WAINWRIGHT

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Feeding biology of sunfishes: patterns of variation in the feeding mechanism

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Fishes are generally believed to differ in their ability to alter (modulate) their feeding behaviour in response to different prey. We investigated modulation quantitatively in four species of sunfishes (Centrarchidae) by evaluating the variation in 11 electromyographic variables measured from recordings of electrical activity in head muscles during feeding on three prey types. The experimental design used allowed us to partition variation between species, among individuals within species, among prey types, and among feedings. Duration of activity of the sternohyoideus muscle was the only variable significantly different among the four species. All variables showed significant differences among individuals within species. The overall range of activity of each muscle activity variable was about the same for all four sunfishes. However, three species showed a significant ability to modulate most muscle variables while a fourth did not change its feeding response with respect to prey type. The results indicate that: (1) intraspecific variation is an important source of variability in functional attributes that should be accounted for in comparisons between species; (2) the ability of some species to modulate appears to be independent of the potential variability in muscle activity possessed by each species; (3) closely related species can differ considerably in their ability to alter muscle electrical activity patterns during feeding; and (4) a quantitative assessment of variation in electromyographic patterns is a powerful approach for asking questions about differences in feeding behaviour.

KEY WORDS:—Functional morphology – feeding – variation – sunfishes – electromyography.

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INTRODUCTION

Functional morphologists studying the feeding mechanism of fishes typically characterize the prey capture event with electromyographic recordings of

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cranial muscle activity and with measurements of bone movements from high-speed films. Over the past two decades these techniques have contributed to the emergence of a general understanding of the roles played by the muscular and skeletal components of the head during feeding.

Many early workers believed the fish feeding mechanism to be relatively stereotyped in its movements and thus to vary little during the capture of different prey (Osse, 1969; Alexander, 1970; Liem, 1970). More recently it has become accepted that some species are capable of altering the patterns of head movement and associated muscle activity in response to different prey locations and prey types (Ballintijn, van den Berg & Egberink, 1972; Elshoud-Oldenhave & Osse, 1976; Liem, 1978, 1980; Lauder, 1981, 1983a).

Liem (1978) coined the term "modulation" to refer to this ability of some species to change the pattern of neuromuscular and kinematic events as a direct response to feeding conditions. He found that some piscivorous cichlid fishes reacted to elusive prey with greater overlap in activity of antagonistic muscles than when feeding on immobile prey. Lauder (1981) showed that the characoid *Lebiasina* possesses a labile feeding response which varies with respect to prey location and type. This was contrasted with *Hoplias* whose feeding behaviour was unaffected by different prey. The most extensive modulation yet reported has been found by Liem (1980) among several genera of rock-scraping African cichlid fishes (Cichlidae), a family that has served as a case study for the evolution of feeding specializations (Greenwood, 1981, 1984). These fishes appear to have at least eight patterns of jaw muscle activity that change according to size, position and type of prey.

The ability to modulate feeding behaviour has been proposed to have significant implications for the trophic ecology of a species (Liem, 1980; Lauder, 1981, 1983a). The hypothesis set forth is that modulating species will have broader diet capabilities than other, more stereotyped taxa, and thus may be able to utilize a wider range of resources than species with stereotyped feeding mechanisms. Modulation and patterns of muscle activity have also been used in an evolutionary context, the latter as characters to test hypotheses of phylogenetic relationships (Lauder, 1983a) and the former in considerations of the adaptive significance of the feeding apparatus (Liem, 1978, 1979, 1980).

Central to the arguments in all of these studies is the importance of an accurate and quantitative assessment of the ability of species to modulate kinematic and/or neuromuscular aspects of feeding behaviour. This assessment should be based on a quantitative evaluation of variability in the parameters of the feeding behaviour under consideration, and yet all studies to date have provided only a qualitative evaluation of the ability of species to modulate feeding behaviour.

An investigation of the effect of any factor (e.g. prey type) on the feeding response must account for other major sources of variation in the feeding parameters of interest. Tests for differences between groups (i.e. different prey types or species) must be based on estimates of within-group variance. For example, comparisons of activity patterns of a particular muscle during feeding on different prey should be based on estimates of the variation among the feedings on different prey types as well as the variation among feedings within each prey type. One important type of within-group variance that has historically been neglected by functional morphologists is variation among

individuals within species. Tests for differences in feeding behaviour in different species should be based on estimates of variation among individuals of each species.

One goal of this study is to describe an experimental design that provides the functional morphologist with a suitable statistical framework for asking questions about differences in feeding responses. We compare cranial muscle activity in four species of sunfishes (Centrarchidae) feeding on three prey types. Variation in the electromyographic parameters measured is partitioned into variation among species, variation among individuals within species, variation among prey types, and variation among feedings for each individual within a single prey type. Based on these estimates of between- and within-group variance we test the significance of the effect each factor (species, individuals within species and prey type) has on muscle activity. The major contribution of this investigation is to quantitatively answer the following question: do fish species differ in their ability to modulate the neuromuscular basis of feeding behaviour in response to different prey, and if so, how? To answer this question we use a statistical analysis of the prey type effect as a test for modulation, and compare the four species of sunfishes for their ability to alter muscle electrical activity during feeding on three types of prey.

MATERIALS AND METHODS

Experimental animals

Four species of the endemic North American freshwater fish family Centrarchidae were compared in this study. Data were collected from two *Ambloplites rupestris*, four *Lepomis macrochirus*, five *Pomoxis nigromaculatus* and six *Micropterus salmoides* (all specimens ranged between 15 and 25 cm total length). Fishes were collected locally in northern Illinois and Indiana and housed separately in 70 litre glass aquaria held at constant temperature (17°C). All fishes were fed a mixed diet of the three experimental prey types for several weeks prior to the study.

Experimental techniques

For each fish simultaneous electromyographic (EMG) recordings of the electrical activity of four muscles were made using a previously described standard protocol (Lauder, 1983c). Briefly, fine wire electrodes were implanted directly into the muscles of anaesthetized fish. All of the muscles were immediately beneath the skin and easily located so there was little danger of electrode misplacement. Electrode wires were glued together into a cable that was sutured to the back of the fish anterior to the dorsal fin. The fish was then returned to the aquarium where it recovered, the electrode cable trailing freely behind.

Electrical signals from the muscles were recorded on a Bell and Howell 4020A tape recorder and played back to a Gould 260 chart recorder at 125 mm/s paper speed. Tape playback speed was 8 times slower than that used for recording (375 mm/s). The amplifier bandwidth (Grass P511J) was 100–3000 Hz, and the electromyograms were amplified 5000 times. Figure 1 shows representative data obtained from two species using this procedure.

Individuals were fed 10 each of the three live prey types: 3–4 cm long pieces of earthworm (*Lumbricus*), 2 cm long adult crickets (*Acheta domesticus*) and 3–4 cm long fathead minnows (*Pimephales promelas*). These three prey were chosen to present a variety of feeding conditions for the fishes. The worms were chosen as a passive prey with little ability to escape. The crickets floated at the surface offering a unique position but like the worms were not usually evasive. In contrast, the minnows were a highly mobile and elusive prey and often elicited an extended pursuit, with several unsuccessful feeding attempts before the final capture.

The order of presentation of the 30 prey items was randomized using a table of random numbers. This allowed us to meet one of the assumptions of the parametric statistics used in data analysis and insured that the fishes would not be able to anticipate the identity of the next prey item. Thus, any effects of different prey on the feeding response are due to events which occurred after the prey had been presented to the fishes. In addition, satiation is known to effect the feeding response of a fish over the course of an experiment (Lauder, 1983b). Since this effect is a function of number of prey eaten (Lauder, 1983b), randomization ensured that there would be no systematic influences of satiation on the results. A total of 510 feedings were used in the statistical analysis.

Four cranial muscles known to play key roles during suction feeding were chosen for consideration in this study. A brief description of their functions follows. All muscle names follow Winterbottom (1974). The levator operculi (LOP) is the primary depressor of the lower jaw, and plays a key role in opening the mouth. The anterior epaxial musculature (EP) inserts on the back of the skull and lifts the head when active. Division 2 of the adductor mandibulae (AM2) closes the jaws. Finally, the sternohyoideus (SH), when active, depresses the hyoid bar and thus the floor of the buccal cavity; a major suction generating movement. This muscle also contributes to depressing the lower jaw via a ligamentous attachment from the hyoid to the mandible. Complete anatomical descriptions and biomechanical analyses are provided in Lauder (1983b).

From the chart recordings, 11 variables (LOP, LOPA, AM2, AM2A, EP, EPA, SH, SHA, LOP–AM2, LOP–EP, LOP–SH) were measured (digitized) for each feeding. These variables quantitatively summarized the overall electromyographic pattern of muscle activity during the successful strike. For each of the four muscles the duration of activity was measured in milliseconds (four variables: LOP, AM2, EP, SH). The maximum amplitude of each muscle burst, scaled in millivolts, was also recorded (four variables: LOPA, AM2A, EPA, SHA). Three final variables characterized the sequence of activity of the four muscles. Using the onset of activity of the LOP muscle as a reference, the difference in time of onset of activity (in milliseconds) was measured between it and each of the other three muscles (three variables: LOP–AM2, LOP–EP, LOP–SH).

Statistical analyses

Our overall experimental design was a two-way analysis of variance with a nested level. Nested within the species were varying numbers of individuals. Crossed with species and individuals was the prey type factor. Ten replicate feedings of each prey type for each fish constitute the contents of a single cell in

this design. From this design the following model equation can be written (Scheffe, 1959):

$$Y_{ijkl} = \mu + \alpha_i^A + a_{ij}^B + \alpha_k^C + \alpha_{ik}^{AC} + a_{ijk}^{BC} + a_{ijkl}^D.$$

Y represents any of the 11 variables, A is the species factor, B the individual within species factor, C the prey type factor, AC and BC are the two interaction terms generated by the experimental design, and D the replicated feedings. Factors with a fixed effect are denoted by α and those with random effects by a. Guided by this model, approximate F ratios were calculated using SAS (Freund & Littell, 1981) type-4 sums of squares. For each muscle activity variable significance tests were performed for each of the three main effects (species, individuals, prey type) as well as the two interaction terms. In tests for the main effects the null hypothesis was that the value of the variable was the same for each of the groups being compared. Interaction terms were tested with the null hypothesis that the effect of prey type was the same for each of the four species (species × prey type) or for each of the individuals within the species (individuals × prey type).

The central purpose of this study was to compare the abilities of the four species to modulate jaw muscle activity in response to different prey types. This was accomplished by analysing the data for each species separately and contrasting the significance of the prey type effect among the four centrarchids. For this analysis the model equation for the two-way analysis of variance was:

$$Y_{ijk} = \mu + a_i^A + \alpha_j^B + a_{ij}^{AB} + a_{ijk}^D.$$

Here, A represents individuals, B is the prey type effect and there is only the single interaction term. Again, the individual factor is a random factor and the prey type factor is fixed. The F ratio used to test the prey type effect was the mean square for the prey type term over the mean square for the interaction term (Scheffe, 1959). If the average value of a muscle variable differed with respect to prey (i.e. a significant prey type effect) we interpreted it as indicative of an ability of that species to modulate that parameter of muscle activity.

Because many significance tests were performed we insisted on a probability value of less than 0.01 to establish significance of all F ratios.

As an aid to interpreting the relationships among the 11 muscle variables and to help identify the major source of variation a principal component analysis (PCA) was performed on the correlation matrix for the data set.

The untransformed data set was used in all analyses. Transformations are usually performed because they often improve the statistical behaviour of a data set. Assumptions of the parametric statistics used were met to our satisfaction with the untransformed data set and were not improved upon by any transformations we experimented with (log, ln, square root).

Calculations for the two-way nested analysis of variance were carried out using the SAS (1982) General Linear Model procedure with type-4 sums of squares.

RESULTS

In all four species there was tremendous variability in the electromyographic variables during feeding (Table 1 and Fig. 1). The overall range of values of

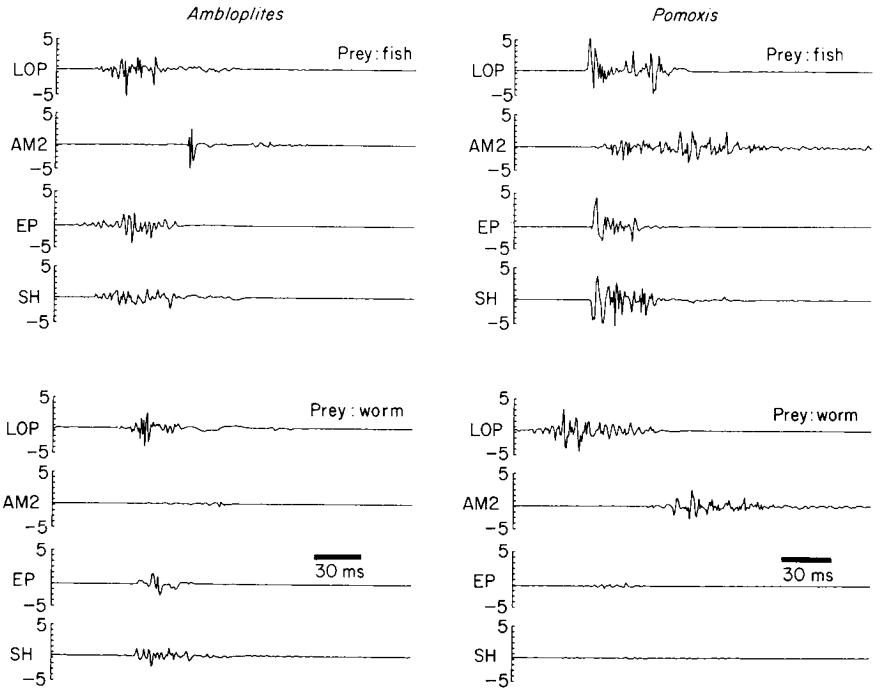

Figure 1. Sample electromyograms from four cranial muscles at the strike during feedings on a non-elusive prey (a worm) and an elusive prey (a minnow). Recordings from a modulating species (*Pomoxis*) and the non-modulating *Ambloplites* are shown. Recordings were taken simultaneously from the four muscles in all cases. The *y*-axis for each myogram is scaled in units of 100 μV. Abbreviations: AM2, division 2 of the adductor mandibulae; EP, epaxialis; LOP, levator operculi muscle; SH, sternohyoideus.

each variable was about the same for each species (Table 1), and at least in the context of this study the inherent variability of muscle activity in the four species was about the same. All species did not use three of the four muscles studied under some feeding conditions. This is indicated by a 0 at the low end of the range in Table 1.

The results from the two-way nested ANOVAs are summarized in Table 2. In tests of the species effect only one variable, the duration of activity of the sternohyoideus muscle (SH), was found to be significantly different among the four species. In contrast, all variables showed significant differences among individuals within species. Similarly, most variables showed significant overall prey type effects. The only exceptions were the duration and amplitude variables for the LOP muscle. Results for the two interaction terms were quite different. The 'species × prey type' term was not significant for any variables while the 'individual × prey type' term was significant in all but two tests.

Table 3 presents the results from the tests of the prey type effect made for each species separately in two-way ANOVAs. *Ambloplites* did not have a significant prey type effect for any of the 11 variables. In contrast the other three species each had significant prey type effects for most muscle activity variables. The duration and maximum amplitude variables of the levator operculi were the only ones that did not show a significant prey type effect in any of the four species.

Table 1. Range of values of 11 electromyographic variables from the strike during feeding in four centrarchids (see text for variable descriptions)

Variable	*Ambloplites*	*Lepomis*	*Pomoxis*	*Micropterus*
LOP*	24–142	12–146	5–134	12–241
LOPA†	7–26	2–26	10–25	2–33
AM2*	0–216	0–251	0–235	0–238
AM2A†	0–20	0–22	0–21	0–27
EP*	0–102	0–103	0–86	0–130
EPA†	0–22	0–22	0–20	0–28
SH*	0–125	0–79	0–94	0–105
SHA†	0–22	0–22	0–23	0–29
LOP–AM2*	5–116	(−4)–141	(−17)–195	(−6)–134
LOP–EP*	(−32)–55	(−13)–92	0–171	(−26)–142
LOP–SH*	(−32)–80	(−32)–52	0–90	(−22)–115

*In milliseconds.
†In millivolts.

The principal component analysis (PCA) yielded two components which together accounted for 53% of the variation in the data set. The first PC explained 35% of the variance in the data (Table 4). PC1 loads significantly on the duration and maximum amplitude variables of the adductor mandibulae, the epaxialis and the sternohyoideus muscles. In addition, the relative onset time between the levator operculi and the other three muscles is negatively correlated with this component. When a second PCA was performed, including prey type as a 12th (dummy) variable, the results were nearly identical to the first analysis (no loading was changed by more than 0.02). Prey type was highly correlated with the first PC (Table 4). A plot of the prey centroids for all species

Table 2. Two-way nested ANOVAs comparing 11 electromyographic variables of the strike during feeding from four species of fish. Significant tests of main effects indicate differences in the average value of the variable among the groups of the factor

	Factor				
Variable	Species (3,14)*	Individuals (13,430)	Prey type (2,24)	Species × prey type (6,24)	Individuals × prey type (24,426)
LOP	N.s.	0.0001	N.s.	N.s.	0.0001
LOPA	N.s.	0.0001	N.s.	N.s.	N.s.
AM2	N.s.	0.0001	0.0001	N.s.	0.01
AM2A	N.s.	0.0001	0.0001	N.s.	0.0001
EP	N.s.	0.0001	0.0001	N.s.	N.s.
EPA	N.s.	0.0001	0.0001	N.s.	0.0001
SH	0.0002	0.0001	0.0001	N.s.	0.0001
SHA	N.s.	0.0001	0.0001	N.s.	0.0001
LOP–AM2	N.s.	0.0001	0.0001	N.s.	0.0001
LOP–EP	N.s.	0.0001	0.005	N.s.	0.0007
LOP–SH	N.s.	0.0001	0.0003	N.s.	0.007

*Degrees of freedom.
N.s. = $P > 0.01$

Table 3. Two-way ANOVAs testing the effect of prey type on 11 electromyographic variables of the strike during feeding. Significant differences indicate an ability of that species to modulate that muscle variable in response to different prey

Variable	*Ambloplites* (2,2)*	*Lepomis* (2,6)	*Pomoxis* (2,8)	*Micropterus* (2,6)
LOP	N.s.	N.s.	N.s.	N.s.
LOPA	N.s.	N.s.	N.s.	N.s.
AM2	N.s.	0.002	0.003	0.005
AM2A	N.s.	N.s.	0.005	0.009
EP	N.s.	0.009	0.001	N.s.
EPA	N.s.	N.s.	0.005	0.001
SH	N.s.	0.008	0.001	0.005
SHA	N.s.	0.008	0.002	0.003
LOP–AM2	N.s.	N.s.	N.s.	0.003
LOP–EP	N.s.	0.001	0.001	N.s.
LOP–SH	N.s.	0.001	0.003	N.s.

*Degrees of freedom.
N.s. = $P > 0.01$.

on the first two PCs (Fig. 2) shows that PC1 tends to contrast the prey types. The first PC is thus considered a prey type axis.

DISCUSSION

Inter- and intraspecific variation

A common approach among functional morphologists interested in analysing the feeding mechanisms of fishes has been to concentrate on patterns of activity of muscles which operate the jaws during feeding (Liem, 1978, 1979, 1980; Lauder & Liem, 1980). Two questions have been answered in this study that

Table 4. Loadings of the first two principal components from a PCA on 11 muscle activity variables. Prey type entry is its loading from a second PCA that included it as a dummy variable

Variable	PC1	PC2
SHA	0.869	0.002
EPA	0.860	0.093
SH	0.790	−0.004
EP	0.711	0.233
AM2A	0.672	0.129
Am2	0.587	0.008
LOP–AM2	−0.526	0.573
LOP	0.225	0.695
LOP–SH	−0.173	0.655
LOP–EP	−0.257	0.632
LOPA	0.174	0.494
Prey type	0.732	−0.166
Variance explained	35%	18%

are frequently addressed only qualitatively: (1) do different species have similar patterns of jaw muscle activity when feeding on the same prey? and, (2) does a given species alter (modulate) its muscle activity in response to different prey? The experimental design used here has allowed us to ask a third question that permits a more accurate answer to the first two: do individuals within species differ? We found that all muscle activity variables measured were significantly different among individuals within species (Table 2).

Our results make it clear that without this estimate of intraspecific variation erroneous conclusions about differences between species could easily be reached. For example, interspecific comparisons could be made based on a sample size of one individual per species. In doing so variation within species is ignored. If differences among species are found there is no way of knowing if the results are due to inter- or intraspecific variation. More often in functional analysis, several individuals within a species are studied, but all individuals are averaged to obtain a mean value for a species. This approach has many pitfalls (for a detailed discussion see Shaffer & Lauder, 1985a), one of which is that lumping data for individuals within a species for the purposes of testing for differences between species confounds sources of variation. One may find highly significant differences between species that do not really exist if variation within species is not taken into account with an appropriate analysis of variance design.

Quantitative studies of feeding in salamanders (Shaffer & Lauder, 1985a, b) found levels of variation among individuals within species comparable to those we describe here for a family of teleosts. It appears that high intraspecific variation in these functional attributes may be a general feature of lower vertebrate feeding mechanisms, and our data provide no support for the notions

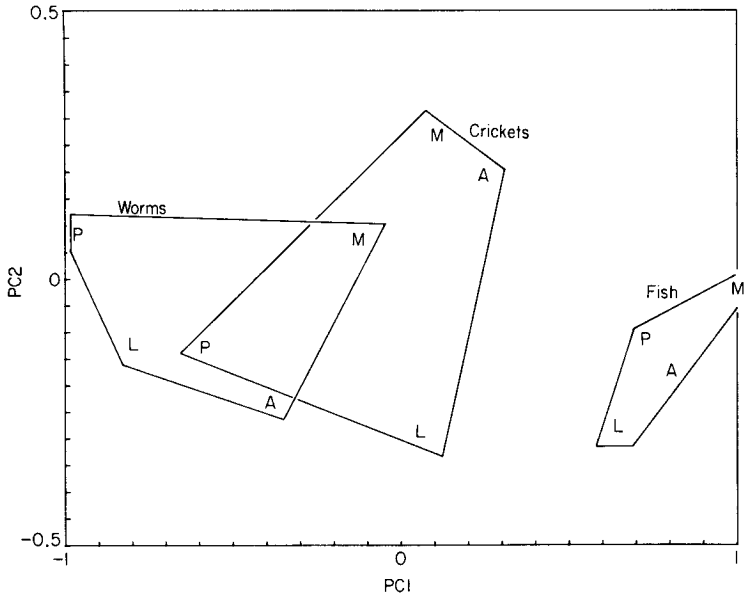

Figure 2. Positions of prey centroids for four centrarchid species on the first two components of a principal components analysis (PCA). The PCA was conducted on 11 variables that summarized the pattern of activity in four cranial muscles during suction feeding (see Materials and methods). Species code: A = *Ambloplites*, L = *Lepomis*, P = *Pomoxis*, M = *Micropterus*.

that high-speed feeding mechanisms are relatively invariant or that individuals within a species differ little in functional variables. Again, this emphasizes the need for interspecific comparisons to account for variation within species.

One cautionary note is warranted concerning our conclusions about individual variation. Differences among experimental preparations could contribute to our 'individual' component of variation. In this experimental design we have not partitioned effects due to experimental preparations from differences attributed to individuals. Shaffer & Lauder (1985a) found significant differences between data obtained on different days from the same individuals for about 20% of their electromyographic variables. Nevertheless, most of the variables still showed significant variation among individuals, supporting the findings reported here.

The results of our comparisons between species suggest that the overall pattern of activity for the four cranial muscles is similar in these four sunfishes. However, the duration of activity of the sternohyoideus muscle (SH) was significantly different among the four species (Table 2), indicating that this was the only variable out of the 11 measured that is useful for distinguishing the species. Two points help to clarify the significance of this result. First, in quantitative studies of suction feeding in ambystomatid salamanders, electromyographic and kinematic variables associated with the sternohyoideus were the only ones found to be significantly different among the species studied (Shaffer & Lauder, 1985a, b). Secondly, data on salamanders (Lauder & Shaffer, 1985) and our unpublished work with sunfishes suggest that, among the muscles investigated, activity of the SH is the most highly correlated with variation in buccal suction pressure measured during the strike. The correlation between buccal pressure and activity of the SH in these taxa is believed on biomechanical grounds to result from a causal relationship. Contraction of the sternohyoideus muscle causes the greatest volume change within the buccal cavity of any cranial muscle and ventral movement of the hyoid occurs at the appropriate time during feeding to result in a negative pressure within the mouth. Thus, adjustments in activity of SH may be the simplest way different species can make changes in the muscle activity pattern that effect changes in generation of negative buccal pressure, and thus feeding performance. The fact that both aquatic salamanders (Lauder & Shaffer, 1985) and the sunfishes studied here assort primarily along the variables associated with the generation of negative pressure within the mouth cavity suggests that differences in feeding performance between species may be achieved by relatively small changes in the activity of one muscle. The hypothesis that variation in function of the sternohyoideus muscle is causally related to differences between species in feeding performance remains to be tested.

Modulation

The major finding of this study is that the four sunfish species differ in their ability to modulate the pattern of jaw muscle activity in response to different prey. For three of the species studied most of the variables responded to different prey while *Ambloplites* shows no significant effect of prey type on the pattern of muscle activity. *Ambloplites* can thus be thought of as the most stereotyped of the species studied.

The feeding repertoire of each species is best viewed as a continuum rather than a specific stereotyped muscle activity pattern for each prey type. Our data provide no indication that each prey type elicits a separate distinct feeding pattern. By using prey of drastically different escape abilities we have elicited predictable changes of muscle activity patterns in three of the species. However, in all four centrarchids, a tremendous amount of variation exists among feeding trials for each prey type. In our tests of the prey type effect we have not investigated the inherent variability in the suction feeding repertoire of each species; rather we have tested the ability of each species to respond to different prey. Indeed, the overall range of values of each variable was about the same for each species (Table 1). The essence of the concept of modulation in this case is that the fish be able to control the pattern of muscle activity as a functional response to feeding conditions and prey type. *Ambloplites* appears to have a generalized feeding response in the sense that, while it is as variable as the other centrarchids (i.e. it has as wide a range of potential EMG values), it does not change muscle activity when feeding on different prey. The ability to modulate appears to be independent of the inherent variability in muscular activity.

What is the effect of prey type on the pattern of jaw muscle activity? As noted earlier, the first principal component (the axis of maximum variation through the data set) from the PCA is a prey-type axis. Because this axis tends to distinguish prey types within each species (Fig. 2) the effects of prey are about the same for the four sunfishes. While PC1 separates prey even for *Ambloplites* (Fig. 2) the variability within each prey type for this species is so high that the differences apparent in Fig. 2 are not statistically significant.

The first principal component contrasts fish feedings and worm feedings. In general the overall activity of muscles is greater and the overlap of muscle activity is greater (low values of LOP–AM2) during fish feedings whereas the opposite is true of patterns associated with worm feedings (Fig. 1). In the modulating species it was quite common for worm feedings to elicit no activity in one or more muscles, typically SH or EP. This pattern of increased muscle activity associated with capture of elusive prey is typical of that reported for other suction feeding actinopterygian fishes (Liem, 1978; Lauder, 1981).

An appropriate experimental design coupled with a quantitative representation of neuromuscular variation during activities such as feeding is emerging as a powerful approach in comparative organismal functional morphology (Gans & Gorniak, 1982; Shaffer & Lauder, 1985a, b; Lauder & Shaffer, 1985). However, still generally unknown is the biological significance of variation in the feeding mechanism. For example, it has usually been assumed that electromyographic modulation represents a fine tuning of the feeding response to capture different prey more 'effectively' (Elshoud-Oldenhave & Osse, 1976; Liem, 1980; Lauder, 1981). This assumption has never been explicitly tested. Thus, a primary objective of future studies will be to clarify the functional implications of modulation in the feeding behaviour of lower vertebrates, and the extent to which other clades exhibit species that differ in their ability to modulate feeding behaviour.

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