

ONTOGENY OF FEEDING MORPHOLOGY AND KINEMATICS IN JUVENILE FISHES: A CASE STUDY OF THE COTTID FISH *CLINOCOTTUS ANALIS*

AMY COOK

Department of Ecology and Evolutionary Biology, University of California at Irvine, Irvine, CA 92717, USA

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Summary

The development of feeding morphology, kinematics and behavior was examined in the juveniles of the cottid fish *Clinocottus analis*. The attacks of 18 juvenile *C. analis*, between 17.59 mm and 42.15 mm in standard length (SL), feeding on brown worms were filmed using high-speed video. Feeding mode, ram- or suction-dominated, kinematic variables and morphology were quantified and compared over the juvenile period. The analysis of these three factors was based on the following questions: (1) do they change over ontogeny; (2) how do their values compare with those of larvae, juveniles and adults of other species; and (3) what is the level of stereotypy, as measured by the variance in these factors, at this stage in ontogeny and does it change? Small *C. analis* juveniles have the small gape and large buccal cavity of a suction feeder, and this morphology becomes more pronounced as they become larger. The kinematic variables of *C. analis* juveniles are similar to those of adult suction-feeding cottids and least-

squares regression analysis showed significant changes in only two variables (time to prey capture and absolute attack predator–prey distance) over the juvenile period. Feeding mode, as measured by the ram-suction index, shows an increase in the suction component of the strike with increasing size. This study demonstrates that, in *C. analis*, suction feeding behavior develops during the juvenile period. Within the juvenile stage, morphology, prey-capture kinematics and feeding mode are not tightly linked ontogenetically such that suction-feeder kinematics (short predator–prey distance and low attack velocity) and basic morphology (small gape, large buccal volume) develop much earlier than the employment of a large suction component during the strike.

Key words: feeding morphology, kinematics, ontogeny, *Clinocottus analis*, behavior, feeding mode

Introduction

Teleost fishes exhibit a wide variety of feeding behaviors and morphologies and have provided material for many studies of the functional morphology of feeding (Liem, 1974; Elshoud-Oldenhavé and Osse, 1976; Rand and Lauder, 1981; Vinyard, 1982; Webb, 1984; Wainwright and Lauder, 1986; Motta, 1988; Harper and Blake, 1991; Norton and Brainerd, 1993). However, most of this research has focused on adult fishes and the functional and behavioral aspects of feeding have not been as well studied for earlier life history stages.

One aspect of larval and juvenile fishes which has been well researched is their morphological development. Using techniques such as the clearing and staining of bone and cartilage, the development of the skull has been analyzed for many species including sparids (Mook, 1977; Matsuoka, 1985), salmonids (Jollie, 1984), serranids (Fritzsche and Johnson, 1980), centrarchids (Mabee, 1993) and hexagrammids (Geerlink, 1989). Likewise, because of the ecological importance of gape changes in young fishes and its effect on prey size, changes in mouth size during ontogeny have been well documented in a wide range of species (Hunter,

1980; Yoshiyama, 1980; Stoner and Livingston, 1984; Keast, 1985). The functional consequences of these developmental changes in morphology are not well understood, however, and for the most part we do not understand how change in a particular morphological feature affects change in the functions associated with it.

Much of what is known about the development of feeding in fishes is based on behavioral observations combined with a few measured variables such as strike distance or strike velocity. These studies indicate several features which appear to be common to the ontogeny of prey capture behavior in fishes: (1) an increase in capture success with age (Blaxter and Staines, 1971; Hunter, 1980; Coughlin, 1994); (2) a decrease in the duration of the feeding event (Hunter, 1972; Coughlin, 1991; Wanzenbock, 1992; Coughlin, 1994); (3) an increase in the distance between the fish and its prey at the initiation of the attack (Hunter, 1972; Coughlin, 1991; Browman and O'Brien, 1992); and (4) an increase in strike velocity (Hunter, 1972; Browman and O'Brien, 1992). Most of these studies were performed on very young larvae and examined a small

range of sizes. Few studies have addressed the development of feeding kinematics in a juvenile fish despite the fact that the juvenile stage is often a period of ecological and morphological transitions.

In this paper, I analyze the functional morphology of feeding in the juveniles of the cottid *Clinocottus analis* as a case study in the ontogeny of prey-capture behavior in juvenile teleost fishes, focusing on ram- and suction-feeding behavior in particular. Many species of fish use some combination of body acceleration and suction to capture their prey (Alexander, 1967; Nyberg, 1971; Lauder and Clark, 1984; Drost, 1987; Norton and Brainerd, 1993). Movement towards the prey constitutes the ram component of the strike (Liem, 1980; Wainwright, 1989) and the proportional contribution of ram and suction to the strike can vary among even closely related species (Norton, 1991; Norton and Brainerd, 1993).

Several studies of larval fishes have found an ontogenetic change in feeding mode from one that is ram-dominated to one that is more suction-dominated (Coughlin, 1991, 1994; Liem, 1991). The morphological transition associated with this change appears to be a common feature in the ontogeny of many fishes and so too may be the behavioral change (Liem, 1991; Von Herbing *et al.* 1996). This evidence supports the hypothesis that the larvae of *C. analis* are ram feeders. Since adult *C. analis* are suction-dominated feeders (Norton, 1991), there are two possible ontogenetic trajectories that could be seen in the juvenile stage. One is that the juveniles are also suction-dominated feeders and show no change during the juvenile period. This would indicate that feeding mode either remains constant throughout ontogeny or changes during the larval stage. A second possibility is that juveniles show a different feeding mode from that of adults and that development of the adult feeding mode occurs during the juvenile period.

I use a quantitative measure of feeding mode, the ram-suction index, to determine which of these trajectories applies to *C. analis*. Developed by Norton and Brainerd (1993), the ram-suction index (RSI) uses the ratio of predator movement minus prey movement to the total movement by both to quantify feeding mode. Movement of the predator may be measured using either a landmark on the body, such as the eye, or the tip of the premaxilla. These two measures represent different aspects of the ram component of the strike. The first represents the movement of the predator's whole body towards the prey. The second represents the combined contribution of body movement and premaxillary protrusion to the ram component of the strike. In some fishes, there is almost no contribution of whole-body acceleration, and the ram component of the strike is exclusively due to premaxillary protrusion in what has been termed 'ram-jaw feeding' (Coughlin and Strickler, 1990). In general, there is a large difference between the RSI of the body and that of the premaxilla in suction-dominated feeders and little or no difference in ram-dominated feeders (Norton and Brainerd, 1993).

The interspecific pattern of relationships between morphology, kinematics, feeding mode and performance is well known in adult cottids (Norton, 1991) and suggests that feeding mode, morphology and kinematics should change together if the fish is to feed effectively. This study investigates whether there are changes in any of these characteristics during the juvenile period and, if there are, whether these changes occur together. The level of stereotypy in the feeding kinematics of *C. analis* is measured to look for changes in variability across the juvenile stage. Finally, to put the results for *C. analis* in perspective, the values for their morphological and kinematic variables and the direction of the changes in these variables during juvenile ontogeny will be compared with those of the adults, juveniles and larvae of other species of fish.

Materials and methods

Collection and maintenance

Juvenile *Clinocottus analis* (Girard) were collected from the intertidal zone during fall and winter at Corona del Mar State Beach and Hearst Memorial State Beach in southern and central California under California Department of Fish and Game Permit number 6228. Fishes between 15 and 42 mm standard length (SL, the length between the tip of the premaxilla and the base of the caudal peduncle) were taken to the laboratory and maintained in 38 and 761 saltwater tanks with undergravel filters. The tanks themselves were not chilled, but the room in which they kept was kept at 18–19°C. *Clinocottus analis* hatch at 3.7–4.5 mm total length (TL, the length between the tip of the premaxilla and the posterior edge of the caudal fin) and settle out of the plankton to take up residence in the intertidal zone by 25 mm TL (Feeney, 1992). Sexual maturity is reached at about 60 mm TL (Wells, 1986). For the purpose of this study, fishes between 15 and 60 mm TL were considered to be juveniles.

Young *C. analis* were maintained on a diet consisting primarily of brown worms (*Lumbriculus* sp.) cut into pieces and supplemented with adult brine shrimp (*Artemia* sp.) and mosquito larvae (*Aedes aegypti*) when available. Fishes had been feeding on brown worms for at least three consecutive days before the actual filming session. All food was presented to the fish through a disposable plastic pipette.

Morphology

Two morphological variables, buccal volume and anatomical gape, were measured from freshly killed specimens. Silicone aquarium sealant was injected into the mouth of a specimen in excess of that needed to fill the buccal cavity. The injected fish ($N=15$) were left for 48 h to allow the sealant to cure thoroughly and then the excess sealant that was outside the mouth was trimmed off and the cast removed from the mouth. The silicone cast was weighed (mass, m) and its volume (V) calculated using the equation: $V = m/0.06$. The value of 0.06 g ml⁻¹ for the density of silicone was determined empirically by measuring the volume of water displaced by

known masses of silicone. The anatomical gape, defined as the distance between the anterior tip of the premaxilla and the anterior tip of the dentary when the buccal cavity is fully expanded, was then measured on the fish using calipers. This is the measure of gape commonly used in the literature and approximates the maximum passive gape of which the mouth is capable with little or no protrusion. Another measure of gape, the functional gape, was measured from the video films of the fish while feeding and is defined as the mean of the maximal gapes achieved by an individual for all feeding events recorded for that individual.

Terminology

The encounter between a fish and its prey can be divided into two parts, the attack and the strike. The attack begins with the acceleration of the predator towards the prey. In cottids, the beginning of the attack is very clearly defined because the fish stops for an extended period that may last several seconds before it begins its acceleration towards the prey. The end of the attack is defined as the time at which the head returns to its pre-attack configuration after prey capture. The strike, a subset of the attack, begins when the fish's mouth begins to open and ends when the mouth closes.

The end of prey capture was defined as the last video field in which any portion of the prey was visible.

Filming and analysis

Attacks of the fish on prey were filmed using a NAC high-speed video system with two strobe lights at a rate of 200 fields s^{-1} . Fishes were filmed in Plexiglas chambers 112 mm × 100 mm × 18 mm for small fish or 120 mm × 140 mm × 40 mm for bigger fish. The chamber was filled with water from the fish's tank and the fish was placed in the chamber and allowed to acclimate for 15–30 min. The prey item, a 2–5 mm piece of brown worm, was then introduced into the chamber through a plastic pipette. When the prey item was captured, the camera and strobe lights were turned off and a new prey item was prepared. Fishes were fed up to 10 prey items per filming session.

The videos were analyzed frame by frame using custom-designed digitizing software. For analysis, sequences had to satisfy the following criteria: (1) the fish was lateral to the camera; (2) a successful capture was made; (3) the prey was on the bottom of the tank rather than in the water column, and (4) the fish approached and attacked the prey rather than taking it just as it emerged from the pipette. The beginning of the sequence was taken as the field prior to that in which the fish began to accelerate towards the prey, and the sequence ended when the mouth was completely closed and the premaxilla had returned to its resting position.

The following coordinates were measured in each field of a feeding sequence: the tip of the premaxilla, the tip of the lower jaw, the center of the eye, a fixed point in the background, a point on the part of the prey closest to the predator in the first field, and a point on the 'posterior' (relative to the predator) of the prey in subsequent fields. From these coordinates, the

distance traveled by the predator from the start of mouth opening to prey capture and the distance moved by the prey were calculated for each sequence.

The ram-suction index (RSI) (Norton and Brainerd, 1993) was calculated from the equation:

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

where D_{predator} is the distance that the predator moves during the strike and D_{prey} is the distance that the 'posterior' portion of the prey moves towards the predator during the strike. The RSI has values between +1 and -1. The value +1 denotes a pure ram strike in which all the movement is on the part of the predator towards the prey, and -1 denotes a pure suction strike in which all the movement is on the part of the prey towards the predator *via* suction by the predator. Two RSIs were calculated for each strike; one basing the movement of the predator on the movement of its eye (RSI_{body}) and the other basing the movement of the predator on the movement of its premaxilla ($RSI_{\text{premaxilla}}$).

Absolute predator-prey distance (mm) and relative predator-prey distance (in body lengths, BL) were calculated as the distance between the tip of the fish's premaxilla and the 'anterior' point on the prey in the first field prior to the attack. Two timing variables, the time from the beginning of the attack to prey capture (initial attack duration) and the time from the beginning of the strike to prey capture (initial strike duration), were measured for each sequence. Absolute (mm ms^{-1}) and relative (BL s^{-1}) attack velocities were calculated as the distance that the fish traveled from the start of the attack to prey capture divided by the initial attack duration. Strike velocity was similarly calculated from D_{predator} and initial strike duration.

Four kinematic variables for the head were measured in each field. Two, functional gape and premaxillary protrusion, were measured from the coordinates described above. Functional gape was measured as the distance from the tip of the premaxilla to the tip of the lower jaw (distance *BC* in Fig. 1A). A comparison of anatomical gapes measured from dead specimens compared with functional gape measured from the video films showed anatomical gape to be $29 \pm 0.02\%$ (mean \pm S.E.M., $N=13$) larger than functional gape. The distance from the eye to the tip of the premaxilla (distance *AB* in Fig. 1A) was used to determine premaxillary protrusion. Hyoid depression and cranial elevation were measured as a line length and an angle, respectively. The depth of the head just behind the eye (line *DE* in Fig. 1B) was used to determine hyoid depression. Cranial elevation was measured as the angle with endpoints at a point just behind the eye and the junction between the first and second dorsal fin with a vertex at the anterior insertion of the first dorsal fin (angle *DFG* in Fig. 1B). Actual premaxillary protrusion and hyoid depression for each field were expressed as the difference between the measured value for that field and the minimum measured value for the sequence.

For each sequence, the duration and time of onset relative to the total attack duration were calculated for four phases of

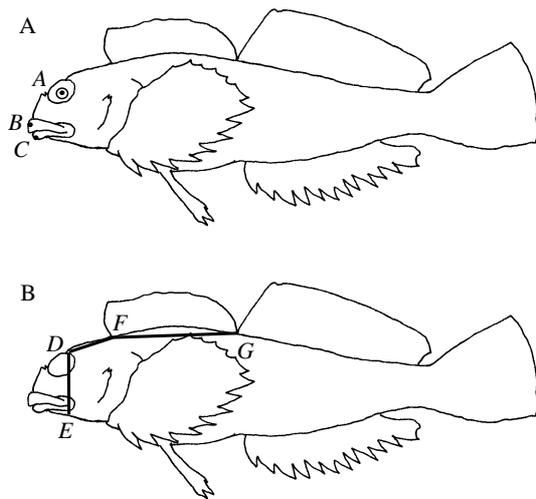


Fig. 1. (A) Coordinates used for calculating functional gape (distance BC), premaxillary protrusion (distance AB) and, with a coordinate on the prey, predator-prey distances. (B) Lines and angle used to measure hyoid depression (distance DE) and head elevation (angle DFG). See text for a detailed explanation of how the kinematic variables were measured.

the attack – preparatory, expansive, compressive and recovery – defined by events of the gape cycle and muscle activity patterns (Liem, 1978; Lauder, 1985). In this case, where there is a clear beginning to the attack, the preparatory phase was defined as the time between the beginning of the attack and the initiation of mouth opening. The expansive phase begins when the mouth begins to open and ends when the gape reaches its maximum. The compressive phase extends from maximum gape to when the mouth closes completely. The recovery phase begins when the mouth closes and, in this study, the end of this phase is defined as when the premaxilla returns to its resting position. This endpoint was chosen because it is almost always the last event leading to the return of the head to its pre-attack configuration and of the body to a resting posture.

In adult fishes, the occurrence of a rapid decrease in buccal cavity volume is considered to be the primary characteristic of the preparatory stage. It can be measured directly using pressure transducers or indirectly using electromyography to measure activity in the adductor arcus palatini and geniohyoideus muscles, whose actions compress the buccal cavity laterally and ventrally. However, these techniques cannot be used on very small fishes. In the *C. analis* juveniles used in this study, movements of the hyoid, and therefore changes in buccal volume, were determined on the basis of measurements of the depth of the head, as described above (Fig. 1B). The magnitude of the change in buccal volume during the preparatory phase was determined by comparing the initial measurement of head depth in the first field of the attack with the measurement just prior to the initiation of hyoid depression.

Statistics

The kinematic variables were analyzed with least-squares

regression analysis using Systat, Version 5.2. The method often used when studying development is to divide the individuals into size classes and to analyze them using an analysis of variance (ANOVA) to look for differences between the size classes. Regression analysis was chosen in preference to this method because no natural size classes were found for juvenile *Clinocottus analis*. Regressions were carried out using mean values of each kinematic variable for each individual and the variances of those variables. The mean difference between $RSI_{\text{premaxilla}}$ and RSI_{body} for each fish was regressed against fish length to test for changes in the relative contribution of premaxillary protrusion to the ram component of the strike.

Regression analysis of the variances was used as a measure of stereotypy through ontogeny. A slope of zero would indicate no change in variance through ontogeny and the behavior would then be considered to be stereotyped.

The timings of maximum gape *versus* prey capture, maximum hyoid depression *versus* prey capture, maximum gape *versus* maximum hyoid depression and maximum gape *versus* maximum premaxillary protrusion were each analyzed using a paired *t*-test to determine whether they coincided. To determine whether there was significant elevation of the hyoid during the preparatory phase, the difference between the initial head depth and head depth at the initiation of hyoid depression was analyzed for individual attacks using a paired-sample *t*-test. The same procedure was used to determine whether there was a significant retraction of the premaxilla during the preparatory phase.

Because many aspects (kinematics and feeding mode) of the same feeding event were measured, a sequential Bonferroni correction was used to determine statistical significance (Rice, 1989). All the variables in Table 1 ($N=22$) were used to calculate the Bonferroni correction. Since they involved a different statistical test and analyzed very different biological phenomena measured at the level of the attack rather than the level of the individual, the *t*-tests were grouped together in a different sequential Bonferroni correction from the regression analyses.

Results

Clinocottus analis juveniles showed a significant increase in absolute functional gape with increasing standard length (Fig. 2). The scaling of absolute functional gape with length showed a slight, but significant, negative allometry (exponent=0.81, $P<0.05$). Buccal volume also increased significantly with length (Fig. 3) and was not significantly different from the expected isometric slope of 3.0 (exponent=3.93, $P>0.05$).

When a juvenile *C. analis* became aware of the presence of the prey, it approached to within 0.24 BL of the prey and paused for a second or less before beginning the attack (Fig. 4A). During the preparatory phase of the attack, when the fish accelerated towards the prey but the mouth was still closed (Fig. 4B), there was a significant elevation of the hyoid ($P<0.001$) and a retraction of the premaxilla ($P<0.001$)

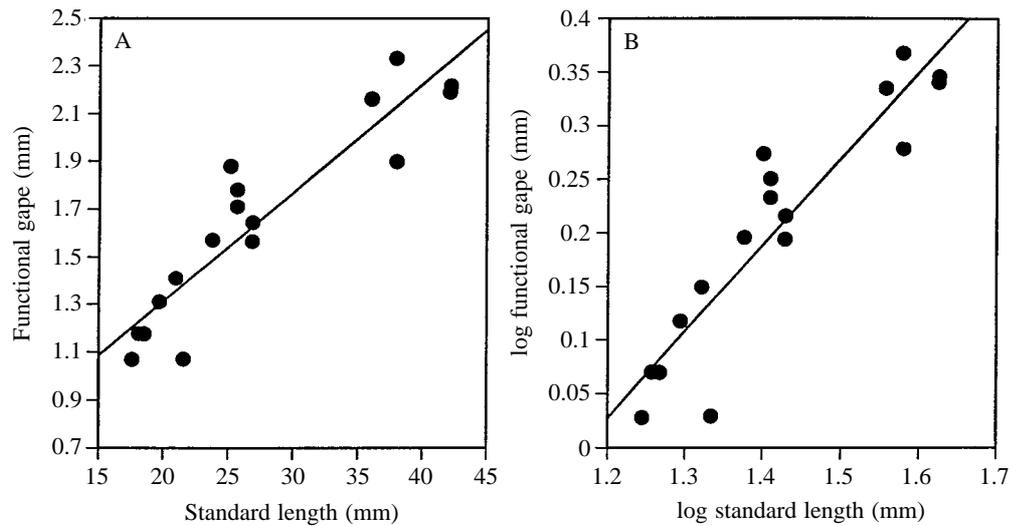


Fig. 2. Development of functional gape in *Clinocottus analis* juveniles. (A) Linear function describing change in functional gape with increasing length: $y=0.045x+0.401$, $r^2=0.85$, $P<0.0001$. (B) log-log plot of gape versus length; the slope is significantly less than 1 at $P<0.05$.

(Fig. 5). The strike was initiated at a mean of 4 mm (0.16 BL; Table 2) from the prey (Fig. 4C). Mean strike velocity was 0.17 mm ms^{-1} (6.5 BL s^{-1}). The initiation of protrusion of the

Table 1. Summary of statistical analyses (least-squares regressions) of the relationships between kinematic variables and standard length in juvenile *Clinocottus analis*

Variable	N	t-value	r ²
Attack kinematics			
Time to prey capture (ms)	18	3.608*	0.45
Absolute predator-prey distance (mm)	16	3.749*	0.50
Relative predator-prey distance (BL)	16	0.579	0.02
Absolute attack velocity (mm ms^{-1})	18	1.254	0.09
Relative attack velocity (BL s^{-1})	18	-2.240	0.23
Absolute protrusion distance (mm)	18	3.126	0.38
Relative protrusion distance (BL)	18	-0.167	0.002
Absolute protrusion velocity (mm ms^{-1})	18	1.046	0.06
Relative protrusion velocity (BL ms^{-1})	18	-1.475	0.12
Strike kinematics			
Absolute predator-prey distance (mm)	17	2.013	0.21
Relative predator-prey distance (BL)	17	-0.878	0.05
Absolute strike velocity (mm ms^{-1})	17	1.600	0.15
Relative strike velocity (BL s^{-1})	17	-1.122	0.07
Ram-suction index, body	17	-3.666*	0.47
Ram-suction index, premaxilla	17	-3.695*	0.47
Phase timing variables			
Duration of preparatory phase	18	0.249	0.004
Duration of expansive phase	18	-1.435	0.11
Duration of compressive phase	18	-1.385	0.11
Duration of recovery phase	18	0.120	0.001
Onset of expansive phase	18	0.251	0.004
Onset of compressive phase	18	-0.645	0.025
Onset of recovery phase	18	-1.618	0.14

N, number of individuals.

Phase timing variables were expressed as a proportion of (durations) or proportion into (onsets) the attack cycle.

*Slope significantly different from zero.

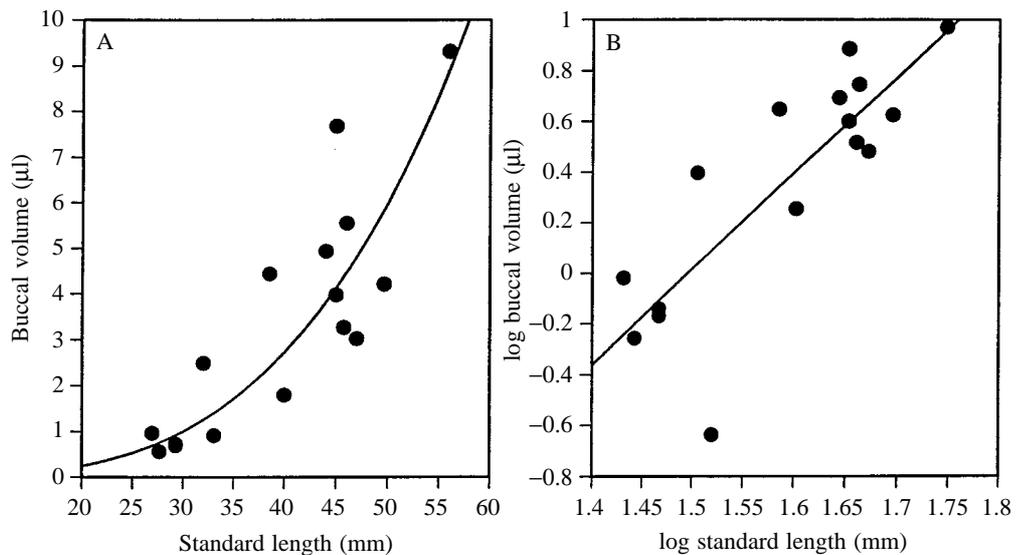
premaxilla and depression of the hyoid occurred at the beginning of the expansive phase, when the mouth was starting to open (Fig. 5). The mouth reached peak gape in 19.7 ms, and depression of the hyoid required 25 ms. Prey capture coincided with peak gape but maximal hyoid depression occurred significantly later than prey capture ($P=0.003$). There was no significant change in head angle during the attack (Fig. 5). After the prey had been captured, the mouth was closed and the premaxilla was then retracted, resulting in a deformation of the head (Fig. 4E) before the skull returned to the pre-attack configuration (Fig. 4F).

There were several clear ontogenetic changes in feeding kinematics. After the Bonferroni correction, two attack variables, time to prey capture and absolute attack predator-prey distance, and two strike variables, RSI_{body} and $\text{RSI}_{\text{premaxilla}}$, changed significantly over the size range

Table 2. Mean values of attack and strike kinematics in *Clinocottus analis* juveniles

Variable	N	Mean	S.E.M.
Attack kinematics			
Time to prey capture (ms)	18	68.51	3.27
Absolute predator-prey distance (mm)	16	6.51	0.85
Relative predator-prey distance (BL)	16	0.24	0.03
Absolute attack velocity (mm ms^{-1})	18	0.03	0.003
Relative attack velocity (BL s^{-1})	18	1.20	0.11
Absolute protrusion distance (mm)	18	0.85	0.08
Relative protrusion distance (BL)	18	0.03	0.002
Absolute protrusion velocity (mm ms^{-1})	18	0.041	0.004
Relative protrusion velocity (BL ms^{-1})	18	0.002	
Strike kinematics			
Absolute predator-prey distance (mm)	17	4.163	0.48
Relative predator-prey distance (BL)	17	0.156	0.02
Absolute strike velocity (mm ms^{-1})	17	0.173	0.02
Relative strike velocity (BL s^{-1})	17	6.55	0.68
Ram-suction index, body	17	0.71	0.07
Ram-suction index, premaxilla	17	0.76	0.06

Fig. 3. Development of buccal volume in *Clinocottus analis* juveniles. (A) Power function describing change in buccal volume with increasing length: $y = -11.97x^{3.52}$, $r^2 = 0.80$, $P < 0.001$. (B) log-log plot of buccal volume versus length; the slope is not significantly different from 3. Each point represents the value for one individual.



examined (Table 1). Time to prey capture increased significantly with increasing fish length, but its timing relative to the total attack duration remained the same (Fig. 6). Absolute attack predator-prey distance increased with increasing fish size, but there was no change in relative attack

predator-prey distance (Fig. 7). Both RSI_{body} and $RSI_{premaxilla}$ decreased significantly with increasing size (Fig. 8). This means that the relative contribution of suction to the strike increased with increasing size. The difference between RSI_{body} and $RSI_{premaxilla}$ was significantly greater in larger fish ($P = 0.008$), indicating that premaxillary protrusion makes a greater contribution to the ram component of the strike in large fish than it does in smaller fish.

Juvenile *C. analis* showed no ontogenetic change in the timing characteristics of the phases of their attacks during ontogeny (Table 1). The mean relative onset times of the expansive, compressive and recovery phases occurred at 48%, 67% and 87% of the attack cycle, respectively. The preparatory phase was the longest in duration, with a mean of 48% of the total attack duration. The expansive and compressive phases were of equal length and approximately half as long as the preparatory phase. The recovery phase had the shortest duration, and four individuals showed no recovery phase in any of their attacks.

The regression analyses of the intra-individual variances of the attack and strike kinematic variables showed no significant change through ontogeny in *C. analis* juveniles. The variance of the timing characteristics of the phases of the attack and the RSI values also showed no change with increasing size.

Discussion

Morphology

The relative gape size of *Clinocottus analis* juveniles was within the range of relative gapes of adult suction feeding cottids measured by Norton (1995) based on upper jaw length. A small gape and large buccal cavity is advantageous to a suction feeder because it allows the fish to produce a higher-velocity suction stream which is effective over a greater distance than for a fish of the same size with a large gape (Alexander, 1967). If gape size and buccal volume in *C. analis* developed isometrically, then smaller individuals would have

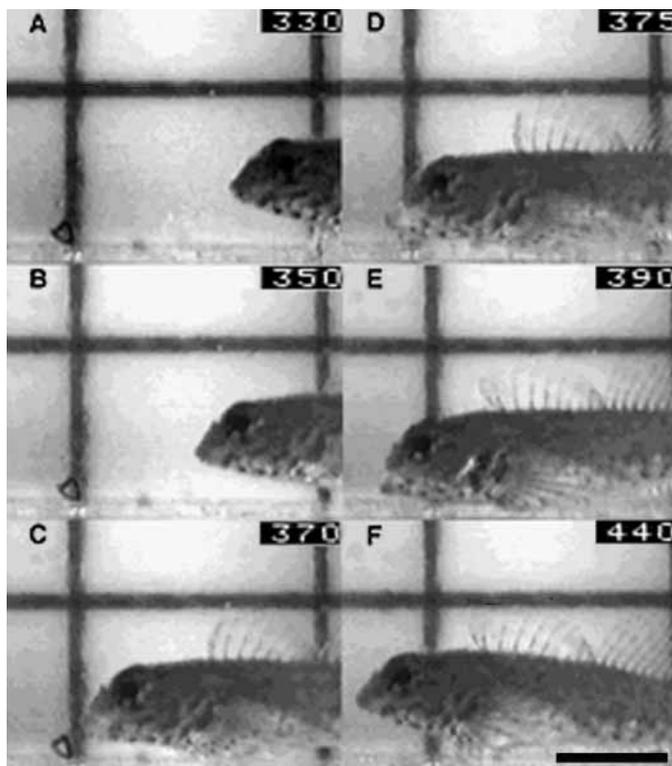


Fig. 4. The prey capture event of a 25 mm SL *Clinocottus analis*. (A) The field before the beginning of the attack. (B) Acceleration towards the prey. (C) The beginning of the strike. (D) Prey capture, the prey is visible within the buccal cavity. (E) The mouth is closed and the premaxilla is retracting. (F) The end of the attack, the head has returned to the pre-attack configuration. Time in the upper right-hand corner of each field is in milliseconds. Scale bar, 5 mm.

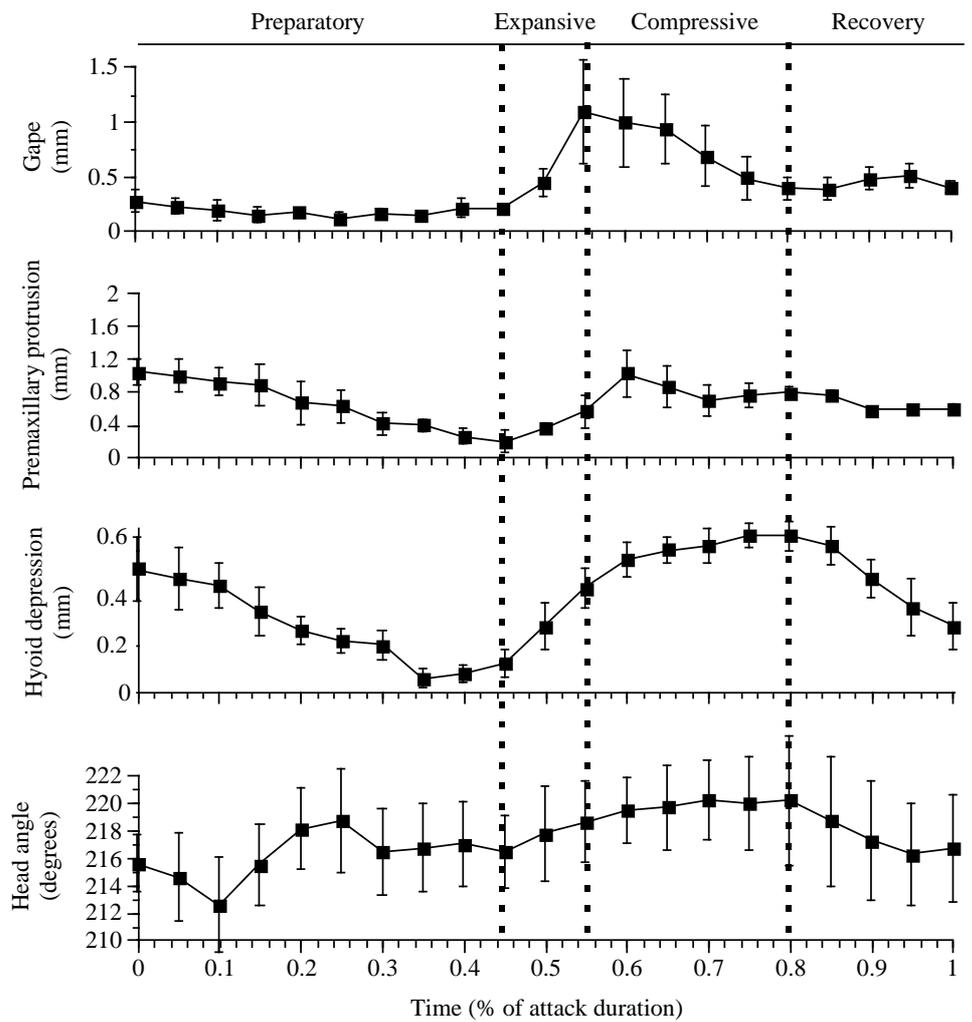
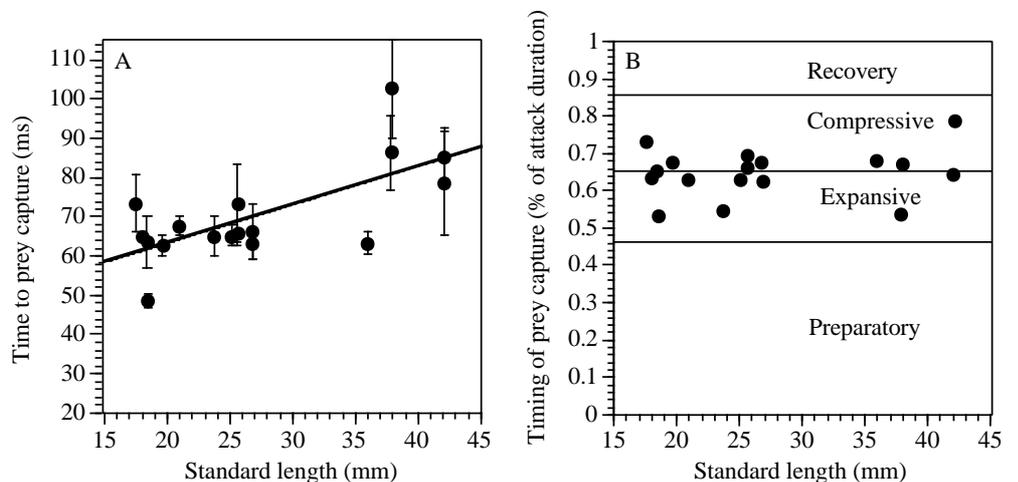


Fig. 5. Kinematic plots based on data from eight attacks by a 36mm SL juvenile *Clinocottus analis*. For each kinematic variable, the mean value (\pm S.E.M.) for all the attacks, at intervals of 5% of the total duration of the attack, are shown. The dotted lines mark the timing of the onset of each phase.

a larger gape relative to buccal volume, and larger individuals would have a smaller gape relative to buccal volume, because of the faster increase in volume compared with gape size. The change in functional gape size with increasing length in *C. analis* juveniles showed a negative allometric scaling (Fig. 2), while buccal volume scaled isometrically with fish length. This combination of isometric scaling of buccal volume and

negative allometric scaling of gape size results in larger *C. analis* juveniles having an even more hydrodynamically efficient morphology for the production of suction (Alexander, 1967) than that predicted by isometry. A comparison of the present data with those of Yoshiyama (1980) for gape size changes in larger *C. analis*, however, indicates that this trend does not continue through adulthood, and for fishes larger than

Fig. 6. (A) Relationship between absolute time to prey capture and standard length for *Clinocottus analis* juveniles. The slope is significant at $P < 0.01$, $r^2 = 0.45$, $y = 1.09x + 39$. (B) Relationship between the timing of prey capture, relative to the total attack duration, and standard length and the phase of the attack in which it occurs. Horizontal lines demarcate the timing of the four attack phases based on the mean values for all individuals. Each point represents the mean value for an individual fish.



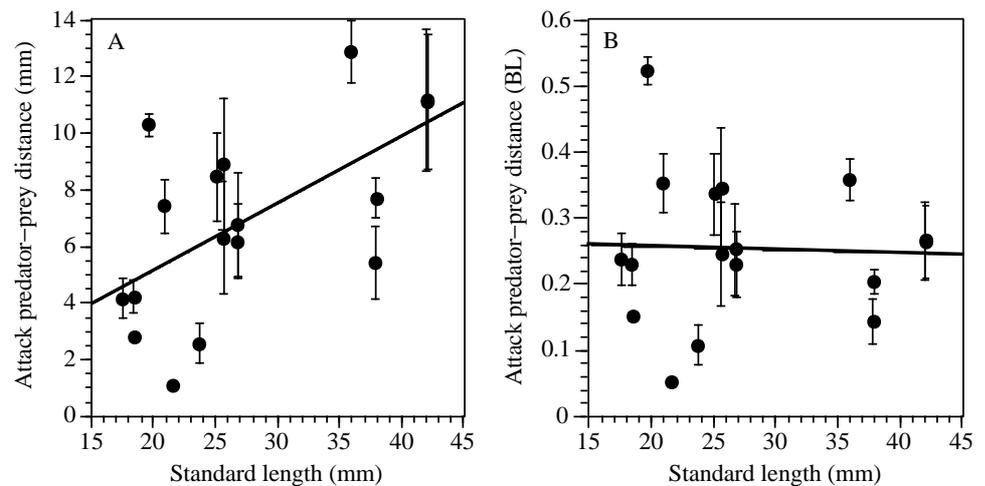


Fig. 7. (A) Relationship between attack predator-prey distance and standard length for *Clinocottus analis* juveniles. The slope is significant at $P < 0.001$, $r^2 = 0.50$, $y = 0.277x - 1.06$. (B) Relationship between relative attack predator-prey distance (in body lengths, BL) and standard length. The slope is not significantly different from zero. Each point represents the mean value \pm S.E.M. for an individual fish.

about 30 mm long the slope of gape size versus SL becomes steeper.

In general, species which have a large relative mouth size compared with other species as adults do not necessarily have larger mouths as juveniles but show a more rapid increase in gape during development (Stoner and Livingston, 1984; Keast, 1985). The slope of the relationship between functional gape size and SL in *C. analis* juveniles was in the lower portion of the range found in juveniles of 15 freshwater fish species (Keast, 1985; Michaletz *et al.* 1987; Scheal *et al.* 1991) based on anatomical gapes. The rate of absolute functional gape

increase in *C. analis* is similar to that of *Lepidesthes sicculus* and *Lepomis* sp. but much slower than that of *Micropterus salmoides*, *Perca flavescens*, *Aplodinotus grunniens* and *Pomoxis nigromaculatus*. Buccal volume in juvenile *C. analis* showed a similar scaling relationship to that of juvenile and adult *Notemigonus crysoleucas* (Ehlinger, 1989) and *Dorosoma cepedianum* (Drenner *et al.* 1982). Both *N. crysoleucas* and *D. cepedianum* are pump filter feeders as adults, a feeding mode functionally similar to suction feeding. So, for the measures of feeding morphology analyzed in this study, *C. analis* shows ontogenetic changes similar to those found in species of fishes which have a relatively small gape and a suction-based feeding mode.

It is important to note that my values for functional gape in *Clinocottus analis* are based on measurements taken during the attack, while almost all the measurements of gape from the literature mentioned above are based on dead specimens. The exception is *M. salmoides*, for which there are data on functional gape (Richard and Wainwright, 1995). Late juvenile *M. salmoides* show a larger functional gape than comparably sized *C. analis* juveniles, and the slope of gape increase with body size is steeper. This indicates that, despite the difference in the method of gape measurement between this study and others, the general trends outlined above are still valid.

Ontogenetic development

Some behavioral development clearly occurs during the juvenile period in *C. analis*. Some of these changes, such as the increase in absolute predator-prey distance with increasing size, are probably due to physiological and physical changes resulting simply from the increase in size. The change in feeding mode, however, is a developmental process not directly caused by the increase in size over ontogeny. Most of the variables measured, however, showed no significant change over the size range studied. For example, although the duration of the feeding event becomes longer as the fish grows, the relative timing of each phase appears to be set prior to or at the onset of the juvenile period. The relative attack predator-prey distance and relative attack velocity showed no significant change with increasing

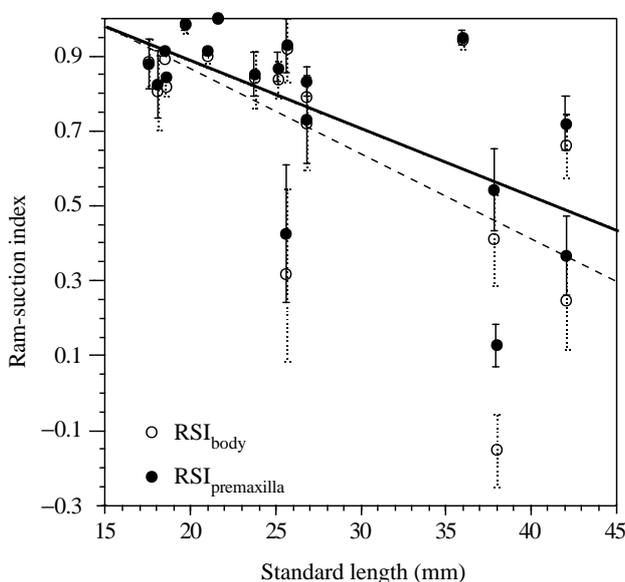


Fig. 8. Relationship between feeding mode, as measured by the ram-suction index, and standard length in juvenile *Clinocottus analis*. Open circles and the dashed line represent the ram-suction index value for the body. The filled circles and solid line represent the ram-suction index value for the premaxilla (see Materials and methods for details). Each point represents the mean \pm S.E.M. for an individual fish. The slopes of both lines are significant at $P < 0.01$ and $r^2 = 0.47$ for both lines. For RSI_{body} , $y = -0.024x + 1.37$. For $RSI_{premaxilla}$, $y = -0.018x + 1.28$.

size and their values were comparable to those of adult suction feeding cottids (Norton, 1991). Therefore, juvenile *C. analis* can be considered to be small adults in all the characteristics measured except for feeding mode.

All aspects of the change in feeding mode in *C. analis* are consistent with a significant change from a ram-feeder to a suction-feeder. The magnitude of the change in RSI_{body} in *C. analis* juveniles was equivalent to the interspecific difference found by Norton and Brainerd (1993) for closely related pairs of ram and suction feeders. In early juvenile *C. analis*, the difference between the RSI_{body} and the $RSI_{\text{premaxilla}}$ was small, as is characteristic of a ram feeder (Fig. 8). The increasing difference between the RSI_{body} and $RSI_{\text{premaxilla}}$ indicates that, in late juvenile *C. analis*, premaxillary protrusion contributes more to the ram component of the strike than in early juveniles. This large difference between RSI_{body} and $RSI_{\text{premaxilla}}$ is characteristic of a suction feeder.

A potentially confounding variable to the decrease in the RSI value over ontogeny is the effect of prey size on feeding mode. Small prey are easier to move using suction than are large prey, so a decrease in prey size relative to predator size might explain the change in RSI over ontogeny. Two lines of evidence, however, support the idea that this is a real behavioral change rather than a response to relative prey size. One is the fact that, over the size range of prey tested (2–5 mm), RSI is not correlated with prey size ($P=0.7$). The second is the result of a pilot study in which the author used brine shrimp as prey rather than brown worms. Brine shrimp are much larger prey than the brown worm pieces used here, but juvenile *C. analis* exhibited lower RSI values in feeding strikes on them.

Interspecific comparisons of kinematics

Of the three common patterns of development of prey capture kinematics outlined in the Introduction, decrease in time to prey capture, increase in attack predator–prey distance and increase in strike velocity, *C. analis* exhibits only one, an increase in attack predator–prey distance. Allometry predicts an increase in attack duration (Richard and Wainwright, 1995), as seen in juvenile *C. analis*, rather than the decrease seen in early larvae of other fish. Many studies include some variables just prior to what is defined as the attack in this study (Hunter, 1972; Brown and Colgan, 1984; Wanzenbock, 1992). Therefore, at least part of the difference between the present results from juvenile *C. analis* and those from the early life history stages of other fishes may be due to differences in terminology. However, two studies which defined the feeding event in the same manner as is used here also show a decrease in time to prey capture (Coughlin, 1991, 1994). It is not clear what physiological or behavioral changes may be behind this phenomenon in very young fishes.

The values for feeding kinematics found for *C. analis* are most similar to those of juvenile *Archoplites interruptus* and *Salmo salar* alevins (Vinyard, 1982; Coughlin, 1991). In comparisons of the feeding kinematics of juvenile *C. analis* with those of the larvae and juveniles of other species, an interesting pattern emerges. In general, for a given value of

predator–prey distance or velocity, individual *C. analis* are larger than the early life history stages of other species for that variable. For example, a *C. analis* juvenile showing a value of 0.04 mm ms^{-1} for absolute attack velocity is 18.1 mm SL, while a *Pomoxis annularis* showing a similar value is 4.5 mm SL (Browman and O'Brien, 1992). There are several possible reasons for this, including a different rate of development in *C. analis*, but the two most probable explanations are the narrow size range examined in previous studies (at least for comparing relative predator–prey distance and velocity) and the effect of prey type. The studies discussed above are based on attacks on prey types that are, to varying degrees, more elusive than the brown worms used in this study.

The characteristics of the phases of the attack and the kinematics of the head have not been quantified for the early life history stages of fishes, so these data on *C. analis* can only be compared with those of adults of other species. The duration of the expansive phase of *C. analis* juveniles is extremely rapid compared with that of adult fishes. The closest value reported for an adult fish is that of *Pomoxis annularis* (Lauder, 1983a) which has an expansive phase of 24 ms, which is 5 ms longer than the mean for juvenile *C. analis*. Since studies looking at locomotion (Archer *et al.* 1990) and feeding (Richard and Wainwright, 1995) in fishes and locomotion in lizards (Marsh, 1988) have found that contraction time increases with the size of the organism, this rapid expansion is most probably due to the small size of *C. analis* juveniles. Unexpectedly, however, the duration of hyoid depression in *C. analis* juveniles is not particularly rapid (25 ms) compared with that of the adults of other fishes. Adult *Lepomis macrochirus*, *Lepisosteus oculatus* and *Hoplerhynchus* sp. all show a much more rapid hyoid depression (Lauder, 1983a, 1985), despite the fact that these fishes are much larger than a juvenile *C. analis*.

This study did not find a change in stereotypy over ontogeny in juvenile *C. analis*. Since, for most of the feeding kinematic variables measured, there was either no change or a change which could be linked to the change in size, this is perhaps not surprising. The change in feeding mode, in contrast, is more complex and potentially involves a number of modifications in the relative onset of hyoid depression, gill arch adduction and opercular expansion (Lauder, 1983a,b). Despite this, there does not appear to be any increase in variance indicative of a period of adjustment during ontogeny. This study was cross-sectional rather than longitudinal so, within an individual fish's ontogeny, there may be some fine tuning associated with the change in feeding mode but it is too brief to impact the ontogeny of juveniles as a whole. Coughlin (1991) found a decrease in variance in the predator–prey distance of Atlantic salmon alevins but, at least over the small size ranges that have been studied, most young fishes show no change in the variance of their kinematic variables with increasing age (Hunter, 1972; Wanzenbock, 1992; Coughlin, 1994).

Previous work on ram and suction feeding has revealed a distinct kinematic repertoire and morphology associated with a species' feeding mode (ram- or suction-dominated) (Norton, 1991) (Table 3). Suction-dominated feeders morphologically

Table 3. *Features of morphology, kinematics and feeding performance associated with ram-dominated and suction-dominated feeding modes in adult cottids*

Characteristic	Feeding mode	
	Ram-dominated	Suction-dominated
Mouth size (BL)	Large	Small
Predator-prey distance (BL)	Large	Small
Attack velocity (BL s ⁻¹)	High	Low
Performance on elusive prey	Good	Poor

Based on Norton (1991).

and kinematically maximize the magnitude of the suction they produce and its effectiveness. Ram-dominated feeders, in contrast, kinematically minimize the prey's ability to detect the predator's approach and morphologically maximize their ability to engulf prey accurately while approaching at high velocity. Since early juvenile *C. analis* use a feeding mode (ram-dominated) that they would not be predicted to use on the basis of their morphology and feeding kinematics (characteristic of suction feeders), this presents a conundrum. There are potentially three ways that this mismatch might have an impact on the ability of *C. analis* juveniles to capture prey. First, without the benefit of 'kinematic stealth', the juveniles may not be very effective against elusive prey. Second, feeding kinematics may have less of an impact on successful capture of elusive prey than the feeding mode used. If this were true, early juvenile *C. analis* would be able to capture elusive prey as effectively as adult ram feeders. A third possibility is that juvenile *C. analis* might use different prey-capture behaviors when attacking elusive prey from those they use on non-elusive prey. Therefore, either by modifying their kinematics to match more closely their feeding mode or by modifying their feeding mode to match more closely their kinematics and morphology, they could be as effective against elusive prey as either adult ram feeders or adult suction feeders, depending on which strategy is used. Further research into the ontogeny of prey capture behavior based on attacks on elusive prey is necessary to identify the strategy used during ontogeny and its effects on juvenile feeding ecology.

The functional morphology of feeding during the juvenile period in fishes can definitely change, and the results from this study illustrate three things about these changes. First, they show that strong interspecific relationships between feeding morphology, kinematics and mode seen in adult fishes may not necessarily translate into a relationship within a species during ontogeny. Early juvenile *C. analis* exhibited a different feeding mode from that predicted by their morphology and kinematics. Second, changes in feeding mode during ontogeny are not simply an increase in the contribution of suction to the strike. Other changes, such as the contribution of premaxillary protrusion to the ram component of the strike, may also occur. Third, and related to the first point, this study illustrates the development of morphology and kinematics prior to feeding mode. Studies that have looked at the development of biting and

filter-feeding in young fishes indicate that this may be a general pattern in fish development (June and Carlson, 1971; Michaletz *et al.* 1982; Stoner and Livingston, 1984). Several new directions for research into the ontogeny of fish feeding are clear, including concentration on the kinematics of the skull (such as hyoid depression and premaxillary protrusion) and investigation into how the scaling of morphologies such as mouth size and buccal volume differ among species using different feeding modes.

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