly different only from fish feeding sequences (Table 1; $P = .01$).

Finally, smelt feedings have a significantly shorter duration than either feedings on mid-

water or bottom mealworms, but take a significantly longer time than fish strikes (Table 1).

Mealworms

Surface.—Strikes at mealworms floating on the water surface are significantly shorter in duration and show consistently greater cranial elevation than strikes on mealworms located in the midwater or bottom (Table 1: $P < .006$). The epaxial muscles are invariably active during feeding from the surface (Fig. 8C) and right and left levator operculi muscles are active symmetrically (Fig. 8C; LOr, l).

Dilator operculi and sternohyoideus activity is variable. The dilator operculi (Figs. 1, 8C: DO) is active from 5 to 75 msec after the onset of activity in the levator operculi while the sternohyoideus is usually active synchronously with the levator operculi (Fig. 8C: SH, LO). Occasionally, however, no activity is detected in the sternohyoideus.

The geniohyoideus is never active during the strike (Fig. 8C: GH) and only during subsequent manipulation and crushing of the prey does activity occur. The adductor mandibulae is active from 50–250 msec ($\bar{x} = 80$ msec) after the start of mouth opening.

Midwater.—Both kinematic and electromyographic profiles of feeding on mealworms in the water column are highly variable (Fig. 3: frames 1–20).

The expansive phase may take as long as 80 msec and is usually longer than the compressive phase (Fig. 7). Cranial elevation is significantly
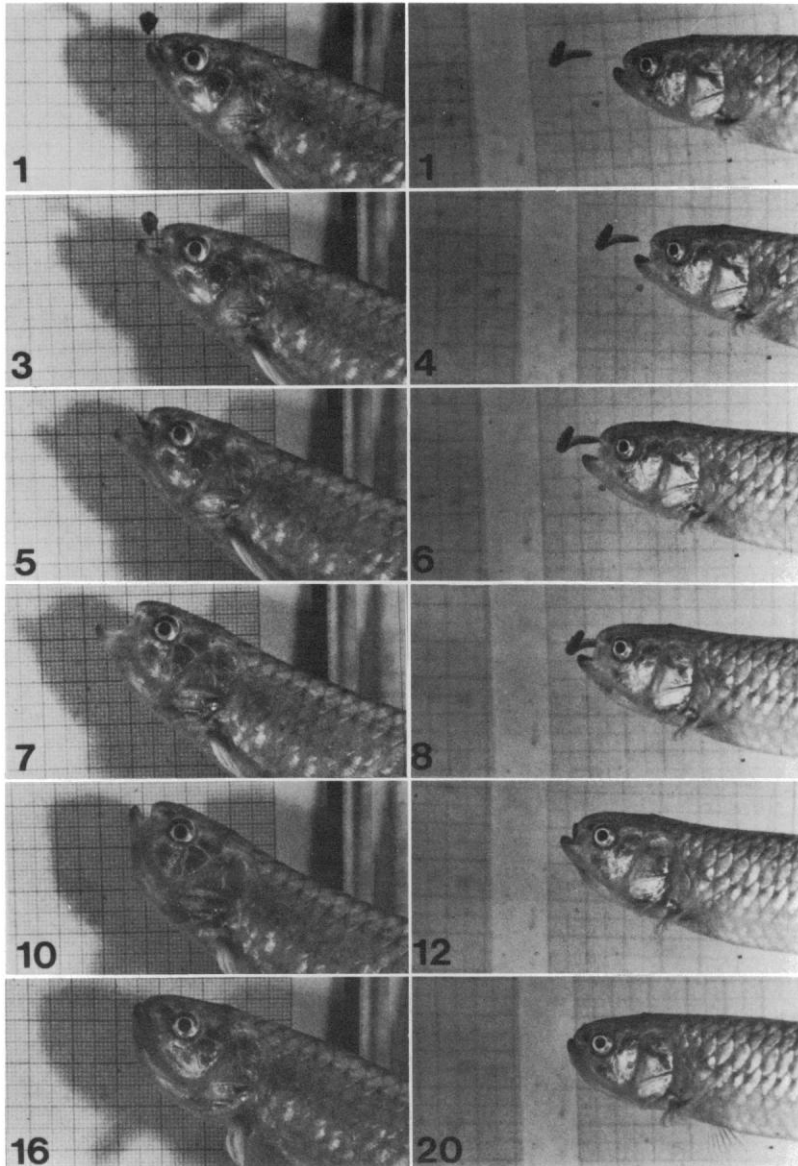
Fig. 3. *Lebiasina boruca*. Representative frames from a high-speed (200 frames per sec) film of the strike at a fish (*Gambusia*), oriented perpendicular to the film plane (on left), and at a mealworm in the midwater (on right). Numbers indicate the frame number in the feeding sequence. Note the different duration, degree of gape, cranial elevation and hyoid depression in the two feeding sequences.

less than during feeding on surface mealworms (Table 1; $P = .004$), and the onset of hyoid depression is delayed until midway through the expansive phase (Figs. 3, 7). The maxilla achieves only a 35°–40° angle with the longitudinal body axis while peak gape is signifi-

cantly less than for all other prey except smelt (Table 1).

The most common pattern of muscle activity during midwater feeding is shown in Fig. 8A. Synchronous activity occurs in the right and left levator operculi followed within 5 msec by the
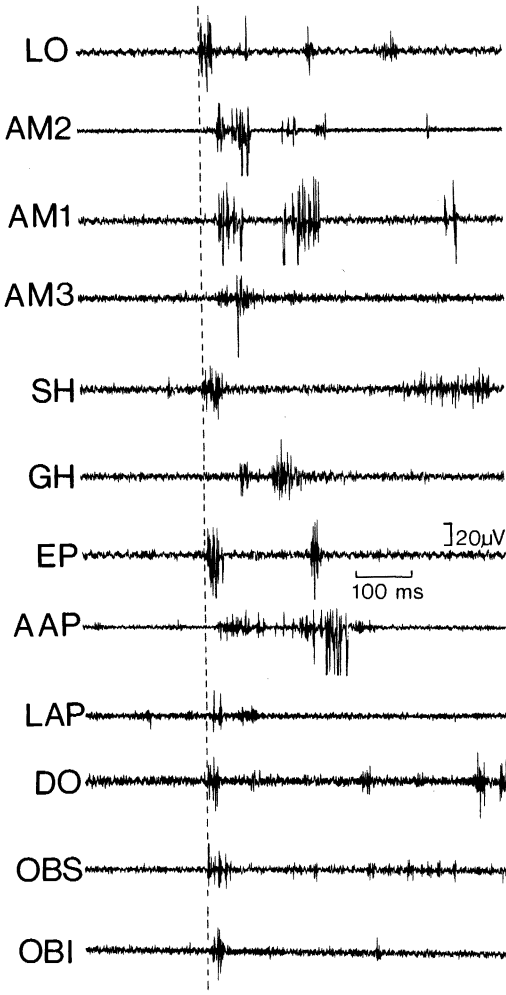
Fig. 4. *Lebiasina boruca.* Pattern of electromyographic activity during the strike at a fish summarized from a number of experiments. Abbreviations as in Fig. 1. The dashed line indicates the time of onset of activity in the levator operculi.

sternohyoideus, epaxial muscles and dilator operculi. The timing of activity in the obliquus superioris is highly variable and depends on the occurrence of lateral head movement just before the strike. The adductor mandibulae (Fig. 8A: AM2) is active 50–60 msec after the levator operculi and may remain active for up to 100 msec.

In less vigorous strikes at midwater mealworms, very little muscle activity is seen. In addition, the levator operculi and epaxial muscles may show asymmetrical activity while the ad-

ductor mandibulae does not (Fig. 8B: LOr, l; EPr, l). Only very low-level activity is seen in the sternohyoideus and obliquus superioris while high-level dilator operculi activity (Fig. 8B: DO) is extremely variable in timing.

After the mealworm is sucked into the buccal cavity at the initial strike, during subsequent "chewing" it is ejected slowly from the mouth in a series of stages, each stage consisting of ejection and then crushing of the prey between the teeth. Usually 3–5 crushing cycles are necessary before the prey has been worked out of the buccal cavity. The mealworm is then turned around by a similar series of movements to those used for fish (Fig. 5), and is sucked back into the buccal cavity in stages interrupted by crushing movements. Strong adduction of the jaws during crushing is accompanied by concomitant high-level activity in the adductor mandibulae.

Bottom.—The key feature of feeding on the bottom is the complete absence of activity in the epaxial muscles (Fig. 8D: EP). Cranial elevation is significantly less than for any other prey type or location (Table 1; $P < .001$), and strike duration is significantly longer than for any other type of feeding (Table 1; $P < .001$), averaging nearly 118 msec.

Symmetrical activity is seen in the right and left levator operculi muscles during mouth opening, and the sternohyoideus is active before or synchronously with the levator operculi (Fig. 8D: LOr, l, SH). The geniohyoideus is inactive during the strike as is the obliquus superioris.

The adductor mandibulae is active from 40–75 msec ($\bar{x} = 60$ msec) after the levator operculi and the timing, amplitude, and duration of activity most closely resemble midwater mealworm feeding.

HOPLIAS MALABARICUS

No differences in the electromyographic pattern were noted during feeding on different prey types.

Initial strike.—The sequence of muscle activity at the initial strike shows very little variability between feeding sequences. Gape is rapidly increased by simultaneous activity in the levator operculi, sternohyoideus, geniohyoideus, epaxial muscles, and obliquus inferioris (Fig. 9: LO,
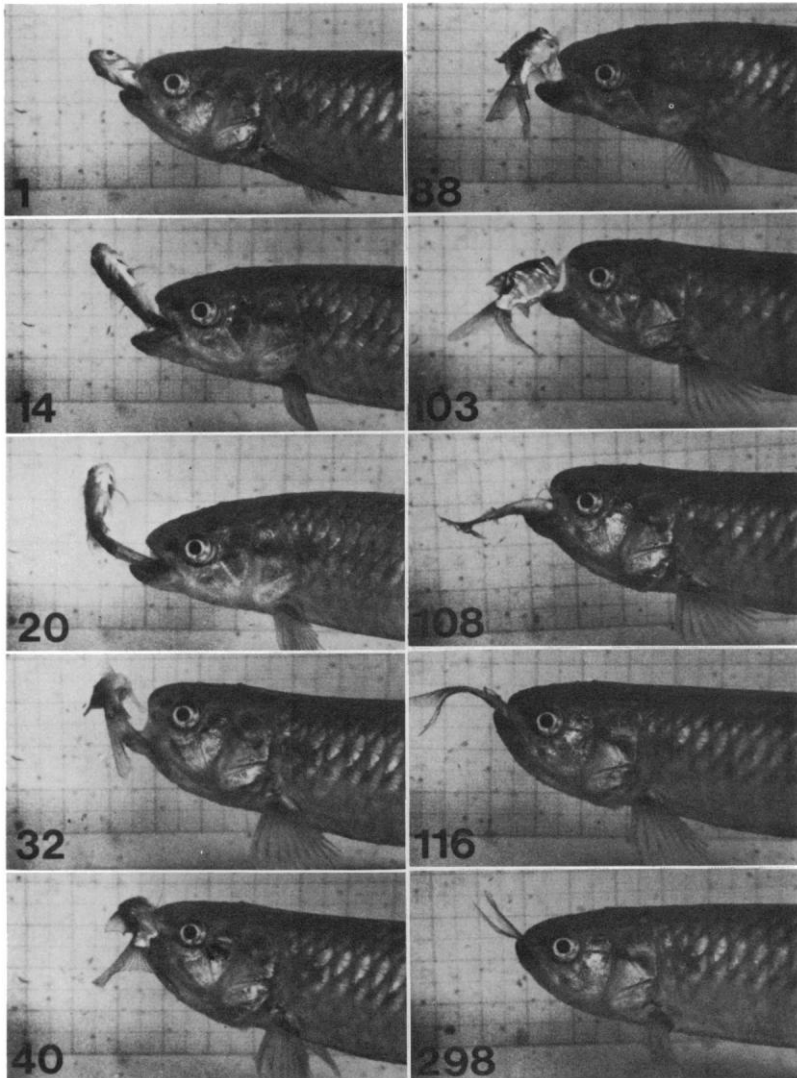
Fig. 5. *Lebiasina boruca*. Representative frames from a high-speed (200 frames per sec) film of prey manipulation following the initial strike. Numbers indicate the frame number in the sequence. See text for explanation.

SH, GH, EP, OBI). All of these muscles are active within 5 msec of each other and this pattern is found during every feeding event. The obliquus superioris is also active at the start of mouth opening (Fig. 9: OBS). The dilator operculi exhibits consistent low-level activity commencing with the onset of levator operculi activity, and lasting for 25 msec before high-level activity begins (Fig. 9: DO). Strong dilation of the operculum may occur following closure of

the jaws. The levator arcus palatini shows a sharp burst of high-level activity for 25 msec at the onset of the expansive phase (Fig. 9: LAP).

The hyohyoideus muscles are the most variable of all cranial muscles in the timing of activity. Usually, the hyohyoideus inferioris is active 10 to 20 msec prior to the hyohyoideus superioris; the onset of activity in the inferioris may occur synchronously with or before activity in the levator operculi (Fig. 9: HHI, HHS).
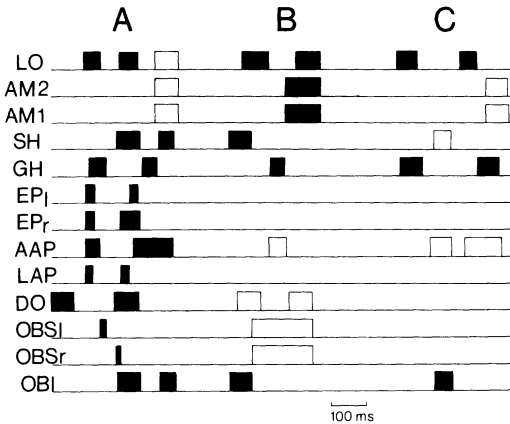
Fig. 6. *Lebiasina boruca.* Block diagram of cranial muscle activity during manipulation of the prey following capture. Three distinct patterns are shown (A, B, C); see text for explanation. Black bars indicate the presence of electrical activity and open bars indicate occasional activity. r and l indicate right- and left-side muscles respectively. Other abbreviations as in Fig. 1.

Fig. 7. *Lebiasina boruca.* Maxillary swing, cranial elevation, hyoid depression and gape versus time during the initial strike at a mealworm in the midwater. Note the delay in hyoid depression and cranial elevation. Time between successive frames is 5 msec.

Occasionally, however, both muscles may lag behind activity in the levator operculi.

Muscles active during the compressive phase include the adductor mandibulae parts one and two, and the adductor arcus palatini (Fig. 9: AM1, 2, LAP). Part two of the adductor complex is active 10 msec after activity in the levator operculi whereas part one activity is delayed for up to 25 msec (Fig. 9: AM1, 2). Although the adductor arcus palatini is quite variable in activity, typically it is active 20–25 msec after activity commences in the levator arcus palatini and is thus entirely active during the compressive phase. Electrical activity in the adductor mandibulae part two extends from the end of the expansive phase into the start of the compressive phase.

Manipulation and deglutition.—Following capture of the prey, two major patterns of muscle activity occur. One pattern is similar to that seen at the initial strike (Fig. 10A). Activity in the levator operculi, sternohyoideus, geniohyoideus, epaxial muscles and obliquus inferioris results in mouth opening, while the adductor mandibulae and adductor arcus palatini are active to compress the buccal cavity (Fig. 10A: AM2, AAP). The levator arcus palatini is inactive. A variation on this pattern often occurs in
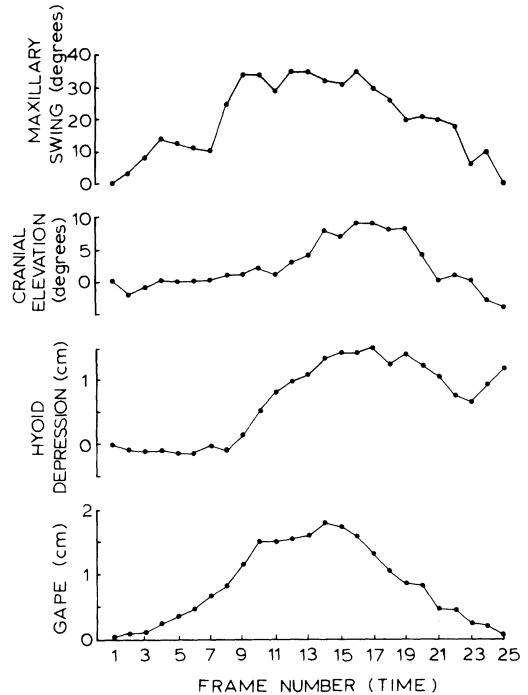
which the adductor mandibulae and epaxial muscles are inactive with only occasional activity in the sternohyoideus and obliquus inferioris muscles (Fig. 10B).

The second major pattern during prey manipulation functions to create a flow of water out of the buccal cavity. The levator operculi and adductor arcus palatini are simultaneously active, and occasional concomitant activity in the adductor mandibulae occurs (Fig. 10C). This is the most common pattern of muscle activity observed during manipulation. The geniohyoideus may also be active in a burst of up to 100 msec in duration with the adductor arcus palatini and levator operculi being the only other muscles active (Fig. 10D).

CHALCEUS MACROLEPIDOTUS

No consistent differences between prey types were noted in the electromyographic profile.
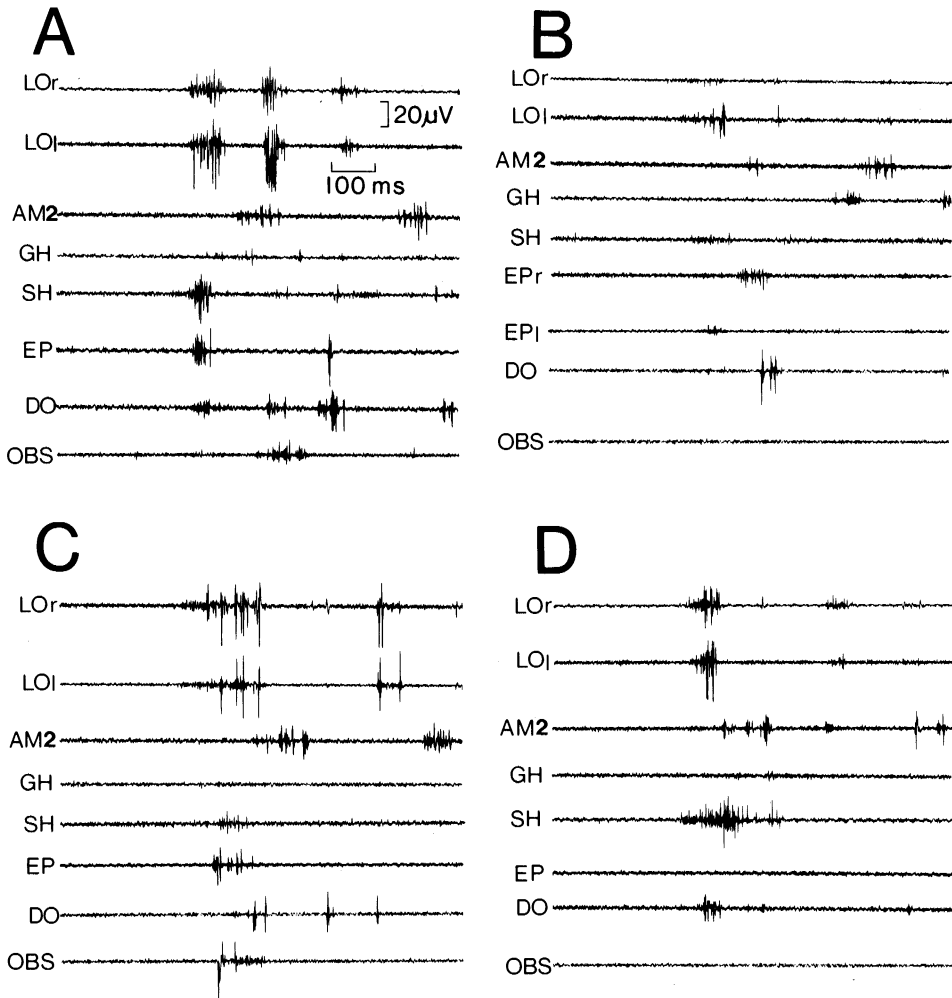
Fig. 8. *Lebiasina boruca.* Patterns of electromyographic activity during feeding on mealworms. A) vigorous midwater strikes; B) midwater strike showing asymmetrical activity between the right and left levator operculi; C) surface feeding; D) bottom feeding. r and l indicate right- and left-side muscles respectively. All other abbreviations as in Fig. 1.

Muscle activity patterns for both mealworms and earthworms are extremely variable and thus both prey types are discussed together.

Initial strike.—The pattern and duration of activity in cranial muscles during the initial strike are highly variable. Even during feeding on a single prey type (mealworms) in a specific location (the midwater), a wide range of activity patterns occurs (Fig. 11: A, B, C). The expansive phase may be initiated by high-level activity

in the levator operculi, sternohyoideus, epaxial muscles, and obliquus inferioris (Fig. 11A: LO, SH, EP, OBI), or the epaxial muscles may be completely inactive (Fig. 11B, C: EP). The levator operculi, sternohyoideus, and obliquus inferioris may also vary dramatically in the pattern of activation (Fig. 11C).

The timing and duration of activity in compressive muscles also is highly variable. In the three examples shown in Fig. 11, the adductor mandibulae (part 2) is active 35 msec, 50 msec
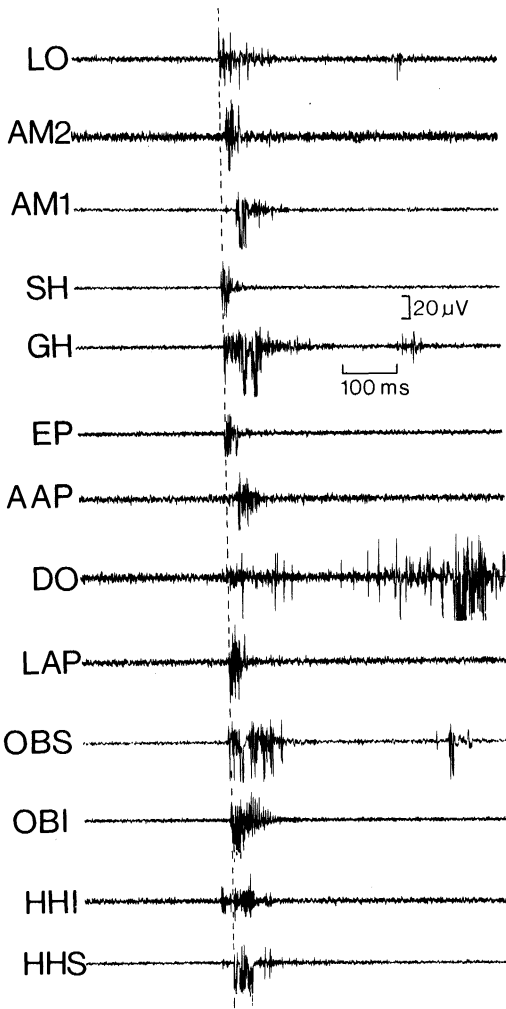
Fig. 10. *Hoplias malabaricus.* Four patterns of electromyographic activity during prey manipulation (described in the text). Black bars indicate the presence of electrical activity and open bars indicate occasional variations. Abbreviations as in Fig. 1.

Mastication and deglutition.—The early phases of prey manipulation involve maceration and crushing of the prey by the front jaws in a pattern very similar to that described for *L. boruca.* The levator operculi, adductor mandibulae, and occasionally the sternohyoideus exhibit nearly synchronous bursts of activity (Fig. 11B, C: LO, AM2, SH).

Once the prey has been crushed by the front jaws, intraoral manipulation and "chewing" occur which are very different from the manip-

Fig. 9. *Hoplias malabaricus.* Pattern of electromyographic activity at the initial strike summarized from a number of experiments. Dashed line indicates the time of onset of activity in the levator operculi. HHI, hyohyoideus inferioris; HHS, hyohyoideus superioris. All other abbreviations as in Fig. 1.

Fig. 11. *Chalceus macrolepidotus.* Three patterns of cranial muscle activity during feeding on mealworms in the midwater (see text). Abbreviations as in Fig. 1.

and remains inactive after activity in the levator operculi. In addition, the right and left adductor muscles may show asymmetrical activity, both at the initial strike (Fig. 11A, B: AM2r, l), and during the early manipulatory phase.

The geniohyoideus is usually inactive during the strike (Fig. 11B, C: GH), although occasionally low-level activity may occur in the compressive phase (Fig. 11A: GH).
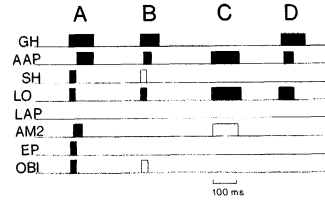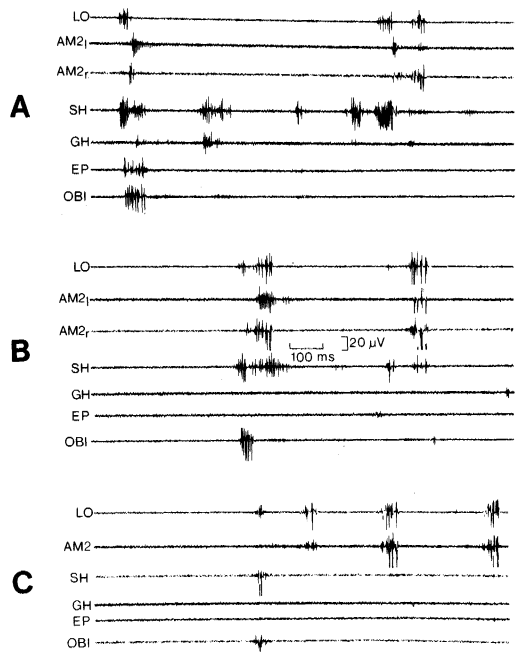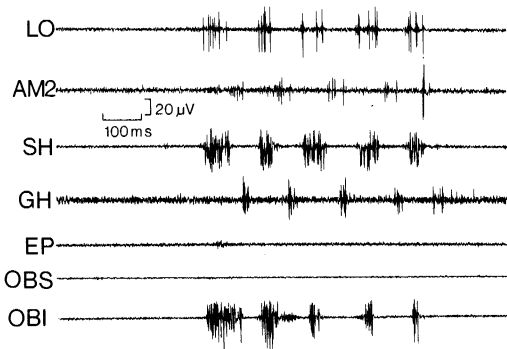
Fig. 12. *Chalceus macrolepidotus*. Pattern of electromyographic activity in selected muscles during intraoral prey manipulation. Abbreviations as in Fig. 1.

ulations described for *Lebiasina* and *Hoplias*. Regular alternating activity of expansive phase muscles (levator operculi, sternohyoideus, and obliquus inferioris) and compressive phase muscles (adductor mandibulae and geniohyoideus) occurs in a remarkably consistent pattern (Fig. 12). The epaxial and obliquus superioris muscles are inactive.

This cyclical pattern reflects the rhythmic expansion and compression of the buccal cavity, and particularly protraction and retraction of the hyoid arch by alternating sternohyoideus and geniohyoideus activity (Fig. 12: SH, GH). Hyoid protraction may contribute to intraoral crushing of the prey between the floor and roof of the buccal cavity.

DISCUSSION

Functional repertoires and modulated jaw dynamics.—Liem (1978) first explicitly considered "modulation" of the jaw apparatus during feeding. Modulation refers to the ability to alter kinematic, electromyographic and pressure profiles of jaw function in response to varying prey position and type.

In the past, prey capture by fishes has generally been regarded as proceeding according to a single preprogrammed pattern of muscle action and jaw movement. This single pattern is presumed to originate in a central nervous system oscillator (by analogy with oscillators producing stereotyped movements during locomotion: Grillner, 1975; Grillner and Kashin, 1976) which initiates motor output to the jaw musculature at a specific, visually-determined time. One manifestation of this belief is the

practice of "averaging" electromyographic data from large numbers of experiments to arrive at the single representative pattern used in prey capture (Lauder and Lanyon, 1980; Osse, 1969).

Recently, Elshoud-Oldenhave and Osse (1976) and Lauder and Liem (1980) have identified differences in the relative timing and duration of electromyographic activity depending on whether the fish was feeding on prey items on the bottom or in midwater.

Liem (1978) identified two patterns of electromyographic activity in piscivorous cichlid fish; these two patterns differed in the timing and duration of muscle activity. More dramatic modulation of jaw dynamics has been reported by Liem (1979, 1980) in rock-scraping and invertebrate-picking cichlids. Jaw modulation in these fishes includes complete asymmetry between activity in right- and left-side jaw muscles, and variability in the occurrence of activity in certain muscles depending on the location of the prey.

One problem common to all previous studies of jaw modulation has been the lack of a quantitative assessment of the differences between each of the postulated patterns in the functional repertoire. In this study, four kinematic parameters of feeding in *L. boruca* have been analyzed with respect to variability during feeding on different prey types in three locations. The data corroborate the hypothesis of Liem (1978, 1979, 1980) that distinct kinematic and electromyographic patterns may exist within the functional repertoire of a species.

When *L. boruca* strikes at pieces of smelt, the location or size of the smelt does not seem to influence the kinematic or electromyographic pattern. However, the patterns elicited by pieces of smelt do differ significantly in respect to duration, cranial elevation, and hyoid depression from strikes at live fish (Table 1; $P < .01$). In addition, the patterns during smelt strikes resemble those during feeding on mealworms in the water column most closely, and differ significantly only in duration (Table 1; $P < .01$). Feeding on live fishes is significantly more rapid and involves greater hyoid depression than feeding on other types of prey ($P < .03$). The electromyographic profile accompanying the capture of live fish (Fig. 4) also differs dramatically from that accompanying the capture of other prey (Fig. 8). These differences are especially clear in respect to temporal overlap in antagonistic muscle complexes.

Within the category of mealworm feeding, the kinematic and electromyographic profiles are modulated depending on the position of the prey (Table 1). All three feeding situations (bottom, midwater and surface) are significantly different from each other in degree of cranial elevation and duration (Table 1; $P < .006$). The epaxial muscles are never active during bottom feeding while they are always active in surface feeding sequences.

Two major conclusions emerge from this analysis. 1) Size of the prey alone does not determine which component of the functional repertoire will be elicited at the strike. Strikes at large pieces of smelt were significantly slower than feedings on equally large fish, and gape, hyoid depression and cranial elevation were all less than during fish feedings. 2) The different components of the functional repertoire are not distinct in all kinematic parameters—nonetheless, the different elements of the repertoire are clearly separable and are non-overlapping in certain features. The most obvious example of this is the consistent presence of epaxial muscle activity during surface feeding and the consistent lack of epaxial activity during bottom feeding.

The major determinant of which particular component of the functional repertoire is used for any given feeding event appears to be a combination of size, position, and prestrike behavior of the prey. An integration of these parameters by the central nervous system results in the recruitment of a particular motor output.

The variability in the electromyographic pattern also changes with prey type. Most muscle activity periods vary less than 5–10 msec during successive strikes at fish. During mealworm feedings, however, between-strike variability in onset of activity is high, especially with the midwater prey position. Elshoud-Oldenhave and Osse (1976) also found more variability during midwater feeding in the ruff, *Gymnocephalus*, than during bottom feeding. Asymmetrical activity between right- and left-side muscles is found only during mealworm feedings.

The electromyographic pattern at the strike in *Hoplias* is invariant even during feeding on widely divergent prey as fish and earthworms (the latter located on the bottom of the aquarium). The functional repertoire of *Hoplias* thus appears to consist of a single component: high-speed inertial suction (Lauder, 1979). This component may be identified as a subset of the functional repertoire in *Lebiasina*. That is, it

closely resembles the "fish pattern" in *Lebiasina* with two additional specializations: greater overlap in antagonistic muscle complexes (essentially tantamount to compression of the time base), and a shift in the time of onset of geniohyoideus activity to the start of the expansive phase (Fig. 9).

Possible ecological correlates of the difference in intraspecific functional repertoires between *Hoplias* and *Lebiasina* are the diversity of foods eaten, and the efficiency with which different foods are captured and handled. A more restricted functional repertoire may correlate with a narrower range of foods eaten in the wild. Saul (1975), in a stomach contents analysis of certain Amazonian fishes found that *Hoplias* ate mostly fishes and some invertebrates, while *Lebiasina* had mostly invertebrates in the stomach and a few fish remains. A more direct test of the hypothesis that functional repertoires correlate with food eaten in the wild would involve a classification of prey into surface, midwater and bottom types, as well as into taxonomic groups, and a measure of prey "elusiveness." A specific correlation between prey category and the presence of an appropriate component in the functional repertoire could then be conducted. Another test of this hypothesis could be executed for fishes in which the range of foods eaten changes during ontogeny. Primarily piscivorous adults should possess a more limited intraspecific repertoire than conspecific euryphageous juveniles.

Chalceus possesses a very different functional repertoire from either *Lebiasina* or *Hoplias*. Although the number of feedings and variety of prey types are too limited to permit an analysis of the number of components in the repertoire, even during feeding on a single prey (mealworms) in one location (midwater), tremendous variability occurs in the pattern of muscle activity between feeding sequences (Fig. 11). This pattern may be indicative of a highly generalized functional repertoire with no discrete nonoverlapping components. In other words, variability within each prey type may span the entire functional repertoire.

Specialization of the functional repertoire as defined by increasing discretization and a concomitant decrease in the number of repertoire components, increases in the series *Chalceus* → *Lebiasina* → *Hoplias*. Variability within repertoire components is inversely correlated with specialization.

A key goal of future studies on characoid

feeding mechanisms will be to examine the distribution of different functional repertoires within the context of phylogenetic hypotheses of characoid relationships. Generalized repertoires may represent a generalized (sensu Nelson, 1978) and thus primitive character. Ontogenetic studies of functional repertoires would provide a test of this hypothesis (Nelson, 1978).

Feeding mechanisms.—One surprising result from electromyographic studies of teleost feeding mechanisms over the last decade has been the discovery of extensive interspecific variability in the activity of the geniohyoideus muscle during the initial strike. This muscle is electrically active during the expansive phase (mouth opening) in cichlids (Liem and Osse, 1975; Liem, 1978) and percids (Osse, 1969; Elshoud-Oldenhave and Osse, 1969), while it is either active only during the compressive phase (mouth closing) or is inactive in *Lepomis* (Lauder and Lanyon, 1980) and *Salvelinus* (Lauder and Liem, 1980). In *Hoplias* (Fig. 9) the geniohyoideus is active during the expansive phase whereas in *Lebiasina* it is only active during mouth closing (Fig. 4) in fish strikes, and shows no activity at all during feeding on mealworms (Fig. 8). *Chalceus* exhibits the latter pattern.

The significance of this variability is unclear. The presence of geniohyoideus activity during mouth opening might be expected to increase the rapidity of mandibular depression, because co-contraction of the sternohyoideus and geniohyoideus would provide a direct posteroventral force at the mandibular symphysis that could rapidly depress the mandible. This hypothesis is not tenable, however: in *Gymnocephalus* where the geniohyoideus is active during mouth opening, the expansive phase lasts 80 msec whereas in *Lepomis* (geniohyoideus only electrically active during mouth closing) the expansive phase averages 20 msec for fish feedings.

The function of the geniohyoideus muscle may be clarified by reference to its working line of action. Both Elshoud-Oldenhave and Osse (1976) and Lauder (1979) have noted that the line of action of the geniohyoideus and sternohyoideus muscles may lie above the quadratomandibular articulation when the jaw is closed. Contraction of the geniohyoideus and sternohyoideus at this time will result in adduction of the lower jaw and protraction of the hyoid. Thus, those fishes in which the genio-hyoideus is active during the expansive phase may be those with the working line of the geniohyoideus and sternohyoideus muscles lying ventral to the quadratomandibular articulation, allowing those muscles to aid in mandibular depression.

One further possible functional correlate of geniohyoideus activity exists. If the working line of the geniohyoideus does lie above the jaw joint, then contraction of the geniohyoideus (and possibly the sternohyoideus) would result in buccal compression. Minimizing buccal volume prior to rapid mouth cavity expansion at the strike constitutes the preparatory phase. To date, preparatory phases have been found only in acanthopterygians and the geniohyoideus, adductor mandibulae, and adductor arcus palatini all reduce buccal volume before the expansive phase. This preparatory reduction in volume allows a greater volume increase during mouth opening and thus a greater velocity of water flow into the buccal cavity. A possible function of the geniohyoideus muscle, then, if it is active before the levator operculi and if the line of action lies above the jaw joint, would be in buccal compression before the mouth is opened. Necessary correlates of this function would be electrical activity in the geniohyoideus at least 10–20 msec before the levator operculi and sternohyoideus fire, and the appropriate working line to allow mandibular adduction.

In *Hoplias*, the line of geniohyoideus action never passes dorsal to the jaw joint during the expansive phase (Lauder, 1979) and contraction of the geniohyoideus and sternohyoideus may contribute directly to rapid mandibular abduction. *Lebiasina* and *Chalceus* do not feed primarily by inertial suction so neither a preparatory phase nor rapid mandibular depression are necessary, and the geniohyoideus remains inactive prior to and during mouth opening.

Liem (1980) reported modulation of epaxial muscle activity in *Petrotilapia* during feeding in different locations. He found that feeding from the bottom involved activity in the epaxial muscles whereas surface feeding did not. This result is the opposite of the modulatory pattern obtained here in *Lebiasina* (Fig. 8C, D). The difference in use of the epaxial muscles during surface and bottom feeding may be correlated with the presence of premaxillary protrusion in *Petrotilapia*. Additional upper jaw protrusion is used during bottom feeding (Liem, 1980), and epaxial muscle activity contributes to protru-

sion (Liem, 1979). In *Lebiasina*, feeding from the bottom is accomplished by scooping up the prey with the lower jaw.

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