Japanese Journal of Ichthyology
Vol. 35, No. 1 1988

魚類学雑誌
35巻1号 1988年

Sound Production in the Anemonefishes, *Amphiprion clarkii* and *A. frenatus* (Pomacentridae), in Captivity

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(Received April 13, 1987)

Pomacentrids are well known for their territorial and acoustic behaviours. A number of papers have been published on the acoustic behaviour of Atlantic species (e.g., Myrberg et al., 1978; Spanier, 1979; Myrberg and Spires, 1980; Myrberg and Riggio, 1985). Study on the sound production in anemonefishes *Amphiprion* can be traced back as early as 1930 when Verwey reported that *Amphiprion akallopisos* and *A. polymnus* emit sounds. Schneider (1964) documented the threatening, fighting, and shaking sounds of *Amphiprion clarkii*, *A. polymnus*, *A. frenatus*, *A. percula*, and *A. bincinctus*. However, no detail data on the acoustic parameters of the latter three species were given in his paper. Allen (1972) described the acoustic behaviour of *A. chrysopterus* and *A. perideraion* by giving the duration, frequency range and repetition of pulses of these sounds. Acoustic data on the remaining 26 *Amphiprion* species are far from complete. The present note gives detail acoustic characteristics of *A. clarkii* and *A. frenatus* and proposals for the producing mechanisms of their sounds.

Materials and methods

Acoustic recordings were made in the laboratory. A total of 16 live specimens of *Amphiprion clarkii* and 9 *A. frenatus* were kept in aquaria ($90\times45\times45$ cm^3) with crashed corals as substrate and water temperature was maintained around 25°C. A 12: 12 hrs light-dark period was maintained. The body length of specimens ranged from 5.2 to 9.5 cm SL in *A. clarkii* and 5.1 to 8.1 cm SL in *A. frenatus*. Three to five individuals of each species were maintained in an aquarium for each recording. Recording time was randomly selected during the day. A miniature hydrophone (Brüel and Kjaer type 8103) suspended in the aquarium was connected to a recording charge amplifier (Brüel and Kjaer type 2651) and cassette recorder (Sony WM D6C). After the sounds were recorded, they were analyzed by a digital sonagraph (Kay 7800) and a high resolution signal analyzer (Brüel and Kjaer 2033) which was attached to a X-Y recorder (Hewlett Packard Model 7015B) for data output.

Results

Quantitative data on the physical parameters of *Amphiprion clarkii* and *A. frenatus* sounds are listed in Table 1. The pop and chirp sounds are distinguishable by their dominant frequency ranges; pops of these two species had a wider frequency range than the chirps (Figs. 1–4). Spectral distribution also differed between these sounds; sound energy was peaked at about 200 to 500 Hz in chirps while energy peak in pop was not prominent (Figs. 2, 4). Species differentiations in frequency range and spectral distinction are insignificant (Figs. 1–4). In both species the pop sound was predominately produced singly although it could be emitted in a set of two (Figs.

Table 1. Physical parameters of pop and chirp sounds in *Amphiprion clarkii* and *A. frenatus*.

Sound type	Sound parameter	Species	
		A. clarkii	*A. frenatus*
Pop	Dominant frequency range (KHz)	<3	<3
	Energy mode (KHz)	—	—
	No. of pulses/call	1–2	1–2
	Duration of a single pulse (msec)	≅80	≅50
Chirp	Dominant frequency range (KHz)	<1.5	<1
	Energy mode (KHz)	≅0.5	≅0.4
	No. of pulses/call	1–17	1–7
	Duration of a single pulse (msec)	≅50	≅50
	Repetition rate (pulses/sec)	16–20	12

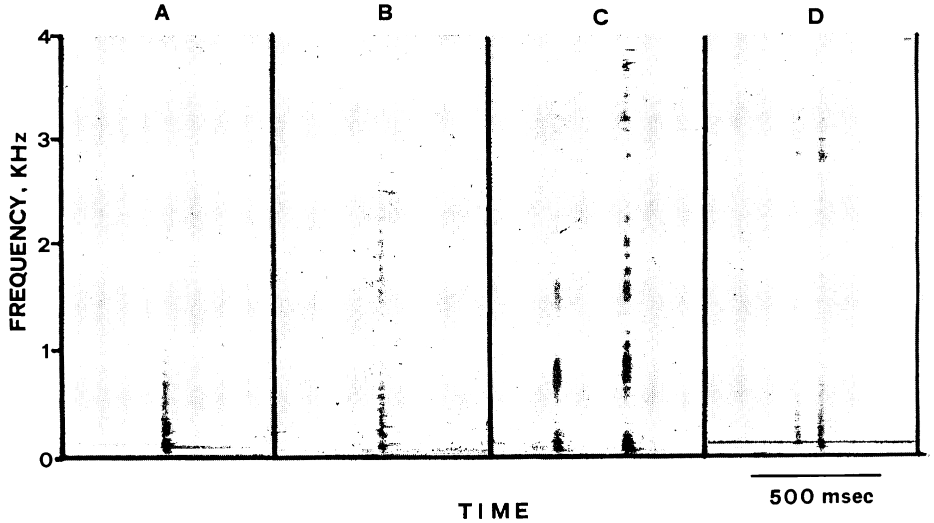

Fig. 1. Sonagrams of single and double pop sounds produced by *Amphiprion clarkii* (A, C) and *A. frenatus* (B, D).

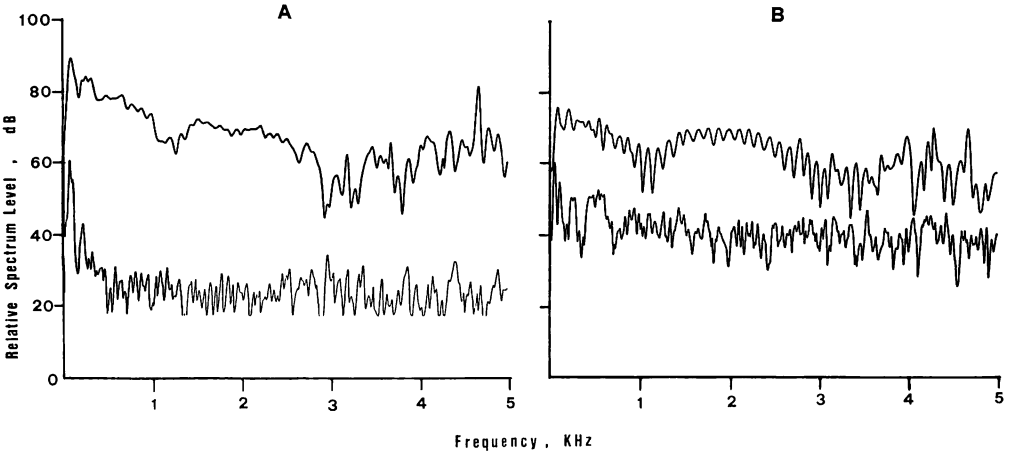

Fig. 2. Spectrograms of single pop sound produced by *Amphiprion clarkii* (A) and *A. frenatus* (B). Bottom spectra: background noise.

1, 5, 6). This sound was often delivered immediately prior to a chirp (Fig. 7) which was composed of a series of pulses (or clicks; Figs. 3, 8). According to its temporal characteristics, chirp is considered an equivalent singal of Allen's "click" of *A. chrysopterus* and *A. perideraion* (Allen, 1972). The composing series often included 1 to 7 pulses in *A. frenatus* (with only one series including 22 pulses; Fig. 9B) and 1 to 17 pulses in *A. clarkii* (Fig. 9A). *A. frenatus* more often emitted chirps with fewer pulses than *A. clarkii* did (Fig. 9A, B). The chirp sounds of these two species are different; the chirps of *A. frenatus* have a lower repetition rate than those of *A. clarkii* (Fig. 3B, C). During an agonistic confrontation, appearance of pops and chirps was accomplished with a slight vertical motion of the dominating contestant's lower jaw. Such motion which is apparently associated with sound production has not been observed in the subordinate contestants (or the loser of the contest). Therefore, it can be concluded tentatively that subdominance inhibits

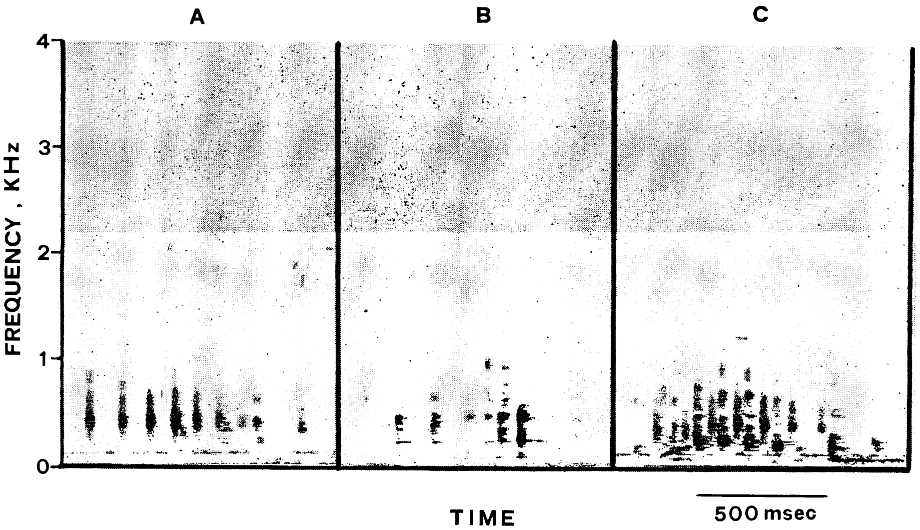

Fig. 3. Sonagrams of chirp sound produced by *Amphiprion clarkii* (A, C) and *A. frenatus* (B).

production of these sounds.

According to our observations, *A. clarkii* was more active than *A. frenatus* in sound emission. The former species produced pop and chirp sounds in 73 out of 112 encounters (65%) while the latter only did so in 62 out of 343 encounters (18%) ($\chi^2=89.77$; $P<0.001$). Unlike *A. frenatus*, *A. clarkii* could emit chirp sound with a higher repetition rate of up to 20 pulses per second (Fig. 3C; Table 1).

Judging from the acoustic properties of the pop and chirp sounds (i.e., short duration, wide frequency range and non-harmonic) and the lack of sonic muscle attached to the swimbladder (pers. obs.), it is believed that grating of pharyngobranchial and ceratobranchial teeth may account for production of these sounds. The ceratobranchial plate and the second to fourth pharyngobranchials carry more long canine teeth in the vocal species (i.e., *A. clarkii*, *A. frenatus*, and *A. perideraion*; Figs. 10A–C, 11A–C), while the non-vocal species (i.e., *A. ocellaris* and *Premnus biaculeatus*) have shorter and fewer teeth in these bones (Figs. 10D, E, 11D, E). Teeth number in *A. clarkii*, which is more active in vocalization and has a longer series of pulses in its chirp sound than *A. frenatus*, is highest among the examined species. This increment in teeth number may be relevant to its vocal characteristics.

In addition to the sounds emitted by the dominant individuals, *A. clarkii* subordinates could produce sound (or the shaking sound) by its submissive display which was a continuous lateral shaking movement with the belly facing the dominant recipient. Sound energy was restricted to a narrow, low frequency band around 200 Hz (Fig. 12). Its duration was about 65 msec (Fig. 12). The shaking sound was detectable only during a vigorous shake of a large subordinate's body. Its low frequency and narrow frequency range suggest that it is a hydrodynamic sound.

Discussion

The present and other published data indicate that *Amphiprion clarkii*, *A. frenatus*, *A. akallopisos*, *A. polymnus*, *A. chrysopterus*, *A. percula*, and *A. bicinctus* are vocal species while *A. ephippium*, *A. ocellaris*, and *Premnus biaculeatus* are non-vocal ones (Verwey, 1930; Eibl-Eibesfeldt, 1960; Schneider, 1964; Mariscal, 1972; Allen, 1972; Chen, 1987). According to Allen (1972), *A. perideraion* is a vocal species. However, we rarely found this species producing sounds in laboratory condition. These specific differences lead to the following inferences. As intraspecific and interspecific interactions inevitably take place in these species, vocal signal is not a compulsory element in the agonistic display of anemonefishes. Our data show that vocal species are also differentiated in their vocal activity towards conspecifics. As vocalization is probably associated

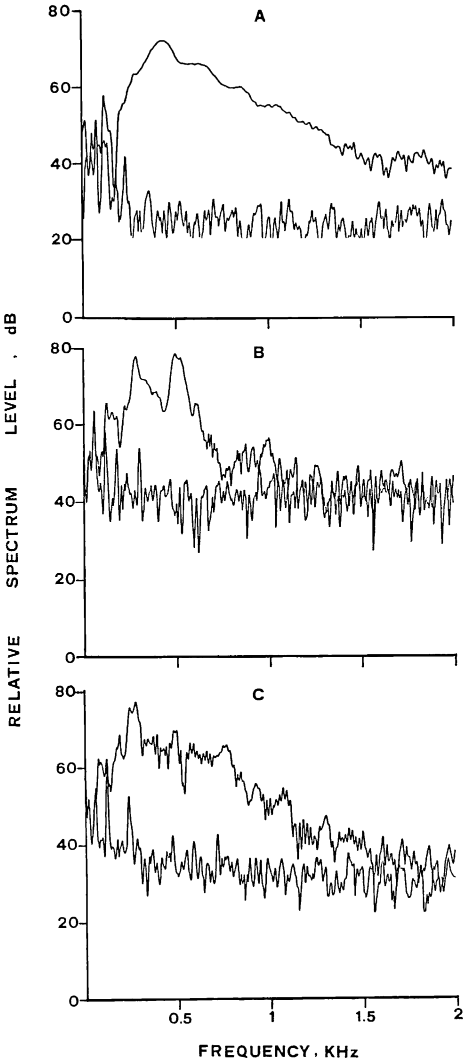

Fig. 4. Spectrograms of chirp sound in Fig. 3. A, Fig. 3A; B, Fig. 3B; C, Fig. 3C.

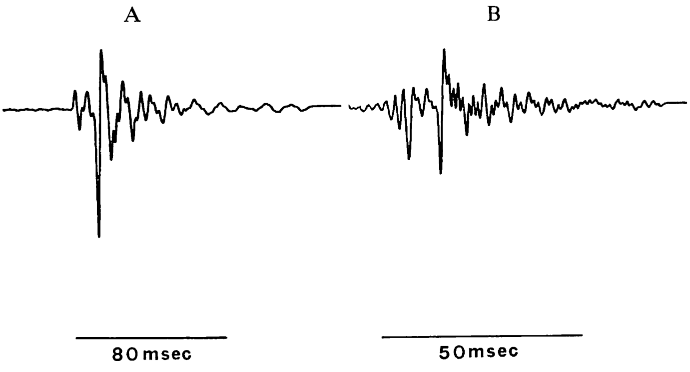

Fig. 5. Oscillograms of single pop sounds produced by *Amphiprion clarkii* (A) and *A. frenatus* (B).

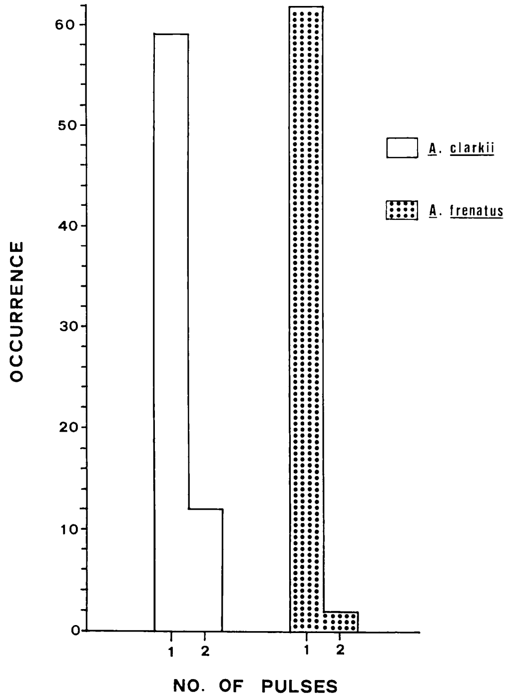

Fig. 6. Occurrence distribution of pulse numbers in pop sounds in *Amphiprion clarkii* and *A. frenatus*.

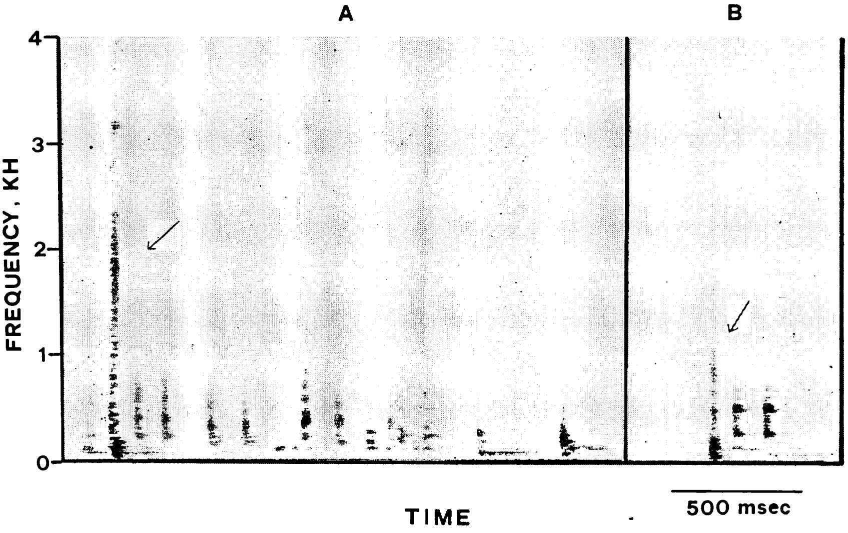

Fig. 7. Sonagrams of chirp sounds preceeded by pop sound (indicated by an arrow) in *Amphiprion clarkii* (A) and *A. frenatus* (B).

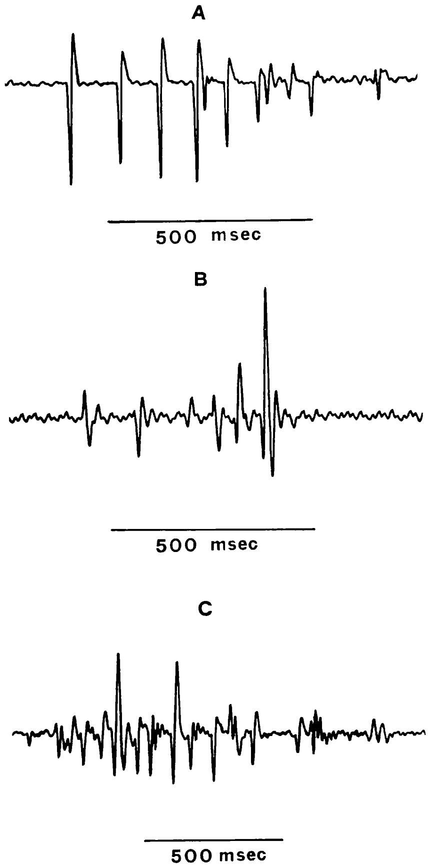

Fig. 8. Oscillograms of chirp sounds in Fig. 3. A, Fig. 3A; B, Fig. 3B; C, Fig. 3C.

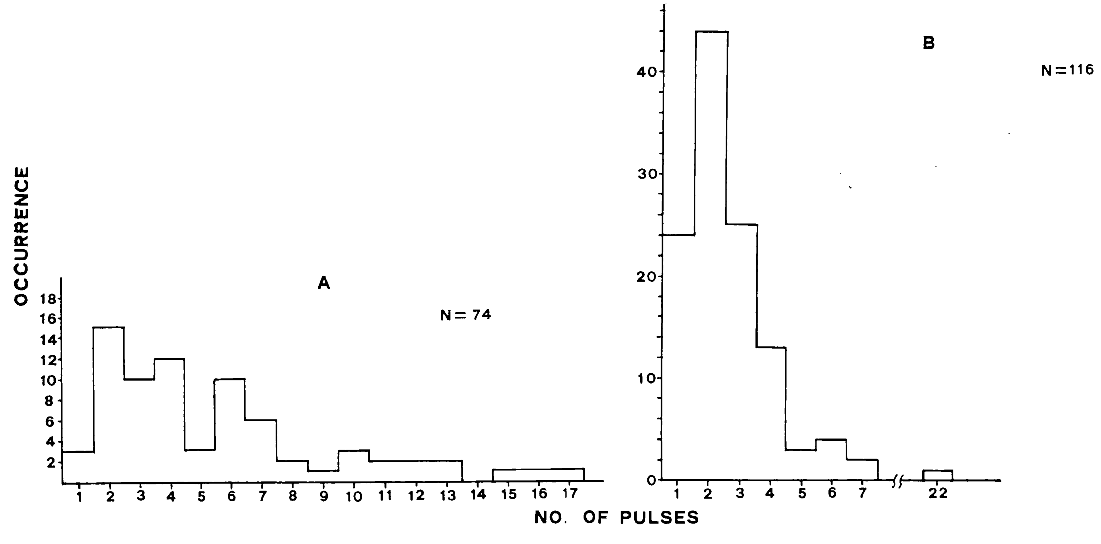

Fig. 9. Occurrence distribution of pulse numbers in chirp sound of *Amphiprion clarkii* (A) and *A. frenatus* (B). N, number of chirp sound analyzed.

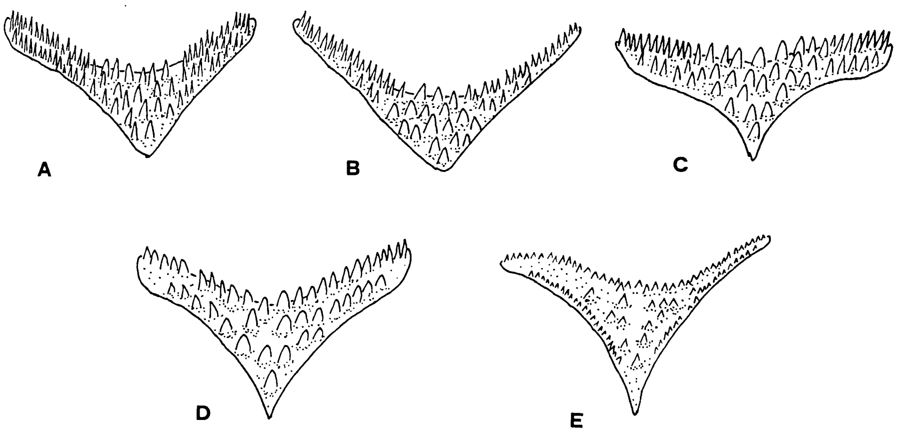

Fig. 10. Tooth patterns of the ceratobranchial plate in *Amphiprion clarkii* (A), *A. frenatus* (B), *A. perideraion* (C), *A. ocellaris* (D), and *Premnus biaculeatus* (E).

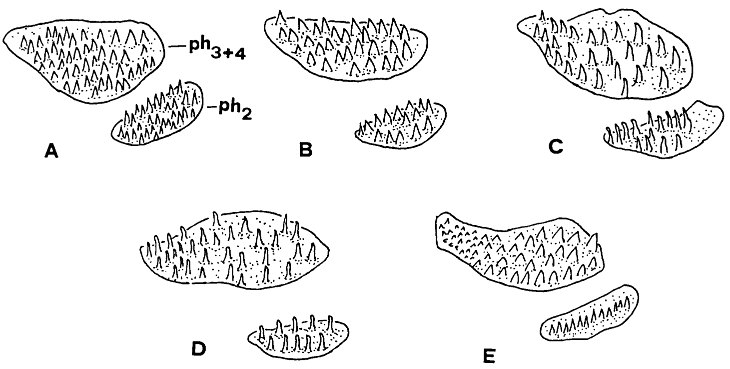

Fig. 11. Tooth patterns of the pharyngobranchial tooth plates in *Amphiprion clarkii* (A), *A. frenatus* (B), *A. perideraion* (C), *A. ocellaris* (D), and *Premnus biaculeatus* (E). ph_2, tooth plate of the second pharyngobranchial; ph_{3+4}, tooth plate of the third and fourth pharyngobranchials.

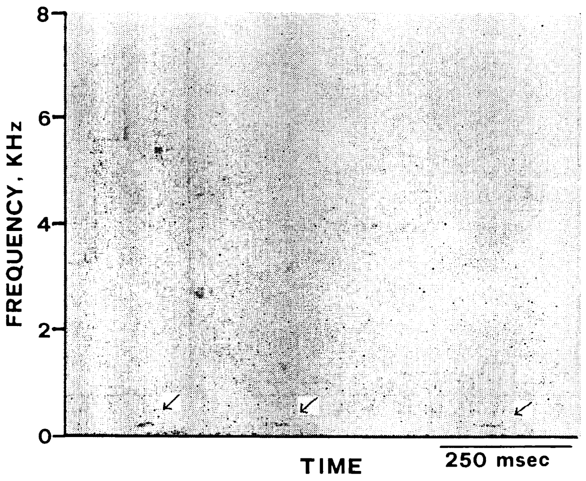

Fig. 12. Shaking sound emitted by an *Amphiprion clarkii* subordinate. Arrows point to this sound.

with aggression, this difference may indicate species-specific variation in aggression towards conspecifics. Difference has also been reported (e.g., Mariscal, 1972) on species-specific aggression shown during interspecific interaction. A thorough understanding of the controlling factors of interspecific and intraspecific aggressions (e.g., interspecific and intraspecific socialities, predator-prey selective pressure, capability on interspecific competition, and utilization of the symbiotic host) and relationship between these aggressive levels may lead to a better knowledge of anemonefish vocalization.

Acknowledgments

We want to thank Drs. Gerald R. Allen of the Western Australian Museum and Richard N. Mariscal of the Florida State University for providing us with many important references. Thanks are also due to the anonymous reviewer for his or her helpful comments on the manuscript. This paper is a portion of the master thesis of the senior author submitted to the National Sun Yat-sen University, Republic of China for the partial fulfillment of the master degree.

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クマノミとハマクマノミの水槽内での発音

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クマノミとハマクマノミの水槽内での発音を記録し，両種の違いを比較した．pop-chirp 発音は優越個体のみにみられ，咽頭歯をすりあわせることにより発生する．クマノミ類の発音する種類は，発音しない種類に比べ，ceratobranchial plate と 2nd to 4th pharyngobranchials に長い犬歯をもっている．クマノミの従属個体は，体を間断なく動かしながら，優越個体に対し，別種の音 (shaking sound) を出す．この音は流体力学的なものであろう．