

CONVERGENCE IN THE FEEDING MECHANICS OF ECOMORPHOLOGICALLY SIMILAR SPECIES IN THE CENTRARCHIDAE AND CICHLIDAE

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Summary

We examined the hypothesis that fish species with similar ecomorphological patterns, but from different taxonomic groups, would use similar feeding modes. We contrasted the feeding behavior of *Micropterus salmoides* (Lacépède) (Centrarchidae) and *Cichla ocellaris* (Block and Schneider) (Cichlidae), both large-mouthed piscivores with a locomotor morphology designed for fast acceleration, with *Lepomis* spp. (Centrarchidae) and *Cichlosoma severum* (Heckel) (Cichlidae), both small-mouthed predators on benthic invertebrates with a locomotor morphology designed for maneuverability. Pressure profiles in the buccal and opercular cavities were more similar for species that shared ecomorphological patterns than for species that shared phylogenetic histories. For small-mouthed predators, minimum buccal pressures were significantly greater and occurred earlier than the corresponding opercular pressures. For both large-mouthed predators, minimum buccal and opercular pressures were similar in magnitude and in timing. We developed the ram–suction index (RSI) to identify the relative contributions of ram feeding (i.e. predator movement) and of suction feeding (i.e. prey movement) to shortening the predator–prey distance during the strike. The RSI values for small-mouthed predators fell closer to the suction end of the ram–suction continuum than did strikes by the large-mouthed predators. The RSI provides a bench mark for evaluating the hydrodynamic consequences of intraspecific, interspecific and interprey variation in strike mechanics.

Introduction

While both functional morphology and ecological morphology are concerned with

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organismal form, each has its own emphasis (see Alexander, 1988). Functional morphology is centered on exploring how structures work and how differences in form influence the mechanical performance of these structures. In ecomorphology, the emphasis is on identifying the relationships between interspecific variation in these structures and ecological differences among species.

The study of the trophic ecomorphology of fishes is an active area of research. Typically, interspecific patterns of diet and distribution are compared to patterns of variation in mouth structure and body form among members of a fish assemblage (e.g. Keast and Webb, 1966; Ebeling and Cailliet, 1974; Gatz 1979*a,b*; Page and Swofford, 1984; Grossman, 1986; Motta, 1988; Winemiller, 1991). Because of their *post-hoc* nature, ecomorphological studies are strictly correlational (Wiens and Rotenberry, 1980); the bridge from correlation to causation depends on providing a mechanism by which these interspecific differences in morphology can influence organismal performance and, thereby, trophic ecology (e.g. McComas and Drenner, 1982; Bentzen and McPhail, 1984; Wainwright, 1988; Norton, 1991).

Functional studies can provide important insights into the biomechanical basis of ecomorphological patterns. Functional morphologists have described three strike modes in fishes: ram feeding, suction feeding and manipulation (Liem, 1980*a*). In manipulation, the oral jaws are used to bite the prey organism from the substratum or a piece out of a larger prey. In ram feeding, the predator engulfs the prey *via* rapid acceleration of the whole body (e.g. *Esox niger*, Rand and Lauder, 1981), often assisted by protrusion of the ascending process of the premaxilla (e.g. *Luciocephalus pulcher*, Lauder and Liem, 1981). During a pure ram strike the predator moves and the prey does not. In suction feeding, subambient pressure generated by rapid expansion of the buccal cavity draws a jet of water into the mouth; this jet drags the prey into the buccal cavity (e.g. *Lepomis macrochirus*, Lauder, 1983*b*). In a pure suction strike, the prey moves but the predator does not.

Ram and suction feeding, described here as discrete modes, represent ends of a continuum. Many fishes can modulate their feeding mechanics in response to prey type and position (e.g. Nyberg, 1971; Elshoud-Oldenhavé and Osse, 1976; Liem, 1978, 1979, 1980*b*; Lauder and Norton, 1980; Vinyard, 1982; Lauder, 1983*a*; Wainwright, 1988; Wainwright and Lauder, 1986; Sanderson, 1988; Coughlin and Strickler, 1990); thus, individual species can be thought of as occupying a range along this continuum. Previous attempts to shoe-horn fish species into strict ram or suction feeder categories have been the source of some controversy in the literature (e.g. Lauder and Liem, 1981, *vs* van Leeuwen, 1984). One of the goals of this paper is to present a quantitative index that can describe the position of individual strikes along this continuum.

Fishes in the family Centrarchidae have received extensive ecomorphological and functional morphological scrutiny. Several studies (Keast and Webb, 1966; Keast, 1978; Gatz 1979*a,b*) have documented a clear ecomorphological gradient, from large-mouthed predators with fusiform bodies that feed on elusive prey (e.g. *Micropterus salmoides* on fishes and crayfish) to small-mouthed species with laterally compressed bodies that feed on grasping, benthic invertebrates (e.g. *Lepomis gibbosus* feeding on benthic insects and snails). Dramatic interspecific differences exist in the magnitude of negative pressures

generated during the strike and in the relationship between minimum pressures in the buccal and opercular cavities (Lauder, 1983b). These interspecific differences in morphology, attack strategy and buccal pressures create differences in the water flow patterns generated in front of the mouth (Lauder and Clark, 1984). These functional studies provide a robust mechanistic basis for the observed ecomorphological pattern in centrarchids.

Convergence in ecomorphological relationships appears to be a common phenomenon in fishes (e.g. Davis and Birdsong, 1973; Ebeling and Cailliet, 1974; Gatz 1979a,b; Page and Swofford, 1984; Winemiller, 1991). Among the neotropical cichlids there are species whose ecomorphological patterns appear to parallel those found among the neotemperate centrarchids (Barlow, 1974). For example, *Cichla ocellaris* shares many aspects of both the morphology and feeding ecology of *M. salmoides* (Knoppel, 1970; Zaret and Paine, 1973). In the speciose genus *Cichlasoma*, many species share the morphology and ecology of *Lepomis* species (Lowe-McConnell, 1969; Barlow, 1974; Loiselle, 1980, 1981; Escalante, 1984).

The goal of this study was to test the hypothesis that predators that had evolved similar ecomorphological patterns would utilize convergent feeding modes despite their separate evolutionary histories. Thus, we would predict that large-mouthed centrarchids (*M. salmoides*) and cichlids (*C. ocellaris*) would be more similar in their feeding mode than either would be to their small-mouthed confamilials, *Lepomis* spp. and *C. severum*, and *vice versa*. To test these interspecific predictions we examined three variables: (1) the magnitude of minimum pressures developed in the buccal and opercular cavities during the strike, (2) the timing of these minimum pressures and (3) the relative position of these predators on the ram-suction continuum. We also investigated, to a limited extent, the relative abilities of these species to modify their feeding mode in response to differences in prey type, elusive vs non-elusive prey.

Materials and methods

The predators and prey

The predator species that we chose from each family represent ecomorphological contrasts and were predicted to occupy opposite ends (but not extremes) along the ram-suction continuum. *Micropterus salmoides* (Centrarchidae) is a specialist on elusive prey (i.e. fishes and crayfish) (Keast and Webb, 1966; Gatz, 1979a; Keast, 1985), with a large gape and locomotor specializations for rapid acceleration (fusiform body, posterior extensions of the median fins, low aspect-ratio caudal fin, Webb, 1984). *Cichla ocellaris* (Cichlidae) is a major piscivore in Central and South American waters (Lowe-McConnell, 1969; Knoppel, 1970; Zaret and Paine, 1973). Like *M. salmoides*, *C. ocellaris* has a large gape and locomotor specializations for acceleration. In contrast, benthic invertebrates are important to the diets of both *L. gibbosus* (Centrarchidae) (Keast, 1978; Gatz, 1979b; Hanson and Qadri, 1984) and *C. severum* (Cichlidae) (Knoppel, 1970; Loiselle, 1980) although, like many Amazonian fishes, *C. severum* will also feed extensively on plant material during the wet season (Lowe-McConnell, 1969;

Goulding, 1980). These species have a small gape and have locomotor specializations for maneuverability (laterally compressed body, anterior extension of the spiny dorsal fin, median/paired fin propulsion; Webb, 1984). Functionally relevant elements of the locomotor morphology (e.g. body shape, fin position) of these four predators are presented in Fig. 1.

The ability of a fish to generate a high-velocity feeding current depends on several factors, including the area of the mouth aperture, the volume change of the buccal cavity and the rates of mouth opening and buccal expansion (Alexander, 1970; Muller *et al.* 1982). To quantify interspecific differences in mouth area and buccal volume, we made casts of the expanded buccal cavities by pumping silicone sealant into the mouths of individuals killed in a solution of tricaine methanesulfonate. Each cast of the fully expanded buccal cavity was allowed to harden inside the fish and then dissected out. We allowed the casts to cure for at least 1 week before trimming off any sealant that had gone through the gill bars or into the esophagus. We measured the buccal volume in a graduated cylinder and the mouth area from the diameter of the round mouth opening. Since it is the relationship between buccal volume and mouth area that affects suction performance, rather than their absolute magnitudes, we divided buccal volume by mouth area to express this relationship. Interspecific differences in the ratio of buccal volume to mouth area are presented in Fig. 1.

The sizes of predators used in various phases of this research are indicated in Table 1. Elusive prey (live goldfish or guppies) and non-elusive prey (pieces of smelt or earthworms) were used to elicit a range of attack behaviors from the predators. Both *L.*

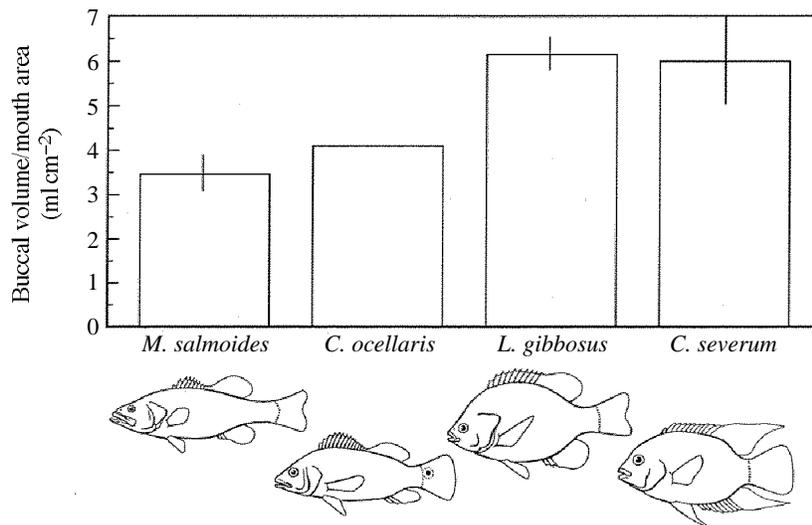


Fig. 1. Diagrams depicting the locomotor morphology of the four predator species used in these experiments (*Lepomis gibbosus* and *Micropterus salmoides*, Centrarchidae, and *Cichlosoma severum* and *Cichla ocellaris*, Cichlidae). Sample sizes are indicated in Table 1. Also depicted are predictions of their relative abilities to generate negative pressure in the buccal cavity calculated as the ratio of potential buccal volume change/the area of the open mouth (means and standard deviation).

Table 1. Sizes of individuals used for various measurements

Species	SL (cm)	BV/MA	RSI	Pressure
<i>Micropterus salmoides</i>	24.4	×	×	×
	21.6	×		
	18.8	×	×	
<i>Lepomis gibbosus</i>	18.0	×		
	13.1	×	×	
	12.9	×	×	
	12.6	×	×	
<i>Cichla ocellaris</i>	21.4	×	×	×
	19.5		×	
<i>Cichlosoma severum</i>	15.5	×	×	×
	12.7	×		
	11.0	×		

SL, standard length; BV/MA, buccal volume and mouth area; RSI, ram-suction index.

The symbol × indicates that the indicated individual was used in a particular analysis.

gibbosus and *C. severum* were fed guppies and goldfish (1–2cm total length, TL) and pieces of earthworms (1–2cm in length). *Micropterus salmoides* were fed goldfish (2–5cm TL) and pieces of either smelt or earthworms (1–2cm in length). *Cichla ocellaris* would only feed on live prey, goldfish (2–5cm TL).

Pressure recordings

Millar Mikro-Tip (Houston, TX) pressure transducers were used to follow changes in buccal and opercular pressures of *M. salmoides*, *C. ocellaris* and *C. severum* (see Table 1). We also present data from G. V. Lauder on the relationship between buccal and opercular pressure minima for the small-mouthed centrarchids (represented by *Lepomis macrochirus*); the patterns of pressure changes in strikes by *L. macrochirus* are qualitatively and quantitatively similar to those generated by other small-mouthed centrarchids, e.g. *L. gibbosus* and *L. auritus* (Lauder, 1980, 1983b).

The sensors of the Millar Mikro-Tip transducers consist of a strain gauge bonded to a membrane with a high natural frequency. By virtue of their high-frequency response (10kHz) and small size, these pressure transducers are ideal for measuring the rapidly fluctuating pressures encountered during aquatic prey capture (van Leeuwen and Muller, 1983). The pressure sensors were threaded through the guide cannulae to within 1cm of the buccal or opercular cavity. This close placement minimized any potential damping due to the cannula.

Guide cannulae for the pressure transducers were implanted into the buccal cavity through the ethmo-frontal region of the neurocranium and into the opercular cavity through the cleithrum (Lauder, 1980). During surgery, fishes were anesthetized in buffered tricaine methanesulfonate. A 2mm diameter hole was drilled through the bone and the cannula tubing (Intramedic, outer diameter 1.9mm, inner diameter 1.4mm) was threaded through the hole such that a flange on the proximal end of the cannula lay flat

against the roof of the buccal cavity or against the anterior face of the cleithrum in the opercular cavity. The guide cannulae were firmly affixed to the fish by a clamp attached to fine surgical-steel wire passed through the epaxial musculature just anterior to the first dorsal spine.

The pressure signals were amplified through Grass P5 series preamplifiers, recorded on a Bell and Howell tape recorder at a tape speed of 38cm s^{-1} , and played back at a tape speed of 4.7cm s^{-1} onto a Gould-Brush 260 pen recorder. We recorded the pressure changes in the buccal and opercular cavities simultaneously. We measured the minimum negative pressure generated in each cavity and the timing offset between the minimum pressures in each cavity.

Calculation and measurement of the ram-suction index

We developed a quantitative index, the ram-suction index (RSI), that allowed us to place individual strikes along the ram feeding/suction feeding continuum. We recorded the x,y coordinates of both the predator and the prey at the start of the strike, i.e. from the film frame or video field at the moment of opening of the predator's mouth. We then recorded the x,y coordinates of the predator and prey (from the point on the prey most distant from the predator) at the last frame or field before the prey disappeared into the predator's mouth.

These coordinates were used to calculate the net distance moved by the predator and by the prey during the strike. The ram-suction index (RSI) was calculated as:

$$\text{RSI} = (D_{\text{predator}} - D_{\text{prey}}) / (D_{\text{predator}} + D_{\text{prey}}),$$

where D_{predator} is the net distance moved by the predator and D_{prey} is the net distance moved by the prey. This index ranges from +1, a pure ram strike in which only the predator moved, to -1, a pure suction strike in which only the prey moved. To assess the contribution made by premaxillary protrusion to the strike, we measured predator position from two body landmarks, the tip of the premaxilla and the anterior edge of the eye, and calculated two indices for each strike: RSI_{body} using the eye as the predator landmark and RSI_{pmx} using the premaxilla as the landmark.

Two motion-analysis systems were employed to gather the data for the RSI. A Photosonics 16mm film camera with two 650W tungsten lights was used initially. Later strikes were videotaped with the NAC 200 high-speed video system with synchronized stroboscopic lights. Both recorded strikes at 200images s^{-1} . Only strikes that were approximately parallel (within 15°) to the plane of the camera or video lens were analyzed. Feeding strikes on film were analyzed frame by frame with a Graf Pen sonic digitizer (Science Accessories Corp., Southport, CT). Feeding strikes on video, analyzed field by field, were first filtered through a ForA F-400 time-base corrector and then digitized using a PC Vision frame-grabbing board (Imaging Technology Inc., Woburn, MA).

Statistical methods

The statistical analysis of both the pressure data and the kinematic data incorporated a similar design, an intraspecific analysis of variance (ANOVA) that contrasted the

influence of the two prey types and an interspecific ANOVA that contrasted the responses of different predators to the same prey types. All statistical tests were run using PC-SAS 6.03 (SAS, 1987). Examination of the descriptive statistics revealed that for all three pressure variables (minimum buccal pressure, minimum opercular pressure and timing offset of minimum pressures) the means were correlated with the variances, a violation of a fundamental assumption of ANOVA (Underwood, 1981); log transformation ($\log+1$ for the former two variables, $\log+100$ for the latter) of the raw data corrected this problem and ANOVA was conducted on the transformed data.

In the intraspecific analysis we used a model I one-way ANOVA in which the prey type served as the independent variable and each of the pressure variables in turn served as the dependent variable (Sokal and Rohlf, 1981). In the interspecific analysis we conducted a separate model I one-way ANOVA for each prey type (i.e. elusive or non-elusive), in which predator species served as the independent variable and each pressure variable in turn served as the dependent variable. In those cases for which a significant predator species effect was found in attacks on elusive prey, we used the Ryan–Einot–Gabriel–Welsch multiple F -test (Einot and Gabriel, 1975) in *a posteriori* comparisons of interspecific differences in pressure variables among the predators. We also contrasted the pressure variables for strikes by *C. severum* that resulted in either misses or captures on elusive prey (guppies), i.e. a model I one-way ANOVA for which strike outcome was the independent variable and the pressure variables were the dependent variables.

In the kinematic analyses we conducted parallel statistical analyses with either kinematic index, RSI_{body} or RSI_{pmx} , as the dependent variable. Because the RSI is effectively a percentage of the initial predator–prey distance, its values may deviate from normality, especially for very low or very large percentages (Sokal and Rohlf, 1981). In this study, most of the RSI values were not extreme and the data and analysis presented here are not arcsin-transformed. Further, statistical analyses conducted with arcsin-transformed data were no different in level of significance or degree of interspecific separation from non-transformed data.

In our analysis of intraspecific differences in attack kinematics, we employed three statistical designs. For *M. salmoides* and *L. gibbosus* we used a mixed-model two-way ANOVA with prey type as the fixed independent factor and predator individual as the random independent factor. For *C. ocellaris*, we used a model II one-way ANOVA with predator individual as the only independent factor. For *C. severum* we used a model I one-way ANOVA with prey type as the only independent factor.

The basic statistical design for the interspecific analysis was a mixed-model nested ANOVA with predator species as the fixed independent effect and replicate individuals nested as the random independent factor. Separate analyses were conducted for each prey type and for each of the indices. The significance of the species effect was evaluated using the mean square of the nested term as the denominator mean square (Sokal and Rohlf, 1981). If this produced a significant species effect, then the Ryan–Einot–Gabriel–Welsch multiple F -test (Einot and Gabriel, 1975) was used to separate the predator species.

Results

Intra- and interspecific comparisons of pressure data

The traces of the time course of pressure changes in the buccal and opercular cavities that we recorded for strikes by *M. salmoides*, *C. ocellaris* and *C. severum* are qualitatively similar to those reported for other species (Alexander, 1970; Lauder, 1980, 1983b; van Leeuwen and Muller, 1983; van Leeuwen, 1984). Near the start of the strike, pressures in both cavities declined below ambient pressure almost monotonically, reaching minimum values after 25–50ms; pressures then returned towards ambient levels during the adduction phase of the strike (Fig. 2).

The relationships between the magnitudes of minimum buccal pressure and minimum opercular pressure were very different between the large-mouthed predators [*C. ocellaris*: reduced major axis (RMA) regression, $y=0.596x-1.67$, $r^2=0.50$; *M. salmoides*: RMA regression, $y=1.27x+0.56$, $r^2=0.44$] and the small-mouthed predators [*C. severum*: RMA regression, $y=0.173x-0.52$, $r^2=0.57$; *L. macrochirus* (data courtesy of G. V. Lauder): RMA regression, $y=0.2191x-1.51$, $r^2=0.64$] (Fig. 3). In a paired sample *t*-test there were no significant differences in the magnitude of minimum buccal and opercular pressures for either *C. ocellaris* ($t_{16}=1.26$, $P>0.20$) or *M. salmoides* ($t_{43}=0.86$, $P>0.35$). However,

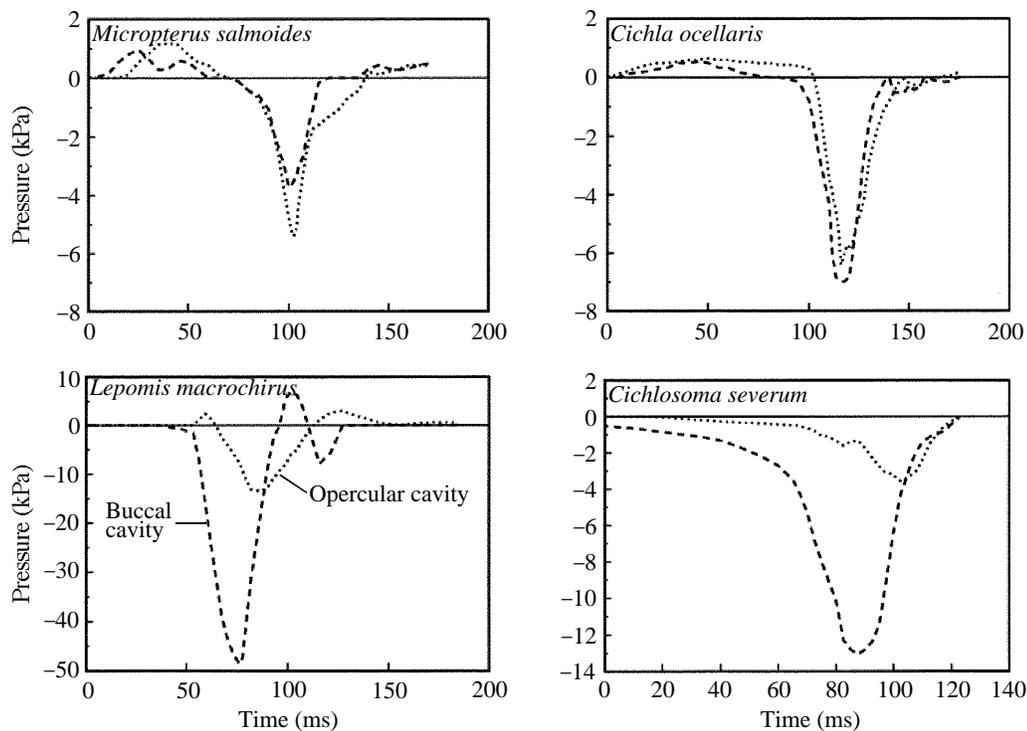


Fig. 2. Representative pressure traces in the buccal (dashed lines) and opercular (dotted lines) cavities during strikes by the four predator species in attacks on elusive prey (live fish). The data on *Lepomis* are from Lauder (1980). Note: in all figures the pressures are given relative to ambient.

minimum buccal pressures generated by *C. severum* were 3–4 times lower than those in the opercular cavity ($t_{70}=10.1$, $P<0.001$). A similar relationship between the buccal and opercular cavity pressures has been reported for several *Lepomis* species by Lauder (1980, 1983b).

While *M. salmoides* did not appear to modify its strike in response to prey type, strikes by *C. severum* on elusive prey created much greater subambient buccal pressures than did those on non-elusive prey (Fig. 3). For *M. salmoides*, neither the magnitude of the minimum pressures generated in buccal ($F_{1,41}=0.75$, $P>0.35$) and opercular cavities ($F_{1,41}=0.14$, $P>0.70$) nor their relative timing ($F_{1,41}=0.42$, $P>0.50$) was different during strikes on the two prey types. By contrast, strikes by *C. severum* on elusive prey resulted in greater subambient pressures in both the buccal ($F_{1,68}=83.9$, $P<0.0001$) and opercular ($F_{1,68}=45.8$, $P<0.0001$) cavities than did strikes on non-elusive prey. Further, the minimum pressures in these two cavities were more synchronous in strikes on elusive prey ($F_{1,68}=22.48$, $P<0.0001$). Finally, comparisons of the relative timing or magnitude of subambient pressures for attacks by *C. severum* on elusive prey that resulted in misses versus captures revealed no significant differences: minimum buccal pressure $F_{1,39}=1.49$, $P>0.20$; minimum opercular pressure $F_{1,39}=0.42$, $P>0.50$; pressure synchrony, $F_{1,39}=3.29$, $P>0.05$.

There were significant interspecific differences (Fig. 4) in the pressure profiles of predators attacking the same prey type in all but one case – buccal pressure in attacks on non-elusive prey (Fig. 4 and Table 2). Subambient buccal pressures were greatest for *C. severum* in attacks on elusive prey, but there were no differences among the predators for non-elusive prey. Subambient opercular pressures were least in *C. severum* regardless

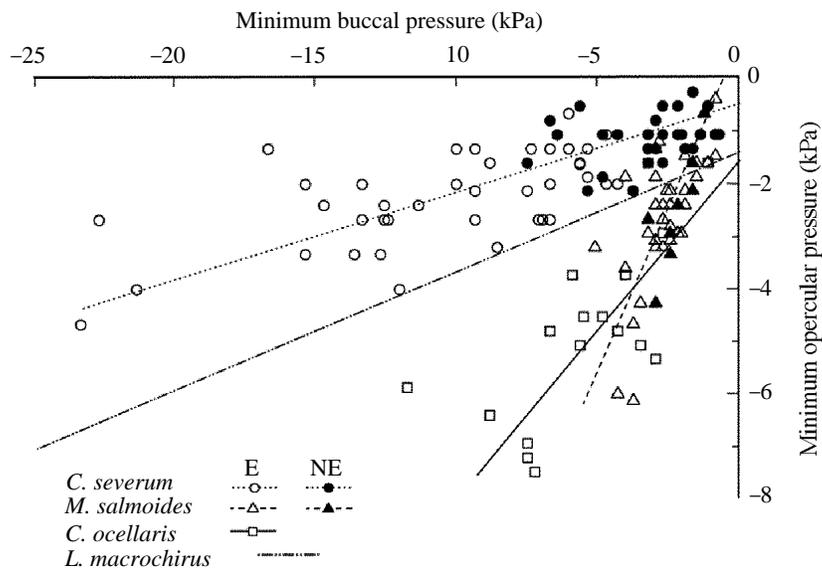


Fig. 3. Relationship between the minimum pressures generated in the buccal cavity and those in the opercular cavity for four predator species in strikes on elusive and non-elusive prey. The lines depict estimates (reduced major axis regressions) of the relationship between minimum buccal and opercular pressures. E, elusive prey; NE, non-elusive prey.

of prey type and greatest for *C. ocellaris* in attacks on elusive prey. The minimum opercular pressures in *C. severum* occurred 10ms (elusive prey) to 15ms (non-elusive

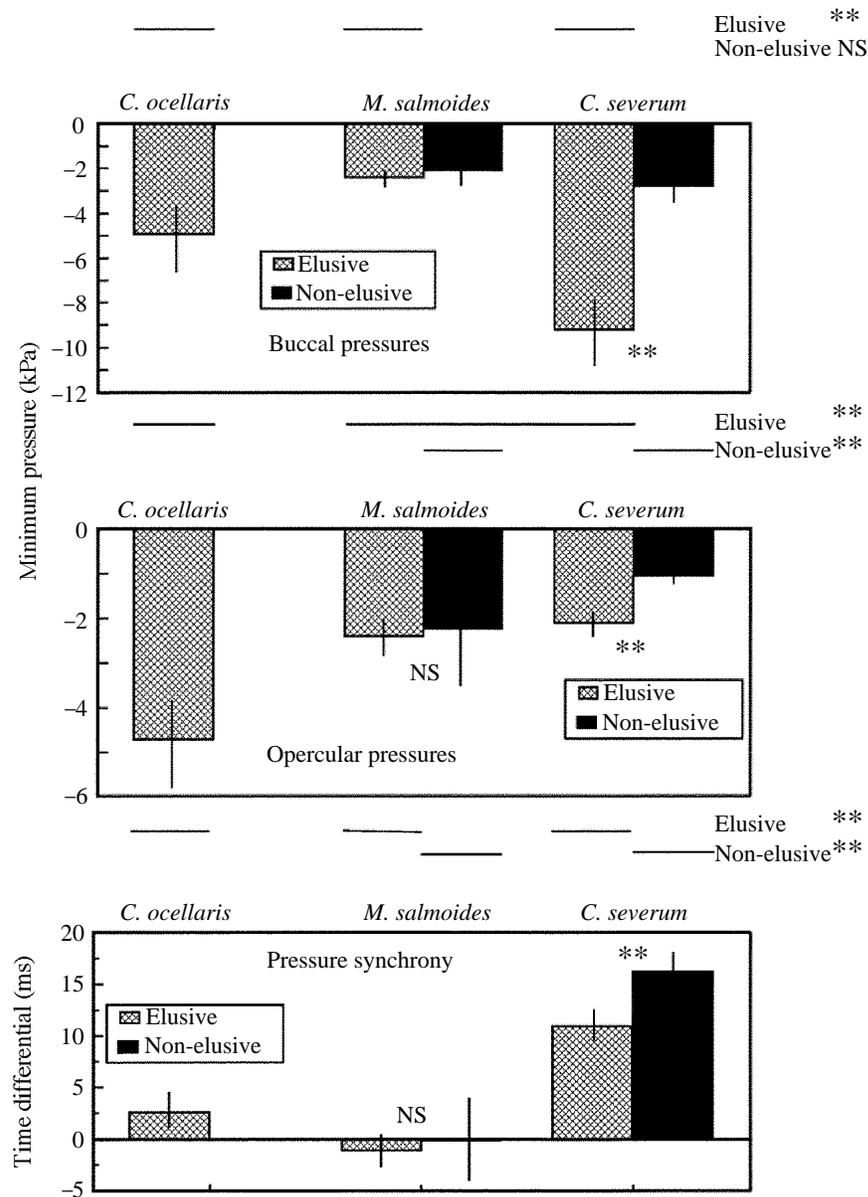


Fig. 4. Interprey and interspecific variation in the magnitude and relative timing of minimum pressures generated in the buccal and opercular cavities. Indicated within the graphs are the results of intraspecific ANOVA tests contrasting prey types. Above each graph are the results of interspecific ANOVA and *a posteriori* tests contrasting these pressure variables for predators feeding on the same prey type. NS, $P > 0.05$; ** $P < 0.01$. Values are mean \pm 95% confidence interval.

prey) after the minimum buccal pressures; opercular pressures were more synchronous with buccal pressures in the two large-mouthed species, approximately 2.5ms behind in *C. ocellaris* and synchronous in *M. salmoides* (all strikes, null hypothesis: offset in timing=0, $t_{43}=1.42$, $P>0.15$).

Intra- and interspecific comparisons of predator and prey movements

There were dramatic interspecific differences in the patterns of predator and prey movement during the strike. In Fig. 5 we show the relative movements of predators and

Table 2. ANOVA tables of pressure variables for interspecific attacks on the same prey types

Dependent variable	Independent variable	d.f.	F	P
Buccal pressure	Elusive prey	2,89	74.7	0.001
	Non-elusive prey	1,35	1.52	0.20
Opercular pressure	Elusive prey	2,89	20.3	0.001
	Non-elusive prey	1,35	15.4	0.001
Pressure synchrony	Elusive prey	2,89	87.1	0.001
	Non-elusive prey	1,35	88.4	0.001

The dependent variables are measures of the magnitude or relative timing of pressures during the strike.

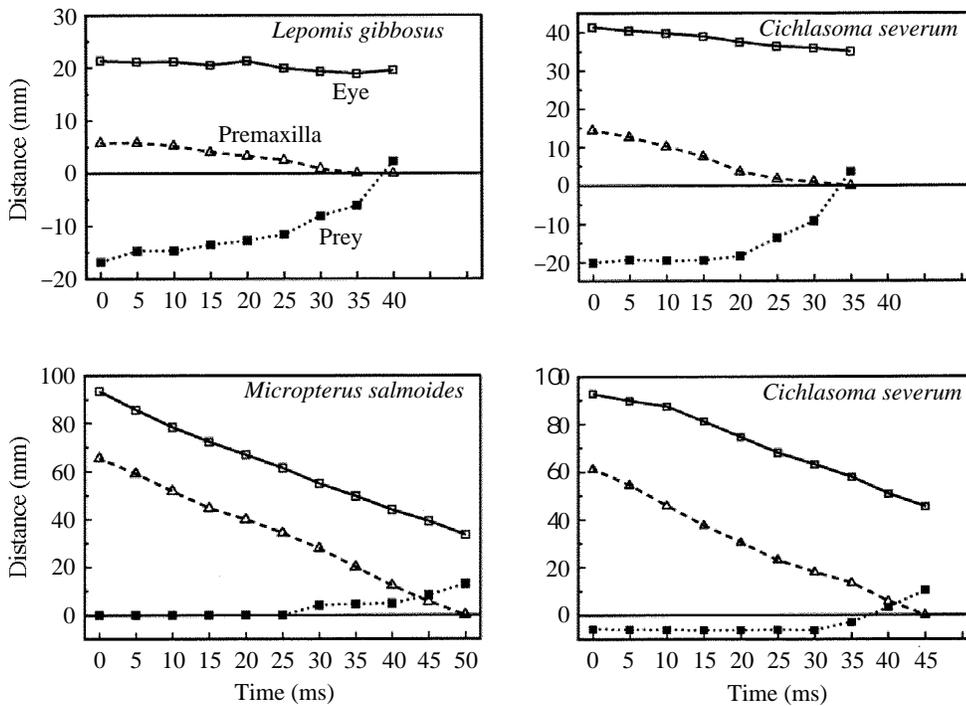


Fig. 5. Representative tracks of predator and prey motion during strikes by the four predators on fish. The plots start at the moment of mouth opening and end at the field (video) or frame (film) where the posterior edge of the prey disappears.

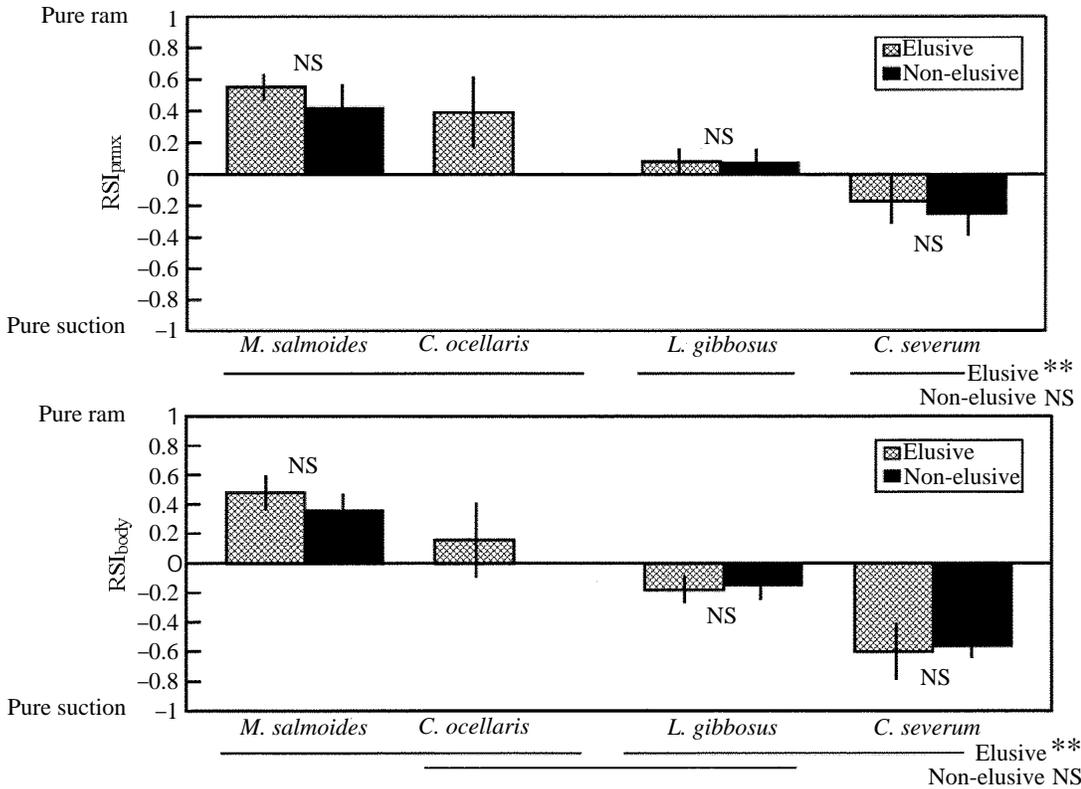


Fig. 6. Interprey and interspecific variation in the ram-suction index calculated from the prey either to the tip of the premaxilla (RSI_{pmx}) or to the eye (RSI_{body}) of the predator. Indicated within the borders are the results of ANOVA tests contrasting prey types. Below each border are the results of ANOVA and *a posteriori* tests contrasting the index values of predators feeding on the same prey type. NS, $P > 0.05$; ** $P < 0.01$. Values are mean \pm 95% confidence interval.

prey during the course of strikes on elusive prey. For both large-mouthed predators, the predator-prey distance is shortened primarily by the movement of the predator's body. For both small-mouthed predators, the predator-prey distance is shortened by movements of both the predator and of the prey. Prey movement is especially pronounced in the last 5 ms.

These patterns are clearly reflected in the ram-suction indices (Fig. 6). There were no inter-prey differences in either RSI for any of the predators (Table 3). However, there were significant interspecific differences in the relative movements of predators and elusive prey as measured by either index (Table 4). Strikes by *M. salmoides* and *C. ocellaris* are more towards the ram feeding end of the ram-suction spectrum, while those by *L. gibbosus* and *C. severum* occupy an intermediate position. If one compares the means of the two indices for each of the four species, thereby focusing on the relative importance of the premaxilla, we can see that premaxilla protrusion contributes the most

to shortening the predator–prey distance in strikes by *C. severum* and the least in strikes by *M. salmoides*.

Table 3. Results of intraspecific analyses of variance for the two versions of the ram–suction index

Independent variable	d.f.	RSI _{body}			RSI _{prmx}		
		MS	F	P	MS	F	P
<i>Micropterus salmoides</i>							
Prey*	1	0.038	0.14	0.77	0.054	0.27	0.65
ind	1	0.306	3.87	0.06	0.391	6.58	0.01
int	1	0.271	3.43	0.07	0.199	0.57	0.07
Error	40	0.079			0.059		
<i>Lepomis gibbosus</i>							
Prey*	1	0.017	0.33	0.67	9.8×10 ⁻⁴	0.04	0.88
ind	1	0.166	1.84	0.18	8.7×10 ⁻³	0.13	0.25
int	1	0.051	0.57	0.46	2.6×10 ⁻²	0.39	0.54
Error	58	0.090			6.7×10 ⁻²		
<i>Cichla ocellaris</i>							
ind	1	0.137	0.68	0.43	1.7×10 ⁻²	0.46	0.51
Error	12	2.43			1.5×10 ⁻¹		
<i>Cichlosoma severum</i>							
Prey	1	1.0×10 ⁻²	0.19	0.67	2.6×10 ⁻²	0.69	0.42
Error	16	1.6×10 ⁻¹			6.4×10 ⁻¹		

*The *F* values for the independent variable prey were calculated using the interaction mean square (int) as the denominator.

Prey, prey type; ind, predator individual; int, interaction term; RSI, ram–suction index; MS, mean square; d.f., degrees of freedom.

Table 4. Results of interspecific analyses of variance for the two versions of the ram–suction index

Independent variable	d.f.	RSI _{body}			RSI _{prmx}		
		MS	F	P	MS	F	P
Non-elusive prey							
spp*	2	3.218	11.8	0.08	1.721	6.14	0.14
ind	2	0.272	3.23	0.05	0.280	4.22	0.02
Error	59	0.084			0.066		
Elusive prey							
spp*	3	3.318	31.6	0.01	1.587	54.3	0.01
ind	3	0.105	1.06	0.37	0.029	0.41	0.74
Error	67	0.099			0.071		

*The *F* values for the independent variable spp were calculated using the mean square of ind as the denominator.

Spp, predator species; ind, predator individuals; MS, mean square; d.f., degrees of freedom.

Discussion

Species in these two fish families (Centrarchidae and Cichlidae) that have comparable ecological niches and similar morphologies also exhibit strong similarities in feeding mechanics. Several features of the pressure profiles (i.e. the absolute and relative magnitudes and the relative timing of minimum buccal and opercular pressures) of strikes by the large-mouthed predators, *M. salmoides* and *C. ocellaris*, were far more similar to each other than they were to those of the small-mouthed, confamilial species, *L. gibbosus* (Lauder, 1980) and *C. severum*. Further, these and other features of the strike not detailed here (e.g. motor patterns in the jaw muscles, attack velocity, etc.) appear to produce similar effects on the prey (i.e. RSI patterns).

Patterns of pressure change

There has been considerable controversy in the functional morphological literature concerning the relative importance of the buccal and opercular chambers in the generation of suction and the direction of flow between these chambers in the strike (see Lauder 1983b, 1986; Muller *et al.* 1985). Theoretical hydrodynamic models presented by Muller and others (Muller *et al.* 1982; Muller and Osse, 1984) predicted that the opercular cavity should be critical to the generation of suction. However, experimental and comparative evidence (Lauder, 1983b) indicates that the gill bars isolate the buccal and opercular chambers during strikes by suction feeders, but do not isolate these chambers during strikes by ram feeders.

Our data for *M. salmoides* are similar to those of Lauder (1983b); the similarities in the magnitude and timing of minimum pressures in the buccal and opercular chambers would indicate that these chambers are connected hydrodynamically. In contrast, the significant differences in timing and magnitude of buccal and opercular pressures in *C. severum* are similar to those found in *Lepomis* spp. by Lauder (1983b). By analogy to *Lepomis*, we hypothesize that the gill bars in *C. severum* isolate the buccal and opercular chambers during the strike. In *C. ocellaris*, the magnitudes of minimum pressures in the two cavities were not significantly different, but the slight, but significant, time lag in minimum pressures may reflect some degree of gill resistance.

The ram–suction continuum

The plots of predator and prey position during strikes by the large-mouthed predators (Fig. 5) show clearly that the approach of the predator is smooth over the interval from the start of the strike (i.e. mouth opening) until prey capture. Little movement of the prey (including potential escape) is detectable. Protrusion of the premaxilla resulted in a net increase in predator velocity (compare the slopes of the body and premaxilla lines in the time–distance plots) and in a shortening of the predator–prey distance (compare the distance from the eye to the tip of the premaxilla at the start of the strike and at prey capture). In strikes by the small-mouthed species, predator movement was primarily due to protrusion of the premaxilla; movement of the prey was first detected 15ms before capture and increased rapidly in the last 5ms. A similar pattern of body and prey movement has been described for the holostean fish *Amia calva* in strikes on live cyprinids (Figs 14 and 15 in van Leeuwen and Muller, 1983).

We have two goals in presenting our ram–suction index. First, we wish to reinforce the concept that ram and suction feeding are not discrete feeding types, but rather ends of a continuum. A firm understanding of this concept may resolve some of the confusion over the definition of suction feeding. Second, the ram–suction index offers a mechanism for quantifying the contribution of ram and suction elements in individual strikes by fishes (this study) and other aquatic predators, e.g. salamanders (Shaffer and Lauder, 1985) and turtles (Lauder and Prendergast, 1992).

The relative importance of ram *versus* suction feeding has been an issue in several recent studies that have attempted to visualize the movement of prey during the strike (Drost and van den Boogart, 1986; Drost, 1987; Coughlin and Strickler, 1990). In one recent study, Drost and van den Boogart (1986) estimated that two-thirds of the initial predator–prey distance was covered by swimming of the predator (larval carp) and one-third by suction of the prey (*Artemia* nauplius) and yet they called this suction feeding. In contrast, Coughlin and Strickler (1990) showed that a planktivorous fish (*Chromis viridis*), formerly assumed to use suction to ‘pick’ plankton, in fact uses ram feeding *via* premaxillary protrusion to capture elusive calanoid copepods, a major element in its diet; a combination of both ram feeding and suction feeding was used to capture less-elusive *Artemia* nauplii. Application of the ram–suction index may remove some of semantic debates that have occurred previously in the literature (Lauder and Liem, 1981, *vs* van Leeuwen, 1984) and provide a mechanism for re-examining previous assumptions concerning the feeding mode used by fishes.

The ram–suction index has enabled us to quantify with some precision the contribution of ram and suction elements to individual strikes. We have confidence in it as a benchmark for evaluating the hydrodynamic consequences of intraspecific, interspecific and interprey variation in strike mechanics. Our index places *L. gibbosus* closer than *M. salmoides* to the suction-feeding end of the spectrum; this result is consistent with our predictions based on fundamental hydrodynamic principles, the morphologies of these species and the pressure patterns of this and similar species. This is also consistent with visualizations of flows generated by large-mouthed (*M. salmoides*) *versus* small-mouthed centrarchids (*L. gibbosus*) during strikes on earthworm pieces (Lauder and Clark, 1984).

As we have formulated it, the RSI focuses on the efforts by the predator to capture prey, through body movement by the predator and through the force imparted on the prey as a jet of water is drawn into the buccal cavity of the predator. However, actions and attributes of the prey may also influence the RSI of an individual strike. Overt actions by the prey (e.g. escape movements or grasping of the substratum) will distort the RSI. In the strikes that we analyzed, the elusive prey did not exhibit any escape movements (i.e. C-starts).

More passive prey characteristics may also influence the RSI. The drag force that carries the prey towards the predator is the sum of the conventional drag and the acceleration reaction (Denny, 1988; Daniel and Meyhofer, 1989; Norton, 1991). Conventional drag is a function of water density, the surface area of the prey, the drag coefficient and the square of the velocity of water passing by the prey. The acceleration reaction is a function of the added mass coefficient, the volume of the prey, the density of the fluid and the acceleration of the fluid past the prey. The flow velocity and acceleration

will depend on the characteristics of the predator, e.g. strike initiation distance, the area of the mouth, the change in buccal volume, and the rate at which the mouth opens and the buccal volume expands. Both the drag coefficient and the added mass coefficient are determined empirically and will change with the size, shape and orientation of the prey to the flow, as well as with the characteristics of the flow (e.g. laminar vs turbulent) (Vogel, 1981; Denny, 1988).

The integration of morphology and behavior

There is no *a priori* reason that predators must use only those behaviors that would appear to maximize the effectiveness of their morphologies (e.g. rapid expansion of the buccal cavity by small-mouthed species at a position close to the prey). There are two alternative strategies. Faced with a difficult prey (e.g. a fish), is capture success likely to be higher for a predator that employs those behaviors that are 'matched' to its morphology (e.g. suction feeding by a small-mouthed predator), even if inappropriate for the functional demands of the prey, or would capture success be higher for a predator that employs a behavioral repertoire (e.g. ram feeding by a small-mouthed predator) that is not 'matched' to its morphology, but might be more appropriate for the prey? In a study of feeding kinematics and capture success among cottid fishes, Norton (1991) has shown that, while most small-mouthed species in his study employed the former strategy, another, *Jordania zonope*, followed the latter. Using these 'unmatched', but appropriate, behaviors (i.e. ram feeding), capture success by *J. zonope* was higher on an elusive prey (shrimp) than that by other small-mouthed species that employed 'matched', but inappropriate, behaviors (i.e. suction feeding). In our study, both the pressure data and the kinematic data indicate that in attacks on fish the small-mouthed predators used those behaviors that 'matched' their morphologies and that accentuated the differences between them and the large-mouthed predators.

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