Acoustic communication in territorial butterflyfish: test of the sound production hypothesis

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Summary

Butterflyfishes are conspicuous members of coral reefs and well known for their visual displays during social interactions. Members of the genus *Chaetodon* have a unique peripheral arrangement of the anterior swim bladder that connects with the lateral line (the laterophysic connection) and in many species projects towards the inner ear. This morphology has lead to the proposal that the laterophysic connection and swim bladder system may be a specialized structure for the detection of sound. However, the relevant stimuli, receiver mechanisms and functions for these putative hearing structures were unknown because butterflyfishes were previously not recognized to produce sounds during natural behavior. We performed field experiments to test the hypothesis that *Chaetodon* produces sounds in natural social contexts. Acoustic and motor behaviors of the monogamous multiband butterflyfish, *C. multicinctus*, were evoked and recorded by placement of bottled fish into feeding territories of conspecific pairs. We demonstrate that territory defense includes the production of agonistic sounds and hydrodynamic stimuli that are associated with tail slap, jump, pelvic fin flick and dorsal-anal fin erection behaviors. In addition, grunt pulse trains were produced by bottled intruders and are tentatively interpreted to function as an alert call among pair mates. Acoustic behaviors include low frequency hydrodynamic pulses <100 Hz, sounds with peak energy from 100 Hz to 500 Hz, and a broadband high frequency click (peak frequency=3.6 kHz), which is produced only during the tail slap behavior. These results provide a biological framework for future studies to interpret the proximate function of the acoustico-lateralis sensory system, the evolution of the laterophysic mechanism and their relevance to butterflyfish social behavior.

Key words: butterflyfish, *Chaetodon*, vocalization, laterophysic, lateral line, hearing, communication.

Introduction

Behavioral displays provide important inter- and intraspecific communication signals that influence the social structure of wild populations. In fishes, visual cues or signals mediate communication during territory defense, reproductive behavior, group aggregations, identification of heterospecifics, and mate or individual recognition (Myrberg and Thresher, 1974; Chiszar, 1978; Guthrie and Muntz, 1993). However, visual displays in fish are often complemented by acoustic stimuli that can improve information transfer or reduce signal ambiguity. For example, in some species a sound or mechanical stimulus produced during visual stimulation by males is necessary to evoke female courtship (Tavolga, 1956; Myrberg et al., 1986; Ladich, 1990; Lobel, 1992; Mann and Lobel, 1998), enhance territory defense (Myrberg, 1997) and

spawning (Satou, 1994a; Satou, 1994b). Thus, it is often necessary to understand the stimuli and functions of multiple sensory systems to interpret the evolution of behavioral displays and social interactions.

Butterflyfishes (family Chaetodontidae, Perciformes) are diverse (~126 spp), highly social and conspicuous inhabitants of almost all coral reefs (Allen, 1980; Findley and Findley, 2001). Members of this family are diurnal and exhibit numerous forms of complex social and mating behaviors that include monogamous pairing, haremic mating systems, solitary behavior and aggregation or schooling (Reese, 1975; Hourigan, 1989). Past studies demonstrate that visual signals in butterflyfishes are important for the recognition of conspecifics (Zumpe, 1965), location and identification of mates (Reese, 1975; Yabuta, 2002), territory defense (Tricas, 1985; Tricas,

1989; Roberts, 1992; Wrathall et al., 1992; Kosaki, 1999), threats from predators (Motta, 1984; Neudecker, 1989) and indicators of behavioral state (Hamilton and Peterman, 1971). These studies on butterflyfish behavior demonstrate that visual signals provide important information in contexts of community ecology, social behavior and fitness.

Although vision is clearly involved in butterflyfish communication, acoustic signals may also be important during behavioral interactions. Members of the genus *Chaetodon* have swim bladder horns and a morphological feature known as the 'laterophysic connection' that may be a unique vertebrate adaptation for processing of acoustic stimuli (Fig. 1). Bilaterally paired anterior horns of the swim bladder project rostrally and near a medial opening of the supracleithrum bone where the head and trunk lateral line systems join (Blum, 1988; Webb, 1998). Among the 12 *Chaetodon* subgenera are several anatomical variations in the length of swim bladder horns, their association with the supracleithrum lateral line canal, and intervening soft tissues (Webb and Smith, 2000; Smith et al., 2003; Webb et al., 2006). This unique morphology in *Chaetodon* has lead to the proposal that their inner ear and part of the lateral line may be sensitive to sound pressure. However, the relevant stimuli, receiver mechanisms and functions for these putative hearing structures were unknown.

A primary stimulus for hearing in fishes is the particle velocity component of sound (the near field) that stimulates the inner ear by whole acceleration of the body (Kalmijn, 1988; Kalmijn, 1989). In some species the inner ear is also stimulated by local particle motion that results from sound pressure-induced pulsations of the adjacent air-filled swim bladder or other gas-filled structures in proximity to the ear (Coombs and Popper, 1979; Denton and Gray, 1993; Yan and Curtsinger, 2000; Fletcher and Crawford, 2001). Therefore, in addition to stimulation of the ear by particle velocity fields, the swim bladder in *Chaetodon* may transform sound pressure into local movement of the anterior horns that stimulate the inner ear. Movement of the swim bladder horns may also displace the adjacent laterophysic tympanum that in turn creates fluid motion within the lateral line in the supracleithrum bone (Webb, 1998). This proposed transduction of sound pressure to the lateral line is novel, but the response characteristics of the laterophysic system to relevant stimuli remain to be tested.

One important assumption of acoustic stimulus processing in *Chaetodon* is that these accessory structures have evolved to enhance the reception of relevant sounds such as those produced during natural social behaviors. Electric shock techniques were used to evoke sounds from several reef fishes, including short pulses from single *Chaetodon* in holding tanks (Fish and Mowbray, 1970). However, to date there are no reports of sound production by *Chaetodon* in natural settings despite the many studies on their well-known and visually mediated social and agonistic behaviors (e.g. Reese, 1975; Tricas, 1985; Tricas, 1989; Fricke, 1986; Hourigan, 1989; Kosaki, 1999; Lobel, 1989; Roberts and Ormond, 1992; Yabuta, 2002). Some possible explanations to explain the failure to detect and identify sounds in naturally behaving

species are that vocalizations are infrequent, of low intensity, masked by ambient environmental noise, or not produced by captive fish. Thus, a test for sound production by butterflyfish in a normal social setting is necessary to establish the natural acoustic repertoire and sound characteristics, and provide insight into possible biological functions of the unique swim bladder and laterophysic morphology.

This study presents an experimental test of the prediction that *Chaetodon* produces weak sounds during their normal social behavior on coral reefs. We used presentations of conspecific intruders into feeding territories of a monogamous species to evoke aggressive visual territorial displays and acoustic behaviors. In addition, we identify sounds produced among intruder fish pairs, thus sound production occurs in contexts of both extra- and intra-pair communication. These findings emphasize the possible importance of weak acoustic signals for social communication in this group, and are consistent with the proposal that the unique laterophysic/swim bladder morphologies evolved to enhance the auditory capabilities of *Chaetodon*.

Materials and methods
Study species and site

The multiband butterflyfish, *Chaetodon multicinctus* Garrett, was selected for this study because of its strong site attachment, monogamous social system and aggressive behaviors associated with defense of a feeding territory (Tricas 1985; Tricas 1989; Hourigan, 1989; Kosaki, 1999). This species is endemic to the Hawaiian Islands and Johnston Atoll, distributed widely over coral-rich reefs of Hawaii, and is easily accessed by divers. It is an obligate corallivore and pairs are known to maintain territories of 50–100 m^2 for periods of >4 years. We expected this species to have enhanced auditory capabilities because it has a well-developed laterophysic system and prominent swim bladder horns that project near the inner ear (Webb and Smith, 2000; Smith et al., 2003; Webb et al., 2006).

Acoustic recording experiments

Field experiments were conducted at Puako Reef on the west coast of the island of Hawaii (19.93°N, 155.86°W). This study site has extensive fields of stony corals (*Pocillopora meandrina*, *Porites lobata* and *Porites compressa*) that extend from the shallow reef flat seaward to depths of about 25 m where pairs of *C. multicinctus* establish permanent and contiguous feeding territories. Scuba divers identified experimental pairs that maintained feeding territories at depths of 8–20 m. Pairs were observed for approximately 15 min to identify the territory boundary and to confirm the pair association. The experimental pair was then challenged by the introduction of conspecific intruders placed in a model bottle, a technique that is known to evoke strong defense behaviors by the resident pair (Tricas, 1989; Kosaki, 1999). Intruder fish were collected each day by hand net >50 m away from the experimental area, placed either singly or in pairs within a
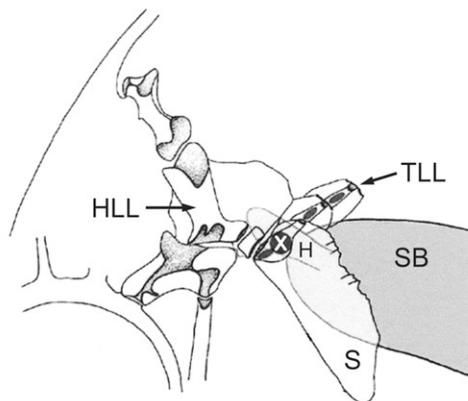
Fig. 1. Schematic diagram of the laterophysic system in butterflyfishes of the genus *Chaetodon*. This unique anatomical feature is a putative acoustico-lateralis hearing mechanism located at the junction of the trunk lateral line (TLL) and head lateral line (HLL) canal systems. The laterophysic connection is formed by gas-filled horns (H) that extend from the anterior swim bladder (SB) and a small tympanum (dark circle and X) on the medial edge of the canal in the supracleithrum bone (S). The swim bladder horns also project towards the otic capsule. Figure modified with permission from Webb and Smith (2000).

Fig. 2. Model bottle method used in field experiments to evoke and record motor and acoustic behaviors produced by *Chaetodon multicinctus*. One or two fish (one shown) were collected by divers, placed in a glass jar and introduced into the territory of a conspecific pair. A hydrophone (H) placed near the bottle detected sounds that were recorded on the audio channel of an underwater video camera (VC). The resident pair quickly discovered the intruders and initiated agonistic acoustic behaviors.

transparent 1-l glass bottle, capped with a perforated lid for ventilation, and positioned near the center of the territory. Acoustic and motor behaviors were recorded with a digital video camera (30 frames s^{-1}, 20–20 000 Hz audio band pass) in an underwater housing and a hydrophone (FishPhone, BioAcoustics, MA, USA; frequency response=8–4000 Hz; sensitivity=–148 dBv/μPa ±1.7 dB) connected to the audio input. This system provided good acoustic recordings but the automatic gain control precluded analysis of absolute sound pressure levels. The hydrophone was placed near or fixed to the side of the bottle, and the camera positioned approximately 1 m away to simultaneously record behavioral interactions and associated sounds (Fig. 2). Since we initially did not know whether sounds would be produced or recordable, we implemented variable time durations for the initial experimental sessions that lasted from 5–43 min. After the start of a recording session, divers swam >50 m away to reduce ambient acoustic background noise produced from the open circuit scuba exhaust. A session was ended when divers returned to the site and moved the setup to the next test territory. To confirm that behavioral responses and sounds were directed at conspecific intruders, control recording sessions were conducted in which the camera, hydrophone and an *empty bottle* were placed in fish territories (*N*=3) for 15 min and the behaviors/sounds recorded. These control tests revealed that resident pairs made brief approaches to the introduced bottle, but showed no agonistic behavior or audible sounds. Thus, the aggressive behavior and acoustic responses observed in our presentation experiments could be attributed to the presence of introduced conspecifics.

Use of animals was approved by the University of Hawaii Institutional Animal Care and Use Committee.

Video tapes were screened for acoustic sounds on a video cassette recorder and monitor in the lab. Each putative acoustic vocalization and any associated locomotor or display behaviors were categorized to identify acoustico-motor behaviors, kinematics, and determine which fish (territory residents or bottled intruders) produced the vocalization. Behavioral sequences were then transferred from tape to a computer and analyzed using Cinestream 3.1 (Autodesk, San Rafael, CA, USA) for the temporal association between motor patterns and sound production. Sound files (raw sample rate=44.1 kHz) were then exported and analyzed with Cool Edit Pro (Syntrillium, Phoenix, AZ, USA) software for temporal and frequency features. Some sounds had strong low frequency content, thus these waveforms were resampled at 4000, 2000 or 200 samples s^{-1} for analysis of low frequencies. Frequency analyses were performed using fast Fourier transformations (FFT Hanning with either a 128 or 256 sample window) and spectrograms. Aggressive behaviors that produced an audible ring caused by contact with the glass bottle were excluded from acoustic analyses.

Results

A total of 4.5 h of behavioral and acoustic data were obtained from 17 different *C. multicinctus* pairs ($\bar{x}$=10.6 min session^{-1}). Prior to the introduction of conspecific intruders, experimental pairs foraged widely across their territory, showed normal movement patterns and intra-pair behaviors and almost no aggressive behaviors with other conspecifics as demonstrated in previous experiments on this species (Tricas, 1985; Tricas, 1989). After placement of bottled conspecific intruders into a territory, resident pairs quickly detected, approached, displayed and attacked the introduced fish [delay=10.0±0.0002 s ($\bar{x}$ ± s.d.; *N*=15 pairs)]. This aggressive behavior resulted in a high proportion of the pair's time budget ($\bar{x}$=80.0%) spent <1 m from the model-bottle and thereby simulated natural but
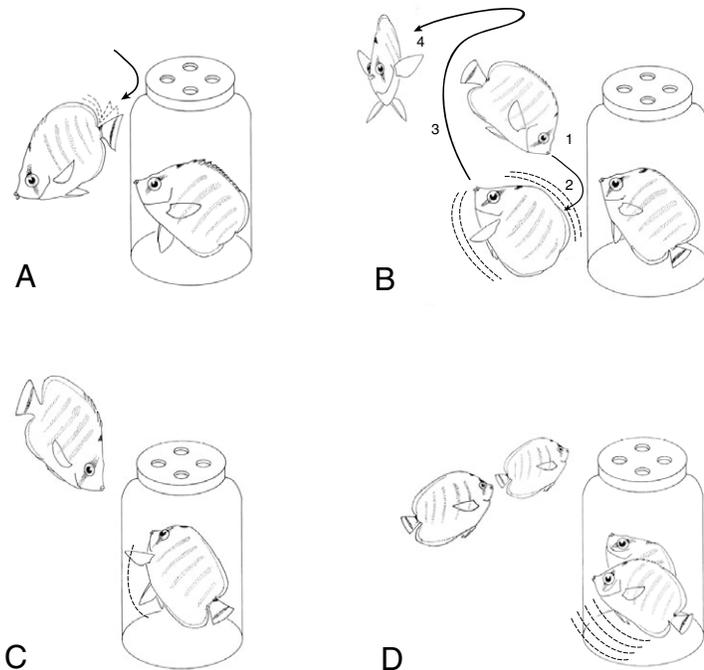
Fig. 3. Behaviors associated with sound production in the multibanded butterflyfish, *Chaetodon multicinctus*. (A) The tail slap behavior occurs after escalated displays and aggression by territorial residents towards bottled intruders and is performed within a distance of one body length from the bottle. The tail slap produces both a low frequency hydrodynamic pulse and a brief broadband acoustic click. (B) The jump behavior is displayed by resident fish and involves several movement patterns: the approach and face (1) and rapid turn (2) are followed by a short swimming ascent (3) and intense lateral display (4). The rapid turn produces a low frequency hydrodynamic pulse that is followed by several rapid acoustic pulses. (C) The pelvic fin flick behavior is produced by both residents and bottled intruders (illustrated), involves the extension of the pelvic fins and a single acoustic pulse. (D) The grunt train sound was produced only by bottled fish when approached by territory residents and may be an alert call to the mate. No body movements were observed during the production of this sound. Broken lines indicate sound production.

prolonged territorial encounters. Bottled intruders typically were stationary when residents were out of sight but faced residents when approached.

Motor and acoustic behaviors of Chaetodon multicinctus

Model bottle experiments always evoked aggressive behavior and often vocalizations from both members of a resident pair. By contrast, the movement of bottled intruder fish was constrained by the container, thus no overt defensive behaviors were recorded for these fish as is commonly seen during territorial disputes on the open reef. However, bottled intruders sometimes produced sounds when approached by residents. Males of this monomorphic species are more aggressive than females (Tricas, 1989) but we did not capture fish to confirm their sex. Acoustic analyses identified five distinct sounds that included both single pulses and pulse trains. Most acoustic behaviors were associated with specific motor patterns.

The tail slap

Territory residents always showed strong aggression that included frontal approaches, static lateral displays and swimming behavior directly in front of or around the intruder fish. Escalated aggressive displays were frequently followed by a strong tail slap delivered at a distance of less than one body length from bottled fish (Fig. 3A). Frame-by-frame analysis revealed that the tail slap behavior begins with a lateral display, slow approach, and flexion of the head and caudal portion of the body away from the intruder. This lateral display behavior is terminated by a quick tail slap at the intruder followed by a turn and forward acceleration of the body. The average duration of the tail slap action pattern was 193 ms (Table 1).

Two distinct acoustic sounds were recorded during the tail slap behavior (Fig. 3A, Fig. 4A). A low frequency pulse sound was produced in association with motion of the body during the tail slap and had an average duration of 154 ms (Table 1). This low frequency sound had a peak frequency between 51 and 109 Hz ($\bar{x}$=69 Hz), and was associated with hydrodynamic flow created by motion of the posterior body that often displaced suspended particulates in the water column and sometimes the nearby mate. However, the hydrodynamic pulse was often difficult to record due to the directionality of the tail slap, the solid wall of the bottle that often blocked hydrodynamic signals to the hydrophone and the rapid attenuation with distance.

An acoustic click was also detected during 97% of all tail slap behaviors (*N*=105) recorded on video. The click sound had a brief duration ($\bar{x}$=10 ms) and most commonly occurred during tail flexion associated with the rapid turn behavior (Table 1, Fig. 4A). The click was broadband and of relatively high peak frequency ($\bar{x}$=3415 Hz). The tail slap behavior was sometimes produced sequentially by the male and female pair as they swam by the bottled fish, thus producing aggressive and complex visual, hydrodynamic and acoustic signals to the intruders. This acoustic behavior was the most frequent observed and accounted for almost half of the recorded sounds (Fig. 5).

The jump

The jump behavior was produced exclusively by resident fish, always directed towards bottled intruders and usually involved a sequence of four motor patterns (Fig. 3B). The jump behavior sequence began with an approach and face of the resident towards the bottled fish followed by a *rapid turn* motion in which the body rotated about 180°. The turn was usually followed by a short ascent in which the fish swam up and away from the intruder to a distance of ~0.5 m and finally
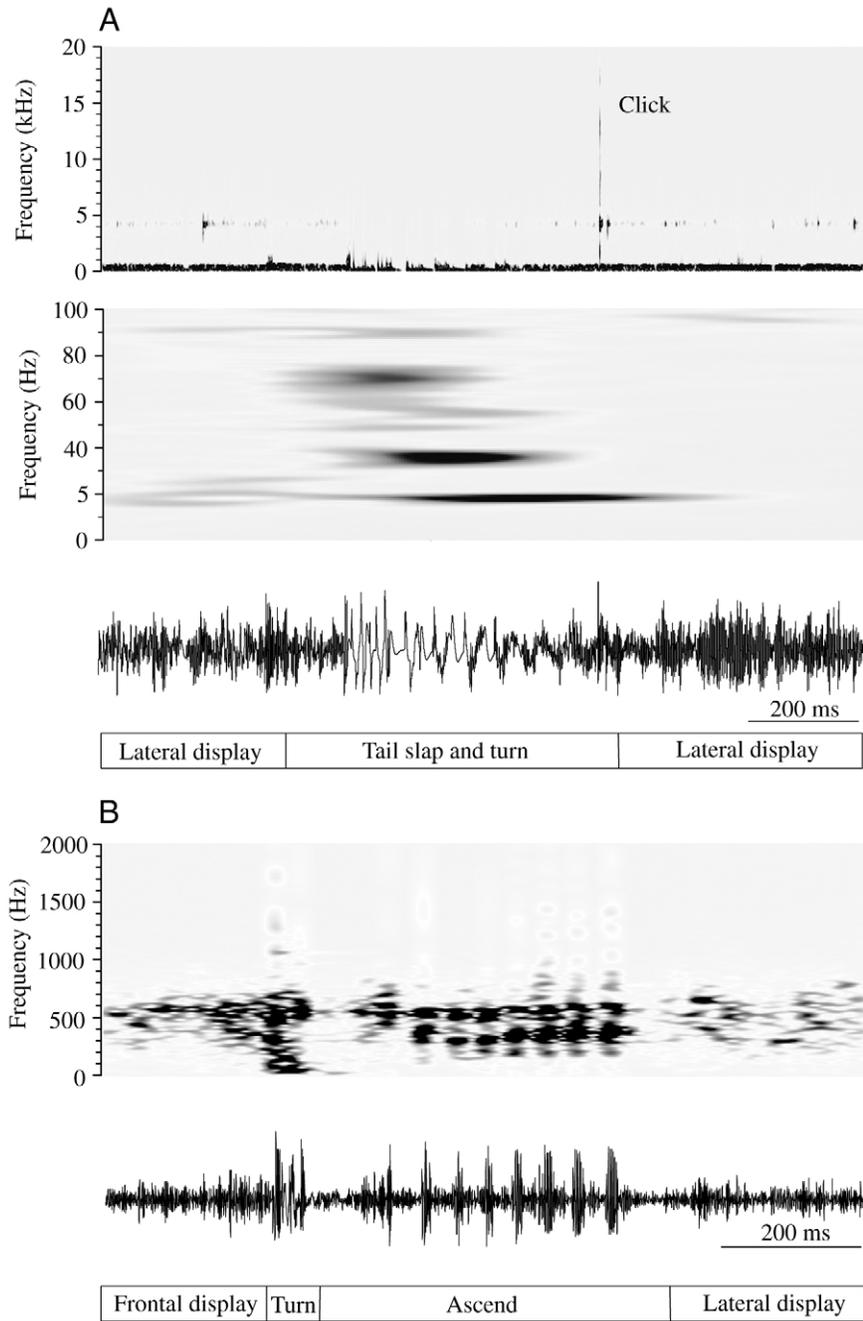
Fig. 4. Motor patterns and sounds produced by multiband butterflyfish, *Chaetodon multicinctus* during agonistic interactions with bottled conspecifics. (A) The tail slap starts with a lateral display followed by tail slap and turn motor patterns (lower panel) that produce acoustic stimuli (waveform on lower trace). A strong hydrodynamic pulse with signals at 20–60 Hz results from the lateral motion of the body towards the intruder (lower spectrogram). The tail slap occurs at the end of the turn that produces a broadband click (upper spectrogram). In this instance the tail slap was immediately followed by a second lateral display. (B) Jump behavior starts with a frontal motor display towards the bottled intruders, a rapid turn of the body, and swimming ascent that is followed by an intense lateral display (lower panel). The turn and ascend behaviors produce acoustic stimuli that include a low frequency component made during the turn followed by a pulse train during the ascent (waveform on lower trace). Note that spectrum of sounds made during both the turn and ascent are from <100–700 Hz, with lower frequencies due to the hydrodynamic pulse made during the turn (spectrogram).

a second turn to start an intense *lateral display.* The display is presented during lateral swimming, involves partial erection of the medial fins, includes a bending of the head away from the bottled intruder, and presents a clear visual signal to the bottled fish. The jump behavior (excluding the approach and lateral display) duration ranged from 231–429 ms ($\bar{x}$=341 ms).
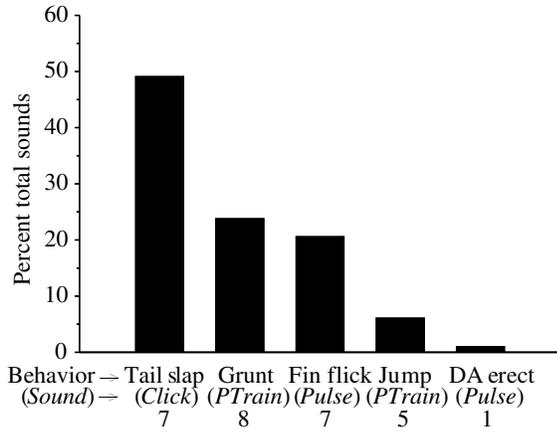
Fig. 5. Relative frequency of sounds produced during aggressive social interactions in the multiband butterflyfish, *Chaetodon multicinctus*. The tail slap, grunt and dorsal-anal fin (DA) erect acoustic behaviors were produced exclusively by territory residents and directed towards bottled conspecifics. Grunt trains were recorded only from bottled fish (most frequently when in pairs) when territory holders came into view and may be an alert or distress signal to the mate. The fin flick acoustic pulse was produced by both resident and bottled fish during confrontations. *N* values are given beneath each behavior.

Acoustic sounds during the jump behavior coincided with either the turn or the ascend motions. Like the tail slap, a low frequency pulsed movement of water is produced during the turn behavior (Fig. 3C, Fig. 4B). The turn was either accompanied or followed by a series of rapid acoustic pulses and a subtle rapid body shake that was not always obvious during upward swimming. The jump sound was a train of four to eight pulses with an average duration of 301 ms (Fig. 6, Table 1). Single pulses were of short duration ($\bar{x}=19$ ms), had usually regular interpulse periods ($\bar{x}=54$ ms), and an average pulse peak frequency of 466 Hz. This behavior was relatively infrequent (Fig. 5) and observed only in highly aggressive resident fish.

Pelvic fin flick

Both residents and bottled fish produced sounds associated with extension of their pelvic fins (Fig. 3C). The pelvic fin flick motor pattern occurred when residents and intruders faced each other, was of relatively long duration ($\bar{x}=238$ ms) and consisted of a rapid ventral extension of both pelvic fins (that occurred in less than one video frame=33 ms) followed by a slower retraction. No other body movements (fin extensions or body motion) were observed during this behavior. The pelvic fin flick produced a brief acoustic pulse that occurred before maximum extension of the fin (Fig. 6A). This sound was of short duration ($\bar{x}=17$ ms), a mean peak frequency of 229 Hz and included 20% of all observed sounds (Fig. 5). No pulse trains were observed with this behavior.

The dorsal-anal fin erect

Partial erection of the medial fins is common during lateral

Table 1. *Motor and acoustic behaviors produced by resident and intruder Chaetodon multicinctus during aggressive interactions*

			Motor pattern	Sound			Pulse train		
Source	N	n	Duration (ms)	Duration (ms)	Peak frequency (Hz)	−10 dB BW (Hz)	Duration (s)	Pulses per train	Interpulse interval (ms)
Tail slap	R	6	13	193±62				–	–	–
Low frequency pulse		3	9		154±132	69±21	40–98	–	–	–
High frequency click		5	12		10±12	3415±1725	2449–5190	–	–	–
Jump	R	3	6	341±77	19±4	466±33	346–593	0.30±0.12	6.2±1.8	41±15
Dorsal-anal fin erect	R	1	1	198	115	125	113–137	–	–	–
Pelvic fin flick	R, I	5	10	238±106	17±8	229±95	179–260	–	–	–
Grunt train	I	5	10	n.o.	42±4	163±32	132–228	5.7±1.9	17.4±9.4	299±41

BW, bandwidth; N, number individuals; n, number of behaviors; n.o., not observed; R, resident; I, bottled intruder.
Values are mean ± s.e.m., except for bandwidth (means only).

Fig. 6. Sound production by multiband butterflyfish, *Chaetodon multicinctus*, intruders during encounters with conspecific territory holders. (A) The pelvic flick behavior by an intruder involves the extension of the pelvic fins that produces an acoustic stimulus during this motion (waveform on lower trace). This sound has a frequency spectrum just below 200 Hz and is also produced during displays by resident fish towards bottled intruders. Arrows show start and end of pelvic fin extension. (B) The grunt train sound is produced by bottled intruder pairs when confronted by territory residents. Unlike all other acoustic signals observed, the grunt train was not associated with any visible body movements, thus most likely is caused by internal muscle movements. This sound included a series of regular spaced pulses (waveform on lower trace) that have a strong frequency component at 400–500 Hz (spectrogram). Note the harmonics associated with each pulse that indicate that this internally generated sound may result in part from resonance of the swim bladder.
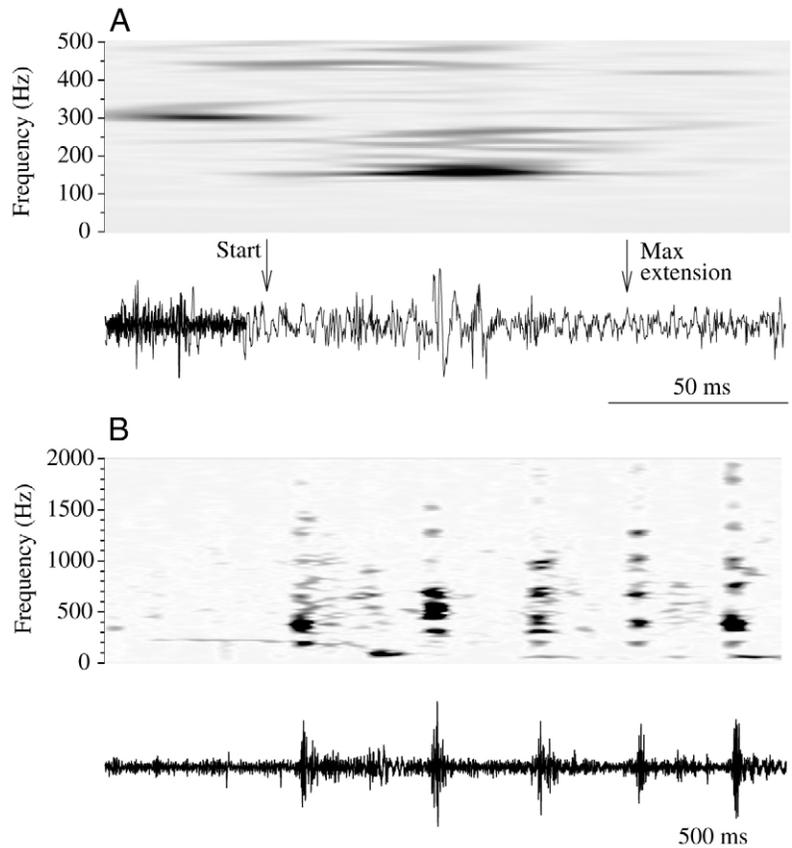
displays among territory residents, primarily involves elevation of the soft caudal portion of the dorsal and anal fins (rarely the spines), and was not observed to include the production of sound. In contrast, the dorsal-anal fin erect behavior included full extension of the dorsal and anal fin spines and was observed in only one fish during an intense lateral swimming display (Fig. 5). This behavior was accompanied by the production of a distinct sound of 115 ms duration and a peak frequency of 125 Hz (Table 1).

Grunt train

The grunt train sound was produced by bottled fish pairs when confronted by territory residents. This acoustic behavior often began when the resident pair approached the bottled intruders (>3 m away), and continued during direct confrontations and displays by residents (Fig. 3D). Unlike all other acoustic behaviors, no clear associated motor movements were observed on video. Thus, the grunt sound is most likely generated by internal muscles that do not influence movement of the fins or body. Although it is possible that free-swimming resident fish could also produce this sound, we have several reasons to conclude that our recorded grunt trains were from bottled intruder fish. First, this grunt sound often began when approaching residents were visible but at large distances from the intruder. Next, we would expect sound amplitude to be relatively constant if produced by bottled fish and variable if produced by the wide-moving territory residents. Our recordings show that the amplitude of grunt pulses, which were detected by the hydrophone that was fixed to the side of the bottle, did not change as free-swimming residents approached, swam in the vicinity, or swam away. Finally, the pulse trains were not interrupted when resident fish produced other acoustic behaviors.

The grunt acoustic behavior was recorded primarily when bottled fish were presented in pairs, and rarely from a single bottled fish. The grunt train was the most common sound produced by bottled intruders (Fig. 5) and consisted of a sequence of individual pulses produced at a rate of about 3 pulses s^{-1} that lasted for an average duration of 5.7 s (Fig. 6B, Table 1). We were unable to distinguish which of the two bottled fish produced the grunt train, but in most cases pulses were of constant amplitude and uniform period, which indicate a grunt train was most likely produced by a single individual. However, in a few records inter-pulse intervals were irregular and thus are probably the result of simultaneous grunts trains produced by both bottled fish. With the exception of the low frequency hydrodynamic pulses produced by territorial fish during the tail slap, single grunt pulses were of the longest duration ($\bar{x}$=42 ms), had a mean peak fundamental frequency of 163 Hz and were of low bandwidth. Several harmonics were often associated with this sound.

Discussion

The proposal that sounds provide important behavioral stimuli for members of the genus *Chaetodon* was derived from systematic and morphological studies that report unique associations between the swim bladder, inner ear and lateral line. However, since sound production was not previously reported during natural butterflyfish behavior, the relevant acoustic stimuli for these structures were unknown. This study

confirms that *Chaetodon multicinctus* produces several distinct sounds and hydrodynamic stimuli during inter- and intra-pair social interactions. These finding provide a biological basis for future studies to test whether the laterophysic system and swim bladder horns enhance hearing capabilities of sounds produced during social interactions.

Acoustic behavior in Chaetodon

This study revealed the production of five sounds that are associated with agonistic visual displays during interactions between territory residents and bottled intruders. The most frequent acoustic behavior was the tail slap made by territory residents and directed towards intruder fish. This behavior was always preceded by a lateral display, a common form of aggression during initial border disputes among territory holders in this and other species *Chaetodon* spp. (Zumpe, 1965; Sutton, 1985; Yabuta, 2002), and in cichlids is an initial signal of low intensity (Baerends and Baerends-van Roon, 1950; Enquist and Leimar, 1983). In escalated encounters by territory resident *Chaetodon*, the lateral display could be followed by the dorsal-anal fin extension behavior or the tail slap behavior at a distance of one to two body lengths from the receiver. The use of relatively weak tail slaps or 'beating' during lateral displays is common in fishes (Chizar, 1978), and is described for some cichlids as stationary swimming with strong undulations (Barlow, 1967), and a low-intensity aggressive behavior (Enquist and Lemar, 1983; Brick, 1998). By contrast, the tail slap behavior by *C. multicinctus* is brief but probably energetically expensive. It is very rapid and intense, usually follows several low-level agonistic lateral displays and occurs at the end of a single bout. The motion of the body during the tail slap produces a strong hydrodynamic pulse with a peak frequency <100 Hz (down to and probably below the 20 Hz limit of our recording system). This transient, low-frequency hydrodynamic stimulus is directed at and can displace the target fish. Low frequency hydrodynamic stimuli were reported up to 100 Hz for startle response (Bleckmann et al., 1991) and up to 300 Hz for rapid swimming (Gray and Denton, 1991) behaviors. Since the force that produces water displacement by *Chaetodon* is likely a function of body size, the hydrodynamic flow from the tail slap together with visual stimulation from the lateral display may provide an integrated honest signal of size or status during territorial challenges as described for tail beating during nesting in the Siamese fighting fish (Halperin et al., 1995).

The late phase of the tail slap behavior in *C. multicinctus* includes a brief acoustic click with a duration of 10 ms, high peak average frequency of 3.6 kHz of high bandwidth that extends up to more than 15 kHz (Fig. 3A), and a peak intensity of ~120 dB re. 1 μPa at a distance of <10 cm from the source (T.C.T. and K. Boyle, unpublished data). The click is within the band of ambient reef noise produced by snapping shrimp which is of much shorter duration (10 μs) but much higher intensity ~180 dB re: 1 μPa (Au and Banks, 1998). The production of high frequency broadband clicks during agonistic interactions with conspecifics was also reported in other fishes (Caldwell and Caldwell, 1967; Valinsky and Rigley, 1981; Crawford et al., 1997). However, the question of whether this high frequency sound is perceived by butterflyfish or serves some other function such as predator deterrence (Vester et al., 2004) remains to be tested.

The jump was a rare but strong aggressive behavior that involved clear visual and pulsed acoustic displays. Single and train pulsed sounds are a common form of aggressive and courtship behaviors in other coral reef species, and are best studied in the damselfishes (Myrberg, 1972; Myrberg et al., 1986; Lobel and Mann, 1995). The humbug damselfish (*Dascyllus albisella*) and the bicolor damselfish (*Stegastes partitus*) produce several different pulsed sounds that are related to aggression, courtship and visiting and can be distinguished by pulse duration, period and number (Myrberg, 1972; Kenyon, 1994; Mann and Lobel, 1998). Although such sounds may be associated with specific behavior contexts, Myrberg provided experimental evidence that the chirp sound produced by male bicolor damselfish serves as a territorial 'keep out' display, and was most effective when paired with the visual presence of a resident fish (Myrberg, 1997). Unlike the variety of pulsed sounds produced by damselfishes that may serve as advertisement for defense of a relatively small territory, the aggressive pulsed sounds in *Chaetodon* were only observed during the jump behavior directed toward bottled fish. Since paired butterflyfishes constantly move about a large feeding territory (Tricas, 1989), this acoustic behavior probably occurs primarily during border disputes and escalated attacks among territory pairs.

The pelvic fin flick behavior was produced by both territory residents and intruders. This behavior occurred when fish were in a face-to-face orientation, produced a coincident visual stimulus created by the ventrolateral extension of the white fins and a short sound pulse, and potentially may function as a mild agonistic display. Pelvic fin 'flickering' in cichlid fishes is not considered to be a socially relevant behavior (Baerends and Baerends-van Roon, 1950; Ostrander and Ward, 1995), thus this needs further investigation in butterflyfish.

The grunt train acoustic behavior was recorded only from bottled fish pairs when territory residents were present or approaching (up to 3 m away), during aggressive attacks, and for a brief time after departure of the resident pair. This vocalization, which unlike all other sounds did not include detectable kinematics, may function as an alert or stress call among monogamous mates. Loud stress sounds were reported for other fishes when they are handled or prodded but biological functions for most of these stress calls need testing (Myrberg, 1981; Smith, 1992). Although our experimental setup could not monitor vocalizations of resident pairs away from the bottle, it is possible that intra-pair grunt trains could be made to alert a free-swimming mate of threats from predators, conspecific intruders or other competitors.

Fishes show a diversity of morphological adaptations for the production of sound stimuli that include direct vibration of the swim bladder, stridulation of bones or teeth, vibration of body parts, and strumming of specialized tendons (Fine et al., 1977;

Myrberg, 1981; Hawkins, 1993; Ladich, 2004). In their survey of sounds of western north Atlantic fishes, Fish and Mowbray (Fish and Mowbray, 1970) used electric shocks to evoke sounds described as small thumps, knocks and toothy clicks from *C. striatus* and *C. ocellatus* isolated in test tanks. That study reported acoustic frequency components of between 100 and 400 Hz and that the swim bladder was the sonic mechanism. However, although sounds may be propagated by resonance of the swim bladder, they must originate from movement of an accessory structure since the swim bladder of *Chaetodon* has no extrinsic or intrinsic muscles (Webb, 1998; Webb et al., 2006). Although we could not resolve the mechanism of sound production, our kinematic analyses demonstrate their association with distinct motor patterns. In the tail slap behavior, gross movement of the body produces a strong pulse of hydrodynamic flow that is followed by an acoustic click. The high frequency broadband characteristics of the click and its association with flexion of the caudal peduncle indicates possible stridulation (Katz, 2002), although we cannot rule out cavitation as occurs in snapping shrimp (Versluis et al., 2000). The sound produced by the pelvic fin flick indicates movement of some internal mechanism linked with structures of the pelvic girdle. Likewise, the sound created during dorsal-anal fin extension was of low frequency and bandwidth, indicating it may not result from stridulation. By contrast, the pulse trains produced during the jump behavior were sometimes associated with slight quivers of the body whereas the grunt train sound had no obvious associated motor patterns. Thus these pulse train sounds are likely generated by movements of internal structures. Further, these latter pulsed sounds showed strong harmonics that indicate movement of internal body parts that vibrate the swim bladder (see Hawkins, 1993).

Acoustico-lateralis stimuli in Chaetodon behavior

Biological sources of sound in water produce two distinct physical stimuli that can stimulate the inner ear and lateral line (reviewed by Kalmijn, 1989). Physical motion at the source–water interface produces an incompressible flow of water commonly of a dipole form. In addition, a sound pressure wave is created that expands outward from the source. The lateral line of teleost fish is sensitive to the velocity and acceleration of water across the surface of the skin (Coombs et al., 1992; Kroese and Schellart, 1992). The fish inner ear is primarily sensitive to the particle velocity fields that accelerate the body and displace the otoliths within it (reviewed by Kalmijn, 1988; Kalmijn, 1989; Schellart and Popper, 1992). In some species secondary particle displacements in the region of the inner ear result from sound pressure-induced pulsations of an adjacent air-filled swim bladder or other gas-filled structures (Denton and Gray, 1993; Yan and Curtsinger, 2000; Fletcher and Crawford, 2001). Such 'otophysic connections' can enhance auditory sensitivity and frequency response of the ear (Coombs and Popper, 1979), may increase the distance over which acoustic stimuli can be detected, but provide no directional information (for a review, see Coombs and

Montgomery, 1999). The genus *Chaetodon* is distinguished by the presence of bilaterally paired diverticulae (horns) of the swim bladder that project in close proximity to the medial surface of the supracleithrum lateral line, and also approach the inner ear (Blum, 1988; Smith et al., 2003) which has well-developed sensory maculae (Popper, 1983). The long swim bladder horns of *Chaetodon multicinctus* (subgenus *Exornator*) project near to the caudal otic capsule and are separated from the supracleithrum lateral line by a layer of muscle (indirect laterophysic connection, Ind2, as per Webb et al., 2006). Therefore, the inner ear of *Chaetodon multicinctus* should be sensitive to hydrodynamic velocity flow fields and sound pressure *via* local displacements of the anterior swim bladder horn, whereas the lateral line is sensitive to hydrodynamic flow across the skin and possibly sound pressure at the level of the laterophysic connection.

Almost all acoustic behaviors recorded in this study were produced within one or two body lengths of the receiver fish and may provide several combinations of multimodal stimuli to the auditory, lateral line and laterophysic systems in addition to strong visual signals. Strong hydrodynamic flow fields produced by body motions of the tail slap (and possibly jump) behavior can displace the receiver's body, stimulate the otolith maculae of the inner ear and provide intensity and directional information about the source. Such low frequency sound may provide important auditory stimuli (Gray and Denton, 1991; Sand and Karlson, 2000) and deserves further consideration in this system. In addition, hydrodynamic flow can differentially stimulate the receiver's ipsilateral lateral line that is known to provide important cues for fish when close to the source. Sounds that have peak frequencies between 100 and 500 Hz (e.g. pelvic fin flick, grunt train, pulse train component of the jump and dorsal-anal fin erection behaviors) may also stimulate the inner ear, which in many species has high sensitivity to particle velocity stimulation in this frequency range (reviewed by Schellart and Popper, 1992). Near field acoustic signals may stimulate both the inner ear and lateral line in a distance-dependent manner to provide directional cues for the source (Coombs and Montgomery, 1999). Such octavolateralis directional information may be important during agonistic interactions among individuals of two or more pairs. In addition, acoustico-lateralis stimuli and communication may be important for butterflyfish reproduction since *C. multicinctus* pairs exhibit body quivers during spawning and a related pomacanthid angelfish produces various sounds ('clicks' and 'grunts') during courtship (Lobel, 1978).

In addition to direct stimulation of the inner ear in *Chaetodon* during social behavior, sound pressure stimuli may induce oscillations of the swim bladder horns (Webb et al., 2006). This transduction of sound pressure to particle motion may produce fluid flow in the supracleithral lateral line or motion of the inner ear. Acoustic pressure stimuli are converted to fluid motion in the lateral line of clupeid fishes by the recessus lateralis in which the anterior lateral line has connections with auditory gas-filled bullae of the inner ear (Blaxter et al., 1981). Sound pressure stimuli from putative acoustic signals in *Chaetodon*

may indeed stimulate motion of the swim bladder horns and adjacent segments of the head lateral line, but the physics of function and any biological importance remain to be demonstrated.

In conclusion, we have shown that a territorial monogamous butterflyfish in its natural habitat reef produces several sounds during visual agonistic interactions with conspecific competitors and mates. This finding is consistent with the hypothesis that sound is important for social communication in *Chaetodon*. Although *Chaetodon multicinctus* produces sounds, the question of whether they provide an adaptive advantage to the sender, receiver or both (*sensu* Myrberg, 1981) now requires experimental confirmation. One possible result of the production of weak sounds by these fish may be the requirement of close associative behaviors for acoustic reception such as pairing and group behaviors that are widespread in *Chaetodon* (Hourigan, 1989; Roberts and Ormond, 1992). Future work is needed to quantitatively characterize the frequency spectra and intensity of sounds produced by *Chaetodon*, determine butterflyfish hearing thresholds and bandwidths, and test whether the laterophysic connection and swim bladder horns enhance hearing capabilities of sounds produced during social interactions. In addition, quantitative measurements of near field particle motion and sound pressures produced by behaviors during their natural interactions are required to determine the relative importance of each stimulus.

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