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KINEMATICS OF PREY CAPTURE IN A FLATFISH, *PLEURONICHTHYS VERTICALIS*

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Summary

Hornyhead turbot, *Pleuronichthys verticalis* (Pleuronectiformes: Pleuronectidae), are morphologically asymmetrical teleosts with substantial bilateral asymmetry in the neurocranium, suspensorium and anterior jaws. In order to quantify the kinematics of prey capture and to test for functional bilateral asymmetries, four individuals of this species were video-taped feeding using a high-speed video system at 200 fields s^{-1}. Frame-by-frame analysis revealed several features not commonly found in prey capture behavior of previously studied ray-finned fishes. These features include (1) extreme lateral compression of the suspensorium and opercular series prior to mouth opening, indicating the consistent presence of a preparatory phase during feeding, (2) apparent dissociation of hyoid retraction and lower jaw depression, (3) prolonged hyoid retraction throughout much of the feeding cycle, and (4) concomitant dorsal rotation of the neurocranium and closing of the jaws. *P. verticalis* also demonstrate a significant degree of functional bilateral asymmetry during prey capture. When approaching prey, fish flex their heads towards the ocular (anatomically the right) side of the body. During prey capture, their jaws bend out of the midline towards the blind (left) side. Comparisons of the displacement and timing for movements of homologous anatomical features on the ocular and blind sides of the head reveal that maximum gape is always larger on the blind side of the head than on the ocular side. In contrast, other kinematic variables measured are similar on both sides of the head. These results suggest that *P. verticalis* possess unique functional features of prey capture behavior and that morphological bilateral asymmetry of the head and jaws is associated with, and perhaps causally related to, the functional bilateral asymmetry present during feeding.

Key words: prey capture, feeding behavior, kinematics, flatfish, hornyhead turbot, asymmetry, *Pleuronichthys verticalis.*

Introduction

Pleuronectiform fishes (flatfishes) hatch as bilaterally symmetrical larvae, but during metamorphosis one eye migrates to the opposite side of the head (Sumida *et al.* 1979; Ahlstrom *et al.* 1984) and the fish come to rest on their blind (or eyeless) side. As a consequence of eye migration, all pleuronectiform fish possess some degree of cephalic skeletal and muscular bilateral asymmetry. In general, the bones and muscles on the blind side of the head are larger than those present on the ocular (eyed) side (Yazdani, 1969). Such bilateral asymmetry is present in the bones and muscles associated with jaw movements and has the potential to affect the feeding mechanism of these fishes. In fact, previous research (conducted by manipulating the jaws of dead flatfish) suggests that varying degrees of cephalic morphological asymmetry can result in varying degrees of functional asymmetry during prey capture (Yazdani, 1969). However, this hypothesis has yet to be tested by examining the feeding behavior of living flatfish.

Most previous studies of the kinematics of feeding in ray-finned fishes have examined one side of the head and body and assumed bilateral symmetry in movements, muscle activity patterns and fluid flow (for example, Liem, 1970; Lauder, 1979; Motta, 1982; Westneat, 1990). Asymmetry could be present in the magnitude or timing of at least three functional aspects of feeding behavior: (1) movements of paired bones of the head, (2) muscle activity in homologous muscles on opposite sides of the head, and (3) flow of water into and out of the head. The few studies that have examined the motor activity patterns of muscles on both sides of the head during feeding events indicate that jaw muscles are active in a bilaterally symmetrical way during rapid prey capture (for example, Liem, 1978). However, several species of fish have demonstrated bilaterally asymmetrical muscle activity patterns during slower methods of food acquisition (e.g. algae scraping) and during manipulation of the prey (Liem, 1979, 1980; Lauder and Norton, 1980).

The possibility of functional bilateral asymmetry has previously been examined in pleuronectiform respiration. Early studies of respiration suggested that breathing in flatfishes is bilaterally asymmetrical (Yazdani and Alexander, 1967) and therefore involves bilaterally asymmetrical head movements and muscle activity patterns. However, a more recent study examining flatfish respiration in *Pseudopleuronectes americanus* has shown that flatfish are symmetrical in both the flow of the respiratory current and in the underlying respiratory mechanisms (Liem *et al*. 1985). For this species, in the case of respiration, functional symmetry is maintained in spite of morphological asymmetry.

Despite the unique questions that pleuronectiform fishes pose for evolutionary and functional morphologists, the basic kinematics of feeding behavior has yet to be described for any species of flatfish. Therefore, this study has three major goals: (1) to describe the kinematics of prey capture behavior in a flatfish, (2) to compare the kinematics with those described in the literature for other ray-finned (actinopterygian) fishes, and (3) to test the hypothesis that functional bilateral asymmetry exists during prey capture in flatfish by comparing movements of features on one side of the head with movements of homologous features on the other side of the head.

Materials and methods

Collection and maintenance of specimens

Pleuronichthys verticalis (Jordon and Gilbert) were chosen for this study because of their asymmetrical cephalic morphology. In the wild, they feed primarily on slow-moving or sessile soft-bodied invertebrates (Kramer, 1991). Earthworms *Lumbricus terrestris* were used as prey because their movement and texture are similar to those of the soft-bodied invertebrates that this species typically consumes.

Specimens of *Pleuronichthys verticalis* were collected during otter trawls conducted at 30 m depths off the coast of Orange County, California, USA. Individuals that died as a result of injuries sustained in the trawl were used for anatomical descriptions. Some specimens (freshly dead specimens) were dissected immediately and others (preserved specimens) were preserved by immersion in a 10 % buffered formalin for several days and then transferred to a 70 % ethanol solution. The head and jaws of freshly dead specimens were manipulated and dissected in order to observe passive movements of bones and muscles. Preserved specimens were cleared and stained in order to observe and describe the bones and cartilage of the head and jaws.

Specimens that were captured alive and in good condition were transferred to the laboratory, where they were maintained in 80 l saltwater aquaria at a temperature of 18–20 °C on a 16 h:8 h L:D cycle. The video-taping chamber used in this study was a 120 l saltwater aquarium (dimensions 90 cm×30 cm×30 cm) with a transparent bottom maintained at a temperature of approximately 20±1 °C. At least 48 h prior to video-taping, fish were transferred to this chamber and allowed to acclimate to it.

Video-taping and digitizing

Four individual *P. verticalis* (HT4, HT8, HT10, HT21; 15.9–18.3 cm standard length) were video-taped using a NAC high-speed video system at 200 fields s^{-1}. They were fed earthworm pieces approximately 2–4 cm in length, placed on the bottom of the chamber. Three views of each individual feeding were recorded: (1) a view of the ocular side video-taped through a front-surface mirror placed at an angle of 45 ° over the tank, (2) a view of the blind side video-taped through a front-surface mirror placed at an angle of 45 ° below the tank, and (3) a view of the gular region (anatomically the ventral portion of the head) video-taped with a camera placed perpendicular to the front of the taping chamber (Fig. 1). The two-camera video system allowed two views to be recorded simultaneously; ocular and blind views were recorded together, as were gular and blind views. When recording the gular and blind views, only sequences in which the long axis of the fish was perpendicular to the camera were analyzed. Four feeding events were recorded using each camera combination for each individual. Thus, in total, eight prey capture events were recorded for each individual. (Individual HT4 was an exception; four feeding events were recorded from the blind and gular views, but only two from the ocular and blind views.)

Video images were analyzed using a customized digitizing program. Points on the neurocranium, jaws, hyoid and opercles were digitized, as well as several reference points on the body. At least 26 frames (which comprised 630 ms total elapsed time) were analyzed for each feeding sequence. For all sequences, time 0 was determined as the time at which the mouth first began to open. The 26 frames analyzed included the following times during the feeding cycle: −300, −200, −150 to −30 (in 30 ms intervals), 0–60 (5 ms intervals), 90–180 (30 ms intervals), 230 and 330 ms.

Kinematic variables

After the video sequences had been digitized, the coordinates of the digitized points were used to calculate the variables of interest. In total, 17 kinematic variables were analyzed. In order to facilitate comparisons with bilaterally symmetrical actinopterygians, all movements of the head and jaws during feeding were determined relative to the anatomical orientation of the fish (Fig. 1).

Seven displacement and timing variables associated with movements of the upper and lower jaws were calculated as follows: (1) maximum gape (cm), the maximum distance between upper and lower jaws during prey capture; (2) time to maximum gape (ms), the interval between the beginning of mouth opening and the maximum gape; (3) gape cycle time (ms), the total time the mouth was open during prey capture; (4) maximum depression of the lower jaw (degrees), the maximum angle calculated between a point on the anterior tip of the lower jaw, a point near the articulation of the lower jaw with the quadrate and a point at the base of the pectoral fin; (5) time to maximum lower jaw depression (ms), the interval between the opening of the mouth and maximum depression of the lower jaw; (6) maximum upper jaw protrusion (cm), the maximum anterior displacement of the premaxilla; and (7) time to maximum protrusion of the upper jaw (ms), the interval between mouth opening and maximum protrusion of the upper jaw.

Two variables associated with movements of the

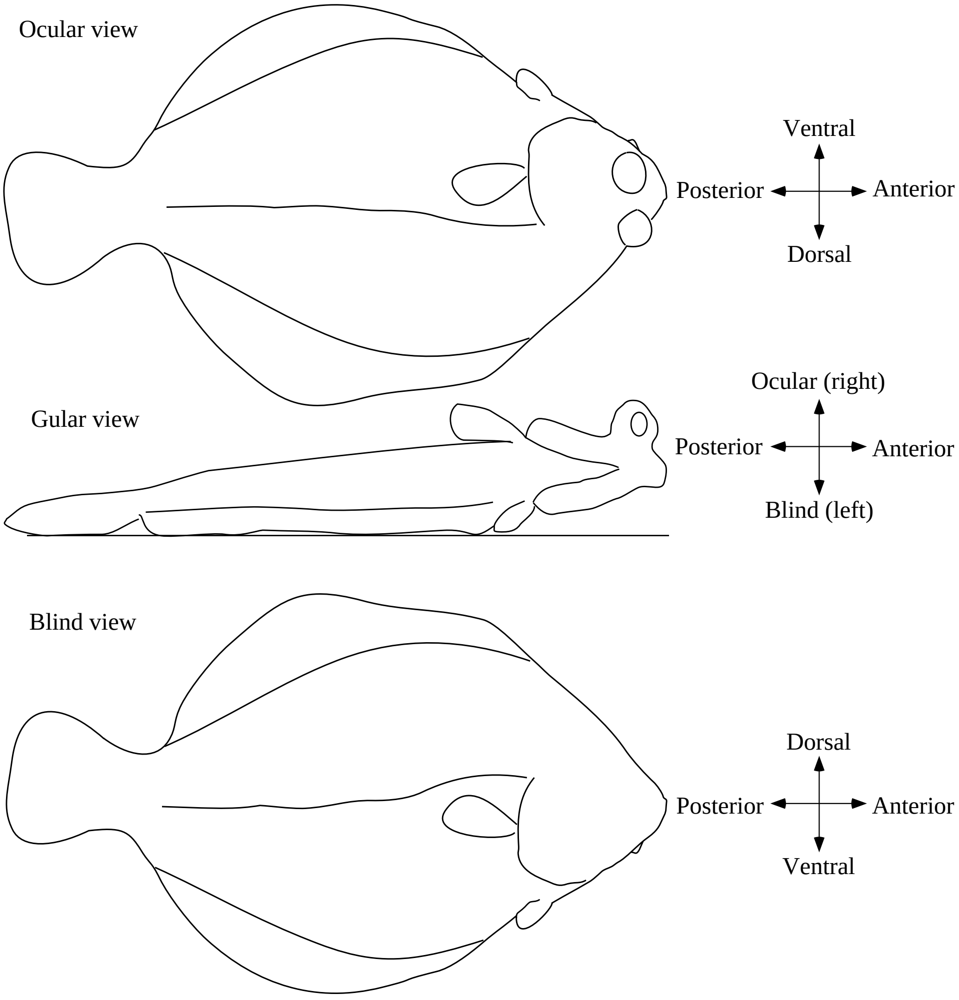

Fig. 1. Schematic diagram of *Pleuronichthys verticalis* indicating relevant directional terms. Note that the directional terms are given with respect to the fish, not with respect to any external frame of reference. The ocular and blind views are shown as viewed through mirrors placed at angles of 45 ° over and under the experimental tank, respectively. This is the same orientation as that in the video images analyzed.

neurocranium were measured. Cranial rotation (degrees) during prey capture (often termed 'head elevation' in previous studies) was measured as the angular rotation of the neurocranium dorsally relative to the rest of the body. The angle of the neurocranium was determined using the following points: an anterior point on the neurocranium near the articulation of the premaxilla, a posterior point on the neurocranium near the attachment of the dorsal fin and a point at the base of the pectoral fin. Time to maximum cranial rotation (ms) was calculated as the interval between the time of mouth opening and the time of maximum dorsal rotation of the neurocranium.

Four variables describing movements of the hyoid were also examined. The maximum depression of the hyoid (cm) was determined using its most ventral position, and maximum retraction (cm) was determined by its most posterior position. The intervals between mouth opening and the most depressed and retracted positions of the hyoid were calculated as the time to maximum hyoid depression and retraction (ms), respectively.

Two variables described timing and displacement of the opercular series during prey capture. Maximum opercular expansion (cm) occurred when the ocular and blind side opercles were maximally laterally displaced. The time to maximum opercular expansion (ms) was calculated as the interval between the beginning of mouth opening and the maximum lateral expansion of the opercular series.

Of the 15 variables described above, six involve movements of unpaired structures. These variables are: maximum hyoid depression, time to maximum hyoid depression, maximum hyoid retraction, time to maximum hyoid retraction, maximum cranial rotation and time to maximum cranial rotation (see Table 1). Since it was unlikely that unpaired structures moved in a bilaterally asymmetrical manner, they were quantified from the blind view only.

Nine of the timing and displacement variables described above involved movements of paired structures with the potential for functional asymmetry during prey capture. Therefore, the following variables were calculated for both the blind and the ocular sides of the head: maximum gape, time to maximum gape, gape cycle time, maximum upper jaw protrusion, time to maximum upper jaw protrusion, maximum lower jaw depression, time to maximum lower jaw depression, maximum opercular expansion and time to maximum opercular expansion (see Table 2).

Two additional angular variables were measured using coordinates from the gular view: (1) maximum lateral flexion of the head (the angle formed by a point at the base of the pectoral fin, a posterior point on the eye and a line parallel with the substratum), and (2) maximum lateral flexion of the lower jaw (the angle formed by a point on the anterior apex of the lower jaw, a point at the base of the lower jaw and a line parallel with the midline of the head). Fig. 2 illustrates how the angular asymmetry variables (lateral flexion of the head and jaw) were calculated in this study.

Statistical analyses

One-way analyses of variance (ANOVAs) were calculated for the six unpaired kinematic variables in order to determine whether there was significant variation among individuals. Two-way ANOVAs were performed on the nine potentially asymmetrical variables (displacement and timing variables). The two-way analyses examined variables for individual and side-of-the-head effects, as well as the interaction of these two effects. Individual was treated as a random effect and the residual was used to calculate the *F*-statistic. Side-of-the-head was treated as a fixed effect and was tested over the interaction term of the two effects. The residual error was used to calculate the *F*-statistic for the interaction term. All ANOVAs were calculated using SuperANOVA on a Macintosh computer.

Using the Macintosh program Statview, one tailed *t*-tests were performed on the two angular variables (head and jaw lateral flexion). The null hypothesis for these tests was that there was no lateral bending of the head or body (angle=0 °).

In order to test for homogeneity of variances, an *F*-max test (Sokal and Rohlf, 1981) was performed on the variables before ANOVAs or *t*-tests were performed. Of all 17 variables analyzed, only one, cranial rotation, failed to meet the criteria of the test. However, the only ANOVA conducted on the cranial rotation data was a one-way ANOVA which examined the data for individual effects. The variances of the four individuals were not homogeneous according to the *F*-max test; however, different variances for the four individuals would appear to support the hypothesis that individual variation was present. Thus, the *F*-statistic for cranial rotation is still included. To account for multiple simultaneous ANOVAs, levels of statistical significance were adjusted for all ANOVAs and *t*-tests using the sequential Bonferroni technique (Rice, 1989).

Results

Morphological asymmetry

It is beyond the scope of this paper to give a complete description of the cranial osteology of *P. verticalis*. However, a brief description of the presence or absence of morphological asymmetry in the functional units of the head and jaws (Liem, 1970) is included here to provide a framework for the results of the kinematic study. A more detailed description of the morphological asymmetry of *P. verticalis* is currently in preparation (A. C. Gibb, unpublished results).

Certain portions of the head and jaws of *P. verticalis* are morphologically bilaterally asymmetrical (Fig. 3). Asymmetry is most extreme in three regions: the neurocranium, the anterior portions of the suspensorium, and the jaws. In the neurocranium, asymmetry consists primarily of a torsion of the dorsal surface towards the ocular side of the body. This torsion is apparently a result of the migration of the eye during metamorphosis (Yazdani, 1969).

The pterygoid process of the suspensorium has a different shape on the ocular and blind sides of the head. On the blind side, the anterior portion of the pterygoid process forms a flat surface which abuts the ventral surface of the palatine bone. On the ocular side, the pterygoid process is rounded and the lateral surface of the palatine does not rest directly against it.

The palatine bone is substantially larger on the blind side than on the ocular side of the head. The maxilla, premaxilla and mandible are also larger (and longer) on the blind side of the head than on the ocular side. In contrast, the hyoid apparatus, the opercular series and the posterior portions of the suspensorium (particularly the hyomandibula and preopercle) do not display a large degree of morphological asymmetry.

Kinematics of prey capture

Pleuronichthys verticalis appear to locate their prey visually and follow its movements with their eyes during capture. During feeding events, *P. verticalis* approach the prey by ‘walking’ along the bottom of the tank using their dorsal and anal fins. When *P. verticalis* are approximately 2 cm away from the prey, they cease to move the body forward; thereafter, primarily their head and jaws move towards the prey item. During capture, the lower jaw is depressed and the upper jaw protrudes anteriorly approximately 1 cm towards the prey (see Table 2). The prey is then sucked into the mouth. During the time (approximately 10 ms total) in which the prey is engulfed, the prey moves an average of 1.4±0.4 cm towards the mouth, while the jaws move an average of 0.2±0.06 cm towards the prey item.

Mean values are given in Tables 1 and 2 for the timing and displacement variables for all sequences for all individuals. Fig. 4 illustrates a typical feeding sequence for one individual (HT8) and Fig. 5 represents the summarized kinematic profile

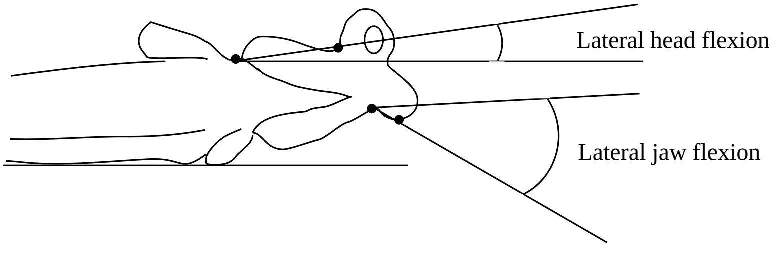

Fig. 2. Schematic diagram of the gular view of the anterior portion of *Pleuronichthys verticalis*. Filled circles indicate points on the head and body that were digitized and used to calculate lateral flexion of the head and jaws. The fish is displayed in this particular posture for ease of presentation of these variables. This combination of head lifting (lateral flexion of the head of approximately 10 °) and jaw bending (lateral flexion of the jaw of approximately −30 °) was never observed during the course of this study.

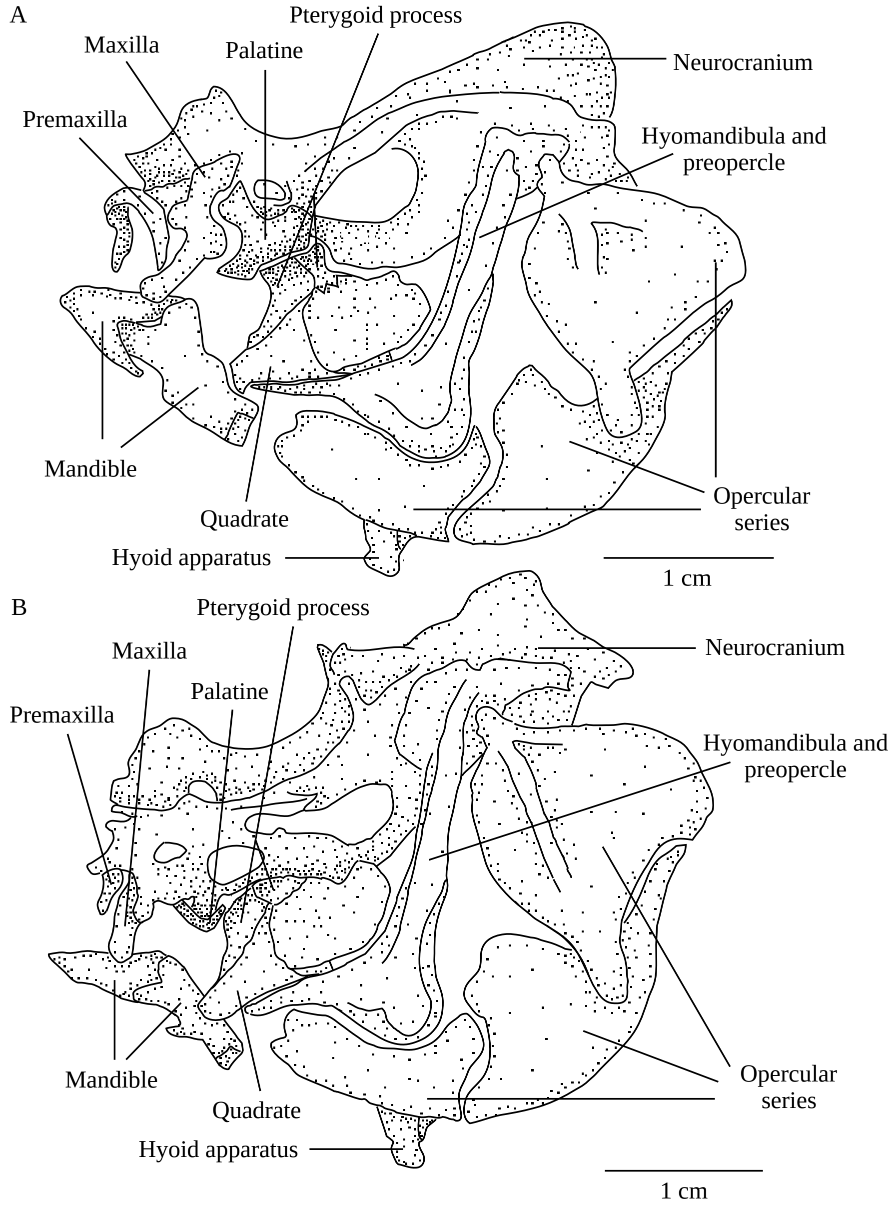

Fig. 3. *Camera lucida* drawings of a cleared and stained skull of *Pleuronichthys verticalis*. (A) The blind side of the head; (B) the ocular side. Note that the ocular side has been reversed horizontally in order to facilitate comparisons with the blind side.

for another individual (HT21) for four prey capture events. The mean values are plotted *versus* time for the feeding cycle. Time 0 was defined by the beginning of mouth opening (Fig. 5), and changes in other kinematic variables will be discussed relative to the gape cycle.

As the fish approaches the prey, the opercles are compressed and reach maximum compression (minimum expansion) during the gape cycle (Figs 4, 5; 0–40 ms). Opercular expansion begins after the mouth is closed, and the opercles continue to expand as the hyoid, neurocranium and lower jaw return to their original positions (Figs 4, 5; 90–180 ms).

Lower jaw depression begins at the same time as mouth opening (Figs 4, 5; 0–20 ms). The lower jaw reaches maximum depression at approximately the same time that the mouth achieves maximum gape (Fig. 5). However, after the mouth is closed, the lower jaw remains slightly depressed at an angle of approximately 20 ° (Fig. 5).

Table 1. *Mean and* S.E.M. *variables measured for unpaired structures during the prey capture behavior of* Pleuronichthys verticalis

Variable	Mean value	S.E.M.
Maximum hyoid depression (cm)	0.89	0.18
Time to maximum hyoid depression (ms)	103.4	21.1
Maximum hyoid retraction (cm)	1.28	0.26
Time to maximum hyoid retraction (ms)	84.1	17.2
Maximum cranial rotation (degrees)	27.6	5.6
Time to maximum cranial rotation (ms)	40.6	8.3

N=16.

Hyoid retraction begins shortly (5–10 ms) after mouth opening (Figs 4, 5; 10–20 ms). The hyoid is retracted rapidly and this posterior movement continues throughout the gape

Table 2. *Mean and* S.E.M. *of variables measured during the prey capture behavior of* Pleuronichthys verticalis *for the ocular and blind sides of the head*

	Ocular (right)		Blind (left)	
Variable	Mean	S.E.M.	Mean	S.E.M.
Maximum gape (cm)	0.50	0.11†	0.73	0.16†
Time to maximum gape (ms)	19.6	4.4†	20.3	4.6†
Gape cycle time (ms)	36.1	8.1†	41.8	9.3†
Maximum upper jaw protrusion (cm)	0.91	0.20†	1.04	0.23†
Time to maximum upper jaw protrusion (ms)	39.3	8.8†	42.1	9.4†
Maximum lower jaw depression (degrees)	33.9	1.1†	33.6	0.8†
Time to maximum lower jaw depression (ms)	20.3	2.1†	20.7	2.0†
Maximum opercular expansion (cm)	0.52	0.11	0.64	0.13
Time to maximum opercular expansion (ms)	66.9	13.7	156.5	32.0

†*N*=14, in all other cases *N*=16.

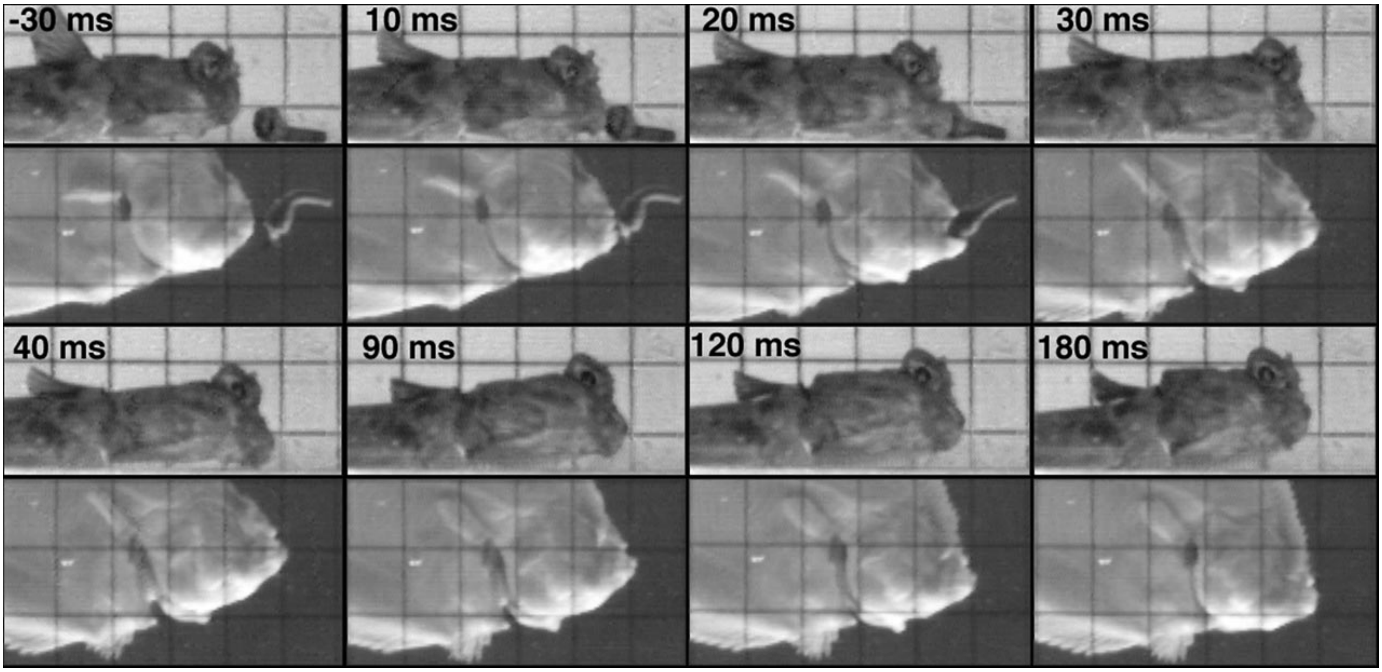

Fig. 4. Selected video frames from a representative prey capture sequence for one individual *Pleuronichthys verticalis* (HT8). Video images have been cropped and the contrast has been manipulated in order to increase the clarity of the image. The gular view is presented in the top half of each panel, and the blind view in the bottom half. Numbers represent time in milliseconds relative to the beginning of mouth opening (time 0).

cycle. The hyoid moves posteriorly a distance of over 1 cm during hyoid retraction (Table 1). The hyoid is not protracted and returned to its original position until well after the mouth has closed (Fig. 4; 120–180 ms). Hyoid depression also begins immediately after mouth opening (Fig. 5) and reaches a plateau shortly after maximum gape is achieved. The hyoid remains at or near maximum depression for some time after the mouth has closed (Fig. 5).

The neurocranium is maintained in a position of slight dorsal rotation as the fish approaches the prey. Rapid cranial rotation begins after the mouth has opened and reaches its maximum value as the mouth closes (Figs 4, 5; 20–40 ms). During this time, the neurocranium rotates dorsally approximately 10 ° in 40 ms. After reaching its maximum value, the neurocranium begins to rotate ventrally (Fig. 5) and reaches minimum cranial rotation near the end of the feeding cycle.

A summary of the results of the one-way ANOVAs performed on unpaired variables is given in Table 3. The only unpaired variable which showed significant individual variation was maximum cranial rotation. Different individuals produced drastically different degrees of cranial rotation; the average maximum cranial rotation during capture in individual HT4 was more than 10 ° greater than that of individual HT21.

Asymmetry variables

The two-way ANOVAs indicated that only one of the nine

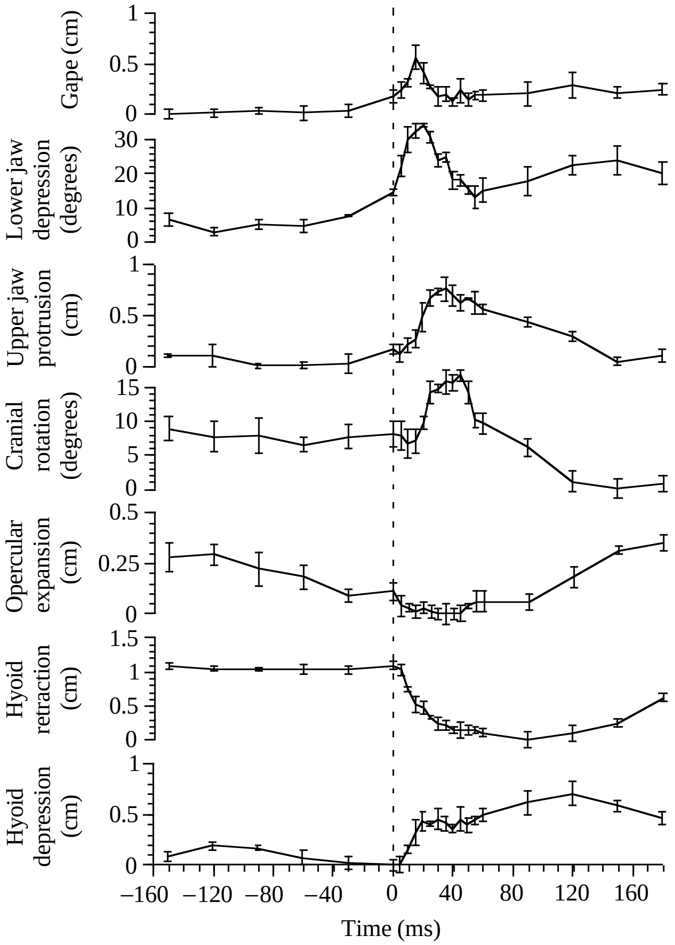

Fig. 5. Kinematic summary of four feeding sequences for one individual (HT21). In order to scale the *x*-axis appropriately, the first two and last two data points collected (−300, −200, +230 and +330 ms) were excluded from this graph. Points on the line represent mean values and the error bars are one standard error of the mean. All variables are given in centimeters, with the exception of lower jaw depression and cranial rotation, which are given in degrees. The dashed vertical line indicates the beginning of mouth opening (time 0) for reference.

displacement and timing variables showed significant bilateral asymmetry (Table 4). Maximum gape was always greater on the blind side of the head than on the ocular side (Tables 2, 4). There was no significant individual variation in this variable, nor was there a significant interaction between side-of-the-head and individual effects.

None of the other displacement or timing variables showed a significant effect of side-of-the-head (Table 4). However, time to maximum opercular expansion showed a strong, but non-significant, trend; maximum expansion of the opercular series occurred on the ocular side before maximum expansion of the blind side (Table 2). This pattern was evident for three of the four individuals (maximum lateral expansion of the ocular and blind side opercles occurred at approximately the same time in individual HT10).

There were no significant side×individual effects for any of these variables and only one variable showed significant individual variation. Maximum lower jaw depression varied significantly among individuals (Table 4); individual HT21 produced an average maximum lower jaw depression more than 5 ° larger than that produced by fish HT4. The variation in lower jaw depression apparently did not produce varying maximum gapes, as this variable showed no significant individual variation (Table 4). However, the pattern of individual variation in lower jaw depression was the inverse of that found for cranial rotation; individuals with a large average maximum cranial rotation generated a small lower jaw depression and *vice versa*.

Table 3. F-*statistics obtained from multiple one-way ANOVAs examining potential individual effects on unpaired kinematic variables*

Variable	Individual d.f. 3, 12
Maximum hyoid depression (cm)	5.87
Time to maximum hyoid depression (ms)	2.68
Maximum hyoid retraction (cm)	5.85
Time to maximum hyoid retraction (ms)	3.72
Maximum cranial rotation (degrees)	12.65*
Time to maximum cranial rotation (ms)	0.45

*Significant at $P<0.05$, using the sequential Bonferroni method described by Rice (1989).

Table 4. F-*statistics obtained from multiple two-way ANOVAs comparing variables obtained for the ocular and blind sides of the head and body*

Variable	Side d.f.=1,3	Individual d.f.=3, 20 (24)	Side×Individual d.f.=3, 20 (24)
Maximum gape (cm)	65.87*	2.44	0.37
Time to maximum gape (ms)	0.27	1.58	0.56
Gape cycle time (ms)	0.60	2.05	0.84
Maximum upper jaw protrusion (cm)	1.56	2.23	3.65
Time to maximum upper jaw protrusion (ms)	0.74	0.56	0.44
Maximum lower jaw depression (degrees)	0.04	8.04*	0.28
Time to maximum lower depression (ms)	0.02	0.83	0.47
Maximum opercular expansion (cm)	5.09	4.51	0.82
Time to maximum opercular expansion (ms)	25.16	3.41	1.37

*Significant at $P<0.05$, using the sequential Bonferroni method described by Rice (1989).

The *t*-tests performed on maximum lateral flexion of the

Table 5. *Values obtained from one-tailed* t*-tests testing the hypothesis that the head and jaws bend significantly out of the sagittal plane of the body during prey capture*

Variables	Mean	d.f.	Critical value	t-value
Maximum lateral head flexion (degrees)	11.3	15	2.602	9.1*
Maximum lateral jaw flexion (degrees)	27.7	15	2.602	13.1*

*Significant at $P<0.05$, using the sequential Bonferroni method described in Rice (1989).

head and jaws indicate that there was substantial bending of these structures out of the midline (Table 5). Before *P. verticalis* begins the gape cycle, the jaws are in line with the rest of the head (Fig. 4). During the gape cycle, the jaws bend out of the midline towards the blind side of the head (Figs 4, 6). The angle between the jaws and the rest of the head increases until it reaches a maximum value of approximately 30° jaw flexion (Fig. 6). As the upper jaw is retracted and the lower jaw elevated, the jaws return to their original positions and are again in line with the midline of the head.

Although the head of *P. verticalis* also bends out of the midline of the body during capture, the timing and magnitude of bending varied between individuals. The individual illustrated in Fig. 6 (HT21) consistently approached the prey with its head flexed towards the ocular side of the body. At the beginning of the feeding event, the head was at approximately 10° to the midline of the body, but during prey capture it was lowered and the angle decreased (Fig. 6). By the end of capture, the head was resting on the substratum, in line with the rest of the body. The individual pictured in Fig. 4 (HT8), however, flexed its head towards the ocular side at the end of the feeding event as well as at the beginning.

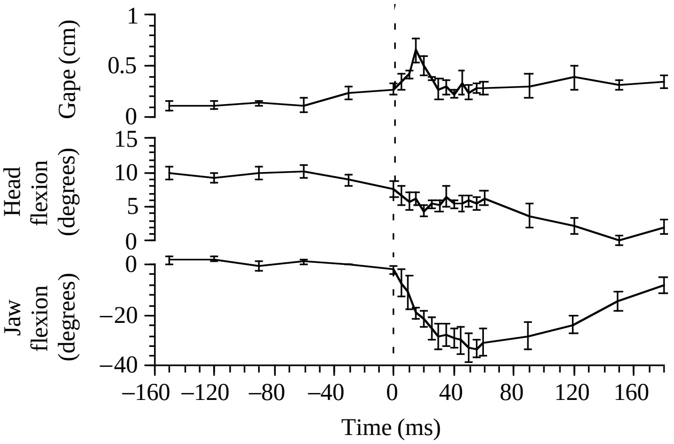

Fig. 6. Summary plot of the angular movements of the jaws and head of one individual *Pleuronichthys verticalis* (HT21) for four feeding sequences. In order to scale the *x*-axis appropriately, the first two and last two data points collected (−300, −200, +230 and +330 ms) were excluded from this graph. A plot of mouth opening (gape) is included for reference. The dashed vertical line marks time 0, the beginning of mouth opening. Positive values indicate bending towards the ocular (right) side of the body and negative values indicate bending towards the blind (left) side of the body. See Fig. 2 for an illustration of how these angles were measured.

Discussion

General kinematics and comparisons with other ray-finned fishes

The kinematics of prey capture in *P. verticalis* will be described with reference to the four phases of the feeding cycle previously described as being common to actinopterygian inertial-suction feeders: preparatory, expansive, compressive and recovery (Liem, 1978; Lauder, 1985). These summary descriptions of suction feeding in actinopterygian fishes use a variety of variables to determine the phases of the feeding cycle. Because of differences between *P. verticalis* and other ray-finned fishes, the phases used here will be defined entirely on the basis of the gape cycle and will be used as reference points in the feeding event. The preparatory phase occurs when the fish locates and approaches the prey before the mouth begins to open. The expansive phase begins when the mouth opens. The compressive phase begins when the mouth begins to close, and the recovery phase occurs after the mouth has closed, as the head and jaws are returning to their original positions.

Pleuronichthys verticalis generate many of the same kinematic movements during capture as do other ray-finned fishes during suction feeding. The fish approaches the prey, the lower jaw is depressed and the upper jaw extends towards the prey. The mouth opens and the hyoid is rapidly depressed. Simultaneous mouth opening and hyoid depression create a rapid expansion of the area inside the buccal cavity and draw the water in front of the mouth, along with the prey, into the buccal cavity. The mouth closes, the jaws are retracted and the opercles expand to allow the water engulfed with the prey to escape from the head. However, *P. verticalis* show several specific features that are unusual or unique among actinopterygian species described to date. These features are primarily related to changes in the relative timing of movements of portions of the head and jaws.

The most striking feature of the initial approach of *P. verticalis* towards its prey is the extreme lateral compression of the opercular apparatus and suspensorium (Figs 4, 5). Compression of the suspensorium and the opercular series is believed to reduce the volume of water inside the orobranchial and opercular cavities prior to mouth opening (Liem, 1978; Lauder, 1985). Thus, the lateral compression of the head of *P. verticalis* suggests a preparatory phase in which the volume of water inside the head is reduced in preparation for the creation of suction during mouth opening. Although the period before mouth opening is usually termed the preparatory phase for all suction feeders, there is little evidence for orobranchial compression in other species (Lauder, 1985). A preparatory phase of this nature has only been described for a few species of cichlid, and was defined for these studies using muscle activity patterns rather than kinematic data (Liem, 1978).

Immediately prior to the expansive phase of feeding in *P. verticalis*, the lower jaw begins to rotate around its articulation with the suspensorium. This rotation produces lower jaw depression, which continues throughout the expansive phase (Figs 4, 5). At the beginning of the expansive phase, the hyoid begins to retract. Previous studies have suggested that the sternohyoideus is the initial depressor of the mandible (Liem, 1970) during prey capture. However, in *P. verticalis*, depression of the lower jaw begins before retraction of the hyoid apparatus. This offset in timing implies that contraction of the sternohyoideus is not responsible for the initial movements of the lower jaw during prey capture.

A possible alternative explanation of early lower jaw depression is the levator operculi–opercular apparatus–mandible coupling (Liem, 1970). According to this model, contraction of the levator operculi pulls the opercular series dorsally and this movement is transmitted to the lower jaw *via* the interopercularmandibular ligament. The interopercularmandibular ligament transmits dorsally directed force to the posterior end of the mandible, causing it to pivot around its articulation with the quadrate and forcing the anterior end of the lower jaw to move ventrally. A similar offset in the timing of jaw depression and hyoid retraction was found in *Amia calva* (Lauder, 1979), suggesting the importance of the levator operculi–opercular apparatus–mandible coupling in jaw depression in the Halecostomi. On the basis of comparative research on aquatic vertebrates, Lauder and Shaffer (1993) have hypothesized that hyoid-mediated mandibular depression is the primitive condition for all gnathostomes and that levator operculi–opercular apparatus–mandible coupling is a synapomorphy of the Halecomorphii and the Teleostei. However, experimental work on nandid fishes (Liem, 1970) and *Chaetodon miliaris* (Motta, 1982) has demonstrated that initial lower jaw depression is generated by contraction of the sternohyoideus and the hypaxial musculature, and later depression is produced *via* the levator operculi–opercular apparatus–mandible coupling. It is difficult to evaluate the role or importance of this possible mechanism in lower jaw ventral rotation in *P. verticalis* without placing markers on the opercular series to facilitate the tracking of individual opercular bones. Clearly, more research is necessary in this area to clarify the relative contributions of these two mechanisms to mandibular depression in teleosts.

The hyoid is rapidly depressed during the expansive phase, but reaches a plateau shortly after peak gape (Fig. 5). Comparative analyses of suction feeding in actinopterygians have suggested that, in general, depression of the hyoid is the main factor creating a volume change in the buccal cavity during suction feeding (Lauder, 1985). Presumably as a result of this functional role, hyoid depression generally peaks shortly after peak gape. Hyoid depression in *P. verticalis* does not reach its maximum value immediately after peak gape, but it does cease to increase rapidly at this time. Hyoid depression hovers at or near its maximal value for the rest of the compressive phase and for most of the recovery phase.

Although hyoid retraction begins at the same time as hyoid depression, retraction of the hyoid does not plateau at the beginning of the compressive phase, nor does it peak near the middle of the expansive phase, as has been found for other ray-finned fishes (Lauder, 1985). In *P. verticalis*, rapid hyoid retraction continues throughout the compressive phase and does not reach a plateau until the recovery phase (Fig. 5). The retraction of the hyoid continues well after the lower jaw is maximally depressed. In fact, as the lower jaw is returning to its original position, the hyoid is still being retracted. This further supports the idea that contraction of the sternohyoideus is not the primary mechanism of lower jaw depression in *P. verticalis*. Therefore, the purpose of this extended period of hyoid retraction is unclear. Since hyoid retraction is apparently not associated with lower jaw depression, it may be linked to another aspect of prey capture. Alternatively, hyoid retraction could be associated with an as yet undescribed type of prey transport.

Initial protrusion of the premaxilla appears to lag behind lower jaw depression (Fig. 5). Maximum depression of the lower jaw also occurs slightly before maximum protrusion of the upper jaw (Fig. 5). This suggests that the ventral rotation of the lower jaw may not be the mechanism for initial protrusion of the premaxilla during mouth opening, as has been found to be the case for many other ray-finned fishes (for a summary, see Motta, 1984). Protrusion of the premaxilla occurs at the same time as dorsal cranial rotation (Fig. 5). The close relationship between premaxilla protrusion and cranial rotation suggests that the premaxilla may be protruded *via* the ‘decoupled’ model of jaw protrusion. This model predicts that upper jaw protrusion can be generated directly by contraction of the epaxial musculature, which raises the neurocranium and causes the premaxilla to slide forward (Liem, 1979). The decoupled mechanism of premaxillary protrusion has previously been documented for some cichlids (Liem, 1979), but not for any other group of teleosts.

The recovery phase of the feeding cycle in *P. verticalis* consists primarily of the bones of the head and jaws returning to their original positions. The premaxilla remains partially protracted after the mouth is closed and is retracted throughout the recovery phase. Premaxillary retraction occurs at the same time as opercular expansion. This suggests that water may be moving from the buccal region, through the pharynx, and finally out of the opercles during the recovery phase. The recovery phase of *P. verticalis* appears to be similar to that described for other teleosts (Lauder, 1985).

Bilateral functional asymmetry

Pleuronichthys verticalis display extreme bilateral asymmetry during prey capture in several functional features. Most individuals approach the prey with their head at approximately 10 ° to the substratum, possibly to facilitate location of the prey. Functionally, this means that the body is flexed towards the ocular side. Presumably, the epaxial and hypaxial musculature on the right side of the body contract in order to maintain this posture, but the precise mechanism of this extended body flexion is unclear.

There was a strong, but non-significant, trend for the opercular series of the ocular side to achieve maximum lateral expansion before the blind side (Tables 2, 4). During early opercular expansion, the head of the fish was positioned almost flat on the bottom of the tank (Fig. 4; 40 ms). Although maximum lateral expansion of the ocular side occurs at this time, this position probably inhibits the expansion of the blind-side opercle. Maximum lateral expansion of the blind side occurred later in the feeding cycle, when the head was often slightly flexed towards the ocular side (Fig. 4; 180 ms).

When engulfing the prey, the upper and lower jaws of *P. verticalis* bend out of the midline of the head at 30 ° towards the blind (left) side. This allows the jaws of *P. verticalis* to extend down towards the prey (which is located on the substratum in the wild and in the laboratory) and suck it into the mouth. Bending the jaws towards the prey item probably facilitates prey capture by allowing the fish to ‘point’ the suction more directly at the prey (as is possible with a vacuum cleaner with a flexible intake hose).

It is not clear how to interpret the consistently larger values for maximum gape measured on the blind side of the head. Two possible mechanisms potentially explain this finding: (1) since the bones of the jaw are larger and longer on the blind side, this side may be able to open wider during prey capture, or (2) because the jaws bend to one side, the difference in gape between the ocular and blind sides could be purely a consequence of the lateral bending of the jaws. In other words, the actual gape of the anatomical right and left sides of the head could be the same but, since the jaws are pointing towards the blind side during prey capture, the gape on the blind side of the head will be measured as larger. It is also possible that a combination of these two mechanisms produces the asymmetrical gape.

It is possible to test the hypothesis that bending of the jaws could entirely account for the observed asymmetry in maximum gape. Cameras recording the ocular (camera O) and blind-side (camera B) views are at 90 ° to the long axis of the fish. As the jaws bend towards the blind side during prey capture, the angle between the blind-side gape and camera B decreases (<90 °), but the angle between the ocular-side gape and camera O increases (>90 °). A decrease in the angle of the jaws to camera B will not change the apparent gape of the mouth; at all angles between 0 and 90 ° the gape will be measured accurately. However, as the angle increases between camera O and the anterior portion of the jaws, the apparent gape will become smaller and smaller, until it is measured as zero at 180 °. Assuming that the decrease in apparent gape between 90 and 180 ° is linear, apparent gape can be predicted.

Mean maximum gape for the blind side of the head was 0.73 cm (Table 2). If apparent gape at 90 ° is 0.73 cm, and apparent gape at 180 ° is 0 cm, then every 1 ° increase in the angle of the jaws to the camera should produce a 0.0081 cm change in apparent gape. Although the maximum angle of the jaw out of the mid-line during prey capture is 28 °, the average jaw angle during maximum gape is approximately 13 ° (Fig. 6). A 13 ° increase in the angle of camera O to the anterior portion of the jaws should produce a decrease in apparent gape of 0.1053 cm, resulting in a measured ocular-side gape of 0.6247 cm. The actual average gape measured for the ocular side was 0.50 cm (Table 2). A one-tailed *t*-test indicates that this value is significantly smaller ($P<0.001$) than the predicted value. This line of reasoning suggests that the smaller gape on the ocular side of the head is a combination of a physically smaller gape on the ocular side and a reduced apparent gape caused by bending of the jaws out of the midline.

A preliminary study entailing manipulation of the jaws in freshly dead *P. verticalis* suggests that lateral bending of the jaws during prey capture may be a functional result of the morphological asymmetry present in the suspensorium and upper and lower jaws. It is beyond the scope of this paper to demonstrate the mechanism by which this unusual asymmetrical movement is produced, but additional studies currently under way will attempt to answer this question. The following investigations are being conducted in order to clarify the functional basis of the asymmetry in jaw movements: (1) an electromyographic analysis of muscle activity patterns in *P. verticalis* will determine whether bilateral asymmetry exists in the timing or magnitude of activity in homologous muscles on opposing sides of the head; (2) a kinematic study using a more morphologically symmetrical flatfish will be compared with the kinematics of *P. verticalis*; and (3) mechanical modeling of the jaws of both species will be used to predict functional asymmetry during feeding.

Prey capture in *P. verticalis* contains significant differences in the timing of kinematic events from that described for other suction feeders. Perhaps more remarkably, these fish display an extreme degree of bilateral functional asymmetry in the movements of the upper and lower jaws which allows them to suck up prey from the substratum. Morphological asymmetry present in the skull is concentrated in the regions involved in opening the mouth and extending and protruding the jaws. Thus, functional asymmetry in feeding behavior is related to, and perhaps caused by, morphological asymmetry in the jaw structures. Although morphological asymmetry is believed to have originated in flatfish as a result of eye migration, at least one species of flatfish has apparently modified it further for a specific feeding behavior.

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