Functional morphology of feeding in the scale-eating specialist *Catoprion mento*

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Summary

The wimple piranha, *Catoprion mento*, has a narrow-range natural diet with fish scales comprising an important proportion of its total food intake. Scales are eaten throughout most of ontogeny and adults feed almost exclusively on this food source. *Catoprion* exhibits a novel prey capture behavior when removing scales for ingestion. Scale feeding strikes involve a high-speed, open-mouth, ramming attack where the prey is bitten to remove scales and the force of the collision knocks scales free. Unique kinematic parameters of scale-feeding strikes include a mean gape angle of nearly 120° and a 'plateau' stage of prolonged maximum displacement for cranial elevation and opercular expansion. When feeding on live fish or loose scales, *Catoprion* performs a typical ram/suction attack that is modulated according to the elusiveness of the prey. Captures of elusive fish elicit faster strikes with greater displacement of cranial elements than do attacks on loose scales sinking in the water column. Despite its specialized diet and suite of anatomical characters, functional versatility in feeding behavior has not been reduced in *Catoprion*, as predicted by many analogous studies in functional morphology. On the contrary, the behavioral repertoire of *Catoprion* has been broadened by the addition of a novel behavior for scale feeding.

Key words: specialization, feeding, biomechanics, fish, lepidophagy.

Introduction

One fruitful approach to animal function has been to investigate the 'unusual' members of a lineage, species that appear to deviate from the typical form, exhibit novel functions or superlative performance, or inhabit extreme environments. This research approach has contributed to the understanding of the form and function of such amazing structures and behaviors as chameleon tongue projection (Schwenk and Bell, 1988; Wainwright et al., 1991; de Groot and van Leeuwen, 2004), tongue protrusion in plethodontid salamanders (Lombard and Wake, 1976, 1977, 1986; Deban and Marks, 2002), water running in basilisk lizards (Laerm, 1973, 1974; Hsieh, 2003), wall climbing in geckos (Russell, 1975; Irschick et al., 1996), extreme jaw protrusion in fishes (Liem, 1979; Westneat and Wainwright, 1989; Westneat, 1991), brain-warming muscles in billfish (Block et al., 1993), and 'flying' in fishes (Fish, 1990; Davenport, 1992), frogs (Emerson and Koehl, 1990) and lizards (Hairston, 1957). Conceptually, these studies explore the limits to biomechanical and behavioral evolution, provide informative and appealing examples of adaptive change, and expand knowledge of functional biodiversity.

Catoprion mento (Cuvier), the wimple piranha, has a strange diet and equally unusual anatomy and feeding behavior. *Catoprion* is a monotypic genus of small South American characin that inhabits clear freshwater streams and lakes with abundant submerged vegetation (Taphorn, 1992). Its specific name, 'mento', is Greek for 'chin', referring to the distinctive protuberance created by the curve in its banana-shaped,

elongate lower jaw (Fig. 1). Its reduced, conical-shaped teeth on the upper jaw project forward when the jaws are closed (Gery, 1977; Sazima, 1983; Taphorn, 1992). The dietary breadth of *Catoprion mento* is one of the narrowest reported for fishes; scales form an important proportion of the diet throughout most of ontogeny, and adults feed almost entirely on this prey (Vieira and Gery, 1979; Sazima, 1983; Nico and Taphorn, 1988). Despite our perception that scales should be an unappetizing meal, lepidophagy is relatively widespread in fishes, having evolved independently in at least five freshwater and seven marine families (Sazima, 1983). Although the functional morphology of scale feeding has not previously been experimentally investigated, anatomical and behavioral observations suggest that a diversity of morphologies and attack behaviors are used by lepidophagous predators (Roberts, 1970; Major, 1973; Liem and Stewart, 1976; Whitfield, 1979; Sazima, 1977, 1983; Peterson and Winemiller, 1997, 1998) and that the behavioral origins of scale feeding may be different for different lineages (DeMartini and Coyer, 1981; Sazima, 1983; Sazima and Machado, 1990).

Surprisingly, scales are a relatively nutritious food source. In addition to layers of keratin and enamel, teleost scales contain a dermal portion and are covered, in life, with a protein-rich mucus layer (van Oosten, 1957; Wessler and Werner, 1957; Harris and Hunt, 1973; Gorlick, 1980; Whitear, 1986). They are a rich source of calcium phosphate (Whitear, 1986), and calorimetry studies by Whitfield and Blaber (1978)
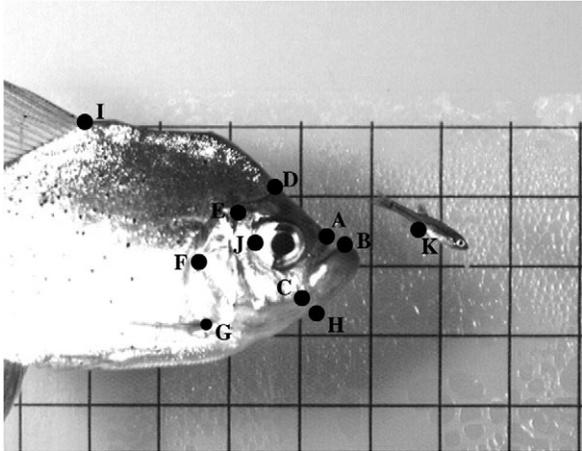
Fig. 1. Landmarks of 11 points digitized on each frame for calculation of the 12 kinematic variables used to describe prey capture behavior. For a description of the points, see text.

and Nico and de Morales (1994) found scales to contain an energy content averaging 8–10 kJ g^{-1}, values approximately two-thirds that of the mass-specific caloric content of whole fishes. Unfortunately, the average mass of scales removed per strike (and therefore the caloric return) and the energy expenditure during scale feeding and other predatory strikes is unknown, but the consumed mass during lepidophagy is likely to be lower. This perhaps explains the observed size limit to scale feeding; lepidophagous fishes seldom exceed 20 cm and most are under 12 cm (Sazima, 1983). Despite their lower energy content, scales have a number of advantages as a food source. Fishes can regrow lost scales relatively quickly – in ~3–4 weeks under laboratory conditions (Sazima, 1983) – so scales represent a renewable resource, ecologically comparable with grazing on plants in many respects. Other benefits to lepidophagy include features that are also conducive to specialization; scales are common, covering the body of most fish species, abundant and seasonally reliable, and their removal requires specific behaviors or morphological structures.

A number of recent studies (Drummond, 1983; Chu, 1989; Meyer, 1989; Sanderson, 1988, 1990, 1991; Ralston and Wainwright, 1997) have investigated the correlation between trophic breadth and the degree of functional versatility (Lauder, 1980; Liem, 1984) in specialist and generalist feeders. The hypothesis of most of these studies is that species with limited diets (trophic specialists) are expected to exhibit a restricted range of behaviors, or show less variability in the kinematics and muscle activity patterns of the strike, compared with generalist species with wider diets. The feeding behavior of *Catoprion* provides an opportunity to test this hypothesis in a species specializing on a derived and specific food source. The fact that specialized scale feeding has evolved independently multiple times may also allow general patterns of form and function in lepidophagous fishes to be identified.

The present study examines the attack behavior and cranial

kinematics of *Catoprion mento* when feeding on three prey items that present different functional challenges for capture and ingestion. The specific goals of the study are threefold: (1) to determine the extent to which *Catoprion* is able to modulate its strike according to the specific demands of different prey; (2) to describe mechanistically the novel prey capture behavior, scale feeding and (3) to test the hypothesis that dietary specialization has resulted in restriction of an ancestral feeding repertoire of greater functional versatility.

Materials and methods

Five *Catoprion mento* Cuvier [standard length (*SL*), 69.7–73.2 mm] were purchased from aquarium suppliers and maintained individually in 22-liter aquaria at temperatures of 25–28°C. Specimens were fed a diet of large goldfish (*Carassius auratus*), from which scales were removed, and small, live cyprinids (*Tanichthys albunubes*; white clouds), which were swallowed whole. A short acclimation period of less than two weeks was required before individuals would feed under experimental conditions. All fishes were filmed in their home tanks. All animal care and research procedures were approved by the Field Museum Institutional Animal Care and Use Committee (protocol FMNH 97-6R).

Kinematics

Individual *Catoprion* were filmed in lateral view while feeding on three different prey: (1) sacrificed goldfish (*SL* 42–45 mm) from which scales were removed by the *Catoprion*, (2) small, live fish (*Tanichthys albunubes*) that were captured whole and (3) loose scales that had been removed with a scalpel from goldfish, placed in the feeding tank and were allowed to sink freely in the water column. Goldfish were tethered with fishing line to a transparent plastic tube and oriented parallel to the camera to ensure attacks occurred within the filming area, but the other prey were not restrained in any way. Fishes were filmed at 250 fields s^{-1} with a high-speed camera (Redlake MotionScope 1000, Indianapolis, IN, USA). A plastic 1-cm grid was placed in the tank to reduce the depth of the filming area and to provide a metric to calibrate the video images.

Images were analyzed field by field in a customized version of NIH Image written by J. A. Walker (www. usm.maine.edu/~walker/software.htm). The field prior to the start of jaw opening was defined as time zero for each strike. Ten coordinates on the predator and one on the prey (Fig. 1) were digitized in each frame and these coordinates were entered into a custom-designed computer program (CodeWarrior, Pascal, J. Janovetz) that calculated the variables used to compare strikes. Cranial displacement variables were calculated as a change in angle over the time of the strike, subtracting the minimum value for each variable from all values for that variable. Angles were used to minimize the effects of size on kinematic variables, especially when comparing strikes from *Catoprion* in this study with published values from other fishes in other studies. The following 10

variables quantifying maximum displacement and time to maximum displacement of cranial movements were calculated: (1) gape angle (A,C,B) between the cranial tips of the jaws and the quadrate/articular joint; (2) cranial elevation (A,E,G), the angle formed by the non-protrusable premaxillla, the attachment of the pectoral girdle to the skull and the anterior attachment of the pectoral fin; (3) hyoid depression (H,C,G), the angle formed by the hyoid, quadrate/articular and pectoral fin; (4) opercular expansion (G,F,E), calculated as the angle between the pectoral fin, posterior point on the suture between the suboperculum and operculum, and attachment of the pectoral girdle to the skull; (5) lower jaw rotation (B,E,C), the angle formed from the tip of the dentary, attachment of the pectoral girdle to the skull, and quadrate/articular joint, and (6–10) time from the frame prior to jaw opening to the maximum displacement for each of the variables above. In addition to these variables quantifying cranial movements, two other variables describing strikes were calculated: (11) prey distance (A,K) in cm, calculated as the linear distance from the premaxilla to the point on the prey that first breaks the plane of the gape, and (12) total gape cycle time (ms), the elapsed time from the frame prior to jaw opening until cranial elements have returned to their resting positions. Individual feeding sequences varied widely (range 128–476 ms) in the total elapsed time of the strike.

To visualize the overall pattern of cranial movement for each prey type, strikes were standardized by aligning each by the time of maximum gape angle. Five strikes from each of the same five individuals were analyzed for each of the three prey types, for a total of 75 strikes. Only successful strikes where the prey was captured or scales were removed were analyzed.

Statistical analyses

A multivariate analysis of covariance (MANCOVA) was performed using prey type and individual standard length as covariates to determine whether prey type and predator size have an effect on strike kinematics. A series of two-way analyses of variance (ANOVAs) were then performed to determine whether mean values for each of the 12 kinematic variables differed among prey types and individuals. If a significant effect was found, individual *t*-tests were performed to determine which pairs of comparisons were significantly different. To control for multiple comparisons, levels of statistical significance were adjusted using the sequential Bonferroni technique (Rice, 1989), resulting in significance values ranging from 0.004 to 0.05 (0.05/12–0.05/1). To describe the major axes of variance in feeding behavior on different prey, a principal components analysis was performed on the 12 kinematic variables. Of the 12 factors extracted from the correlation matrix, only two have an eigenvalue greater than 1 (Norman and Streiner, 1994) and were used to describe feeding behaviors. A scatter plot of these two axes (PC 1 and PC 2) was constructed to illustrate the position of each feeding sequence in multivariate space. All statistical analyses were performed using JMP 3.1 (SAS Institute, 1995) or StatView 5.0.
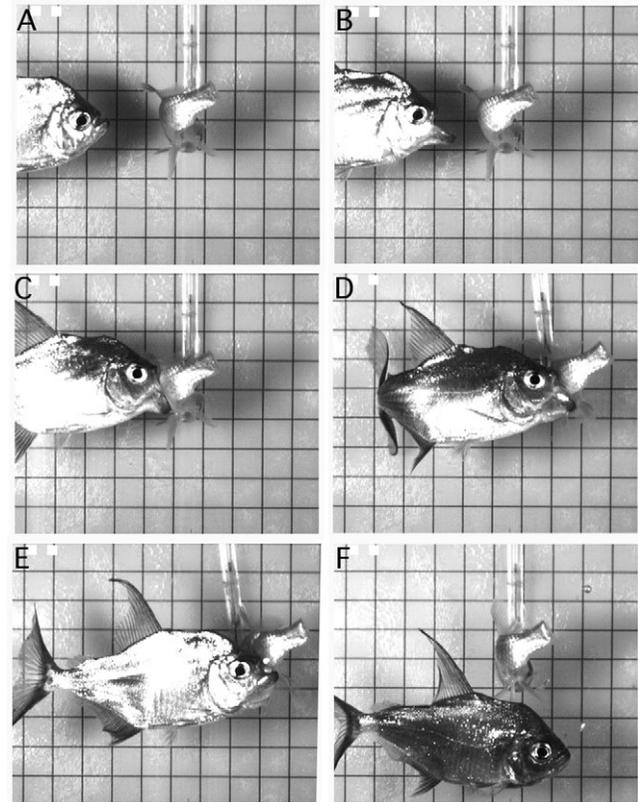

Fig. 2. Representative sequence of *Catoprion mento* scale feeding on a goldfish. (A) Time zero marks the start of jaw opening; (B) 52 ms later, gape angle exceeds 90° well before contact is made with the prey; (C) 76 ms, maximum gape angle; (D) 136 ms, maximum opercular expansion as the teeth rasp the flank of the fish; (E) 164 ms, jaw closing and ingestion of scales during the bite; (F) 260 ms, post-strike, cranial elements have returned to resting position. Note the loose scales in the water column removed during the strike. Note also the integrated use of body and tail undulations throughout the strike to power the ramming attack.

Results

Scale feeding

Under laboratory conditions, *Catoprion* would readily scale feed on fishes longer than three times their own standard length, size differences greater than those reported by Sazima (1988), and scale-feeding cannibalism was observed multiple times in a group of 10 *Catoprion* housed together in a 110-liter aquarium. *Catoprion* began most prey capture attempts on whole prey (goldfish and white clouds) by stalking slowly to within a few centimeters of the prey. The actual attack involved a rapid acceleration towards the prey item, with maximum predator attack velocity averaging 0.86 m s^{-1}. Jaw opening began well before rapid acceleration towards the prey (Fig. 2A) at a mean distance of 1.98 cm (Table 1). Gape angles, while still more than a centimeter away (Fig. 2B), were greater than 90°, which is higher than mean peak gape while feeding on other prey types. Scale-feeding attacks on both tethered and untethered fish were directed near the center of gravity of the

Table 1. *Mean values for 12 kinematic variables measured for* Catoprion mento *strikes on three prey types*

Variable	Fish (F)	Scale (L)	Scale feeding (S)	
Displacement (deg.)				
Gape angle	83.07±7.96	55.51±9.98	119.60±7.03	F, L, S
Hyoid depression	17.42±2.79	13.64±2.68	22.50±3.70	F, L, S
Cranial elevation	17.28±2.90	10.14±2.98	17.64±3.98	F/S, L
Opercular expansion	38.16±10.14	21.89±7.92	30.79±7.98	F, L, S
Jaw rotation	80.80±9.42	52.46±9.70	112.84±6.06	F, L, S
Prey distance (cm)	1.11±0.36	1.09±0.39	1.98±0.36	F/L, S
Timing (ms)				
Time to gape angle	72.64±21.75	101.76±27.84	208.64±57.62	F, L, S
Time to hyoid depression	77.44±25.00	119.20±30.09	216.16±54.35	F, L, S
Time to cranial elevation	77.60±22.98	121.76±29.33	234.40±61.81	F, L, S
Time to opercular expansion	84.96±22.31	129.28±29.41	248.48±68.38	F, L, S
Time to jaw rotation	72.00±20.88	103.20±27.54	208.80±57.19	F, L, S
Total gape cycle time	181.76±33.47	232.16±65.67	337.76±48.67	F, L, S

Values are means ± S.D. (*N*=25 for each prey type).
Variables that are not significantly different are united with a backslash (F/S), statistically different variables are separated by commas (F, S). A sequential Bonferroni-corrected value of *P*<0.05 was used for all comparisons.

prey, similar to predatory behavior reported for other fish species (Rand and Lauder, 1981). A gradual increase in gape angle, largely due to increased lower jaw rotation (Fig. 3), occurred until prey contact was made. At that point, the rate of

Fig. 3. Plots of mean kinematic values (± S.E.M.) for 25 scale-feeding strikes from five *Catoprion mento* individuals. All variables for all strikes were standardized by time of maximum gape angle. The broken line marks the time of prey contact, while the solid line marks the time of maximum gape angle in each plot. Note the plateau stage of stability at near-maximum displacement for cranial elevation and opercular rotation.

lower jaw rotation and gape angle expansion increased as the lower jaw was fitted to the side of the prey (Fig. 2C). The linear gape distance during scale feeding for these similarly sized individuals averaged 1.47±0.14 cm (mean ± S.D.) and mean maximum gape angle was nearly 120° (Table 1). A largely vertical plane was formed between the upper and lower jaws, a posture that orients the everted premaxillary and reduced maxillary teeth of *Catoprion* perpendicular to the body wall of the prey. Maximum hyoid depression and cranial elevation followed approximately 8 and 26 ms, respectively, after peak gape, with maximum opercular rotation following 40 ms later (Table 1). Both cranial elevation and opercular rotation were maintained at values near maximum for prolonged periods, until jaw closing was nearly complete, resulting in a 'plateau' phase in the strike profiles for these variables (Fig. 3). Mouth closing, again largely accomplished by lower jaw rotation (Figs 2, 3), began while the jaws remained in contact with the prey, scraping the teeth along the flanks of the goldfish (Fig. 2D,E). Scales were ingested during the strike (Fig. 2E), and loose scales removed by the impact of the attack (Fig. 2F) were also swallowed as they settled from the water column or were collected from the bottom substrate. Attacks removed only scales; untethered goldfish taken from tanks after repeated attacks showed that the underlying musculature was not bitten. Unlike scale-feeding behavior in the morphologically asymmetric cichlid *Perissodus eccentricus* (Liem and Stewart,
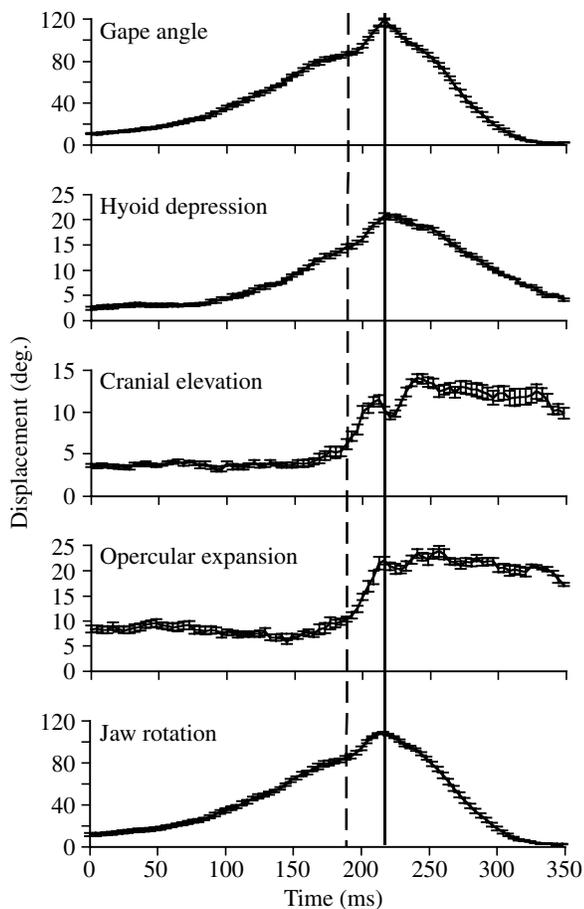
1976), attacks by individual *Catoprion* were made on both left and right sides of the prey.

Feeding behavior on fish and loose scales

In contrast to scale feeding, the kinematic patterns of *Catoprion* capturing whole fish (Fig. 4) and loose scales (Fig. 5) were similar to patterns reported for other fishes while suction feeding. Maximum mean attack velocities were lower than during scale feeding, averaging 0.38 m s^{-1} for strikes on fish and 0.17 m s^{-1} for strikes on loose scales. Prey capture followed the general anterior-to-posterior sequence of cranial movement (Figs 6, 7) well documented for suction-feeding fishes (Lauder, 1985; Lauder and Shaffer, 1993). Strikes began with an increase in gape due to lower jaw rotation, followed by nearly synchronous raising of the head and depression of the hyoid, expanding the volume of the buccal cavity and creating a vacuum that draws in water and prey (Lauder, 1985; Liem, 1993). Finally, the opercular apparatus expanded laterally, allowing the volume of water that entered the buccal cavity during prey capture to drain. Displacement of cranial

elements were greater during feeding on fish but the time to reach these excursions was shorter than when feeding on scales (Figs 6, 7), a pattern that has been consistently reported for other fish species when feeding on evasive *vs* non-evasive prey (Lauder, 1981; Sanderson, 1988, 1990, 1991; Chu, 1989).

When feeding on fish, *Catoprion* again stalked to within a short distance of the prey before accelerating rapidly during the attack (Fig. 4). Predator velocity remained high throughout the strike, indicating that a combination of ram and suction feeding modes was used (Norton and Brainerd, 1993). Jaw opening did not begin until *Catoprion* were an average of 1.11 cm from the fish. Jaw opening proceeded rapidly, averaging a maximum value of 83° (linear gape distance 1.08±0.17 cm), which is well below the functional gape limit for the species, after 73 ms. Maximum gape was achieved after the prey had entered the mouth. Mean values for cranial elevation and hyoid depression during capture of evasive prey were also high, and the mean value for maximum opercular expansion at 38° was the only variable higher during fish
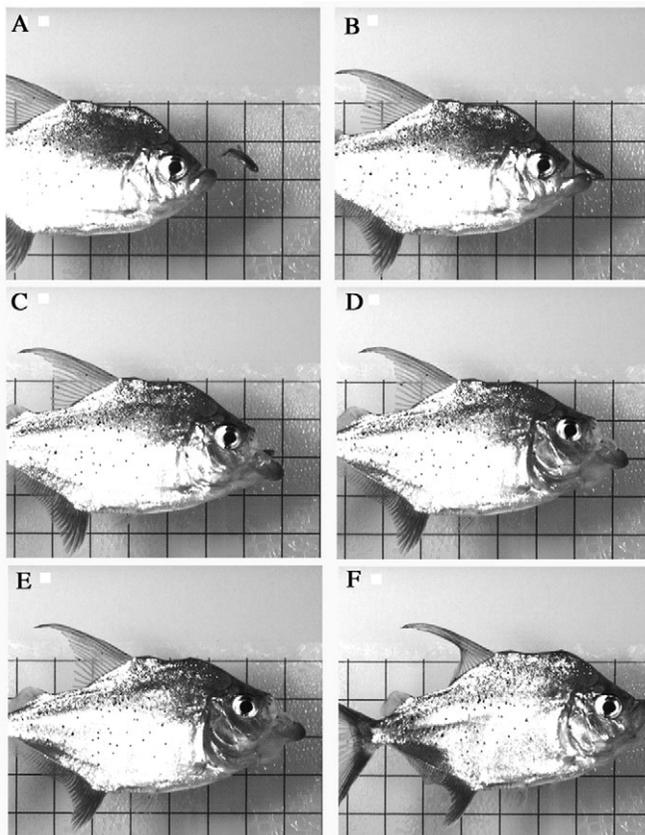

Fig. 4. Representative sequence of *Catoprion mento* capturing a live fish. (A) Time zero marks the start of jaw opening; note the fast-start behavior of the prey; (B) 36 ms later, gape angle widens but most of the distance between *Catoprion* and the fish has been closed by movement of the predator; (C) 52 ms, at maximum gape, most of the fish is within the buccal cavity; (D) 60 ms, maximum hyoid depression; (E) 64 ms, maximum opercular expansion; (F) 116 ms, post-strike, cranial elements have returned to resting position.
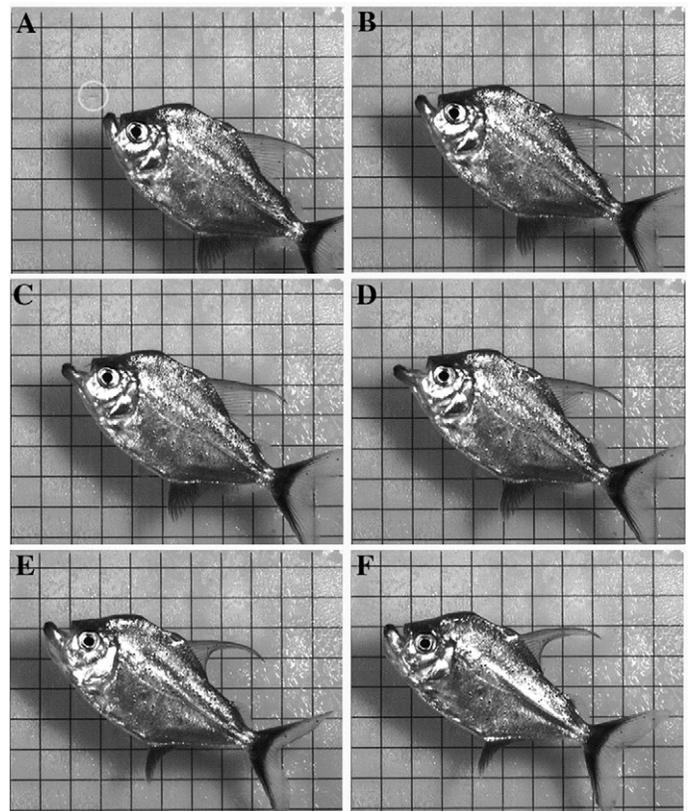

Fig. 5. Representative sequence of *Catoprion mento* capturing a loose scale. (A) Time zero marks the start of jaw opening. The circle identifies the scale prey, which is also visible in B and C. (B) 40 ms later, gape angle widens but most of the distance between *Catoprion* and the scale has been closed by movement of the predator. Note the smaller distance moved by *Catoprion* compared with during strikes on fish; (C) 52 ms, continued lower jaw rotation at a slower rate than fish strikes; (D) 64 ms, maximum gape; (E) 92 ms, maximum opercular expansion; (F) 112 ms, slow return of cranial elements to resting position.

feeding than scale removal. Maximum values for all cranial displacement variables were lower when feeding on loose scales (mean linear gape, 0.81±0.097 cm) than on fish despite taking a longer time to reach that maximum value. Only distance from the prey at the start of jaw opening was not statistically different between the two behaviors (Table 1). There was no evidence of a preparatory phase of constriction of cranial elements to reduce buccal volume prior to the onset of jaw opening, as has been reported in some derived groups of fishes (Gibb, 1995).

Comparisons among prey capture behaviors

MANCOVA results revealed a highly significant effect of prey type ($P<0.0001$, $F=28.37$, d.f.=24,120) and a non-significant effect of predator standard length ($P>0.16$, $F=1.48$, d.f.=12,60) on strike kinematics in these *Catoprion* individuals specifically chosen for their similarity in size. The overall patterns of suction feeding on scales and fish are similar, with differences between the two behaviors due largely to the lower rates of movement of cranial elements in feeding on loose scales. Rates of displacement of cranial elements appear similar between feeding on loose scales and scale removal for gape angle, hyoid depression and lower jaw rotation during
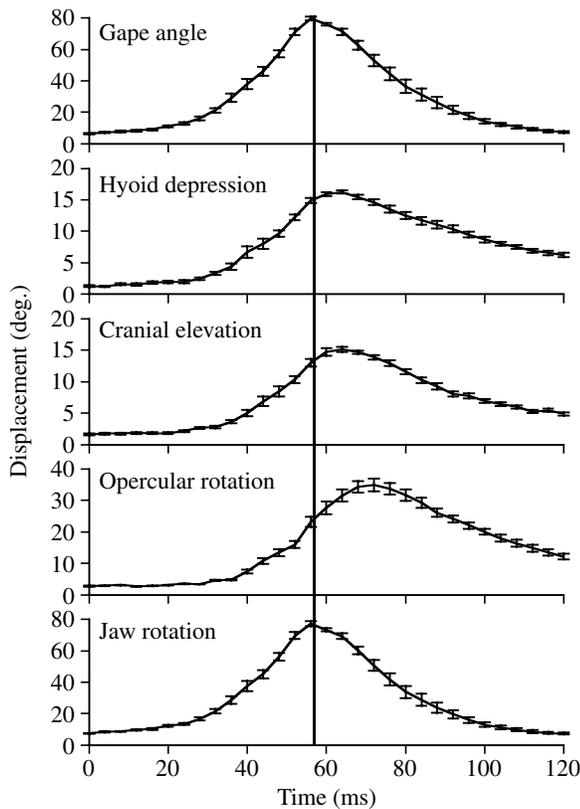
most of the strike. Rates of displacement for these three variables increase as prey contact is made during scale feeding, appearing more similar to the slopes of the gape profiles for fish feeding. The plateau phases of prolonged maintenance of cranial elevation and opercular expansion at angles near maximum during scale feeding are apparent from these graphs, with this stage lasting approximately one-third of the entire gape cycle time. Cranial and opercular elements begin to return to their resting positions only after the jaws are almost completely closed by retraction of the lower jaw.

Histograms comparing mean values for the six displacement (Fig. 8) and six timing (Fig. 9) variables used to compare prey capture behavior clearly show that *Catoprion mento* is able to modulate characteristics of the strike to match the demands of different prey. All 12 variables were highly significantly different between prey types (Table 2) while only two variables, maximum opercular expansion and time to maximum hyoid depression, differed significantly among individuals. Of the 36 pair-wise comparisons among the three prey types (Table 1), only two are not significantly different:
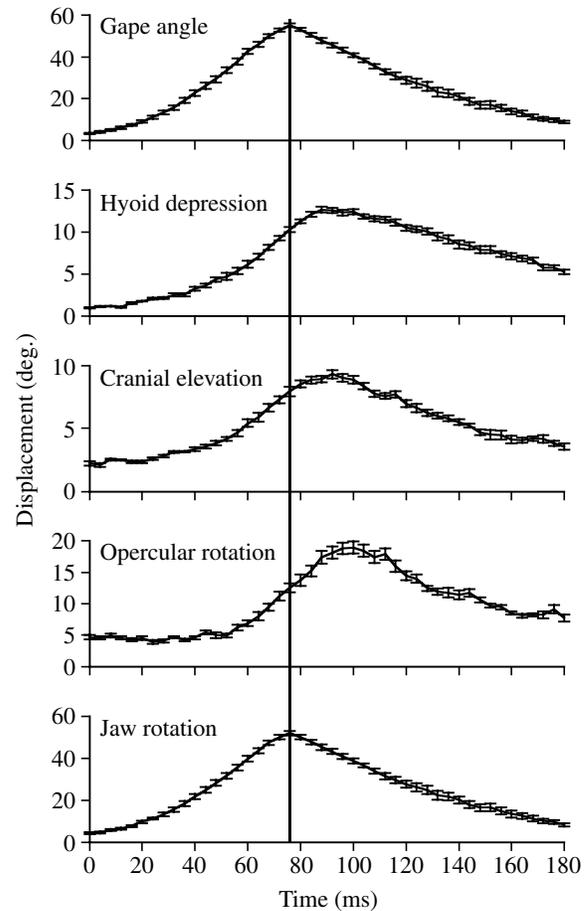

Fig. 6. Plots of mean kinematic values (± S.E.M.) for 25 strikes on live fish from five *Catoprion mento* individuals. All variables for all strikes were standardized by time of maximum gape angle, marked by the vertical line in each plot. Note the bell shape of all kinematic plots and the anterior-to-posterior sequence of cranial movements.

Fig. 7. Plots of mean kinematic values (± S.E.M.) for 25 strikes on loose scales from five *Catoprion mento* individuals. All variables for all strikes were standardized by time of maximum gape angle, marked by the vertical line in each plot. Note the lower displacements and longer durations of cranial movements compared with fish strikes.

cranial elevation during scale feeding and fish feeding, and distance from the prey at the start of the strike during captures of fish and loose scales. The uniformly longer times to maximum displacements during scale feeding are not surprising given the greater distances the cranial elements are moving during this prey capture behavior. The consistently lower magnitudes but longer times to maximum for cranial movements when suction feeding on loose scales compared with capturing fish are consistent with compensations in behavior shown by other fishes when capturing prey capable of performing escape behaviors.

A principal components analysis of all 75 strikes supports the ANOVA results that the dietary specialist *Catoprion mento* is able to modify the kinematics of prey capture according to the demands made by different prey. The two major axes of variation, which together account for nearly 85% of the variation in strike kinematics (Table 3), almost completely separate strikes by prey type (Fig. 10). Variables loading highly on PC1 (63.8% of variance) largely separate scale feeding from strikes on fish and loose scales. That 10 of 12 variables, all but angles of maximum cranial elevation and opercular expansion, load similarly and relatively highly on

Table 2. *Results of two-way ANOVA for all strikes comparing levels of variation due to prey type and individual predator*

Variable	Prey d.f.=2,4	Individual d.f.=4,4	Prey × individual d.f.=8,75
Displacement (deg.)			
Gape angle	358.20**	0.60	1.03
Hyoid depression	61.11**	3.54	1.36
Cranial elevation	40.44**	1.25	0.85
Opercular expansion	29.54**	6.26**	1.61
Jaw rotation	305.78**	0.60	1.03
Prey distance (cm)	42.38**	2.18	1.93
Timing (ms)			
Time to gape angle	106.08**	3.97	1.85
Time to hyoid depression	121.66**	4.75*	3.05*
Time to cranial elevation	114.27**	1.86	2.50
Time to opercular expansion	121.87**	2.97	3.36*
Time to jaw rotation	112.36**	4.04	2.19
Total gape cycle time	52.22**	1.38	0.78

Table entries are *F*-ratios.
*Significant at sequential Bonferroni-corrected value of *P*<0.05.
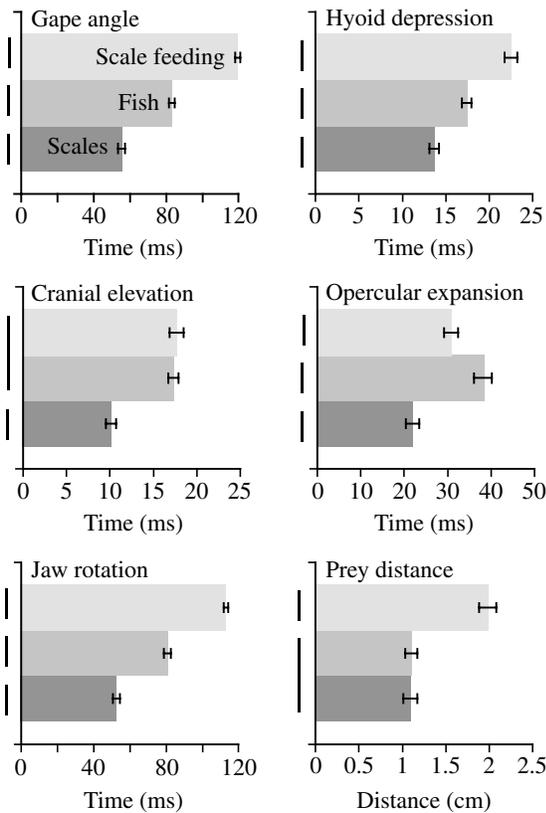**Significant at sequential Bonferroni corrected value of *P*<0.001.

Fig. 8. Histograms comparing mean values (± S.E.M.) for kinematic displacement variables for each prey. The key for all graphs is as given in the gape angle plot. Vertical lines connect prey whose means are not significantly different according to a Bonferroni-corrected value of *P*<0.05; separate lines indicate that means are significantly different.
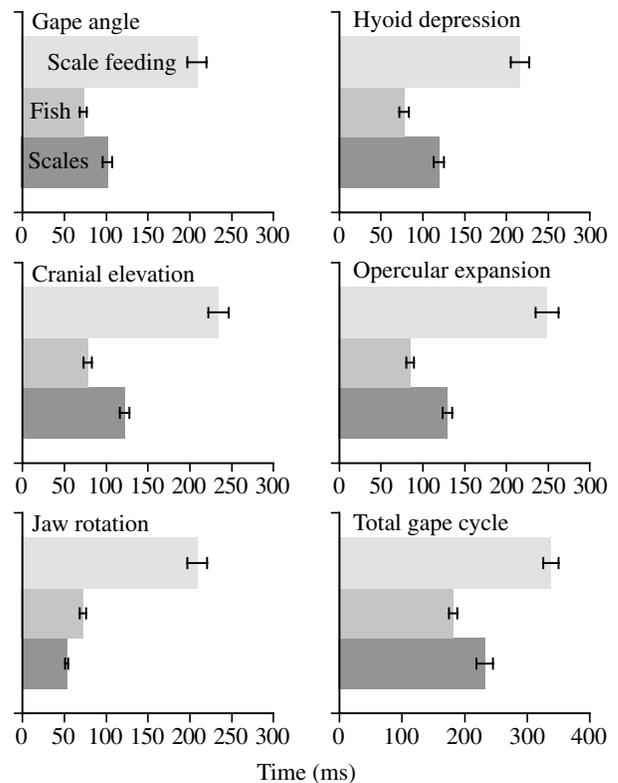

Fig. 9. Histograms comparing mean values (± S.E.M.) for kinematic timing variables for each prey. The key for all graphs is as given in the gape angle plot. All pair-wise comparisons are statistically different according to a Bonferroni-corrected value of *P*<0.05.

Table 3. *Factor loadings from principal components analysis of kinematic variables for all 75 strikes*

| Variable	PC1 (scale feeding)	PC2 (suction feeding)
Displacement (deg.)		
Gape angle	0.30	0.31
Hyoid depression	0.25	0.33
Cranial elevation	0.14	0.47
Opercular expansion	0.004	0.53
Jaw rotation	0.29	0.32
Prey distance (cm)	0.28	0.04
Timing (ms)		
Time to gape angle	0.34	−0.16
Time to hyoid depression	0.34	−0.20
Time to cranial elevation	0.34	−0.19
Time to opercular expansion	0.33	−0.20
Time to jaw rotation	0.34	−0.17
Total gape cycle time	0.31	−0.14
Variance measures		
Eigenvalue	7.66	2.54
Percent	63.84	21.13
Cumulative percent	63.84	84.97

Fig. 10. Principal components analysis of all 75 strikes by *Catoprion mento* on three prey. Each symbol represents one feeding sequence; F, live fish; L, loose scales; S, scale feeding. Boundary lines surrounding each prey category are subjectively drawn. Factor loadings for all kinematic variables are listed in Table 3.

this factor supports the uniqueness of this behavior from other types of prey capture. PC2, which accounts for 21.1% of total variance among prey capture behaviors, effectively distinguishes strikes on live fish from strikes on loose scales. The displacement variables maximum opercular expansion and cranial elevation load particularly highly on this factor, although all displacement variables except linear distance from prey at the start of jaw opening load positively and have relatively high coefficients for PC2. Loadings for all timing variables are similar in magnitude and negative in sign for this factor. PC2 is interpreted as differentiating strikes that rapidly reach large cranial displacements from strikes that proceed to lower angular excursions at a slower rate.

Discussion

Three major conclusions can be drawn from this study of the feeding behavior of *Catoprion* on prey that place different functional demands on both the trophic anatomy and strike kinematics necessary for their capture and ingestion. First, *Catoprion* is able to modulate strike kinematics and attack behavior according to prey type. Second, the kinematics of scale removal is a novel feeding behavior, different from suction feeding and other forms of biting not simply by the extreme displacement of many cranial elements during the strike but also by differences in the timing of movements of functional units relative to each other. Third, the derived specialization of *Catoprion* for lepidophagy has not limited the ability of this species to recognize different prey or to behaviorally adjust strike kinematics according to the specific demands of that prey. Specialization has not resulted in limited functional versatility but resulted instead in the evolution of a novel feeding behavior
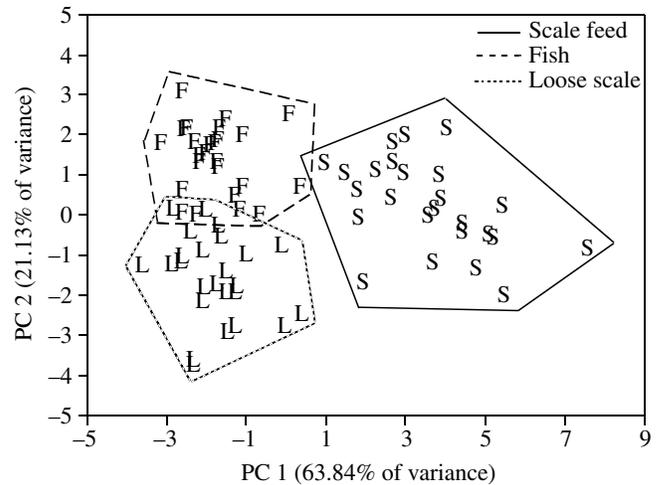
that has been added to the ancestral repertoire. Possible trade-offs in feeding performance appear to be largely the result of modification in trophic anatomy, not in feeding behavior.

Modulation of suction feeding

The ability to create negative intra-oral pressure has been found in all ancestrally aquatic osteichthyans (fishes) studied to date, and the retention of this ability may be required for transport of captured food even if the prey is actually captured by a behavior other than suction feeding (e.g. biting). Many secondarily aquatic tetrapods also capture prey underwater by suction feeding and show a pattern of cranial movement similar in sequence and magnitude to that seen in fishes (Shaffer and Lauder, 1985; Lauder and Shaffer, 1993; Lauder and Prendergast, 1992). As expected, *Catoprion* retains this ability to generate negative pressure by increasing the volume of the buccal cavity. Video images clearly show that prey are sucked into the mouth along with a volume of water and are not simply overtaken by the predator. Suction feeding, and modulation of the kinematic movements that generate negative pressure, have been retained in this dietary specialist from a biting lineage.

The amount of negative pressure generated during suction feeding depends on both the magnitude and speed of volume change in the buccal cavity, with greater pressures produced by larger, more rapid displacement of cranial structures (Lauder et al., 1986; Grubich and Wainwright, 1997). Most fishes possess the ability to modify feeding behavior and kinematics of the strike according to the evasiveness of the prey (Liem, 1978, 1979; Vinyard, 1982; Sanderson, 1990; Norton, 1991; Nemeth, 1997b), as well as size of the prey (Lauder, 1981; Ferry-Graham, 1997) and position of the prey in the water column (Lauder, 1981). Among those fishes able to modulate feeding behavior, without exception, more evasive prey elicit faster strikes with greater displacement of the cranial

elements responsible for buccal expansion, as would be predicted by hydrodynamic theory (Vogel, 1989; Denny, 1993). The fewer studies that directly measure changes in buccal pressure during feeding confirm that strikes on evasive prey are characterized by decreases in intra-oral pressure of greater magnitude than strikes on non-evasive prey (Nemeth, 1997a; Grubich and Wainwright, 1997).

Comparison of strikes in *Catoprion* feeding on non-evasive loose scales with strikes on evasive fish supports this pattern. All displacement and timing variables are significantly different between the two prey types and differ in the direction predicted by the functional demands of creating a powerful vacuum underwater; during strikes on fish, the buccal cavity is expanded to a greater magnitude, and at a faster rate, than strikes on scales. However, unlike the response of other fishes to evasive prey (Norton, 1991, 1995; Cook, 1995), *Catoprion* does not initiate the strike from a greater distance from the prey, although attack velocities during the strike are higher. Suction-feeding strikes on fish or loose scales are statistically different in most variables and easily separable along an informative axis of principal component space, confirming that *Catoprion* is able to assess the escape potential of prey and directionally modify feeding behavior to increase capture success.

Functional morphology of scale-feeding behavior in Catoprion

A diet of scales and the ability to remove them from other fishes are derived features in *Catoprion*. Phylogenetic hypotheses for the Serrasalminae (Machado-Allison, 1982; Orti et al., 1996) suggest that a largely herbivorous diet of seeds, leaves and aquatic vegetation is primitive for the subfamily. Ancestral serrasalmines have the ability to both generate effective suction that is used for prey capture and intra-oral transport of food to the esophagus and to produce a forceful bite (Janovetz, 2001). Many aspects of the scale-feeding strike in *Catoprion* differ from capture of the other two prey items used in this study as well as previously reported feeding behaviors in other fishes. Scale feeding in *Catoprion* is, to date, the most extreme example of what has been described in the literature as 'ram feeding' (Liem, 1980a; Norton and Brainerd, 1993). Ram and suction feeding are considered as two ends of a continuum in one axis of prey capture that is defined by the relative movements of the predator and the prey (Norton and Brainerd, 1993). In pure ram feeding, only predator movement is used to capture stationary prey, while in pure suction feeding the stationary predator draws the prey towards it and into the mouth using only negative pressure. The tethered prey used in this study are unable to move, but as *Catoprion* often attacks fish 2–3 times its own length (Sazima, 1983; J.J., personal observation), prey movement is likely to range from extremely small to non-existent. The term 'ram feeding' is particularly appropriate for *Catoprion* as, unlike in other ram-feeding fishes where predator velocity is used to merely overtake and engulf prey whole, *Catoprion* actually uses the force of its strike during collision with the prey to knock scales free (Janovetz, 2003; Janovetz and Westneat, manuscript submitted for publication).

Many of the unusual kinematic features of scale feeding can be understood in light of the different functional demands of this feeding mode compared with suction feeding. A very gradual increase in gape by lower jaw rotation begins while *Catoprion* is still nearly 2 cm from the prey. This slow rate of gape increase lasts for approximately 150 ms (Fig. 3) before prey contact is made, which is almost longer than the average time for the entire gape cycle when feeding on fish. Low rates of cranial expansion allow water to 'leak' into the buccal cavity and prevent the explosive volume change necessary to generate suction. Typically, a gape angle of over 80° is achieved, almost solely due to lower jaw rotation, before the *Catoprion* begins a rapid acceleration towards the goldfish. After this, lower jaw rotation does not appreciably increase until contact is made with the prey. After rapid acceleration to strike velocity but just before collision with the goldfish, cranial elevation begins and is followed soon after by lateral expansion of the opercular series. That lower jaw rotation stabilizes briefly near the maximum angle for fish strikes, increasing again only after prey contact, may suggest that a lower jaw angle of near 80° is the functional limit for active, muscular control of jaw rotation but that the jaw is anatomically capable of being passively rotated a further 30°. Measurement of muscle activity in the jaw abductors with electromyography or sonomicrometry or estimates of the potential shortening capabilities of fibers from the levator operculi and geniohyoideus muscles from anatomical dissection would help answer this question.

The upper jaw (premaxilla and maxilla) of all serrasalmines is non-protrudable due to the derived condition of a ligamentous attachment of these ancestrally mobile elements to the neurocranium (Machado-Allison, 1982). Cranial elevation serves to orient the everted, tusk-like premaxillary teeth of *Catoprion* into a forward-facing position to effectively rasp scales from the flanks of fish. While lower jaw adduction begins and is nearly completed during prey contact, very little upper jaw depression occurs during contact, resulting in a plateau stage of stability. Beneski et al. (1995) describe a period of relative stability in gape angle in some ambystomatid salamanders of the subgenus *Linguaelapsus*, during which time the tongue pad is protracted, reshaped to fit the prey and retracted. They conclude that this period of stability is necessary for the accurate aiming of the tongue pad. In *Catoprion*, stability of the upper jaw during prey contact probably provides a firm 'battering ram' for force transfer.

Momentum from the initial approach, as well as added force from tail and body undulations during prey contact, is probably transmitted to the prey largely through the upper jaw. A non-protrudable premaxilla, which may have evolved initially to withstand the high bite forces generated while feeding on seeds, is a putative preadaptation for the ramming strike of *Catoprion* during scale feeding. In this sense, the ligaments responsible for binding the upper jaws are analogous to the 'collagen tract within the lower lip' of Liem and Stewart (1976), who hypothesized that the tract stabilized the jaws of scale-eating cichlids from Lake Tanganyika during bites. This anatomical shift in biological design, while advantageous for withstanding the force of a scale-

feeding attack, prevents upper jaw protrusion, a character that has been widely hypothesized to increase suction-feeding performance in teleost fishes (Motta, 1984).

In most Halecostome fishes (*Amia* + teleosts), the mobile maxilla and descending arm of the premaxilla swing forward during prey capture to laterally occlude the gape and restrict the flow of water that is sucked into the mouth largely to a volume in front of the predator (Lauder, 1980, 1985; Liem, 1993). The inability of *Catoprion* (and all piranhas) to occlude the gape means that water lateral to the mouth, and therefore not useful for prey capture, will enter the buccal cavity and reduce the effective suction force for prey capture. The enormous gape of *Catoprion* compounds this problem, creating an equally large lateral area on each side to admit water. Despite early debate (Muller et al., 1982; Lauder, 1983b), it is now generally agreed that the gill bars isolate buccal and opercular cavities during suction feeding (Muller et al., 1985; Lauder, 1986). The gill bars remain closed early in the strike, preventing reverse flow into the buccal cavity from the operculum, and open after peak gape, providing an exit through the operculum for excess water engulfed during the strike (Lauder, 1985). Throughout most of the acceleration and prey-contact phases of scale feeding, the opercular series remains laterally expanded in *Catoprion*, exhibiting a plateau phase similar to cranial elevation. Although direct measurement of gill bar spacing was not done, this probably indicates that buccal and opercular cavities are hydrodynamically linked during scale feeding, allowing the efficient exit of the large volume of water engulfed during attacks covering such a large distance. *Catoprion* appears able anatomically to segregate buccal and opercular cavities and behaviorally appears to do this while feeding on fish and loose scales. That this sequence of kinematic events, crucial for effective suction feeding, is not performed during scale feeding is further support that scale feeding in *Catoprion mento* is a novel and distinct form of prey capture.

Is specialization limiting for Catoprion mento?

Recently, there has been great interest in functional morphology in relating the functional versatility (the range of kinematic, muscle activity or other behavioral responses) of organisms to a measure of their resource utilization in the wild (e.g. Sanderson, 1988, 1990, 1991; Ralston and Wainwright, 1997; Ferry-Graham et al., 2002). The expectation of most of these studies is that specialists will have less functional versatility than generalists. Specifically in feeding studies, the hypotheses are that species with narrow dietary breadth will have a more stereotypical or restricted range of feeding responses to prey and that this limited repertoire results in reduced performance when feeding on prey other than those typically found in the diet.

Catoprion mento, according to both an ecological and morphological definition, is a trophic specialist. Its natural diet throughout most of ontogeny contains scales and, as adults, *Catoprion* feeds almost exclusively on this derived food source (Sazima, 1983; Taphorn, 1992; Vieira and Gery, 1979). Anatomically, *Catoprion* has a longer jaw with a distinctive curve, reduced and everted pedicel-like teeth and an even less protrudable maxilla than its vegetarian serrasalmine ancestors. Has the functional versatility of *Catoprion* been restricted in conjunction with this specialization of diet and anatomy? Despite extreme modification of the feeding system and a natural diet of very narrow breadth, *Catoprion* actually appears to have an increased range of feeding behaviors in its repertoire. *Catoprion* has retained the ancestral ability to generate suction to capture prey, to modulate the specific kinematics of a ram/suction attack, but has also evolved a novel feeding behavior, with distinct kinematic parameters, when removing scales from fish. In the case of *Catoprion*, specialization appears to have *added* to the range of feeding modes behaviorally available.

If behaviorally able to feed on a variety of prey, why does the natural diet of *Catoprion* contain such a reduced subset of the available resources and why does *Catoprion* specialize on nutritionally less profitable prey (Futuyma and Moreno, 1988; Robinson and Wilson, 1998)? For *Catoprion*, the costs of specialization may be largely anatomical. Many derived features of the trophic anatomy, both autapomorphic for *Catoprion* and synapomorphic for the Serrasalminae, alter the biological design of the feeding apparatus in a direction predicted by biomechanics to compromise effective suction feeding or forceful biting. The enormous gape of *Catoprion*, coupled with the inability of the non-protrudable upper jaw to laterally occlude the gape, should result in reduced water flow from directly in front of the mouth and therefore in reduced suction-feeding performance. The reduced teeth, small adductor muscles and velocity-emphasizing (Barel, 1983; Westneat, 1995) lever design of the long lower jaw will limit effective bite force. Although prey capture performance was not quantified and *Catoprion* is able to feed effectively under the restricted conditions necessary for filming, in more natural settings these functional consequences of its derived trophic anatomy may reduce the ability of wimple piranha to capture evasive prey using suction or to remove more than scales during biting.

When can the Jack-of-one-trade have his cake and eat it too?

While most studies comparing trophic specialists and generalists have found an equal ability to modulate feeding behavior (Sanderson, 1988, 1990; Ralston and Wainwright, 1997), some have not (Lauder, 1981; Chu, 1991; Sanderson, 1991, but see Sanderson, 1988 for comparison of the same three species). Liem (1984, 1990) proposed the intriguing hypothesis that suction feeding is an extremely flexible feeding mode that is so useful and effective in a wide variety of feeding situations that the assumed advantage of specialization, increased efficiency, is rarely a selective pressure. All fishes appear to use suction for hydraulic transport of captured food to the esophagus (Bemis and Lauder, 1983), and this behavior, although using the same mechanism as feeding, is usually considered distinct from feeding (Gillis and Lauder, 1993). This dual biological role for suction generation suggests that loss of this ability would affect not just prey capture but also prey transport and implies an almost inherent modulation capability.

Recent functional studies of fishes from a range of phylogenetic positions confirm that the ability to modulate feeding behavior according to the functional demands of the prey is ancestral for teleosts. The presence of modulation, even in specialists, should therefore be the null hypothesis in fish feeding studies, and expectation of its loss should be explained in the context of providing a selective advantage. The rarely stated but presumed advantage of a specialized feeding mode is that this single behavioral response is optimal for feeding on the few items in the diet and that maintaining behavioral flexibility somehow compromises this behavior, perhaps by slowing the behavior to allow for sensory feedback. This neural cost of behavior has never been demonstrated for a vertebrate, however. Morphological trade-offs in biological design are well documented, and it is perhaps more likely that anatomy limits the range of behavioral responses that allows a species to forage efficiently. Additional studies of fish feeding behavior, which mechanistically explain the complex function of the vertebrate skull, are a valuable contribution to our understanding of the evolutionary and ecological processes that create and maintain organismal diversity.

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