

FEATURE ARTICLE



Acoustic behaviors in Hawaiian coral reef fish communities

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ABSTRACT: Coral reef fish communities often include hundreds of sympatric species which are of great interest to reef conservation and fisheries managers. Long-term acoustic monitoring of fish sounds can be used to infer periodic reproductive activity and changes in population abundance. However, limited records of sound production by coral reef species have precluded the application of acoustic monitoring at the population or community levels. We used rebreather and digital acoustic/video techniques to produce a sound library for fishes on coral reefs of west Hawai'i Island, HI, USA. We documented 85 sounds produced by 45 (47%) of the 96 resident species that were associated with agonistic interactions and resource defense, reproduction, nest defense, feeding, and vigilance behaviors. Most non-feeding sounds consisted of single or trains of pulse events <100 ms long that were distributed across a spectrum of <100 to 1000 Hz with the majority of peak frequencies between 100 and 300 Hz. Agonistic sounds created during competitive interactions over food, space, or nest brood resources were identified for damselfishes, surgeonfishes, butterflyfishes, and triggerfishes, among others. Reproductive sounds associated with courtship, spawning, or nest defense were produced by damselfishes, goatfishes, butterflyfishes, parrotfishes, and surgeonfishes, as well as wrasses and Moorish idols. The distinct adventitious feeding sounds recorded for some parrotfishes and triggerfishes occurred in a higher frequency band (2–6 kHz) and may be useful indicators of feeding activity and rates of reef bioerosion. This is the first study to characterize the species-specific behavior soundscape that can be applied to acoustic monitoring of a coral reef fish community.

KEY WORDS: Bioacoustics · Rebreather · Reef fish · Sound production · Fish behavior · Coral reef

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Rebreather divers record sounds produced by coral reef fish during resource defense, reproduction, predator avoidance and feeding for acoustic monitoring of population activities.

Images: Timothy C. Tricas and Kelly S. Boyle

INTRODUCTION

Coral reef fish communities include sympatric populations of hundreds of species that are concentrated in small geographic areas (Allen & Werner 2002, Bellwood & Wainwright 2002). Fish acoustic behaviors are a prominent feature of coral reef environments and provide a potential tool for monitoring and management of fish populations. Many fish produce sounds during agonistic interactions with competitors, responses to predators or threats, and during courtship and spawning (reviewed by Fine et al. 1977, Myrberg 1981). Passive acoustic recordings of

such species-specific sounds can provide valuable information on the onset, duration, and periodicity of reproductive activities and changes in abundance of local fish populations (Rountree et al. 2003a,b, 2006, Luczkovich et al. 2008). However, despite the many thousands of fish species known to inhabit coral reefs worldwide, sound production is currently described (or hypothesized to exist) for fewer than 300 species, which represents a great underestimate (Lobel et al. 2010). Furthermore, the majority of coral reef fish sounds are anecdotal, qualitative, and lack information on sound waveforms with few records taken from sympatric populations (e.g. Steinberg et al. 1965, Bright 1972). Thus, much work is needed to adequately characterize sonic species, sound repertoires, acoustic features, and behavioral contexts that contribute to the soundscape of coral reef fish communities.

The application of sound libraries to passive acoustic monitoring of fish communities was previously limited by several factors. In many cases, the bioacoustic capabilities of marine species are only partially characterized, and the identities of sonic species are often inferred, misidentified, or unknown (e.g. Steinberg et al. 1962, McCauley & Cato 2000, Sprague & Luczkovich 2001, Mann & Jarvis 2004, Anderson et al. 2008). For many coral reef species, the behavioral context of specific sounds in wild populations is often unknown or incomplete (Fish & Mowbray 1970, Myrberg & Fuiman 2002, Lobel et al. 2010). One important feature of fish sounds is their low-frequency spectrum (<50 Hz to several kHz) and competing background noise from wind, waves, and other sources in this frequency band (Wenz 1962, Cato 1980). The direct observation of bioacoustic behaviors by scuba divers is limited by the exhalant bubble noise and limited bottom time. This affords a great advantage for the use of rebreather life-support systems that produce no exhalant bubble noise and provide extended bottom time (Bright 1972, Lobel 2005, Radford et al. 2005) and also for recent digital video/audio recording equipment and analysis software. These technological enhancements now facilitate the creation of species-specific and context-specific acoustic libraries for coral reef fish communities.

More than 600 species of marine fishes inhabit the inshore and reef areas of Hawai'i, HI, USA (Randall 2007), but details of sound production (waveforms, intensity, frequency spectra) are reported for only a few species: 2 soldierfish *Myripristis* spp. (Salmon 1967); 2 bigeyes *Priacanthus* spp. (Salmon & Winn 1966); 3 damselfishes (Lobel & Mann 1995, Mann &

Lobel 1998, Lobel & Kerr 1999, Maruska et al. 2007), 1 trunkfish (Lobel 1996), 2 wrasses (Boyle & Cox 2009), 3 butterflyfishes (Tricas et al. 2006, Boyle & Tricas 2010, 2011), and 1 triggerfish (Salmon et al. 1968). The purpose of this study was to develop an acoustic library of the acoustic behavior of fish species on shallow Hawaiian coral reefs for future use in the interpretation of long-term passive acoustic monitoring data. We used closed-circuit rebreathers to closely approach visually identified species and record sound production in synchrony with their natural behavior. Results show that approximately half of the observed species produce sound in biologically relevant contexts that may be used for identification of social interactions, reproduction, and activity patterns of species in Hawaiian coral reef fish communities.

MATERIALS AND METHODS

Study locations

Acoustic behaviors of fish were recorded at Puako Reef on the island of Hawai'i (19.93° N, 155.86° W) during the spring and summer of 2008 and 2009. This fish management area is characterized by large fields of hard corals that slope to a reef edge at about 15 m and extend steeply to a sand interface at about 30 m. Many species engage in feeding and social interactions in the water column, near the reef surface, on sand patches, and in caves. Large aggregations of fishes were observed in periodic broadcast spawning activities along the reef edge and deeper slope areas. We also obtained some fish sounds at Papawai Bay in Kona, Hawai'i (19.64° N, 156.02° W), and the outer reefs of Kaneohe Bay and Honolulu on the island of Oahu.

Dives and data recording

Divers used Evolution (Ambient Pressure Diving) closed-circuit rebreathers that do not release exhaust bubbles that interfere with acoustic recordings, extend bottom time up to 3 h, and allow very close approach to fish. Most dives were conducted at 8 to 40 m depth with 1 decompression excursion to rocky outcroppings at 80 m. Acoustic behaviors were recorded with digital video cameras (Sony TRV-950 and Canon Optura) in Amphibico underwater housings equipped with an external hydrophone (HTI min96 High-Tech) that recorded coincident

sounds on 1 audio channel (48 kHz sample rate, 20–24 000 Hz audio band pass). Dives were conducted between 09:00 and 19:30 h and were often scheduled to observe spawning behaviors in the afternoon, dusk, or on outgoing tides. We evoked aggressive sounds from the normally shy coral-feeding blue-eye damselfish *Plectroglyphidodon johnstonianus* by placement of a coral-feeding multiband butterflyfish *Chaetodon multicinctus* within a glass bottle near the territory. The animal use protocol was approved by the University of Hawai'i Institutional Animal Care and Use Committee.

Video and acoustic analyses

Digital video recordings were imported to a computer in the lab with Windows Movie Maker and saved as an uncompressed AVI file. The entire video and audio recordings were then pre-screened individually by at least 2 reviewers, who logged the times of acoustic events and behavioral context for identified species into a spreadsheet. Discrepancies among these observations of sound production were reviewed and discussed by 2 or more individuals and either collectively accepted as a fish sound or discarded. In cases where fish sounds were not associated with overt body motions, multiple sound events were required to classify a species as acoustically active. Audio was extracted from the video with Cool Edit Pro 2.0 or Adobe Audition and saved in an uncompressed WAV format. When present, camera hum noise was notch filtered at 149.8 Hz at ~100 dB attenuation. The associated sound waveform was visually inspected, the duration above background noise measured, and the sound waveform saved. Spectrograms showed that the acoustic energy for most sounds was <2 kHz; thus, sounds were low pass filtered in the 'high quality' setting and down-sampled to 4 kHz. Feeding and social sounds that showed higher spectra were analyzed at the original 48 kHz sampling rate.

Many sounds were emitted as a single continuous waveform (e.g. pulse, growl, blended pulse series that occurred without separation by non-acoustic intervals), whereas others consisted of a series of non-continuous acoustic events (e.g. pulse train, discrete blended pulse events separated by brief non-acoustic intervals). In order to characterize the temporal features of interrupted sounds, we defined a sound type as either (1) a single independent sound event that is separated from subsequent sound events by inter-pulse intervals ≥ 0.5 s, or (2) a sound

event train that consisted of a series of sound events (such as single pulses in series or growls with short silent intervals between portions of the overall sound) separated by inter-event intervals <0.5 s. For sound event trains (most commonly pulse trains), the total number of separate wave events (events or pulses train⁻¹) was first enumerated. The onset and offset times of the first 4 events (or the entire train if ≤ 4 wave events) were then measured for calculation of (1) mean event duration, (2) event train segment duration (for entire trains with 2 to 4 events or the first 4 events in longer trains), (3) event rate s⁻¹, and (4) mean inter-event interval.

Previously unreported sounds were first assigned a descriptive name type based primarily on its acoustic features (e.g. pulse, high-frequency pulse, blended pulse, half-pulse) in order to avoid onomatopoeias and anthropomorphic interpretations that have added to the great non-uniformity of sound nomenclature in the literature as reviewed by Lobel et al. (2010). We secondarily assigned a behavioral descriptor to some sounds that were produced in clear behavioral contexts (e.g. spawning pulse, courtship pulse) especially when there was overlap in acoustic features of sounds within a species (e.g. courtship and spawning pulses in yellow tang *Zebrasoma flavescens*). The high-frequency broadband sounds produced during feeding by some parrotfishes and triggerfishes were always associated with a scraping behavior of the jaws on the food substrate and were named based purely on the associated 'scrape' behavior. We also assigned sound names in accordance with previously reported sounds for Hawaiian species when possible, and to new and presumed homologous sounds produced by related species (e.g. several pomacentrids and holocentrids).

Relative intensity (the intensity of a sound event relative to background noise), power spectra (the relative power of different frequencies within a single sound event), and spectrograms (the temporal distribution of frequency spectra across the duration of a sound event) were calculated from sound waveforms with custom Matlab 7.0 scripts. Sound power spectra were determined from 1024-point fast Fourier transforms with a Hanning window of 0-padded sounds. Peak frequency (frequency with the highest intensity) and the minimum, maximum, median, and quartiles of all frequencies ≤ 10 and ≤ 6 dB intensity of the peak frequency were determined from power spectra data.

Mean and standard error were determined for each acoustic character from averages of each individual (if more than a single sound was recorded from a single fish) and then averaged for individuals of a spe-

cies. In some cases, sounds were recorded among a group of individuals in small shoals/schools for which it was not possible to determine the vocalizing individual. In such cases, we treated 1 sound recorded from each encountered group as an independent observation to avoid pseudoreplication. Statistical comparisons were made for the acoustic features of sounds produced among some species and behavior categories. Parametric samples were tested for differences with 2-sample *t*-tests. In many cases, sound duration, peak frequency, or bandwidth samples did not meet the assumptions of normality or homoscedasticity and thus were tested for differences with the non-parametric Mann-Whitney test. We describe the relationship between sound event duration and peak frequency among the observed acoustic species in 13 families with an inverse polynomial regression model. Statistical tests were performed using SigmaPlot v.11.0 and 12.5.

RESULTS

Rebreather divers logged approximately 180 h during daylight and dusk hours and identified 96 teleost species (24 families) in the study area at the Puako and Papawai Hawai'i reef sites (see Table S1 in the Supplement; www.int-res.com/articles/suppl/m511/p001_supp.pdf). Analysis of 22 h of video/audio recordings showed that 45 species (47%) in 12 families (50%) produced 85 sound types (Table S2 in the Supplement) in several behavioral contexts (Fig. 1). Below we report the characteristics of sounds colated in behavioral categories by family.

Agonistic behaviors—aggression and defense

Nearly half (39 = 45%) of the documented acoustic behaviors were recorded from 24 species during agonistic (aggressive–submissive) interactions that involved the defense of feeding resources or nest sites, chases and retreats during other social interactions, or interactions with potential predators (Fig. 1, Table S2).

Groupers (Serranidae). The peacock grouper *Cephalopholis argus*, which occurred at depths of approximately 5 to 25 m, produced loud, low peak frequency (104 Hz) pulse sounds and trains during agonistic interactions with conspecifics (Fig. 2A).

Butterflyfishes (Chaetodontidae). Pulsed agonistic sounds were recorded for 5 of 6 acoustic butterflyfishes. The coral-feeding multiband butterflyfish

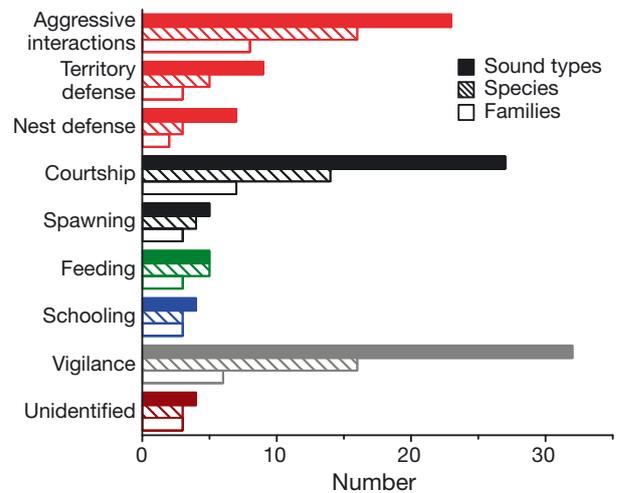


Fig. 1. Behavioral contexts of 85 sound types recorded from 45 species of Hawaiian coral reef fishes. Data are shown for the total number of sounds produced by all species (solid bars), number of species that produced sound associated with a behavior category (hatched bars), and number of fish families the produced sound associated with a behavior category (open bars). Fish sound categories are agonistic behaviors separated into aggressive interactions among individuals and defense of territories or nests (red bars), reproductive interactions separated into courtship and spawning behaviors (black), feeding (green), schooling (blue), vigilance (gray), and unidentified behavioral contexts (burgundy). Several sound types were produced in multiple behavior categories

Chaetodon multicinctus and the ornate butterflyfish *C. ornatissimus* produced brief pulse sounds 36 to 56 ms in duration with average peak frequency between 184 and 346 Hz during agonistic encounters with conspecifics and reproductive activities (described below) (Table S2, Fig. 2B). A unique pulse sound of very brief duration (7 ms) and the highest high peak frequency (3609 Hz) recorded in this study was produced by the blacklip butterflyfish *C. kleinii* during interactions with conspecifics. We also recorded pulse sounds during conspecific agonistic interactions in the pyramid butterflyfish *Hemitaurichthys polylepis*, but these aggressive sounds were more frequently associated with disturbance and reproductive behaviors (described below).

Damselishes (Pomacentridae). Five damselfish species produced sounds associated with agonistic interactions among conspecifics or during defense of egg nests (Table S2). Three sound types were produced by males of both the Hawaiian sergeant *Abudefduf abdominalis* and the Indo-Pacific sergeant *A. vaigiensis* that establish breeding (sometimes heterospecific) colonies. Two sounds produced during agonistic encounters with conspecific and heterospecific individuals were the aggressive short

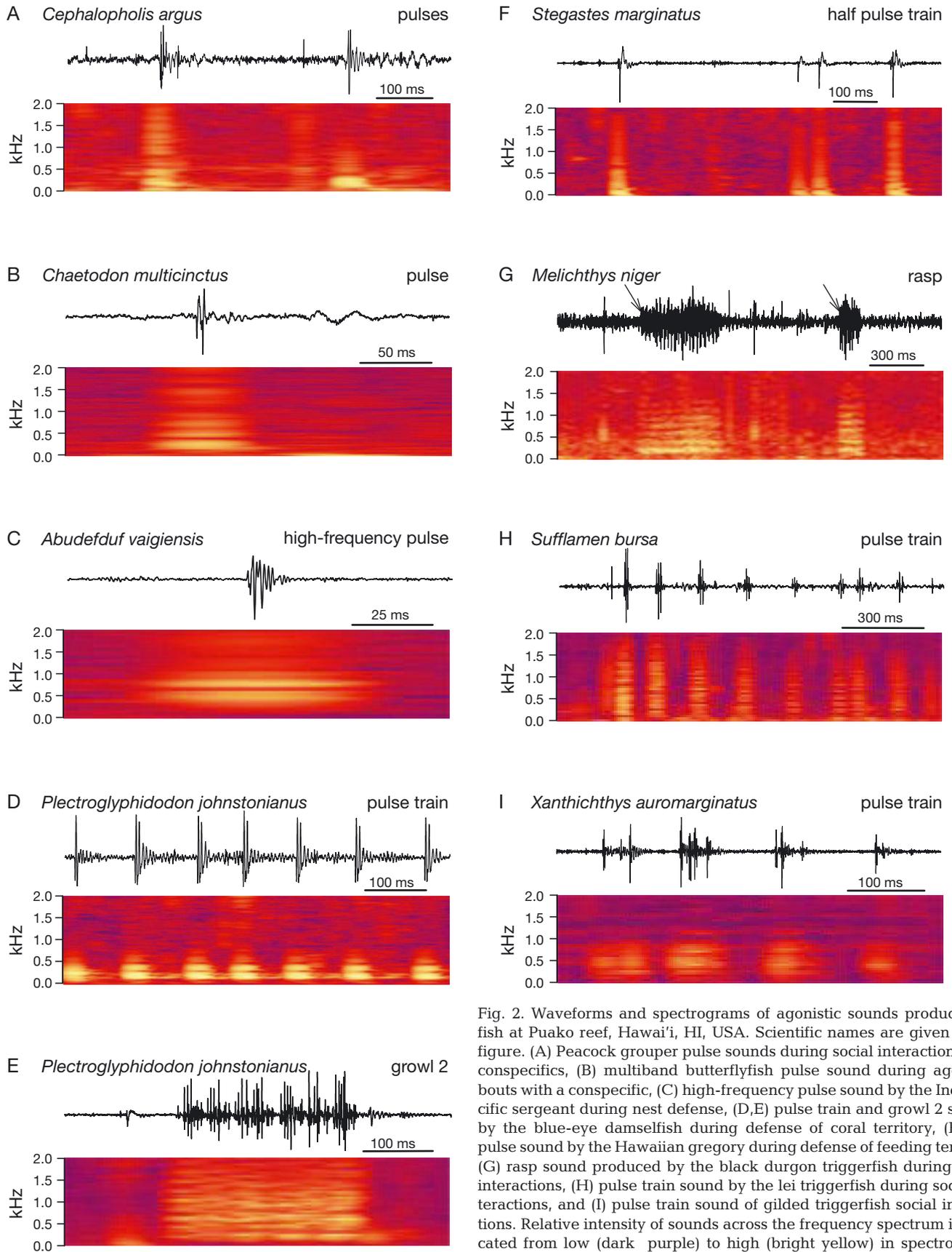


Fig. 2. Waveforms and spectrograms of agonistic sounds produced by fish at Puako reef, Hawai'i, HI, USA. Scientific names are given in the figure. (A) Peacock grouper pulse sounds during social interactions with conspecifics, (B) multiband butterflyfish pulse sound during agonistic bouts with a conspecific, (C) high-frequency pulse sound by the Indo-Pacific sergeant during nest defense, (D,E) pulse train and growl 2 sounds by the blue-eye damselfish during defense of coral territory, (F) half pulse sound by the Hawaiian gregory during defense of feeding territory, (G) rasp sound produced by the black durgon triggerfish during social interactions, (H) pulse train sound by the lei triggerfish during social interactions, and (I) pulse train sound of gilded triggerfish social interactions. Relative intensity of sounds across the frequency spectrum is indicated from low (dark purple) to high (bright yellow) in spectrograms

pulse (Agg12) identified by 1 to 2 pulses per sound and longer pulse trains (Agg>2) identified by >2 pulses as reported by Maruska et al. (2007). A new agonistic high-frequency pulse sound (Fig. 2C) was of much shorter duration (18–23 ms) and higher peak frequency (805–1162 Hz) but was not produced in pulse trains.

The most prolific production of agonistic sounds was observed in the territorial blue-eye damselfish *Plectroglyphidodon johnstonianus*. These coral-feeders produced single pulse and train sounds directed towards neighboring conspecifics and when experimentally evoked by introduction of a bottled coral-feeding multiband butterflyfish *C. multicinctus* near their territory (Table S2). The single pulse sound was of short duration (33 ms) with a peak frequency of 284 Hz and is similar in characteristics with the pulses produced in a pulse train (Fig. 2D). We also recorded 2 growl sound types, which occurred as a series of contiguous pulses of much longer event duration (125–403 ms) and higher peak frequency (125–403 Hz) than the half pulse sound. The growl 1 sound had a rapid regular pulse-emission rate and pulse amplitude, whereas the growl 2 sound (Fig. 2E) had more variable pulse emission rates and pulse amplitudes. A half pulse sound waveform was identified by a distinctive single, strong, and rapid negative peak followed by a slower positive half cycle. Half pulses were of similar short duration (40 ms) to single pulses but were lower in peak frequency (49 Hz; $p = 0.024$, t -test, $t = -3.0$, $df = 6$). Very similar pulse and half pulse sounds (Fig. 2F) were recorded for the Hawaiian gregory *Stegastes marginatus* that defends algal turf feeding and breeding territories (Table S2). Pulse train sounds were recorded for threespot chromis *Chromis verater* during agonistic interactions with a conspecific and the 'aggressive' sound (Mann & Lobel 1998) produced during agonistic chases by the Hawaiian dascyllus *Dascyllus albisella* (Table S2).

Wrasses and parrotfishes (Labridae). Pulsed sounds and trains were recorded during agonistic chases with conspecifics for the male bird wrasse *Gomphosus varius* and the male bullethead parrotfish *Chlorurus spilurus* (Table S2) and are described below in the section on reproductive behaviors.

Surgeonfishes (Acanthuridae) and Moorish idol (Zanclidae). The Moorish idol *Zanclus cornutus* produced sounds during aggressive interactions and during apparent courtship behaviors (Table S2). These included both single pulsed sounds and trains that ranged from 30 to 102 ms in duration and peak frequencies from 176 to 520 Hz. Brief pulsed sounds

of average peak frequency from 200 to 556 Hz were recorded during agonistic (and courtship) behaviors primarily directed toward conspecifics for the orange-band surgeonfish *Acanthurus olivaceus*, the Hawaiian bristletooth *Ctenochaetus hawaiiensis*, the gold-ring bristletooth surgeonfish *C. strigosus*, and the yellow tang *Zebrasoma flavescens* (Table S2). A long pulse sound that was of longer duration (120 ms) than the single pulse (30 ms) was recorded for a single *C. hawaiiensis*.

Triggerfishes (Balistidae). Agonistic acoustic behaviors during social interactions were recorded for 3 triggerfishes (Table S2). The loud thump-like pulse sound produced during agonistic chases among black triggerfish *Melichthys niger* was of relatively short duration (68 ms) and low peak frequency (86 Hz). In contrast, the rasp-like pulse sound was of longer duration (319 ms) and higher peak frequency (313 Hz; Fig. 2G). The lei triggerfish *Sufflamen bursa* readily produced pulsed sounds when engaged in agonistic chases, territory defense, and nest-guarding behaviors (by females) and occurred as single pulses or pulse trains ($9.8 + 2.8$ SE pulses train⁻¹; Fig. 2H) with a peak frequency of 583 Hz. The planktivorous and territorial gilded triggerfish *Xanthichthys auromarginatus* produced pulses of relatively short duration (58 ms) and 287 Hz peak frequency primarily in trains during chases with conspecifics (Fig. 2I).

Reproductive behaviors—courtship and spawning

A total of 32 reproduction-related sounds were recorded for a total of 18 species across the butterflyfish, damselfish, parrotfish, and surgeonfish families, as well as wrasses and Moorish idol. The majority were associated with courtship behaviors and spawning (Fig. 1).

Butterflyfishes. The planktivorous pyramid butterflyfish *H. polylepis* was not acoustically active during daytime feeding in the water column. However, late in the afternoon on some days, males established courtship territories on the bottom (>15 m deep) that they defended from other males and that were visited by pre-spawn females (identified by their swollen abdomen filled with hydrated eggs). During these interactions, males produced loud single and train pulse sounds as recently reported (Boyle & Tricas 2011). Further analyses showed that these sounds (peak frequency = 144–147 Hz) are produced as either discrete pulses (84 ms duration) or blended pulses that have no interpulse separation (186 ms duration; Table S2). We recorded a pulse sound dur-

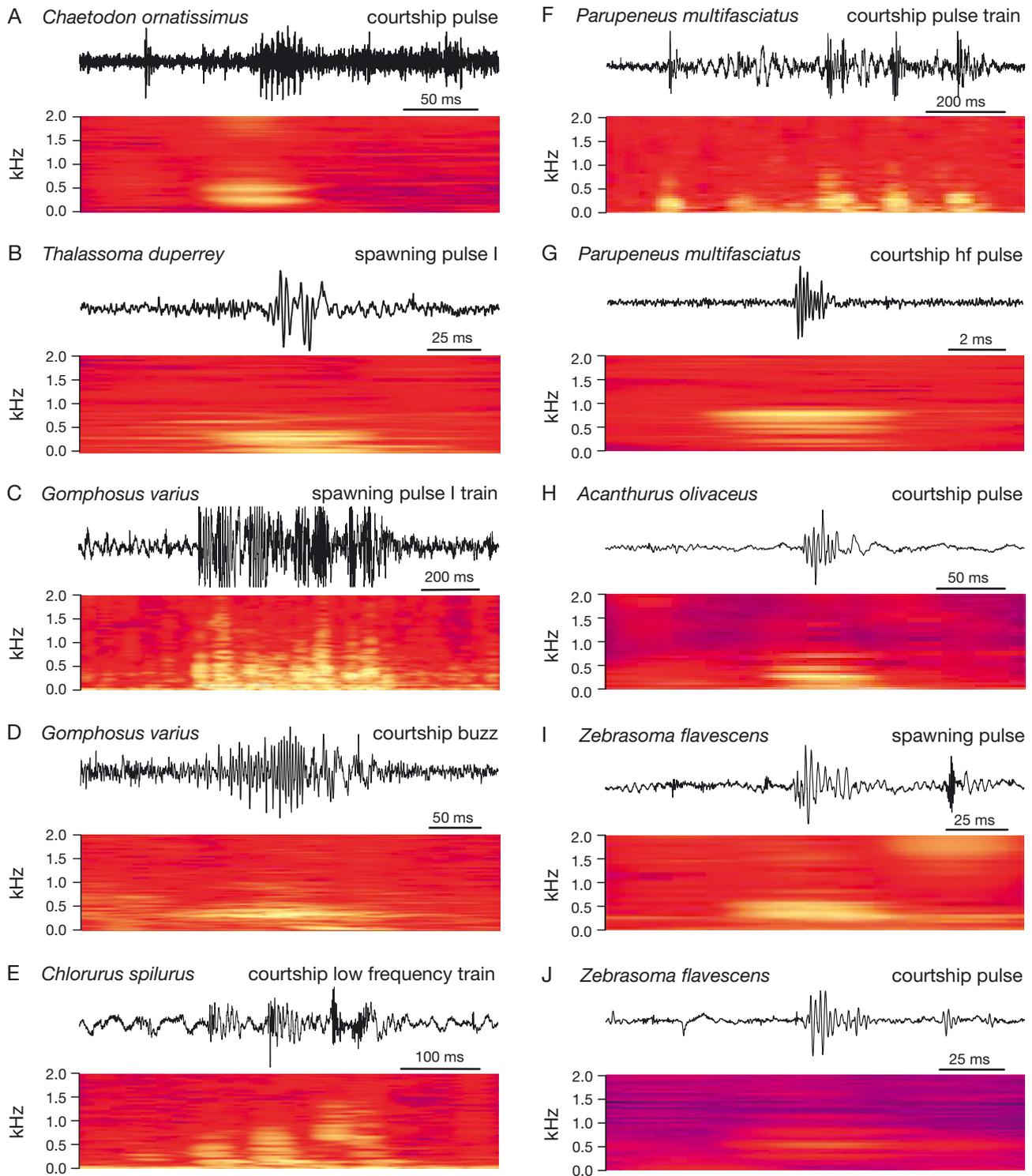


Fig. 3. Waveforms and spectrograms of reproductive sounds produced by fish at Puako reef, Hawai'i, HI, USA. Scientific names are given in the figure. (A) Courtship pulses by the ornate butterflyfish, (B) pulse I sound during spawning by the saddle wrasse, (C) spawning pulse I train during spawning by the bird wrasse, (D) courtship buzz sound by a male bird wrasse, (E) low-frequency pulse train by the bullethead parrotfish during courtship with females, (F,G) pulse train (peak frequency ~140 Hz) and brief high-frequency (hf) pulse (peak frequency ~830 Hz) by male manybar goatfish during courtship, (H) short pulse by olive surgeonfish during courtship, (I) pulse sound produced by yellow tang during a spawning rush, (J) pulse sound produced during courtship by a pair of yellow tangs. Relative intensity of sounds across the frequency spectrum is indicated from low (dark purple) to high (bright yellow) in spectrograms

ing courtship by a pair of ornate butterflyfish *C. ornatissimus* (Fig. 3A) which was similar to their agonistic sound (described above).

Damselfishes. Three previously reported sounds (Lobel & Mann 1995, Mann & Lobel 1998) were recorded for the Hawaiian dascyllus *D. albisella*. The 'signal jump' was produced by courting males and the mate/visit sound during visits and spawning by females at the coral nest site. The aggressive pulse was indistinguishable from the signal jump, so these 2 sounds were pooled in our analysis (Table S2).

Wrasses and parrotfishes. Several single pulse and train event sounds were recorded during reproductive behaviors of the bird wrasse *G. varius* and the saddle wrasse *Thalassoma duperrey* (Table S2). Single pulse I sounds (Fig. 3B) were produced by both species during courtship and spawning behaviors and discriminated by their relatively long duration (57–85 ms) compared to the shorter pulse II sound (11–28 ms) that was recorded only during courtship (per Boyle & Cox 2009). Both pulse types were also produced in trains (Fig. 3C) that were of similar peak frequency and pulse duration as single pulses (Table S2). One courting *G. varius* male produced a unique buzz sound that lasted for 141 ms and had a peak frequency of 371 Hz (Fig. 3D), but this acoustic behavior was very rare. Our recordings of male *T. duperrey* in courtship also identified a new blended pulse I sound that lacked clear interpulse intervals.

Large terminal-phase male bullethead parrotfish *C. spilurus* establish feeding territories with female harems along the reef slope at ≥ 20 m depth. Males produced distinct sounds associated with both aggressive chases of other males and during reproductive behaviors with females (Table S2). Loud, single low-frequency pulses were of relatively long duration (252 ms) compared to those produced in trains (45 ms; Fig. 3E) but were of similar peak frequency (111 vs. 137 Hz, respectively). Similar sounds were recorded during spawning events high in the water column, but we were unable to analyze spawning sounds due to poor signal to noise ratios.

Goatfishes. Recurrent sounds associated with reproductive activities were identified for the island goatfish *Parupeneus insularis* and manybar goatfish *P. multifasciatus* (Table S2) primarily near peak and outgoing tides. Males of both species produced low-frequency single pulse and train sounds during courtship chases of females (Fig. 3F). Single and train sound events within these 2 species were similar in duration ($p = 0.38$, Mann-Whitney U -test, $U = 5.0$, $n = 3$ and 6 , respectively, for *P. insularis*; $p = 0.62$, t -test, $t = -0.53$, $df = 6$ for *P. multifasciatus*) and peak fre-

quency ($p = 0.71$, Mann-Whitney $U = 7.0$, $n = 3$ and 6 , respectively, for *P. insularis*; $p = 0.88$, $t = 0.156$, $df = 6$ for *P. multifasciatus*). Male *P. multifasciatus* also produced a courtship high-frequency single pulse sound (Fig. 3G) which was of very short average duration (18 ms) and of higher peak frequency (833 Hz) than the other pulsed sounds (139 Hz) recorded for this species ($p < 0.001$, $t = 8.80$, $df = 8$).

Surgeonfishes and Moorish idol. Similar but infrequent courtship and agonistic sounds were recorded from the Moorish idol *Z. cornutus* and several acanthurids (described above, Table S2): the orangeband surgeonfish *A. olivaceus* (Fig. 3H), the Hawaiian bristletooth *C. hawaiiensis*, the goldring bristletooth *C. strigosus*, and the yellow tang *Z. flavescens* (Table S2). In contrast, high numbers of sounds were recorded during the pronounced reproductive activity of *Z. flavescens* at the Puako study site where hundreds or thousands of fish formed widespread aggregations above the deep reef slope (Table S2). Individual females with hydrated eggs were approached and courted by males, and then spawned in a rapid upward spawning rush often with several males. We identified short pulse sounds associated with spawning (Fig. 3I) and courtship (Fig. 3J) behaviors which were of similar duration (40–42 ms) and peak frequency (274–349 Hz; Table S2), but we were not able to confirm whether sounds were made by males, females, or both sexes. We also observed a longer and more variable 'collision' pulse sound that occurred during fast movements of fish in small groups as they engaged in agonistic and spawning interactions (Table S2), and assume that this sound was caused by the physical impact of the bodies of individual fish. Large populations of the lavender tang *A. nigrofuscus* formed similar spawning assemblages during the study, but no reproductive sounds were identified for this species.

Feeding behaviors

Parrotfishes. Broadband sounds that resulted from the scraping of teeth on hard benthic substrate during feeding were recorded for adult bullethead parrotfish *C. spilurus*, palenose parrotfish *Scarus psittacus*, and ember parrotfish *S. rubroviolaceus* (Table S2, Fig. 4A–C). Average duration of feeding sound scrapes for these species ranged from 87 to 181 ms, and were of relatively high peak frequency (1277–3387 Hz) and broad bandwidth. Note that a single bite usually produced interrupted sound waveforms presumably caused by motion of the teeth over small

Fig. 4. Waveforms and spectrograms of feeding sounds produced by the bite action of oral jaws and teeth upon hard food substrates by benthic feeding fish on Hawaiian coral reefs. Scientific names are given in the figure. (A) Feeding bite sound by the bullethead parrotfish, (B) feeding bite sound by the redlip parrotfish, (C) feeding bite sound by the palenose parrotfish. Note high peak frequency and bandwidths produced as parrotfish scrape algae and diatoms from dead coral rock. (D) Feeding bite sound by the black durgon triggerfish that feeds on benthic invertebrates, (E) feeding bite sound by the barred filefish that feeds on live hard coral. Relative intensity of sounds across the frequency spectrum is indicated from low (dark purple) to high (bright yellow) in spectrograms. Start of bite waveforms is indicated by arrows

irregularities in the substrate. These feeding sounds showed the highest frequency spectrum (max. bandwidth quartile range = 6157–8860 Hz, Table S2) of all sounds recorded in this study.

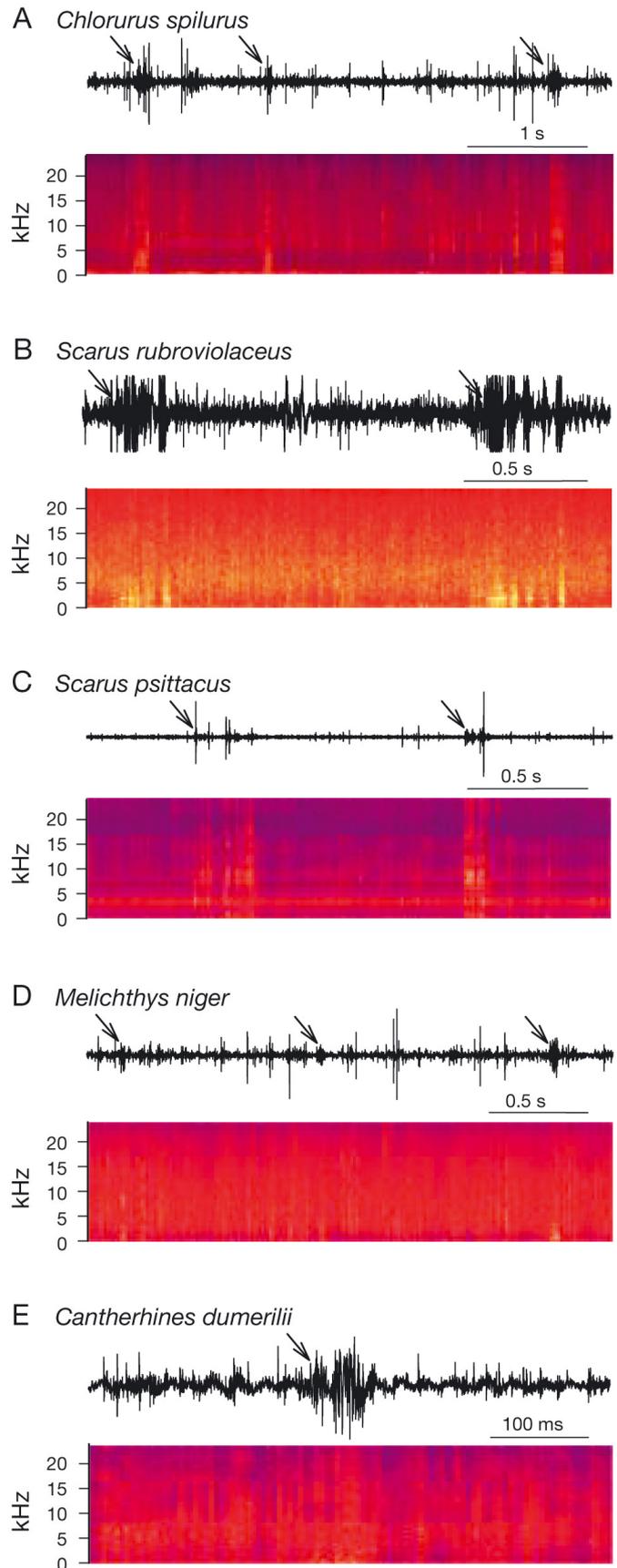
Triggerfishes and filefishes. Sounds were produced during benthic feeding by filefish and triggerfish. The black triggerfish *M. niger* produced a scrape sound when feeding on hard benthic substrates (Fig. 4D) that was of relative short duration (63 ms) but of high peak frequency (3973 Hz) similar to parrotfish feeding. The barred filefish *Cantherhines dumerilii* also produced an audible scrape sound (Fig. 4E) when feeding on live coral *Pocillopora* spp. but was of very low peak frequency (35 Hz).

Schooling

We recorded pulse sounds produced by species in schools or aggregations near the reef. The bicolor anthias *Pseudanthias bicolor* and bluestripe snapper *Lutjanus kasmira* formed schools at depths >20 m that produced infrequent short pulse sounds (Table S2). Single pulse and train sounds were produced by white saddle goatfish *Parupeneus porphyreus* that foraged in groups of <5 individuals and larger non-feeding schools over the reef. Large schools of yellowfin goatfish *Mulloidichthys vanicolensis* and the yellowstripe goatfish *M. flavolineatus* were frequently encountered on the reef, but only 1 poor-quality pulse sound was recorded for the latter species.

Vigilance behavior—responses to divers or predators

Several species produced sounds in response to the approach of a diver or a potential fish predator. In these cases, we categorized the diver's presence as a disturbance stimulus and the response of the fish as vigilance (alert) behavior.



Squirrelfishes and soldierfishes. Numerous holocentrid species were observed on the open reef or within/near reef crevices during daylight hours and produced a wide range of vigilance sounds (Table S2), many of which were reported previously (e.g. Winn et al. 1964, Salmon 1967, Horch & Salmon 1973). Large groups of ~3 to 20 epaulette soldierfish *Myripristis kuntee* formed stationary and relatively inactive aggregations over the coral reef bottom and produced sounds when approached by divers or large predatory fish (e.g. carangids). Knock pulses (Fig. 5A) were usually first produced by the fish nearest to the diver (identified by the coincident erection of the dorsal fin or turning behavior) followed by more knock sounds from other individuals as they moved towards shelter. The grunt (Fig. 5B) and staccato sounds were produced more intermittently. Similar acoustic vigilance responses were observed for the soldierfish *M. berndti* and *M. amaena*, which inhabit caves or reef shelters during the day. The more solitary Sannara *Neoniphon sammara* and goldlined *N. aurolineatus* squirrelfish produced loud pulsed growls, grunts, knocks or staccato sounds. Growl sounds consisted of a rapid series of contiguous pulses that decreased in rate over time. On several occasions, additional sounds were recorded after alert and vocalizing *N. sammara* or *Myripristis* entered the reef with other holocentrids, but the source of those sounds could not be confirmed.

We recorded several new vigilance sounds from blue-lined squirrelfish *Sargocentron tiera* found under exposed ledges or within small spaces of the reef (Table S2, Fig. 5C–E). The growl sound was of relatively long duration (395 ms) and had a mean peak frequency of 202 Hz. The grunt occurred as a single pulse with a shorter mean duration (74 ms) but similar peak frequency (191 Hz). The knock sound was produced as a train of pulses with a peak frequency of 387 Hz. We also observed sounds from the larger congener, the saber squirrelfish *S. spiniferum*, but poor recording quality precluded analysis.

All growl, grunt, knock, and staccato sounds were recorded from *M. berndti*, but all remaining holocentrids produced at least 3 sound types (Table S2). The growl was produced by at least 1 species of all 4 genera and consisted of 1 to 9 events with a relatively long duration (80–591 ms). Although there are indications of possible pulse duration and frequency differences among sound types (e.g. knock: 7–28 ms, 387–926 Hz vs. other sound types), our low sample sizes precluded statistical comparisons among sounds and species.

Angelfishes and butterflyfishes. Vigilance sounds were recorded for 2 of 3 angelfish species (Table S2).

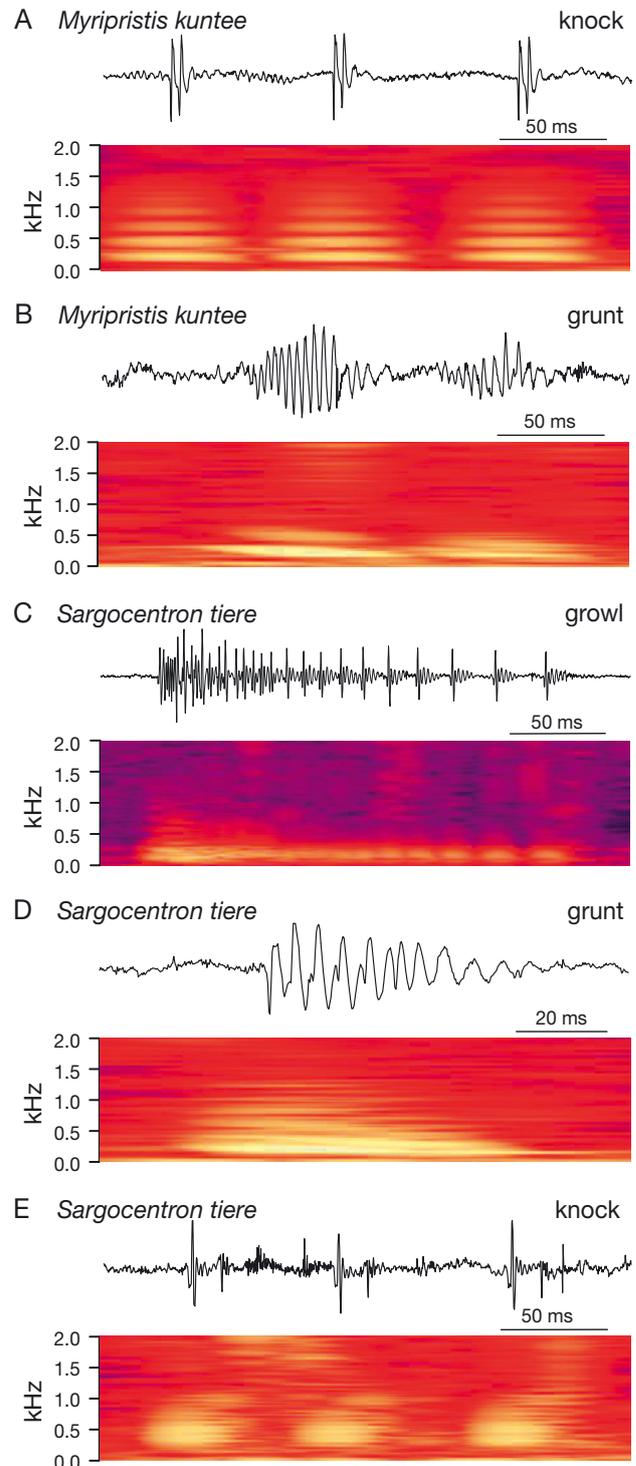


Fig. 5. Waveforms and spectrograms of sounds associated with vigilance that are produced by fish on Hawaiian coral reefs after approach by divers or predators. Scientific names are given in the figure. (A,B) Grunt and knock sounds by epaulette soldierfish that rest unsheltered near the coral substrate during daylight hours; (C–E) growl, grunt, and knock sounds by blue-lined squirrelfish within shelter of the reef. Relative intensity of sounds across the frequency spectrum is indicated from low (dark purple) to high (bright yellow) in spectrograms

The flame angel *Centropyge loriculus* and bandit angelfish *Apolemichthys arcuatus* produced similar short pulse sounds when approached by divers, but these were rare. Short pulse sounds were produced by the multiband butterflyfish *C. multicinctus* (indistinguishable from the agonistic sound), the pyramid butterflyfish *H. polylepis* (similar to the courtship sound), and Thompson's butterflyfish *H. thompsoni*. Overall, there was a narrow peak frequency range for single pulse, pulse train, and blended pulse sounds (144–170 Hz) produced by both species of *Hemitaurichthys*. A pulse disturbance sound was recorded from the forcepsfish *Forcipiger flavissimus*, which showed the highest recorded peak frequency (840 Hz) of any butterflyfish vigilance sound.

Damselfishes. Three species of planktivorous damselfish produced pulsed sounds when approached by divers near the reef substrate (Table S2). Single pulses of similar duration (154–186 ms) and low peak frequency (27–35 Hz) were recorded for the oval chromis *C. ovalis*, and threespot chromis *C. verater*. A high frequency vigilance pulse produced by the chocolate-dip chromis *C. hanui* was also of short duration (22 ms) but higher peak frequency (1012 Hz).

Triggerfishes. Pulse train sounds were recorded for the lei triggerfish *S. bursa* (previously described in agonistic behaviors) and a single pulse sound for the gilded triggerfish *X. auromarginatus* when some fish were approached by divers.

General characteristics of reef fish sounds

Single event sounds were recorded for at least 1 species in 12 fish families and were of short duration (range = 7–385 ms, median = 59 ms, $n = 39$). In comparison, the mean number of events in trains ranged from 1.15 to 10.5 among species, and their duration (median = 52 ms, $n = 45$) did not differ from single pulse events (total range = 7–591 ms, $p = 0.94$, Mann-Whitney $U = 868$). The 85 sound types covered a broad spectrum of peak frequencies from 27 to 3609 Hz with a mean of 475 ± 75 SE Hz (Table S2, Fig. 6). However, peak frequencies were not normally distributed (Kolmogorov-Smirnov test, $p < 0.001$) and were biased towards a low-frequency range with a mode of 100 to 300 Hz and median of 285 Hz.

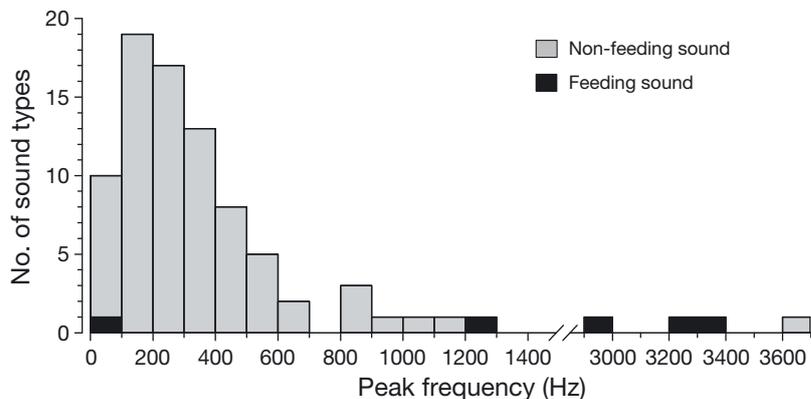


Fig. 6. Peak frequency of sound types recorded for 45 species of reef fishes on Hawaiian coral reefs. Sounds were produced during non-feeding behaviors (gray bars) and scraping of reef substrate during feeding by parrotfish, black durgon triggerfish, and barred filefish (black bars). Note that the peak of the frequency distribution for most non-feeding sounds is ≤ 1200 Hz with a peak between 100 and 300 Hz. Sounds produced during feeding by parrotfish and black durgon are of higher peak frequency

A bivariate plot of pulse duration and peak frequency for non-feeding sounds shows a non-linear and inverse relationship with great overlap among fish families (Fig. 7). Sounds with peak frequency > 500 Hz were generally of short duration (< 50 ms) and were produced by several damselfishes, squirrelfishes, butterflyfishes, and goatfishes, with the exception of 2 labrid sounds of longer duration (L symbols in Fig. 7). In comparison, several low-frequency sounds could be distinguished by their relatively long pulse duration (> 100 ms); these were made by several species that include squirrelfish, damselfish, surgeonfish, and triggerfish.

There was great overlap in sound frequency spectra among species and behavioral contexts (Fig. 8). Low-frequency sounds < 100 Hz were recorded for several unrelated species that include *Sargocentron spiniferum* soldierfish (alert call), bluestripe snapper *L. kasmira* (shoaling), peacock grouper *C. argus* (aggression), Hawaiian bristletooth acanthurid *Ctenochaetus hawaiiensis* (courtship aggression), and the barred filefish *C. dumerilii* (feeding on live coral). The feeding sounds of parrotfishes were of higher peak frequency than social sounds of all reef fishes (range = < 47 –8156 vs. 18–3609 Hz, median = 2953 vs. 245 Hz, $n = 29$ and 164, $p < 0.001$, Mann-Whitney $U = 928$). Parrotfish feeding sounds occupied a wider portion of the 0–24 kHz frequency band than did social sounds of reef fishes as shown in Fig. 8: -6 dB bandwidth (range = 0.46–7.42 vs. 0.05–7.62%, median = 3.0 vs. 1.0%, $n = 29$ and 164, $p < 0.001$, Mann-Whitney $U = 518$) and Table S2: -10 dB bandwidth (range = 1.57–16.67 vs. 0.11–12.31%, median = 7.0 vs. 1.0%, $n = 29$ and 164, $p < 0.001$, Mann-Whitney $U = 141$).

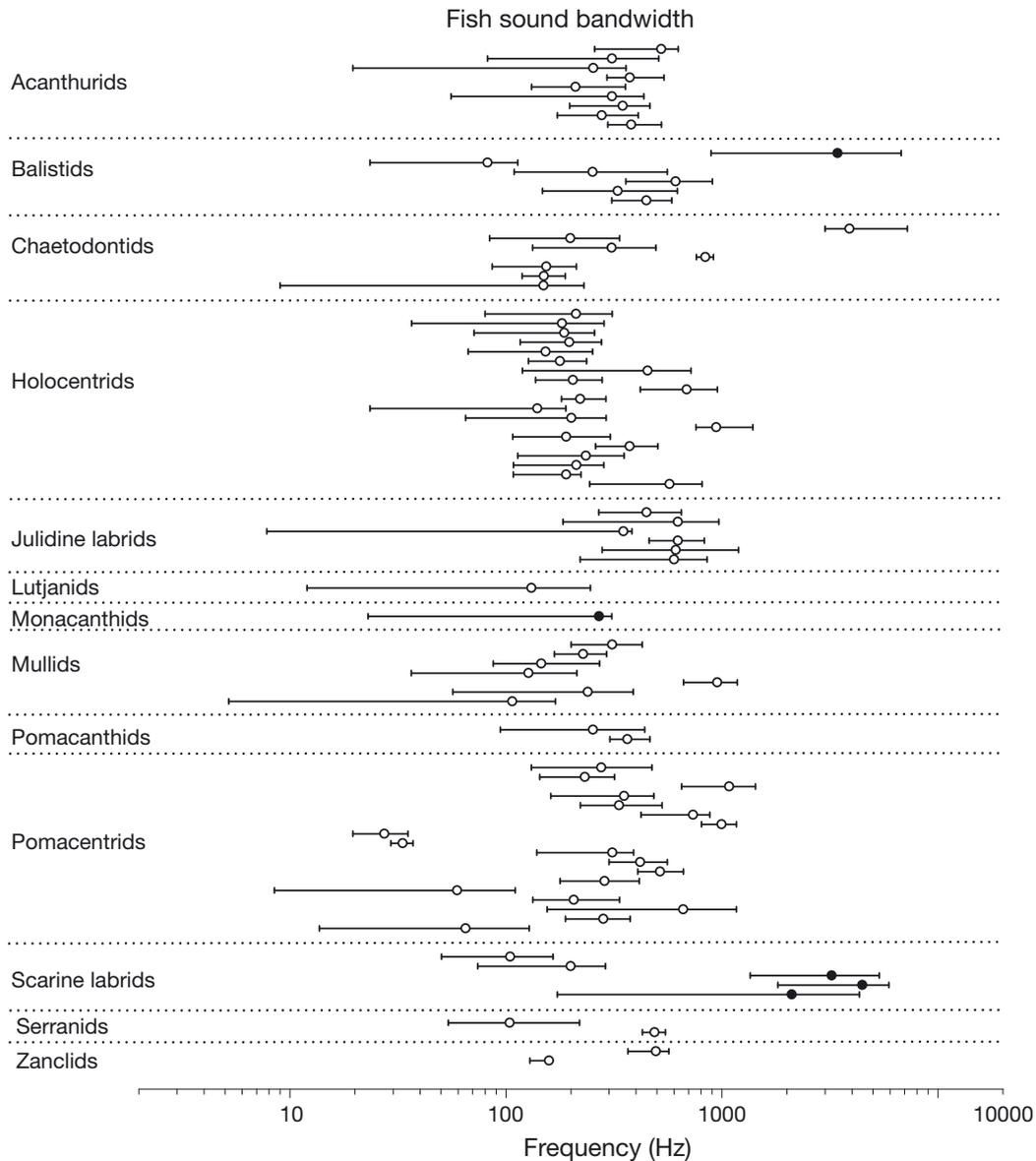


Fig. 8. The 6 dB bandwidth of non-feeding and feeding sound types recorded for 45 species of fishes on Hawaiian coral reefs. Median peak frequency is indicated for non-feeding (open circles) and feeding (solid circles) sounds. Note high peak frequency and bandwidths for feeding sounds of parrotfishes (scarines) and 1 balistid

results reveal a diversity of sounds associated with courtship behaviors for several reef species. Future studies should focus on recording species-specific acoustic behaviors associated with the spawning act.

Vigilance, alarm, or alert calls

The production of sound after physical disturbance, handling, or electric shock is often used to identify sonic species in the lab (Fish & Mowbray 1970). Many species in our study produced sounds

in response to the close approach by a diver which we conservatively categorized as vigilance or alert sounds. Most notable were the squirrelfish and soldierfishes, which are highly vocal and known to make many of these calls in the presence of predators (Salmon 1967), and many are produced during agonistic and social communication. The production of pulsed sounds in response to divers was observed for several damselfish, triggerfish, and filefishes and likely functions in an agonistic context, as with many other members of these families. Further experiments are necessary to place the new calls

produced in response to divers into a biologically relevant context for each species.

Feeding sounds

The production of adventitious sounds during feeding is best described for parrotfishes (Lobel et al. 2010, their Table S2). We recorded similar incidental feeding sounds for 3 species of parrotfish during their normal foraging on dead coral substrates. These sounds were distinctive primarily by their long bite duration (87–181 ms) and high peak frequency spectrum (1277–3387 Hz). Acoustic analyses of feeding sounds of several Caribbean parrotfishes showed the production of high-frequency scrape and crunch sounds that can be used to distinguish feeding activities of small and large individuals (but not species) based on sound duration, frequency spectra, and the temporal spacing of sound waves within a bite sound (Sartori & Bright 1973). The occurrence of these distinctive sounds is a good indicator of the feeding activity by this important family of herbivorous fishes and may be used as a potential measure of reef bioerosion. Our few observations of the coincident production of feeding sounds by the corallivorous barred filefish *Cantherines dumerilii* and the hard-benthos feeder black durgon *Melichthys niger* are consistent with feeding sounds reported for other triggerfishes and filefishes (Moulton 1958, Steinberg et al. 1965, Fish & Mowbray 1970). Sounds from these and other benthic feeding hard-tooth species may also be of potential use in estimates of their feeding activity in coral reef environments and rates of fish-induced bioerosion.

Reef noise and fish sound spectra

The peak frequency of most pulse sounds in our study ranged from 100 to 300 Hz and was near or within the low-frequency band of ambient noise that is generated by wind, tidal flow, and anthropogenic activities (Wenz 1962, Myrberg 1980, Urick 1983). Several fish sounds showed peak frequencies <100 Hz, the band which can be dominated by wind-generated noise at the surface. Thus high signal-to-noise fish sounds in this low-frequency band are best recorded in calm wind and wave conditions as occurs on leeward rather than the windward reefs that are subject to relatively strong and continuous trade winds.

The higher frequency band of 100–2000 Hz is dominated by fish sounds on other coral reefs (Cato 1980)

and includes the peak frequencies and bandwidth of most of our fish sounds. Although most sounds in this study had peak energy at the low end of this range, the –6 and –10 dB bandwidths span a much broader spectrum and are similar to that reported for fish vocalizations on a north Australian reef (Cato 1980). Many of those sounds were uninterrupted tones of several seconds in duration, showed strong harmonics, and occurred primarily during nocturnal hours. Of note was the diurnal sound type ‘C,’ which was described as a steady rhythmic pulsing knock sound. These low-frequency energy peaks observed in our study are generally below the 400 Hz to 4 KHz band of evening acoustic choruses of biological origin reported for coral reefs in the Timor Sea and west Pacific Ocean (Cato 1978). Recent work on the soundscapes of a Pacific reef in Panama shows a strong diurnal peak near 400 Hz that was attributed to acoustic activity of *Stegastes acapulcoensis* (Staaterman et al. 2013). Further work should focus on determining the sources and spectrum of nocturnal fish sounds that may provide sensory cues to larval fish for recruitment (Simpson et al. 2008) and vary across reef habitats and diel periods (Radford et al. 2014).

Future passive acoustic monitoring

The ability to distinguish sounds to the levels of species and behavior confirms the potential value for acoustic monitoring of reproductive activities of target species on Hawaiian reefs. For example, sounds produced by the male Hawaiian dascyllus *Dascyllus albisella* can be used in conjunction with acoustic monitoring to demonstrate the correlation between rates of sound production and spawning season (Mann & Lobel 1995, Lammers et al. 2008). Our records of sounds produced during courtship, spawning, and nest defense indicate this potential application to at least 20 other species of Hawaiian reef fish (Fig. 1). Species such as the yellow tang, Moorish idol, butterflyfishes, and angelfishes are important to the aquarium trade (Tissot & Hallacher 2003), and we have shown that many species produce sounds during reproductive activities. In addition, the acoustic behavior of the peacock grouper *C. argus* may be used to monitor the activity of this invasive and often ciguatoxic species for management over wide spatial areas (Dierking & Campora 2009). On a broader scale, monitoring the production of fish sounds over long periods of time may be used to assess populations and fishing impacts on reef fishes of management concern in Hawai'i (Williams et al. 2008). Fur-

thermore, bioacoustic recordings can be combined with other observations such as reproductive behaviors, gonad condition, spawned zygotes, lunar cycles, visual censuses, and fish movement patterns to provide estimates of species' reproductive activity or abundance (e. g. Saucier & Baltz 1993, Gilmore 2003, Mann et al. 2009, Rowell et al. 2012). Thus the use of fish sound libraries is of future value to estimate the population activities and abundances of threatened, endangered, and other species of concern to managers. We are currently using these species-specific behavior sounds as acoustic templates to identify periodic population behaviors across several years of continuous passive acoustic recordings in our Hawaiian study reef communities.

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