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# Morphology and kinematics of prey capture in the syngnathid fishes *Hippocampus erectus* and *Syngnathus floridae*

**Abstract** The mechanism of prey capture in two syngnathid fishes, the lined seahorse *Hippocampus erectus* (Perry) and the dusky pipefish *Syngnathus floridae* (Jordan and Gilbert), is described based on anatomical observations and high-speed video recordings (200 and 400 images s$^{-1}$) of feeding events by four seahorses and three pipefish. The fish were collected near Turkey Point, Florida, U.S.A., in January 1994 to March 1995. The dominant features of the morphology of these and many other syngnathiform fishes include extreme elongation of the suspensorium and neurocranium with a small mouth located at the anterior tip of the head. In the seahorse, a preparatory phase of prey capture consisted of slow ventral head flexion. This was followed by rapid elevation of the head and snout as the prey was drawn into the mouth by suction. Both *H. erectus* and *S. floridae* capture prey rapidly, with peak head excursions and mouth opening occurring within 5 to 7 ms of the onset of the strike. There was no upper jaw protrusion. In both species the time to recovery of the cranium and hyoid apparatus to resting positions was highly variable but took at least 500 ms. Manipulations of freshly dead specimens indicated a biomechanical linkage between head elevation and hyoid depression. However, the predictions of a previously proposed four-bar linkage model that couples hyoid depression to head elevation were not fully supported by kinematic data from one seahorse, suggesting that additional linkages act during the expansive phase of prey capture. These species exhibit the generalized kinematic pattern of prey capture in bony fishes, with head elevation, hyoid depression and mouth opening occurring almost simultaneously. The derived morphology results in a unique feeding behavior, in which prey are captured during a sudden up-swing of the head, which brings the mouth to the prey. Suction is used to draw the prey into the buccal cavity.

## Introduction

Among the characteristic morphological features of seahorses and pipefishes (family Syngnathidae) are an elongate tubular snout and small terminal mouth. The possession of a pipette-like feeding structure has been interpreted as a specialization for suction feeding by a number of workers (Branch 1966; Osse and Muller 1980; Muller and Osse 1984; Muller 1987). Analyses of the mechanical consequences of head shape in syngnathid fishes have indicated that the elongate buccal cavity will result in higher flow velocity and lower buccal pressures during suction feeding than would be seen in a more generalized fish feeding system (Osse and Muller 1980; Muller and Osse 1984). In addition, a rounded mouth aperture reduces drag as water enters the mouth, and a smaller mouth results in a greater velocity of water influx than a similarly designed system with a larger mouth (Alexander 1967). In spite of this general perception in the literature that seahorses and pipefishes are specialized suction feeders functional data on the feeding mechanism of these fishes are lacking. In particular, it is not known how the unusual morphology of the syngnathid head is employed during prey capture.

Among the structural models that have been proposed which consider the mechanical aspects of feeding and permit some insight into the consequences of morphological diversity, "four-bar linkage" may allow the further understanding of the syngnathid feeding behavior. "Four-bar linkage" is a principle derived from mechanical engineering in which four "bars", with four common joints, move in a coordinated fashion (Westneat 1994). Assuming one of these bars is fixed, the active movement of at least one input bar, initiates a chain reaction in which the other components must compensate for the change in joint angles by also moving. The

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result is the passive movement of a fourth output bar. In teleosts, four-bar linkage models have been proposed to explain the association of movements within the skull during suction feeding as well as to explain the transmission of muscle activity into force and velocity of those movements (Westneat 1994).

Muller (1987) concluded that head elevation was largely responsible for the expansion of the buccal cavity via a linkage with the hyoid apparatus. The existence of a four-bar linkage was proposed to link hyoid depression to cranial elevation in several teleost taxa, including syngnathid fishes (Muller 1987).

In the case of hyoid depression via head elevation, the four components of the four-bar linkage model in the syngnathid skull (Fig. 1) include: the hyomandibula (A–B), an input bar; the pectoral girdle (D–A), the fixed bar; the sternohyoideus muscle and urohyal (pectoral girdle to urohyal/ceratohyal, C–D), a secondary input bar; and the ceratohyal (hyomandibula/ceratohyal to ceratohyal urohyal, B–C), the output bar (Muller 1987). At the onset of a prey-capture sequence, head elevation begins due to contraction of the epaxial muscles (Lauder 1985). Bar A–B, the hyomandibula bone, articulates with the neurocranium in a fashion that does not permit anterior–posterior rotation of the bar on the skull. The four bar chain compensates for the pull of the epaxial muscles by allowing the hyomandibula to rotate anteriad and dorsally, increasing the angle in the joint between the hyomandibula and the pectoral girdle (Fig. 1). However, the activity of the epaxial muscle is balanced by the hypaxial musculature, causing the system to remain rigid (Muller 1987). Because the forces exerted onto the four-bar system by the epaxial muscle are not converted into motion immediately, the entire four-bar system becomes stressed (Muller 1987). Slight opening of the angle be-

tween the hyomandibula and the ceratohyal (B), caused by shortening of bar C–D due to contraction of the sternohyoideus muscle, abducts the urohyal resulting in an explosive response of the prestressed four-bar system (Muller 1987). The hyomandibula bar releases and rotates anteriad and dorsally as joint angle A increases with head elevation. In compensating for the movement of the hyomandibula and the change in angle of joint C, the ceratohyal snaps out of position and its dorsal end rotates anteriorly, forcing the structures at joint C, the anterior end of the ceratohyals and the urohyal, to rotate ventrally and posteriorly. Thus, the hyoid apparatus, comprised of the ceratohyal and urohyal bones, is depressed via cranial elevation (Fig. 1).

In spite of the potentially broad significance of the four-bar linkage proposed by Muller (1987) to account for hyoid depression by cranial elevation in teleost fishes, few studies have critically tested for the presence of this linkage. Westneat (1990) verified the presence of the linkage in several species of cheiline wrasses by comparing the predictions of the four-bar model to actual kinematic data. In this study we use an approach similar to Westneat's (1990) and ask whether the four-bar linkage adequately models movements of the neurocranium and hyoid apparatus in the seahorse.

The present study describes the kinematics of the syngnathid feeding mechanism and assesses the role of a four-bar linkage in coupling hyoid depression to head elevation. The prey capture kinematics and morphology of the lined seahorse, *Hippocampus erectus*, are described, supplemented with similar observations of the dusky pipefish, *Syngnathus floridae*. We address three questions: (1) What are the kinematics involved in syngnathid prey capture? (2) What are the effects of possessing the elongated tubular snout and small terminal mouth on the movements of the feeding mechanism? (3) Does Muller's (1987) four-bar linkage model account for hyoid movement?
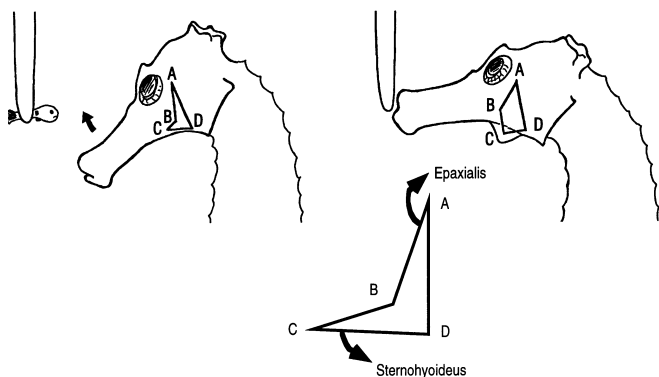


**Fig. 1** *Hippocampus erectus.* Proposed four-bar linkage model for cranial elevation and hyoid depression in the seahorse feeding mechanism (based on Muller 1987; Westneat 1994). The pectoral girdle bar (*D–A*) remains in a fixed position while the hyomandibula bar (*A–B*) moves anteriad and dorsally with head elevation because of contraction of the epaxialis muscle, resulting in the passive movement of the ceratohyal (*B–C*) anteriad and ventrally. Slight shortening of the urohyal-sternohyoideus bar (*C–D*) by contraction of the sternohyoideus muscle causes the release of the four-bar system from an initially stressed and rigid condition

## Materials and methods

### Morphology

Two *Hippocampus erectus* (Perry), with standard lengths (SL) of 25 and 96 mm, and one *Synganthus floridae* (Jordan and Gilbert) (SL = 162 mm) were cleared and stained using a modification of the procedures of Dingerkus and Uhler (1977). This allowed us to examine the topography of ossified structures (stained red) and cartilaginous structures (stained blue) in the syngnathid skulls. Skeletal and muscular nomenclature follows Branch (1966), Winterbottom (1974), and Fritzsche (1980).

One seahorse (SL = 96 mm) and two pipefish (SL = 154 mm, 162 mm), all freshly dead, were manipulated to explore the movements of the skeletal elements and examine the mechanical linkages of the feeding mechanism. The heads were cocked and elevated to simulate a strike at prey, so that passive reactions of the other structures within the feeding mechanism, such as the hyoid apparatus and the oral jaws, could be observed. Similarly the hyoid was manually retracted, and the mouth opened to reveal linkages of hyoid depression with mouth opening as well as hyoid depression with head elevation.
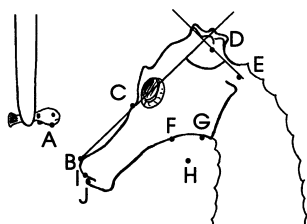
Kinematics

All seahorses and pipefish were collected in seagrass beds located in the northeastern Gulf of Mexico, near Turkey Point, Florida in January 1994 to March 1995. Individuals used in video recordings were maintained in 100-liter aquaria at room temperature (22 + 2 °C). Plastic tubing was placed in the seahorse aquaria so that the fish had structures that they could grasp with their prehensile tails. The seahorses were fed daily with live juvenile sailfin mollies (*Poecilia latipinna*), and occasionally live adult brine shrimp except for the day before a filming session. We assumed that the natural diet of seahorses included small benthic prey and copepods, but no diet data were available. The seahorses were trained to feed on single mollies held with forceps in front of a plastic filming grid (1 cm²), while strobe lights were on.

Feeding sequences were recorded from four seahorses (SL = 66 mm, 110 mm, 132 mm, 141 mm) using a NAC HSV-400 high-speed video system operating at 200 or 400 images per second. Subsequently, prey capture sequences were digitized image-by-image and stored on computer disk. At least six feedings per individual were analyzed. Good sequences (determined by the lateral orientation of the seahorse with respect to the camera, the inclusion of all important trophic structures within the field of view, and the sharpness of the image) of 12 to 20 images around the prey capture event were analyzed image-by-image with a custom computer program. The following five variables were measured on every image (Fig. 2). (1) *Distance to prey* was the distance in millimeters from the tip of the premaxilla to the nearest point on the prey item (A–B). (2) *Angle of head elevation* was the angle formed by one line connecting the tip of the premaxilla to a spot on the neurocranium just anterior to the eye (B–C) and a second line connecting the posterior tip of the crown with the position of the first vertebra (D–E). (3) *Hyoid depression* was the distance in millimeters of the distal tip of the hyoid (H) from a horizontal line drawn along the ventral arm of the preopercle bone (F–G). (4) *Gape distance* was the distance in millimeters between the anterior tip of the premaxilla and the anterior tip of the dentary (I–J). (5) *Time* was calculated as a function of the number of video images and the imaging rate.

The changes in angle of head elevation, hyoid depression, gape, and distance to prey were separately plotted against time for each sequence. Times to peak values of hyoid depression, head elevation, and gape were determined by calculating the time from Time 0. "Time 0" was defined as the image immediately prior to the image of the first head elevation movements of the strike. The peak values for each variable were also determined.

Feedings of three pipefish (SL = 126 mm, 145 mm, 154 mm) were recorded following a protocol similar to the seahorse. The pipefish were fed live adult brine shrimp because the mollies were generally too large for them to consume. The brine shrimp were



**Fig. 2** *Hippocampus erectus*. Variables measured for kinematic study. Distance to prey was the distance in millimeters from the tip of the premaxilla to the nearest point on the prey item (*A–B*). Angle of head elevation was the angle formed by one line connecting the tip of the premaxilla to a spot on the neurocranium just anterior to the eye (*B–C*) and a second line connecting the posterior tip of the crown with the position of the first vertebra (*D–E*). Hyoid depression was the distance in millimeters of the distal tip of the hyoid (*H*) from a horizontal line drawn along the ventral arm of the preopercle bone (*F–G*). Gape distance was the distance in millimeters between the anterior tip of the premaxilla and the anterior tip of the dentary (*I–J*)

held in a clear glass micropipette in front of the filming grid and released immediately prior to a feeding sequence. *Syngnathus floridae* is assumed to have a similar diet to that of the short-nosed Florida pipefish, *Syngnathus scovelli*, which shares the same habitat and consumes amphipods, copepods and small shrimp (Joseph 1957; Motta et al. 1995). Measurements of variables from the videos differed from those of *Hippocampus erectus* in that the angle of head elevation was measured as the angle between a line connecting the tip of the snout and a point above the eye and a line drawn from the joint of the neurocranium with the first vertebra along the vertebral column.

Four-bar linkage model

In order to determine if a four-bar linkage accounts for the movements involved in prey capture of *Hippocampus erectus* a customized computer program was employed courtesy of M. Westneat. The program accepts morphological data (bar lengths and the angles between them) and constructs a four-bar linkage model. The program was used to predict hyoid movements that result from head elevation based on the four-bar linkage for hyoid depression proposed by Muller (1987). Lengths of the four components of a stained *H. erectus* (SL = 96 mm) were used, and the model provided hyoid movement within the four-bar linkage. Predicted hyoid depressions and head elevations were compared with actual kinematic data of feeding sequences from one seahorse (SL = 110 mm). Four models were explored that varied in the percent shortening of the sternohyoideus muscle from 10 to 40%.

## Results

Morphology

The skulls of *Hippocampus erectus* and *Syngnathus floridae* are typical of syngnathid fishes (Kindred 1921; Branch 1966; Fritzsche 1980). Only features central to a discussion of the feeding mechanism will be described here.

As in other syngnathids, the opercular slit of the two species is reduced to a small opening, dorsal and posterior to the opercle. Teeth are lacking on the jaws, and the upper part of the cleithrum forms part of the external armor. Elongation of neurocranial and suspensorial bones, such as the interopercle, preopercle, suborbital, lacrimal, dermethmoid, vomer, and frontal, make up the rigid tube snout (Figs. 3, 4).

The large hyomandibula of *Hippocampus erectus* (Fig. 3) extends ventrally from the anterior margin of the opercle. The long preopercle lies beneath the hyomandibula and extends anteriorly under the eye. The ceratohyals are also large, and there is cartilaginous tissue in the interhyal at the articulation with the hyomandibula. The ceratohyals are joined at their ventral tips to form the hyoid arch. The hyoid arch normally rests in a position parallel and ventral to the snout and perpendicular to the pectoral girdle. The short stubby urohyal is unpaired, lies posterior to the hyoid arch and is connected to the ventral tip of each ceratohyal by short stout ligaments. Contraction of the sternohyoideus muscle, which originates from the cleithrum and inserts on the urohyal, pulls the urohyal back and causes the hyoid bars to rotate posteriad and ventrally at the ar-

**Fig. 3** *Hippocampus erectus.* Diagram of the seahorse skull. (*ART* articular; *BSTL* branchiostegal rays; *CH* ceratohyal; *CL* cleithrum; *CRN* crown; *DETH* dermethmoid; *DT* dentary; *ECT* ectopterygoid; *ENT* entopterygoid; *FR* frontal; *HM* hyomandibula; *IOP* interopercle; *LAC* lacrimal; *MX* maxilla; *NCR* neurocranium; *OP* opercle; *PAL* palatine; *PFR* prefrontal; *PMX* premaxilla; *POP* preopercle; *QU* quadrate; *SBO* suborbital; *SPHN* sphenotic; *SYM* symplectic; *UH* urohyal; *VM* vomer)
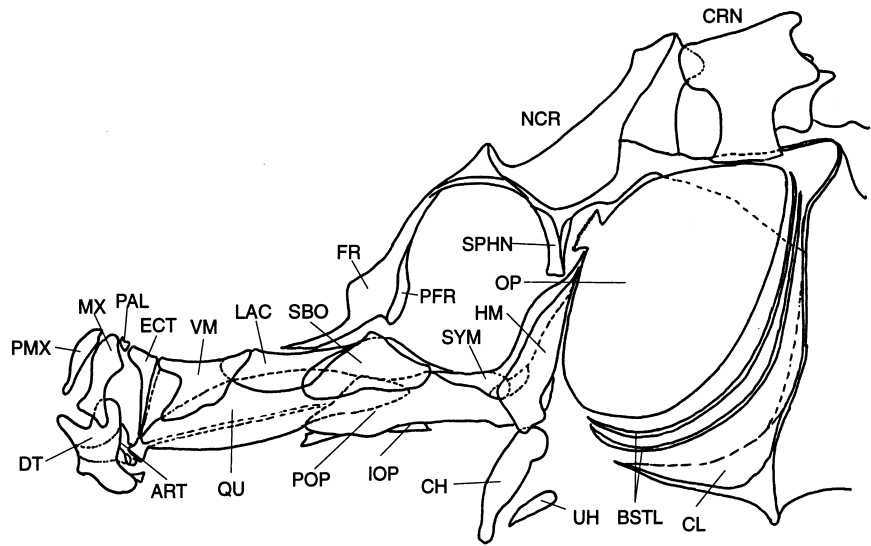
**Fig. 4** *Syngnathus floridae.* Diagram of the skull of the dusky pipefish. *Abbreviations* as in Fig. 3
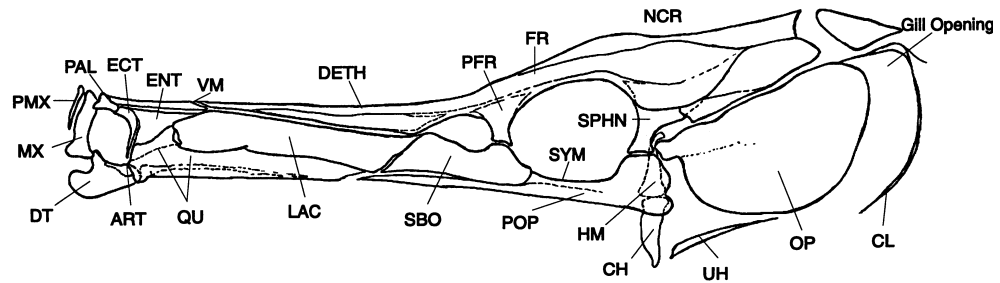
ticulation with the hyomandibula. As the hyoid arch rotates from its resting position, it also twists outward forcing the hyomandibula bones apart. The dentary and articular are fused to an extent that they are hard to differentiate except that the articular bone articulates with the quadrate. The neurocranium is modified so that it forms a coronet.

A major osteological difference between the two species is the placement of the hyomandibula beneath the preopercular plate in *Syngnathus floridae* (Fig. 4). The large hyomandibula extends from the dorso-anterior margin of the opercle ventrally below the sphenotic and underneath the preopercle. The dorsal portion of the ceratohyal and the small portion of cartilaginous tissue at the articulation with the hyomandibula, also lie beneath the preopercle. The unpaired urohyal of *S. floridae* is long and tapered, extending ventrally medial to the opercles. The interopercle, not shown in the diagram, is ventral and beneath the quadrates extending from midpreopercle to midquadrate.

By manual manipulations of fresh specimens of *Hippocampus erectus*, we found that movements of the hyoid and mandible were linked, so that when the hyoid arch is manually retracted, the mandible also depresses and the mouth opens. Also, when the mouth was manually opened we found that the entire snout widened via the lateral spreading of the suspensorial bones constituting the snout. Similar results were found in manipulations of *Syngnathus floridae*.

Head elevation and hyoid movement were found to be linked. The head of *Hippocampus erectus* elevated at a pivot point between the first vertebra and the neurocranium. When the head was manually lifted, the hyoid apparatus "popped" out of its resting position once a certain angle of head excursion was reached. Manipulation of the hyoid resulted in elevation of the head only when extreme retractive movements were applied to the hyoid apparatus.

### Kinematics

As with many other suction-feeding fishes, three phases can be described in the seahorse and pipefish strikes, a preparatory phase, an expansive phase, and a recovery phase (Lauder 1985). In the preparatory phase, the seahorse slowly approaches the prey in an upright orientation, slowly flexing its head ventrally. During the expansive phase, prey capture is accomplished by simultaneous elevation of the head and expansion of the buccal cavity. When the mouth is opened, the prey item is sucked in. The morphological study showed that mouth opening is sufficient in causing lateral expansion of the head, however, it can not be responsible for head expansion during prey capture because it is necessary for the mouth to remain closed in order to produce suction. Depression and spreading of the hyoid are responsible for ventral and lateral changes in buccal volume. The

kinematic data support this by showing that hyoid depression begins before mouth opening. During recovery, the jaws, head and hyoid apparatus return to their starting positions.

The seahorse strike involves an explosive elevation of the head that occurs at the same instant as hyoid depression and jaw depression (Fig. 5). The expansive phase of prey capture occurred in an average of 5.8 ms after the onset of the strike (Table 1). In the graph depicting head elevation against time (Fig. 5), no significant movements were made during the preparatory phase. During the expansive phase the head was elevated to a peak angle of 29.1° in about 6.5 ms. During head elevation the hyoid depressed to its lowest position 4.7 ms after the onset of the strike. Maximum gape occurred in 4.9 ms. The recovery phase was quite protracted, sometimes taking more than 1 s as the head and the hyoid returned to their resting positions (Fig. 5).

The pipefish showed similar patterns of movement during feeding events when compared to the seahorses (Fig. 5). Maximum hyoid depression, the maximum change in head elevation, and maximum gape occurred at or within a few milliseconds of prey capture. The rapid prey strike was also followed by a relatively slow recovery phase. Overall, prey capture by the seahorse was slightly faster than the pipefish (Table 1).

Four-bar linkage

Calculations of hyoid depression as a function of head elevation from four-bar linkage models assuming 10, 25, 30, and 40% sternohyoideus shortening are shown along with data from several prey capture sequences of *Hippocampus erectus* (Fig. 6). Increasing the percent of sternohyoideus shortening increased the maximum hyoid depression distance, and all versions of the model, except the 25% model, predicted that maximum hyoid depression would occur at about 30°. The 25% model predicted peak hyoid depression at 35°. However, in the feeding sequences analyzed peak hyoid depression always occurred before head elevation reached 30°. The model assuming a 10% sternohyoideus muscle shortening gave the best fit to the kinematic data, but peak hyoid depression still always occurred before head elevation reached the predicted 29° (Fig. 6). Furthermore, hyoid depression was overestimated by the model at all head angles above 5°.
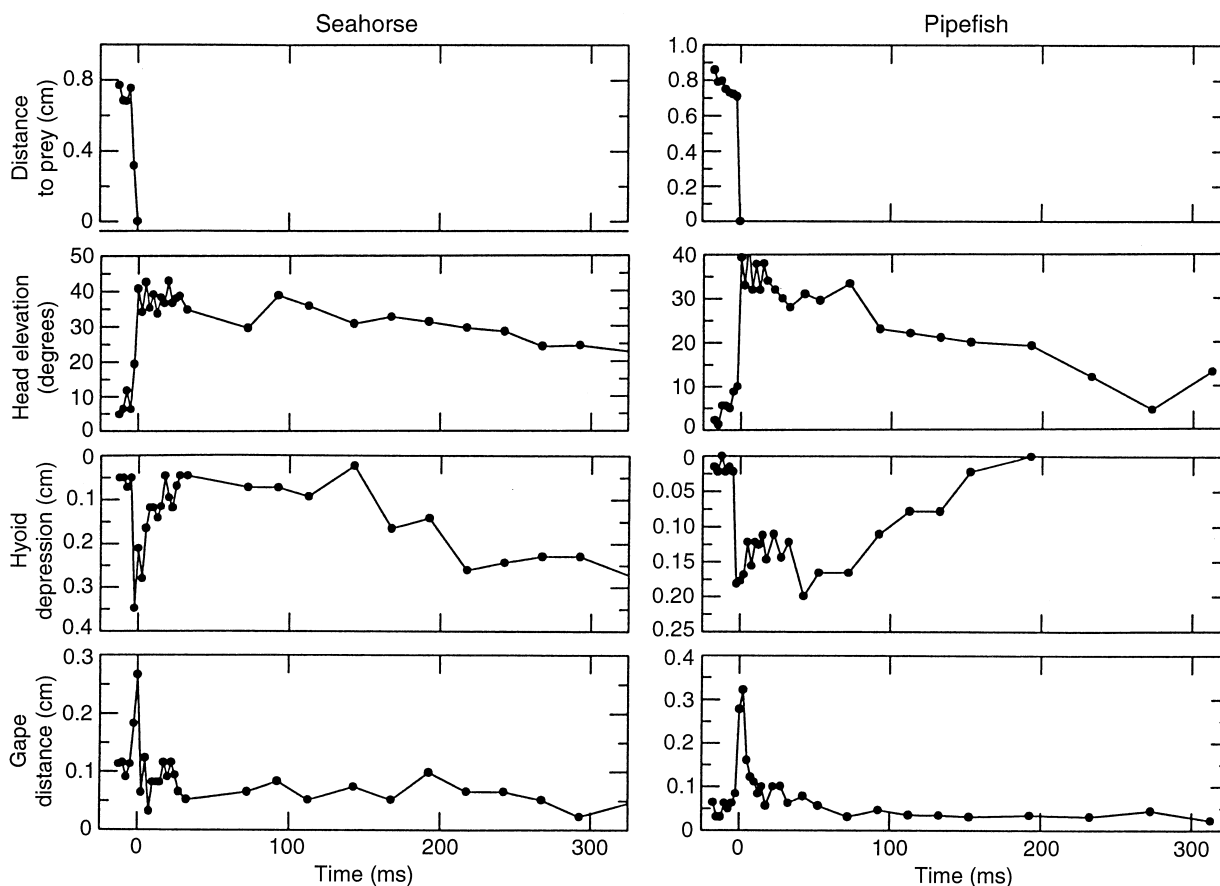


**Fig. 5** *Hippocampus erectus, Syngnathus floridae*. Kinematic plots for a seahorse and a pipefish, including the distance to prey, angle of head elevation, depth of hyoid depression, and gape for a single feeding event

| Variable | H. erectus (N = 25 feeding sequences) | S. floridae (N = 7 feeding sequences) |
|---|---|---|
| Time to prey capture (ms) | 5.8 (2.3) | 7.9 (2.2) |
| Time to peak values (ms): | | |
|   Head elevation | 6.5 (2.4) | 7.5 (2.9) |
|   Hyoid depression | 4.7 (1.3) | 6.1 (2.0) |
|   Gape | 4.9 (1.8) | 6.8 (2.8) |
| Peak head elevation (°) | 29.1 (6.9) | 29.2 (8.5) |
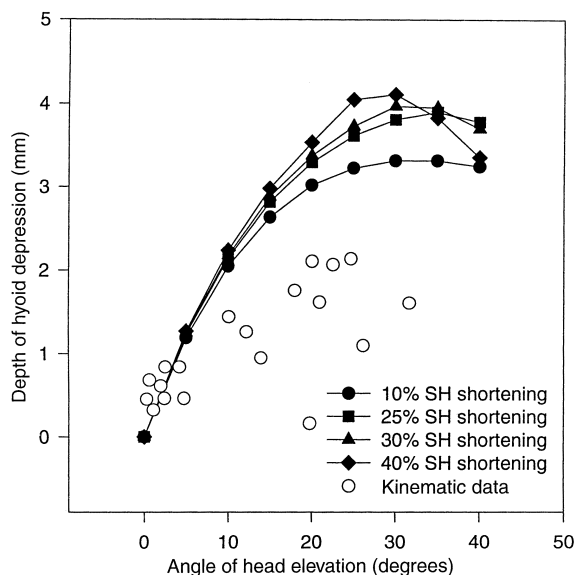


**Fig. 6** *Hippocampus erectus*. Four-bar linkage model predictions of hyoid depression as a function of head elevation plotted with actual kinematic data from six strike sequences by a 110 mm SL seahorse. Morphological data for the computer model were taken from a stained individual (SL = 97 mm). The four versions of the model varied in the assumed percent shortening of the sternohyoideus muscle. Note that all versions of the model substantially over-estimated the extent of hyoid depression

## Discussion

The unusual tube snouts of *Hippocampus erectus* and *Syngnathus floridae* (and other syngnathid fishes) consist of a small terminal mouth at the end of elongate neurocranial and suspensorial bones. Remarkably, this highly modified morphology undergoes a sequence of movements during prey capture that represents the generalized prey capture kinematics of actinopterygian fishes (Lauder 1985). As with other fishes, both *H. erectus* and *S. floridae* begin a prey-capture sequence with nearly synchronous head elevation, mouth opening and hyoid depression. The maximum angle of head elevation at prey capture was about 30° in both syngnathids. Similar angles of peak head elevation have been described in more generalized forms such as *Amia calva* (Lauder 1980), the largemouth bass, *Micropterus salmoides* (Richard and Wainwright 1995), and several cheiline wrasses (Westneat 1990).

The unusual feeding behavior of the seahorse and pipefish is a consequence of coupling the generalized teleostean kinematic sequence with the specialized cranial morphology of syngnathid fishes. With the small mouth mounted on the anterior end of an elongate neurocranium, cranial elevation rotates the mouth with the head, bringing it into a position close to the prey. This is in contrast to the generalized pattern in teleosts in which the effect of cranial elevation on the mouth is simply to elevate the upper jaw, contributing to widening of the gape. The use of rapid cranial elevation permits these fish to maintain a constant body position while their mouth is thrust toward the prey, covering the final 1 to 2 cm of the approach to the prey by rotating the head.

Once the small mouth reached the prey, suction was used to move the prey into the buccal cavity. These events happened rapidly, with prey capture occurring in an average of 5.8 ms in the seahorse and 7.9 ms in the pipefish. Given that the size of the two species studied was about 100 mm, prey capture times in the range of 6 to 8 ms make these species among the fastest feeding fishes reported to date, comparable to the fastest reported capture-times of 5 ms in antennariid anglerfishes (Grobecker and Pietsch 1979). The novel use of cranial elevation as the mechanism of rapidly moving the mouth toward the prey, rather than the more typical forward body lunge, permits these fishes to capture elusive prey in spite of their slow swimming speeds.

Four-bar linkage

Our manipulations of fresh specimens clearly suggested a mechanical linkage between head elevation and hyoid depression. Manual elevation of the cranium resulted in passive flexion of the hyoid apparatus into the depressed position, and the general synchrony of hyoid depression and head elevation in the feeding sequences supports the manipulation evidence of a linkage. Quantitative results of the four-bar analysis with data from one seahorse, however, suggest that the linkage cannot be modeled simply by the four-bar model of Muller (1987), even when allowances were made for contraction of the sternohyoideus muscle, as suggested by Westneat (1990, 1991).

The four-bar model failed to predict key aspects of the kinematic data from one seahorse. Although the

general shape of the relationship between the variables was predicted by the four-bar model (i.e., hyoid depression always increased with head elevation up to angles of 25°), the relationship was not precise. Another prominent feature not accounted for by the model involved movements toward the end of the strike. Following prey capture the head continued to elevate until it reached a maximum angle of excursion of about 30°. During this time the hyoid continued to retract posteriorly, sometimes reaching a position parallel to the skull, 180° with respect to its resting position. This was not a conformation predicted by the four-bar model. Often, further depression of the hyoid occurred after the initial lowering of the head in the recovery phase. In sum, the four-bar model does not seem sufficient to account for the movements of the hyoid during feeding in the seahorse. Our anatomical observations confirm that the linkages that are part of the four-bar model proposed by Muller (1987) are present in the head of *H. erectus*. The failure of the model to predict accurately hyoid movements suggests that unknown factors influence the workings of this system. One possible difficulty is that we analyzed the skull as a two-dimensional system, not accounting for the consequences of lateral expansion of the suspensorium. Lateral movements of the suspensorium would be passed on to the dorsal end of the ceratohyal through their mutual attachment (Fig. 1, joint B). The net effect of lateral movement of B would be a reduction in the depression of the ventral tip of the hyoid. Hence, three-dimensional movement may potentially account for the discrepancy between the four-bar model and our kinematic data.

Sound production during prey capture

Seahorses are known to make a snapping sound during head movements (Fish 1953), and we heard this noise during particularly forceful strikes by *Hippocampus erectus*. Snapping sounds were made by *Hippocampus hudsonius* as it rapidly elevated its head and Fish (1953) proposed that the noise was created by the rubbing of the neurocranium against the ossified coronet. Fish (1953) dissociated sound production from feeding behavior because no sound was heard while the seahorse fed on plankton and detritus in the tank. Fish (1953) believed the sound to be a mode of communication used for orientation to new surroundings or in courting behavior.

We suggest two possible mechanisms for the production of the snapping sound made by seahorses. First, it could be created by the initial, rapid depression of the hyoid from its resting position. We observed sound being made only during prey-capture attempts and only during what appeared to be particularly forceful strikes. Fish (1953) fed plankton to *Hippocampus hudsonius*, prey items which may not require the effort needed to capture small, free-swimming fish. The second possibility is that the sound is caused by cavitation inside the buccal cavity. Many species of fish have been observed to cavitate water during particularly forceful prey-capture attempts (Muller and Osse 1984; Lauder 1985). We have observed snapping or explosive sounds occasionally during suction-feeding attempts by species in diverse teleost families including species in the genera *Lepomis*, *Balistes*, and *Lagodon*. It may prove difficult to distinguish between these two hypotheses experimentally because both invoke a central role for forceful expansion of the feeding apparatus.

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