

Sound production during feeding in *Hippocampus* seahorses (Syngnathidae)

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Synopsis

While there have been many anecdotal reports of sounds produced by *Hippocampus* seahorses, little is known about the mechanisms of sound production. We investigated clicking sounds produced during feeding strikes in *H. zosterae* and *H. erectus*. Descriptions of head morphology support the idea that feeding clicks may represent stridulatory sounds produced by a bony articulation between the supraoccipital ridge of the neurocranium and the grooved anterior margin of the coronet. Analysis of high-speed video and synchronous sound recordings of *H. erectus* indicate that the feeding click begins within 1–2 msec of the onset of the rapid feeding strike (4 msec mean duration). Surgical manipulations of the supraoccipital-coronet articulation resulted in a decreased proportion of feeding strikes that produced clicks. This study provides several lines of evidence in support of the hypothesis that feeding clicks in *Hippocampus* seahorses are stridulatory in origin and are produced by the supraoccipital-coronet articulation. Our results are not consistent with previous suggestions that sounds may be produced by cavitation due to rapid pressure changes within the buccal cavity during the feeding strike.

Introduction

Acoustic signals are known to play a key role in intraspecific and interspecific communication in many organisms (reviewed by Sebeok 1977). In teleost fishes, sounds are produced in a variety of ecological contexts (Myrberg 1981). For example, sound production has been observed during agonistic encounters (de Amorim 1996, Ladich 1990), courtship (Tavolga 1956, Myrberg et al. 1986, Kenyon 1994, de Amorim 1996), spawning (Lobel 1992), and defense against predators (Myrberg 1981, Fine et al. 1977). Teleost fishes make sounds by bone stridulation, swimbladder vibration, and

grinding of pharyngeal teeth, as well as by other means (reviewed by Schneider 1966, Fine et al. 1977).

Anecdotal reports of sound production by *Hippocampus* seahorses have existed for more than a century. Dufossé (1874) observed *Hippocampus brevirostris* males and females making vibrational sounds during the quivering motion that typically accompanies *Hippocampus* courtship (Fiedler 1954, Masonjones & Lewis 1996). Several other seahorse species have been observed to produce a rapid clicking sound resembling a finger-snap (Gill 1905, Fish et al. 1952, Fish 1953). The frequency distribution of sounds recorded from *H. hudsonius*

ranged from 50 to 4800 Hz, the principal frequency varied between 400 and 800 Hz (Fish 1954). Seahorse clicking sounds have been observed in a variety of contexts: introduction of fish to new surroundings (Fish 1954), courtship and copulation (Fish & Mowbray 1970), inter-male competition (D.J.C. personal observation), and feeding (Fish & Mowbray 1970, James & Heck 1994, Bergert & Wainwright 1997).

Little is known about how seahorses make clicking sounds. Two main hypotheses have been proposed, but neither had been tested prior to this study. Fish (Fish et al. 1952, Fish 1953, 1954, Fish & Mowbray 1970) was first to suggest a stridulatory mechanism involving the articulation of two bones in the head, the supraoccipital and the coronet. Gill (1905) and James & Heck (1994) proposed that clicks were produced by cavitation, which produces sound due to the collapse of vapor bubbles in fluid, and may be caused by rapid pressure changes within the buccal cavity during suction feeding (Urick 1983, Muller & Osse 1984, Lauder 1985).

We examined these hypotheses in two species of seahorses, *Hippocampus erectus* and *H. zosterae*, which both produce sound during feeding strikes. We provide descriptions of head morphology which have not been previously published for these species. We tested the stridulation hypothesis using a novel combination of kinematic, surgical, acoustic and morphological analyses.

Materials and methods

Study organism

Seahorses were maintained in artificial seawater (Instant Ocean, specific gravity 1.023) in the laboratory in 38 liter (50 x 30 x 25 cm) or 70 liter (60 x 38 x 30 cm) aquaria, at 25 °C and a 13L:11D photoperiod. *Hippocampus zosterae* were collected in Card Sound, Florida and were fed *Artemia* nauplii with a lipid supplement (Super Selco, INVE) once daily. *Hippocampus erectus* were collected in Apalachee Bay, Florida and these were fed approximately 40 adult *Artemia* per fish, three times per day.

Morphology

Description of head morphology in *H. zosterae* was based on eight adult specimens that had been cleared and double-stained for bone and cartilage (Dingerkus & Uhler 1977, Song & Parenti 1995). Total lengths (TL, measured from the tip of coronet to the tip of the extended tail) of *H. zosterae* specimens ranged from 34 to 47 mm. Drawings were made using a camera lucida on a stereo microscope at 40x. Osteological terminology follows Jungersen (1910), Gregory (1933), Ginsburg (1937), and Azzarello (1989). Dissections of the head and neck regions were made on three ethanol-preserved *H. erectus* (TL 16-20 cm) and major muscle groups were identified following Azzarello (1990).

Feeding strike kinematics

We studied the movements which occur during feeding strikes using synchronous audio and video recordings of two *H. erectus* which was chosen for study because of its relatively large size. We used a Kodak Ektapro EM 1000 high-speed video system to record at either 500 or 1000 frames sec⁻¹. Acoustic recordings were made with a Benthos RDA hydrophone (sensitivity: -194 dBV re 1 μPa; Benthos, Inc., North Falmouth, MA). Audio signals were recorded and synchronized with video signals using a MacADIOS II analog-to-digital conversion board (12 bit) and SuperScope II software (GW Instruments, Somerville, MA). Audio signals were recorded on a Power Macintosh 7100 computer at a sampling rate of 10000 points sec⁻¹. We determined the timing of click production with respect to the feeding strike motion using two channels which displayed both the acoustic signal and a 1 msec video frame marker. Time comparisons between the video frame markers and the acoustic signal allowed for precise determination of when during the feeding strike the click was produced.

We analyzed movement across consecutive frames of the high-speed video by digitizing short video clips using a Radius VideoVision Studio board and Adobe Premiere 4.0. The clips were converted to numbered PICT files and imported into

NIH Image for measurement of distances and angles.

To describe conformational changes in the head during feeding strikes, we measured the angle (Figure 1, $\angle A$) between a line connecting the coronet to the tip of the snout (Line 1) and the body axis (Line 3). We also measured the angle ($\angle B$) between a line connecting the supraoccipital bone (SOC) to the snout (Line 2) and the body axis (Line 3). These two angles were measured for each video frame starting just prior to feeding movement and continuing until maximal head elevation before returning to rest position. Angle measurement error was less than 1.4%, determined by ten repeated measurements each for seven different angles. During a feeding strike, the total angular change of the SOC and coronet, each measured relative to the body axis, was calculated by summing angular changes across consecutive frames. We then compared the angular movements of the SOC and coronet relative to each other by subtracting the total angular change of the coronet (Δ angle A) from the total change of the SOC (Δ angle B) during the entire feeding sequence. A value of zero for the calculated relative angular movement of the SOC and coronet would indicate that these two bones moved in the same conformation during the strike, or did not move at all. A negative value for the calculated relative angular movement would indicate that the SOC had moved upward relative to the coronet, while a positive value would indicate that the SOC had moved downward relative to the coronet.

Feeding click characterization

H. zosterae feeding clicks were recorded in a 70 liter aquarium with a Benthos RDA hydrophone and a Sony digital tape recorder (DTC-7). We simultaneously recorded feeding behavior with a Sony Hi8 video recorder. To decrease mechanical and electrical background noise, the tanks were placed on 40 mm thick flextube foam and were lit by two 40 watt incandescent bulbs. All aquaria heaters and air supplies were turned off during recording. The battery-powered tape recorder was connected to the water surface with a single ground. Acoustic recordings

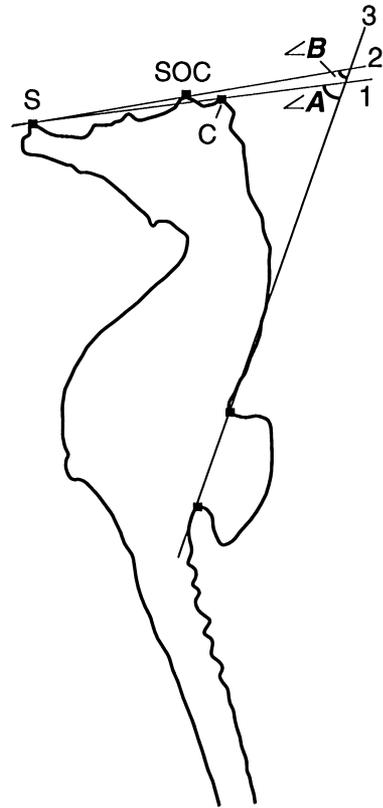


Figure 1. *Hippocampus erectus* outline designating lines and angles measured for kinematic analysis. Points used to determine each line are indicated by filled boxes. Line 1 = coronet to tip of snout; Line 2 = SOC to tip of snout; Line 3 = body axis; A = angle between Lines 1 and 3; B = angle between Lines 2 and 3; SOC = supraoccipital; S = snout; C = coronet.

were digitized and analyzed using Canary 1.2 (Cornell Laboratory of Ornithology, Ithaca, NY) on a Macintosh IIsi computer.

Underwater recordings in small aquaria can be complicated by background noise and artifacts due to tank characteristics (Parvulescu 1966, Yager 1992), although it is possible to measure some acoustical characteristics using small tank recordings (e.g. de Amorim 1996). Two parameters frequently used to characterize acoustic signals are dominant and peak frequency (Myrberg et al. 1986, Lobel 1992, de Amorim 1996). Dominant frequency is measured from amplitude spectra and represents the frequency with the greatest cumulative amplitude throughout the signal. Peak frequency, measured from signal spectrograms, is the instantane-

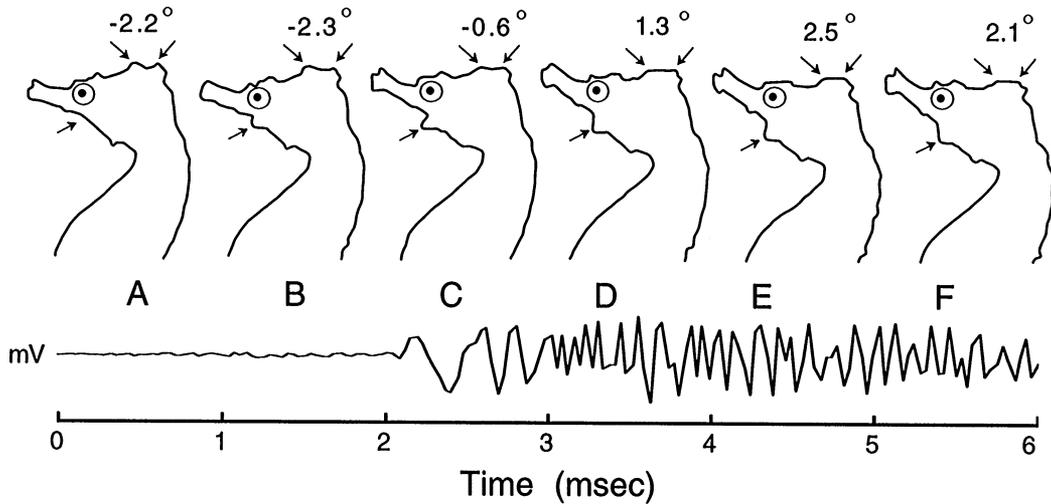


Figure 3. Feeding strike of *Hippocampus erectus* with synchronous acoustic and high-speed video recordings [letters indicate simultaneous time points (± 1 msec) on acoustic and video recordings]. Lower panel: Oscillogram of click produced during feeding strike: the duration of the click includes tank artifacts. Upper panel: Changes in head and body position during consecutive 1 msec high-speed video frames. Arrows indicate hyoid depression and the relative movement of the SOC and coronet. Measurements represent $\angle B$ minus $\angle A$ (as defined in Figure 1): the positive change during the sequence indicates that the SOC has moved ventrally relative to the coronet.

crown-shaped bone at the top of the head, articulates with the SOC, which forms the posterior process of the neurocranium. The anterior margin of the coronet bears a narrow, medial groove that fits over a posterior ridge on the SOC. Ventrally, the coronet has a fixed articulation with the first nuchal plate (NP1) that prohibits any posterior movement

or rotation. Neither the SOC nor the coronet exhibit lateral mobility.

In *H. erectus*, epaxial muscles attach along the ventral posterior margin of the SOC and extend between the coronet and vertebral column with no attachments to the coronet. These muscles originate at various points along the vertebral column. In manipulations of dead *H. zosterae* and *H. erectus* specimens, head elevation caused the SOC ridge to slide posteriorly under the medial groove of the coronet.

Feeding strike kinematics

Bergert & Wainwright (1997) describe feeding strikes in *H. erectus* as consisting of a preparatory phase, an expansive phase, and a recovery phase (discussed in Lauder 1985). The expansive phase of the *H. erectus* feeding strike consists of extremely rapid head elevation coupled with depression of the hyoid apparatus (Bergert & Wainwright 1997). We found that during the expansive phase, hyoid depression and head elevation occurred simultaneously (within the same msec, $n = 12$) and hyoid depression continued for 0.72 sec ($n = 5$, range 0.30–1.76 sec). Maximum head elevation occurred within

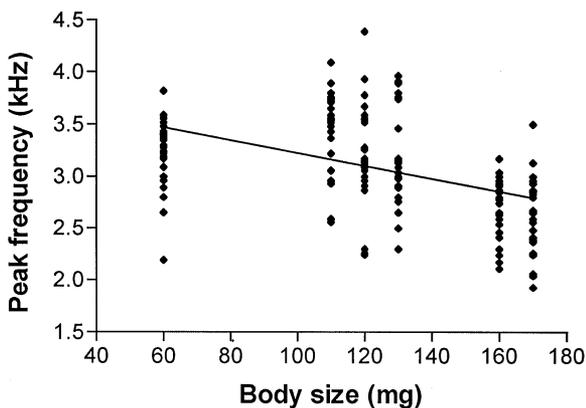


Figure 4. Relationship between *Hippocampus zosterae* feeding click peak frequency and body size (blotted wet weight). Thirty clicks produced during feeding strikes were recorded for each of six individuals. Regression equation; peak frequency = $3.883 - 0.006$ (wet weight), $F = 57.0$, $p < 0.001$.

Table 1. Sound production during feeding in untreated and surgically-manipulated *Hippocampus zosterae* seahorses. The untreated group consisted of two fish recorded without surgical treatment. In the surgery group, two fish were recorded while feeding 3 and 6 days after surgical removal of the posterior supraoccipital ridge. The surgery control consisted of one fish recorded one week after surgical removal of the dorsal anterior SOC process.

Treatment	<i>Hippocampus zosterae</i> feeding strikes:			
	With click	Without click	Total # of strikes	Percentage strikes producing clicks
Untreated	70	5	75	93.3
Surgery	0	29	29	0.0
Surgery control	50	0	50	100.0

4 msec (mean of 5 feeding sequences, range 3-6 msec) of the first upward head movement. *H. erectus* feeding clicks began within 2 msec of the initiation of head elevation ($n = 9$, range 1-5 msec) (Figure 3).

The relative angular movement of the SOC and coronet (Figure 3), calculated by subtracting the total angular change of the coronet from the total angular change of the SOC, averaged 3.9° ($n = 5$, range 1.8° - 4.8°), indicating that the SOC moved downward relative to the coronet during feeding strikes. A single recorded *H. erectus* feeding sequence that failed to produce a detectable sound showed reduced relative angular movement of the SOC and coronet, measuring 1.6° .

Feeding click characterization

H. zosterae feeding clicks ranged from 5 to 20 msec in duration (including tank artifacts). Mean peak frequencies of feeding clicks from six *H. zosterae* (30 clicks per individual) ranged from 2.65 kHz (\pm

SE = 0.078) to 3.43 kHz (\pm 0.066). Peak frequency declined significantly as *H. zosterae* body size increased (Figure 4: $r^2 = 0.245$, $p < 0.001$). For the considerably larger *H. erectus*, lower peak frequencies (1.96-2.37 kHz) were observed for four clicks produced by one individual.

Both *H. zosterae* and *H. erectus* produced similar clicks in other situations. *H. zosterae* frequently clicked when placed into a new aquarium. During courtship, competing *H. zosterae* males often clicked while snapping at each other. Snaps included a head motion similar to the feeding strike. Both *H. zosterae* and *H. erectus* produced a series of clicks when held out of water.

Surgical manipulation of the SOC-coronet region

We recorded 75 feeding strikes from two untreated *H. zosterae* and 93% of these feeding strikes were associated with clicks (Table 1). For the two seahorses in which the SOC articulation with the coronet was surgically removed, 29 feeding strikes were

Table 2. Sound production during feeding in pre-surgery and surgically-manipulated *Hippocampus erectus*. One seahorse was recorded while feeding prior to surgery, and then at 1 and 7 days following surgical removal of the posterior SOC ridge.

Treatment	<i>Hippocampus erectus</i> feeding strikes:			
	With click	Without click	Total # of strikes	Percentage strikes producing clicks
Pre-surgery	52	0	52	100.0
1 day post-surgery	2	24	26	7.7
7 days post-surgery	1	16	27	3.7

recorded but no clicks were observed. For the surgical control seahorse in which the anterior process of the SOC was removed, clicks accompanied all of the 50 feeding strikes recorded one week following surgery. The surgical removal of the dorsal posterior process of the SOC bone resulted in a significant reduction in sound production during feeding strikes in *H. zosteræ* (contingency table analysis, $G = 94.7$, $n = 104$ feeding strikes, $df = 1$, $p < 0.001$)

In a single *H. erectus* prior to surgery, clicks accompanied all of the 52 recorded feeding strikes (Table 2). Following surgical removal of the SOC-coronet articulation, 7.7% (1 day) and 3.7% (7 days) of the feeding strikes had associated clicks. The few clicks that were observed post-surgery in *H. erectus* were much lower in amplitude than those recorded prior to the surgery. For this *H. erectus*, surgical removal of the dorsal posterior process of the SOC significantly reduced the proportion of feeding strikes associated with clicks both one day ($G = 82.19$, $n = 78$, $df = 1$, $p < 0.001$) and seven days following surgery ($G = 91.55$, $n = 79$, $df = 1$, $p < 0.001$).

Discussion

Feeding strikes in *H. erectus* and *H. zosteræ* resemble those described for other syngnathid pipette feeders (Muller & Osse 1984, Bergert & Wainwright 1997). Our study supports the previous finding that in *H. erectus*, head elevation during the expansive phase of prey capture is extremely rapid (4 msec) and occurs simultaneously with hyoid depression (Bergert & Wainwright 1997). Such rapid head elevation is accomplished by contraction of the epaxial musculature which results in a dorsal rotation of the neurocranium (Lauder 1985). Based on our manipulations of dead seahorses and kinematic analyses of feeding strikes, a ridge along the posterior portion of the supraoccipital appears to slide ventrally under the coronet during this head movement.

Previous hypotheses that have been proposed for mechanisms of click production in *Hippocampus* seahorses include: (1) stridulatory sound production from the bony articulation between the su-

praoccipital and the coronet (Fish 1953) and (2) cavitation produced by rapid pressure changes within the buccal cavity during the feeding strike (Gill 1905, James & Heck 1994, Bergert & Wainwright 1997).

Hydrodynamic cavitation may produce sound due to the collapse of vapor bubbles in fluid resulting from rapid decrease in pressure (Urlick 1983, Lauterborn 1997). Cavitation events can be highly variable depending on the conditions of the fluid (Smith 1994, Lauterborn 1997), and due to their small size it would be extremely difficult to directly measure cavitation in seahorses. However, several observations suggest that cavitation is not likely to account for click production during seahorse feeding. Patterns of pressure changes measured in the buccal cavity of other suction-feeding fishes (Muller & Osse 1984, Lauder 1985) suggest that cavitation might occur during or following the late expansive phase when pressure within the buccal cavity decreases most rapidly. However, our results indicate that clicks generally occur within 2 msec of the start of the expansive phase, when the pressure is increasing. In addition, both *H. zosteræ* and *H. erectus* produce a series of audible clicks when out of water. It is unlikely, in these conditions, that sufficient water remains in the buccal cavity for cavitation to occur.

This study provides several lines of evidence supporting a stridulatory origin for the feeding click. The anterior portion of the coronet in *H. zosteræ* forms a groove which articulates with a ridge on the SOC at the posterior region of the neurocranium. While the coronet itself exhibits little mobility, the SOC ridge slides postero-ventrally under the medial groove of the coronet during the rapid head elevation that characterizes the seahorse feeding strike. In *H. erectus* feeding strikes that produced clicks during head elevation, the SOC moved downward relative to the coronet by an average of 3.9° , apparently due to the SOC ridge sliding under the coronet. Although based only on a single observation, the one recorded *H. erectus* strike that failed to produce a click showed a lower relative movement (1.6°) of the SOC and coronet perhaps insufficient for stridulatory sound production.

The results of surgical removal of the posterior

ridge of the SOC also provide support for the stridulation hypothesis. In both *H. zosterae* and *H. erectus*, surgical removal of the SOC posterior ridge decreased the proportion of feeding strikes that produced clicks. Continued sound production during feeding strikes in a surgical control *H. zosterae* indicated that surgery itself or minor bone trauma does not reduce the ability to produce clicks. However, it is possible that lack of sound production following removal of the SOC posterior ridge could have resulted from other changes associated with the surgery, including removal of muscle attachments from the SOC. In addition, seahorses in which the SOC posterior ridge had been removed showed a reduced range of motion during feeding strikes compared to both the surgical control and untreated seahorses, although all fish were capable of feeding. It is possible that this reduced range of motion may have decreased pressure changes in the buccal cavity and prevented cavitation.

The ecological and behavioral implications of the seahorse feeding click are currently unknown. However, seahorses have been observed to produce similar clicks in many circumstances, as described above. Several aspects of seahorse reproductive biology, including a monogamous mating system (Vincent 1994) and elaborate courtship behavior (Vincent 1994, Masonjones & Lewis 1996), suggest a possible role for acoustic communication in intraspecific interactions. Future investigations may provide insight into the functional significance of acoustic signals in seahorses.

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