

# Sound Production in the Clownfish *Amphiprion clarkii*

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Although clownfish sounds were recorded as early as 1930 (1), the mechanism of sound production has remained obscure.

Yet, clownfish are prolific “singers” that produce a wide variety of sounds, described as “chirps” and “pops” in both reproductive and agonistic behavioral contexts (2). Here, we describe the sonic mechanism of the clownfish *Amphiprion clarkii*.

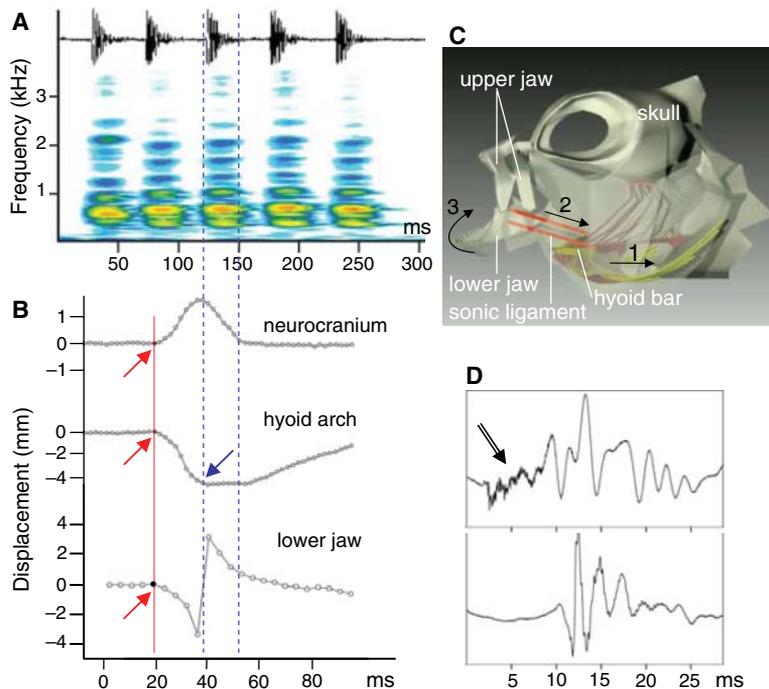
We studied sounds (from three males and one female) directed toward conspecifics that approach their sea-anemone hosts. Sound recordings, synchronized with high-speed video (500 fps) coupled ( $n = 9$ ) or not ( $n = 22$ ) with an x-ray system, allowed us to quantify movements of skeletal elements (3).

*A. clarkii* sounds (Fig. 1) are produced in trains of one to eight pulses (means for duration, 26 ms; pulse period, 35 ms; and energy, between about 450 to 800 Hz). These parameters do not correspond with typical stridulatory mechanisms (4) and have higher frequency components than swimbladder sounds driven as a forced response to sonic muscle contraction (5).

Sounds ( $n = 14$ ) were typically accompanied by rapid (<30 ms) movements that include an elevation of the head, lowering of the hyoid bar and anterior part of the branchial basket, a backward movement of the pectoral girdle, and lastly a closing of the lower jaws (movie S1). Synchronization of sound pulses with the video images indicates that sound is produced when the hyoid apparatus is rapidly lowered (23.8 m/s<sup>2</sup>,  $n = 50$  frames) and the mouth simultaneously closed (Fig. 1).

Manipulations of specimens show that low-amplitude elevations of the skull lower the jaws and branchial basket, a phenomenon well known in fish feeding (3, 6). Rather than accentuating this movement, a higher-

amplitude elevation of the head actually forces the mouth to close by a previously unknown mechanism.



**Fig. 1.** Sound production in *A. clarkii*. (A) Oscillogram and sonogram of a train of pulses. (B) Graphs of the movements of different skeletal elements during sound production. The red line indicates the beginning of the sonic movement; the blue arrow, the pulse onset; and double dotted lines, the sound duration. (C) Schematic representation of the sound-producing mechanism, illustrating the relative movement of skeletal components. Lowering the hyoid bar (1) stretches the sonic ligament (2), and the jaw closes the mouth (3) by rotating around the mandible articulation on the quadrate. See also movies S1 and S2. (D) Oscillogram of a pulse. Top selection is sound from an intact fish; bottom selection, sound from the same fish after the jaw teeth were cut. The bottom pulse is shorter and deprived of the high-frequency onset (arrow).

Dissections reveal that an unusual sonic ligament is responsible for the rapid lower jaw elevation. The ligament joins the hyoid bar (ceratohyal) to the internal part of the mandible (coronoid process of the articulo-angular) and can be compared to a drawbridge (movie S2). The ligament, acting as a cord, forces the mandible to turn around its articulation during the lowering of the hyoid bar, forcing the mouth to close (Fig. 1). Sound results from the collisions of the jaw teeth, transferring energy to the jaws that are presumably the sound radiator. Transecting the right and left sonic ligaments muted the

fish, supporting our hypothesis. Furthermore, cutting upper and lower jaw teeth resulted in shorter sounds (23 versus 48 ms,  $P < 0.0001$ ,  $n = 38$  pulses) without the typical low-amplitude high-frequency onset. This result indicates that intact sounds start with teeth collisions (Fig. 1).

Species-specific sounds are produced by all 27 *Amphiprion* species and appear to be supported at least by interspecific variation in teeth shape. The sonic ligament is present in other members of the damselfish family (7), many of whom produce communication sounds (8). The homologous ligament mechanism is likely involved in sound production throughout this large family and represents a novel skeletal adaptation for a new behavioral function. This functional movement seems to be an exaptation of the feeding mechanism.

## References and Notes

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## Supporting Online Material

www.sciencemag.org/cgi/content/full/316/5827/1006/DC1  
Movies S1 and S2

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