Courtship and spawning sounds in bird wrasse *Gomphosus varius* and saddle wrasse *Thalassoma duperrey*

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Acoustic signals from the bird wrasse *Gomphosus varius* and saddle wrasse *Thalassoma duperrey* were recorded on coral reefs in Hawaii. Terminal phase males in both species emit two types of pulse trains (type I and type II). Type I pulses were produced during spawning and courtship, while type II pulses were associated only with courtship behaviours. *Gomphosus varius* type I pulses were of lower frequency than *T. duperrey* type I pulses (271 *v*. 840 Hz) and were of narrower band. Discriminant function analyses revealed interspecific differences between type I pulse trains and individual pulses of both types. This study is the first documentation of courtship and spawning sounds in sympatric labrids and shows divergence in acoustic signals.   © 2009 The Authors

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Key words: acoustic signals; coral-reef fishes; Labridae; reproductive behaviour; sound production.

INTRODUCTION

Courtship signals are used by a variety of animals for mate assessment, mate attraction and synchronization of reproduction and to provide a species-specific cue to prevent hybridization of closely related sympatric species (Bradbury & Vehrencamp, 1998). The production of courtship sounds to attract mates has been described from many fish species such as gadoids like Atlantic cod *Gadus morhua* L. (Nordeide & Kjellsby, 1999) and haddock *Melanogrammus aeglefinus* (L.) (Hawkins & Amorim, 2000); sciaenids such as weakfish *Cynoscion regalis* (Bloch & Schneider) (Fish & Mowbray, 1970; Connaughton & Taylor, 1995) and red drum *Sciaenops ocellatus* (L.) (Guest, 1978); callichthyid catfishes (Kaatz & Lobel, 1999); the striped blenny *Chasmodes bosquianus* (Lacépède) (Tavolga, 1958); gobiids (Lugli & Torricelli, 1999). Among coral-reef fishes, the damselfish (Pomacentridae) is the best studied family for use of acoustic communication during courtship. Males of several damselfish species produce courtship sounds, either during a signal-jump courtship display in which the male rapidly ascends into the water column and descends back down while emitting a pulsed sound (Myrberg, 1972; Lobel & Mann, 1995),

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during zig-zag displays (Lobel & Kerr, 1999), or while a male escorts a female fish towards the nest (Maruska *et al.*, 2007). While damselfishes have been examined extensively, studies that describe the courtship sounds from other coral-reef fishes are limited in number and entirely absent for other coral-reef labroid fishes, such as wrasses (Labridae) (Rice & Lobel, 2003).

The spawning behaviour of many wrasse species has attracted much attention from behavioural ecologists (Warner *et al.*, 1975; Robertson & Hoffman, 1977; Warner, 1982; Ross, 1983; van den Berghe *et al.*, 1989). Most species are protogynous sequential hermaphrodites, are broadcast spawners and initial phase males, that sneak spawn, exist in some species (Warner, 1982; van den Berghe *et al.*, 1989). Individual spawning bouts may occur in pairs in which a single large territorial male spawns with a female (Robertson & Hoffman, 1977; Eckert, 1987) or in groups where several smaller initial phase males spawn with a female (Warner, 1982). Both spawning patterns can occur within a single species (van den Berghe *et al.*, 1989). Courtship for many wrasse species, including wrasses in the genera *Gomphosus* and *Thalassoma*, involves displays in which terminal phase (TP) fishes hover and circle above the reef substratum while fluttering pectoral fins until an initial phase (IP) female joins the male in a spawning rush (Robertson & Hoffman, 1977; Eckert, 1987). Additionally, group spawning occurs in some species including the saddle wrasse *Thalassoma duperrey* (Quoy & Gaimard) (Ross, 1983). Despite much scientific interest in the stereotyped patterns of visual courtship displays and easily observed spawning behaviour of coral-reef wrasse species, no accounts of spawning or courtship sounds have been described.

The bird wrasse *Gomphosus varius* Lacépède and *T. duperrey* are sympatric in Hawaii (Randall, 2007) and spawn at the same time (Ross, 1983; pers. obs.). Males of *T. duperrey* occur as both TP and IP (Ross, 1984), and IP males may also exist for *G. varius*. Furthermore, both species exhibit similar courtship and spawning behaviours and have been observed to hybridize (Randall, 2007). Thus, acoustic signalling may be a mechanism to synchronize reproductive behaviour and to prevent hybridization. This study tests predictions of the hypothesis that *G. varius* and *T. duperrey* produce acoustic signals during courtship and spawning, and that these signals are species-specific. In addition, the rapid movement of pectoral fins during courtship hovering is examined as a possible sound production mechanism.

MATERIALS AND METHODS

STUDY SITE

Observations and recordings were made on a coral reef at Puako, Hawaii ($19°58'11''$ N; $155°50'55''$ W) at a depth range of $2–12$ m. *Gomphosus varius* courtship behaviour and spawning bouts were observed on 19 and 22 August 2005, and *T. duperrey* courtship and spawning were observed on 23, 26 and 27 August 2006. Spawning and courtship were observed between 1500 and 1700 hours at $0·5–0·8$ m tidal height during the full lunar phase for *G. varius* and between 1500 and 1700 hours at $0·4–0·7$ m tidal height during the new lunar phase for *T. duperrey*.

SOUND AND VIDEO RECORDING

For each species, a single TP male (18 individuals of *G. varius,* 22 individuals of *T. duperrey*) was followed at a $1–3$ m distance by a diver using scuba or snorkel and

recorded on video with a housed (www.amphibico.com) Sony TRV950 digital video camera (www.sony.com), while sounds were recorded simultaneously with two HTI Min96 hydrophones (http://home.att.net/~hightechinc/index.html) ($-163 \cdot 7$ and $163 \cdot 8$ dB re 1 V μPa^{-1}) connected to a housed digital audio tape recorder (Sony PCM-M1) with a 48 kHz sampling rate. Fishes moved quickly and were at times difficult to follow. Thus, single TP males were observed for an average of 3 min (range of 16 s to 11 min), and after several behaviours (*e.g.* courtship, chases and spawning) were observed, a new focal TP individual was followed.

DATA ANALYSES

Digital video and audio records were uploaded to computer. Video of fish behaviour was reviewed and associated audio files were examined aurally for the presence of sounds. Only sounds recorded from focal fishes at close proximity and with obvious behaviour or movements were used in the analysis. In addition, characteristic sounds were only audible when fishes were in close vicinity to the receiver. Initial review of fish sound spectrograms indicated that all energy was <3 kHz; hence, files were low-pass filtered with Cool Edit Pro 2.0 software (http://www.adobe.com/special/products/audition/syntrillium.html) at the highest quality setting and downsampled to 6 kHz. Sound recordings were then high-pass filtered above 20 Hz with a Butterworth filter with a transition bandwidth of $1 \cdot 01$ Hz and a stop attenuation of 1000 dB to reduce low-frequency noise.

The onset and offset of each fish sound were estimated by examination of waveforms and spectrograms relative to background noise levels. Individual sound files were analysed using Matlab (www.mathworks.com) for duration and spectral content. Power spectra were determined with an N-point, zero padded Hanning window FFT. From the power spectra, the following variables were calculated in order to characterize the spectral features: peak frequency (the frequency with the highest energy), bandwidth (the spectral bandwidth measured as the proportion of all frequencies within 10 dB from the peak) and median frequency (the median frequency value of all frequencies within 10 dB from peak, as the peak frequency is not always centred within the distribution of spectral energy). These three variables were chosen because they represent acoustic features that are likely to be biologically relevant based on known properties of frequency selectivity of fish hearing (Popper & Fay, 1999).

Sounds for both species were often emitted as rapid trains. In order to characterize the temporal features of sound emission, several characteristics of sound events were analysed. A train was defined as a group of pulses in which the interevent time for each pulse was shorter than the total train duration; thus trains were separated by interevent times longer than the trains themselves. The duration of trains, number of pulses per train, the pulse rate (number of pulses s^{-1}) within each train and the interpulse interval (IPI, amount of time between pulses) were characterized. Qualitative aural, waveform and spectrogram observations of sounds from both species indicated that two types of pulses were observed: type I and type II. Differences between these two pulse types were tested quantitatively, and trains containing each pulse type were considered separately (*e.g.* pulse type I followed by pulse type II and then more type I pulses were considered as two type I pulse trains and one type II train).

Type I and type II pulse-train features (train duration, number of pulses, pulse rate and IPI) and individual pulse features of type I and type II pulses (pulse duration, peak frequency, median frequency and bandwidth) were averaged for each fish, and univariate statistical comparisons were made with individual fish as sample data. Differences in type I and type II pulse-train features and differences between individual type I and type II pulses were examined within *G. varius* with paired *t*-tests because individual fish made both sound types. Type II pulses were only recorded from two *T. duperrey* males; hence, intraspecific differences between pulse types were not examined with *t*-tests. Interspecific differences in type I pulse train features and individual type pulse features (above) were assessed with two-sample *t*-tests assuming unequal variances. Data were tested for normality and were $\log_{10}$ transformed if possible, or tested with non-parametric statistics: Wilcoxon signed rank test or Mann–Whitney *U*-test. Type I error was adjusted for multiple comparisons (16 initial comparisons) using a sequential Bonferroni (Rice, 1989).

A linear discriminant analysis (LDA) was used to determine further which features best distinguish individual trains and individual pulses from each species. Backwards stepwise LDA with an alpha 0·15 to enter and 0·15 to remove variables was performed in Systat 12·0 (www.systat.com) separately for type I and type II pulse trains with train length, number of pulses, pulse rate, and IPI used as variables and species as classification groups. To identify which features best distinguish individual pulses of each species, LDA was performed separately for each pulse type (I and II) with duration, peak frequency, bandwidth and median frequency as variables and species as classification groups.

RESULTS

SOUND PRODUCTION BEHAVIOUR

Both species produced sound associated with courtship and spawning behaviours (Table I). Most sound events occurred during courtship when TP males hovered above the reef near IP females. In *G. varius,* 25 (*n* = 16 individual fish) of 28 or 89% of unambiguous sound events occurred during courtship. In *T. duperrey*, 23 (*n* = 7) of 26 (*n* = 10) or 88% unambiguous sound events occurred during courtship. Spawning rushes were also associated with sound. Five of five (*n* = 4) *G. varius* spawning rushes observed were associated with sound (Table I). Recordings of two individuals (one event each), however, were not analysed because the video and acoustics were not robust quality (*i.e*. low signal to noise ratio or confounded by second TP nearby). *Thalassoma duperrey* spawn rushes were less associated with sound events (Table I).

Two types of sound were produced with these reproductive behaviours referred to as type I and type II pulse trains (Table I and Fig. 1). For both species, type I pulse trains were produced with courtship and spawning behaviours, but type II pulse trains were uniquely associated with courtship and did not occur with spawning rushes. In 74 sound trains produced during courtship by 17 individual *G. varius*, 51% were pulse type I and 49% were pulse type II. Whereas in *T. duperrey*, of the 44 sound-train events produced from eight individuals in courtship, 91% were type I pulse trains and only 9% were type II pulse trains.

TABLE I. Behavioural context of *Gomphosus varius* and *Thalassoma duperrey* sound-train emission, frequency of occurrence of each sound-train type (%) and summary of observed individual fishes (*n*)

| Species	*n*	Number of sound events observed	Behaviour spawning	Sound train produced (frequency of occurrence, %)		Spawns observed with sound
				Pulse I train	Pulse II train	
G. varius	4	5	Spawning	100	–	5 of 5
	16	25	Courtship	51	49	–
T. duperrey	2	3	Spawning	100	–	3 of 14
	7	23	Courtship	91	9	–

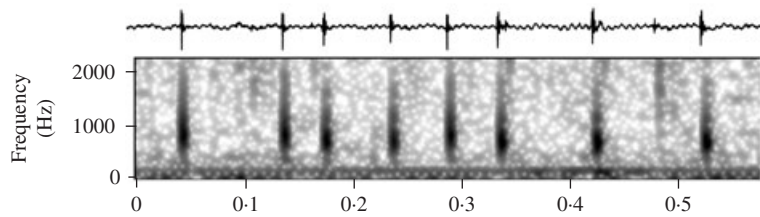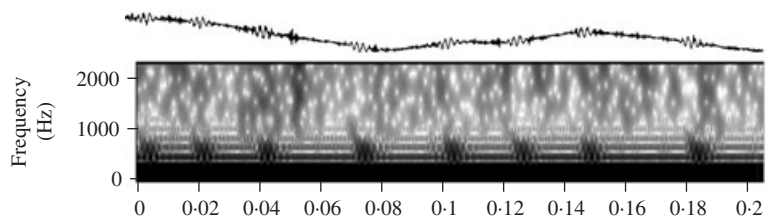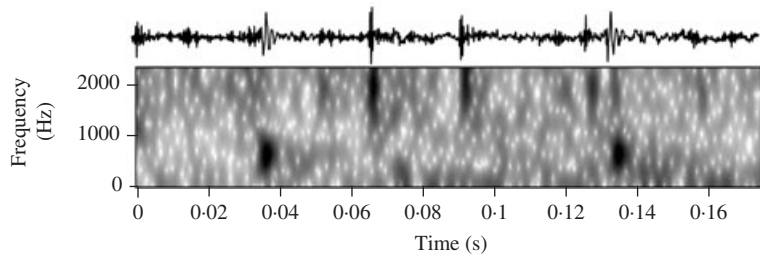*n*, number of individuals.

G. varius type I pulse train
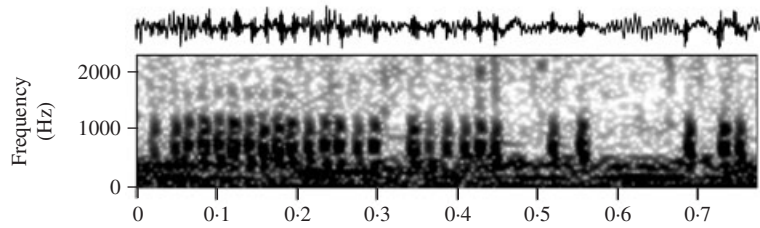
G. varius five pulse segment of type I pulse train
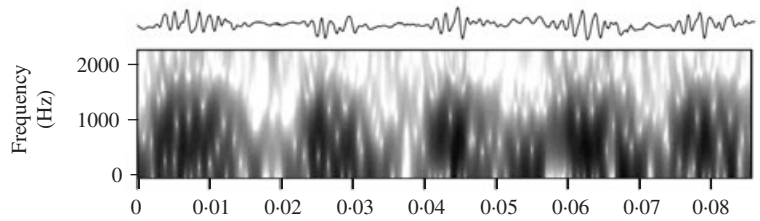
G. varius eight type II pulse train

T. duperrey eight pulse segment of type I pulse train

T. duperrey two type II pulse train

Time (s)

FIG. 1. Type I and type II pulse trains of *Gomphosus varius* and *Thalassoma duperrey*. Sound wave forms (top) and corresponding spectrograms (below) for portions of representative trains are shown. Spectrogram settings: 2·5% window length, 95% window overlap, Hanning window, 1024 point FFT.

TABLE II. Features of type I and type II pulse trains produced by *Gomphosus varius* and *Thalassoma duperrey*. Number of terminal phase males recorded (*n*), number of individual trains mean ± S.E. of train duration, number of pulses per train, pulse rate and interpulse interval (IPI)

	n	Number of trains	Duration (s)	Number of pulses	Pulse rate (pulses s^{-1})	IPI (s)
G. varius type I pulse trains	15	41	1·0 ± 0·2	15·8 ± 2·7	21·7 ± 2·9	0·06 ± 0·01
G. varius type II pulse trains	12	36	0·5 ± 0·1	3·7 ± 0·5	14·9 ± 3·6	0·15 ± 0·04
T. duperrey type I pulse trains	8	43	0·4 ± 0·1	14·8 ± 3·0	41·8 ± 8·5	0·04 ± 0·01
T. duperrey type II pulse trains	2	4	0·2 ± 0·1	1·8 ± 0·2	10·3 ± 3·4	0·19 ± 0·08

SOUND CHARACTERISTICS

The two types of sound trains produced by *G. varius* have distinctive characteristics. *Gomphosus varius* type I pulse trains (Table II) contained more pulses per train (paired *t*-test, d.f. = 10, $P < 0.001$), and trended towards a lower IPI (Wilcoxon signed rank test, $n = 9$, $P < 0.05$, but not below adjusted sequential Bonferroni $\alpha = 0.004$). In addition, *G. varius* type I pulses trended towards a lower median frequency (paired *t*-test, d.f. = 10, $P < 0.05$, but not below adjusted sequential Bonferroni α). Individual type I pulses (Table III) of *G. varius* were longer duration than type II pulses (paired *t*-test, d.f. = 10, $P < 0.001$). Peak frequencies of *G. varius* type I pulses were not different than *G. varius* type II pulses (paired *t*-test, d.f. = 10, $P > 0.05$); however, type II pulses of *G. varius* were broader band (bandwidth mean ± S.E. 0·38 ± 0·04 *v.* 0·18 ± 0·02, paired *t*-test, d.f. = 10, $P < 0.01$). Mean ± S.E. sound pressure level at the hydrophone in the 0–3 kHz band was 109 ± 8 dB$_{rms}$ (referenced to, re, 1 μPa) for *G. varius* type I pulses and 121 ± 35 dB$_{rms}$ (re: 1 μPa) for *G. varius* type II pulses. Sound source levels, however, were not obtained because the distance from the fishes to the hydrophone was not constant.

The features of the two types of sound trains produced by *T. duperrey* are summarized in Tables II and III. No statistical comparisons could be made between the two train types because recordings of type II events were from only two individuals. Mean ± S.E. sound pressure level at the hydrophone for *T. duperrey* type I pulses was 105 ± 8 dB$_{rms}$ (re: 1 μPa) and 116 ± 0 dB$_{rms}$ for *T. duperrey* type II pulses.

INTERSPECIFIC DIFFERENCES

Train features

No differences in type I pulse train features (train duration, number of pulses, pulse rate, IPI) were found between species with *t*-test comparisons; however, some differences were revealed with stepwise LDA. The best LDA model to distinguish *G. varius* type I pulse trains from *T. duperrey* type I pulse trains (LDA, Wilks' λ 0·7; $F_{2,78}$ 16·7, $P < 0.001$) used two variables: pulse rate (*F*-to-remove 27·6) and number of pulses (*F*-to-remove 4·6). This model predicted 74% (74% jackknifed) of

TABLE III. Individual characteristics of type I and II pulses produced by *Gomphosus varius* and *Thalassoma duperrey*. Number of terminal-phase males recorded (n), number of individual pulses, mean ± S.E. of duration, peak frequency and proportion of bandwidth within 10 dB of peak frequency (10 dB BW) proportion

	n	Number of pulses	Duration (s)	Peak frequency (Hz)	Median frequency (Hz)	10 dB BW proportion
G. varius type I pulses	15	551	0·013 ± 0·002	271 ± 42	391 ± 36	0·2 ± 0·0
G. varius type II pulse	12	138	0·006 ± 0·002	478 ± 90	704 ± 69	0·4 ± 0·1
T. duperrey type I pulses	8	873	0·012 ± 0·002	827 ± 90	1248 ± 160	0·3 ± 0·0
T. duperrey type II pulses	2	7	0·009 ± 0·003	509 ± 98	1321 ± 709	0·3 ± 0·1

G. varius type I pulse trains and 74% (71% jackknifed) of *T. duperrey* pulse trains correctly. LDA was not successful in separating *G. varius* type II pulse trains from *T. duperrey* type II pulse trains (LDA, Wilks' λ 1·0; $F_{1,36}$ 1·5, $P > 0.05$), because overall time of occurrence and number of type II pulses were similar between species.

Pulse features

Mean individual type I pulses (Table III and Fig. 2) of *G. varius* were of lower peak frequency than *T. duperrey* (t-test, d.f. = 16, $P < 0.01$), lower median frequency (t-test, d.f. = 16, $P < 0.001$), and occupied a narrower proportion of total recorded bandwidth (t-test, d.f. = 16, $P < 0.001$). Interspecific differences between individual type I and type II pulses revealed by LDA were best predicted by median frequency and pulse duration. The best LDA model to distinguish individual type I pulses (LDA, Wilks' λ 0·8; $F_{3,1,471}$ 103·3, $P < 0.001$) used median frequency (F-to-remove 205·6), duration (F-to-remove 12·2) and bandwidth (F-to-remove 8·7). This model classified 77% (77% jackknifed) *T. duperrey* type I pulses correctly, but only 42% (42% jackknifed) *G. varius* pulses correctly. The best LDA model to discriminate individual type II pulses between species (LDA, Wilks' λ 0·7; $F_{2,1,145}$ 25·1, $P < 0.001$) used duration (F-to-remove 36·2), median frequency (F-to-remove 5·5) and bandwidth (F-to-remove 1·0). This model classified 97% (97% jackknifed) *G. varius* type II pulses correctly, but only 57% (57% jackknifed) *T. duperrey* pulses correctly.

DISCUSSION

This study is the first to characterize sound production in social contexts for the labrid genera *Gomphosus* and *Thalassoma*. Wrasses are the second largest marine fish family (Nelson, 1994) and are conspicuous on coral reefs, but prior to this finding, there has been little evidence of sound production during social behaviours. The presence of sound emission during courtship behaviour by TP males of both *G. varius*
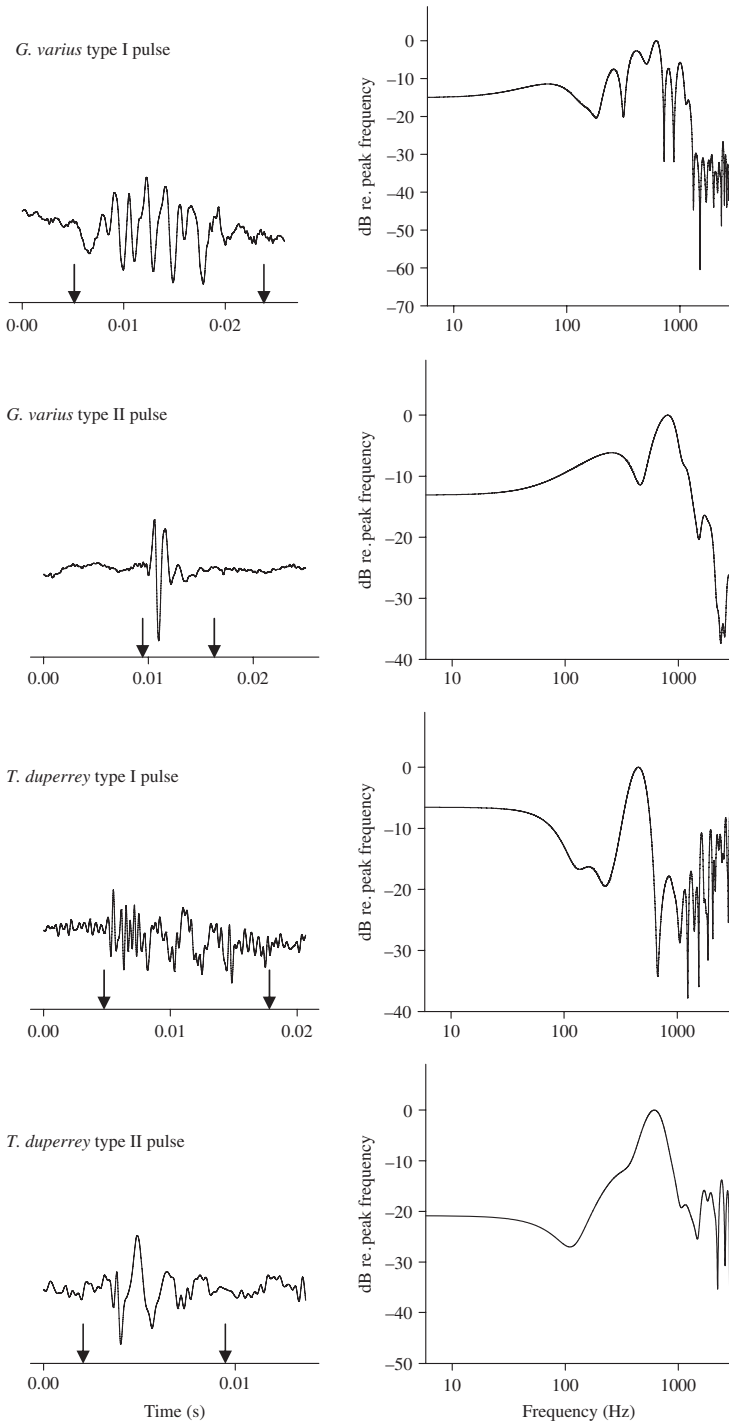
FIG. 2. *Gomphosus varius* and *Thalassoma duperrey* pulse wave forms and power spectra from representative individual type I and II pulses. Arrows indicate pulse onset and offset times estimated from relative background noise levels (re, referenced to).

and *T. duperrey* provides an opportunity for future studies that test the importance of acoustic signalling for mate attraction in wrasses. The flutter behaviour of TP wrasses, at least in these two species, involves not only a visual display of the fish body and moving pectoral fins, but also an acoustic display of two pulse types for each species. These sounds may attract the smaller IP females that are often within close range, but closer to the coral substratum. The courtship sounds may also serve an agonistic function in spawning territoriality behaviour between competing TP males. In addition to courtship displays, type I pulse trains also were produced during the brief spawning rush into the water column. Spawning sounds may be important for synchronizing gamete release for males and females in these species, as was suggested for serranids (*Hypoplectrus* spp.) (Lobel, 1992), Mozambique tilapia *Oreochromis mossambicus* (Peters) (Amorim *et al.*, 2003) and *M. aeglefinus* (Hawkins & Amorim, 2000). It is possible that IP females also produce acoustic signals during courtship and spawning. Yet the observations from this study are most consistent with TP males as the sound source because pulse trains during the spawning rush and flutter-hover were similar, and the latter sometimes occurred before IP females were near the observer and hydrophones. Thus, the labrid acoustic signals recorded in this study may play an important role in reproductive behaviours although further experiments are needed to test directly the functions of these sounds.

This study revealed several quantifiable interspecific differences between type I and type II pulse sounds. This finding of species-specific acoustic signals is consistent with the hypothesis that *G. varius* and *T. duperrey* may use species-specific acoustic signals to prevent hybridization with closely related wrasses, but further study is required to test this hypothesis directly. *Gomphosus varius* and *T. duperrey* type I pulse trains differed in terms of pulse rate and number of pulses. Individual *G. varius* type I pulses differed from *T. duperrey* with respect to high-frequency spectral components: third quartile 10 dB frequency and maximum 10 dB frequency, and *G. varius* and *T. duperrey* type II pulses differed in duration and max 10 dB BW. These differences in acoustic features of male sounds would be predicted if acoustic signalling was important for female mate choice and species recognition. Other interspecific differences in acoustic variables have been recorded in courtship sounds from cichlids of Lake Malawi (Lobel, 1998; Amorim *et al.*, 2004). Myrberg & Spires (1972) showed that male bicolour damselfish *Stegastes partitus* (Poey) respond more readily to calls from other male conspecifics than calls from sympatric congeners. Six species of *Thalassoma* are sympatric on Hawaiian coral reefs (Randall, 2007), and molecular phylogenetic evidence suggests that *G. varius* is nested within the *Thalassoma* clade (Bernardi *et al.*, 2004). Both *G. varius* and *T. duperrey* often spawn at the same time (Ross, 1983; pers. obs.) Furthermore, *T. duperrey* sometimes hybridizes with *G. varius* and the uncommon sunset wrasse *Thalassoma lutescens* (Lay & Bennett) in Hawaii (Randall, 2007). Thus, an investigation in acoustic differences among sympatric, closely related julidine wrasses coupled with experiments to test the discriminatory and auditory preferences of females may determine whether sound is an important cue for reproductive isolation.

Each sound type (I and II) within a species may have a contextual role during reproductive activities. For both species, type II pulse trains only occurred during courtship, prior to spawning. Type I pulse trains, however, occurred in both courtship and the spawning rush. Thus, type II pulse trains may have a specific role earlier in agonistic behaviour and courtship as males set up spawning territories.

Hearing thresholds of *G. varius* and *T. duperrey* have not been tested behaviourally or physiologically; so the response and discriminatory ability of these species to each sound type remains speculative. Most of the spectral energy for both the *G. varius* and *T. duperrey* sounds lies at <1000 Hz, which is typical of most teleost sounds (Hawkins, 1993). These low-frequency sounds are within the bandwidth of greatest auditory sensitivity for fishes without known adaptations for high-frequency hearing (Schellart & Popper, 1992). Labrids have no known structural mechanisms for coupling the swimbladder to the inner ear, a feature that is necessary for enhanced sensitivity to sound pressure, and little is known about their auditory sensitivity. Behavioural hearing thresholds to pure tone sounds have been measured in the blue-head wrasse *Thalassoma bifasciatum* (Bloch), a closely related species to the wrasses in this study, and best sensitivity is from 200 to 600 Hz, with measurable thresholds from 100 to 1200 Hz (Tavolga & Wodinsky, 1963). Most of the energy of *G. varius* and *T. duperrey* type I and II pulses occurs within this area of best acoustic sensitivity for *T. bifasciatum*.

As with many sound-producing teleosts, the mechanism of sound generation in these wrasses remains unknown. The most widely suggested mechanism of sound production in other labroid species has been stridulation of pharyngeal tooth plates with amplification provided by the swimbladder (Rice & Lobel, 2003). Recent evidence from Clark's anemonefish *Amphiprion clarkii* (Bennett), however, has shown that rapid head elevation lowers the hyoid bar, which is connected to the lower jaw by a novel ligament that produces rapid jaw closure (Parmentier *et al.*, 2007). Thus, oral jaws may be the mechanism, or at least part of the mechanism of sound production for many pomacentrids. It is not clear whether a similar ligament system may be present in wrasses that would allow for an oral jaw role in sound production. A percussive system of sound production that involves pectoral fin drumming against the side of the body has been proposed for sound production in triggerfishes (Balistidae) (Moulton, 1958). Spawning striped parrotfish *Scarus iseri* (Bloch), which are labrids *sensu* Streelman & Karl (1997) and Westneat & Alfaro (2005), produce hydrodynamic noise that occurs from the swimming movement of the fish (Lobel, 1992). These observations and the fast movements during *G. varius* pectoral fin flutter (8–10 Hz in rostral-caudal plane) (unpubl. data) compared with moderate labriform swimming (4·9 Hz in dorso-ventral plane) (Walker & Westneat, 1997) suggest a role of fin flutter in wrasse sound generation. *Gomphosus varius* type I pulse trains, however, are emitted more than twice as fast as the flutter rate. Thus, sound generation cannot be explained by pectoral flutter alone.

It is uncertain whether other labrids produce social sounds, but given the diversity of the wrasse family (*c*. 600 spp.) and the fact that fish sound production is widespread, it is likely that others produce acoustic signals. While this underscores how much remains uncertain in coral-reef fish acoustics, it suggests potential for the use of passive acoustics (Luczkovich & Sprague, 2002; Lammers *et al.*, 2008) to monitor labrids, a major component of coral-reef fish populations.

References

Amorim, M. C. P., Fonseca, P. J. & Almada, V. C. (2003). Sound production during courtship and spawning of *Oreochromis mossambicus*: male-female and male-male interactions. *Journal of Fish Biology* **62,** 658–672.

Amorim, M. C. P., Knight, M. E., Stratoudakis, Y. & Turner, G. F. (2004). Differences in sounds made by courting males of three closely related Lake Malawi cichlid species. *Journal of Fish Biology* **65,** 1358–1371.

van den Berghe, E. P., Wernerus, F. & Warner, R. R. (1989). Female choice and the mating cost of peripheral males. *Animal Behaviour* **39,** 875–884.

Bernardi, G., Bucciarelli, G., Costagliola, D., Robertson, D. R. & Heiser, J. B. (2004). Evolution of coral reef fish *Thalassoma* spp. (Labridae). 1. Molecular phylogeny and biogeography. *Marine Biology* **144,** 369–375.

Bradbury, J. W. & Vehrencamp, S. L. (1998). *Principles of Animal Communication*. Sunderland, MA: Sinauer Associates.

Connaughton, M. A. & Taylor, M. H. (1995). Seasonal and daily cycles in sound production associated with spawning in weakfish, *Cynoscion regalis*. *Environmental Biology of Fishes* **42,** 233–240.

Eckert, G. J. (1987). Spawning in *Anampses* (Pisces: Labridae). *Copeia* **1987,** 789–790.

Fish, M. P. & Mowbray, W. H. (1970). *Sounds of the Western North Atlantic Fishes*. Baltimore, MD: Johns Hopkins Press.

Guest, W. C. (1978). A note on courtship behavior and sound production of red drum. *Copeia* **1978,** 337–338.

Hawkins, A. D. (1993). Underwater sound and fish behaviour. In *Behaviour of Teleost Fishes* (Pitcher, T. J., ed.), pp. 129–169. New York, NY: Chapman & Hall.

Hawkins, A. D. & Amorim, M. C. P. (2000). Spawning sounds of the male haddock, *Melanogrammus aeglefinus*. *Environmental Biology of Fishes* **59,** 29–41.

Kaatz, I. M. & Lobel, P. S. (1999). Acoustic behavior and reproduction in five species of *Corydoras* catfishes (Callichthyidae). *Biological Bulletin* **197,** 241–242.

Lammers, M. O., Brainard, R. E., Au, W. W. L. & Wong, K. B. (2008). An ecological acoustic recorder (EAR) for long-term monitoring of biological and anthropogenic sounds on coral reefs and other marine habitats. *Journal of the Acoustical Society of America* **123,** 1720–1728.

Lobel, P. S. (1992). Sounds produced by spawning fishes. *Environmental Biology of Fishes* **33,** 351–358.

Lobel, P. S. (1998). Possible species specific courtship sounds by two sympatric cichlid fishes in Lake Malawi, Africa. *Environmental Biology of Fishes* **52,** 443–452.

Lobel, P. S. & Kerr, L. M. (1999). Courtship sounds of the Pacific damselfish, *Abudefduf sordidus* (Pomacentridae). *Biological Bulletin* **197,** 242–244.

Lobel, P. S. & Mann, D. A. (1995). Spawning sounds of the damselfish *Dascyllus albisella* (Pomacentridae) and relationship to male size. *Bioacoustics* **6,** 187–198.

Luczkovich, J. J. & Sprague, M. W. (2002). Using passive acoustics to monitor estuarine fish populations. *Bioacoustics* **12,** 289.

Lugli, M. & Torricelli, P. (1999). Prespawning sound production in Mediterranean sand-gobies. *Journal of Fish Biology* **54,** 691–694.

Maruska, K. P., Boyle, K. S., Dewan, L. R. & Tricas, T. C. (2007). Sound production and spectral hearing sensitivity in the Hawaiian sergeant damselfish, *Abudefduf abdominalis*. *Journal of Experimental Biology* **210,** 3990–4004.

Moulton, J. M. (1958). The acoustical behavior of some fishes in the Bimini area. *Biological Bulletin* **114,** 357–374.

Myrberg, J. A. A. (1972). Ethology of the bicolor damselfish, *Eupomacentrus partitus* (Pisces: Pomacentridae:) A comparative analysis of laboratory and field behavior. *Animal Behaviour Monographs* **5,** 197–283.

Myrberg, A. A. & Spires, J. Y. (1972). Sound discrimination by the bicolor damselfish, *Eupomacentrus partitus*. *Journal of Experimental Biology* **57,** 727–735.

Nelson, J. S. (1994). *Fishes of the World*, 3rd edn. New York, NY: John Wiley & Sons.

Nordeide, J. T. & Kjellsby, E. (1999). Sound from spawning cod at their spawning grounds. *ICES Journal of Marine Science* **56,** 326–332.

Parmentier, E., Colleye, O., Fine, M. L., Frédérich, B., Vanderwalle, P. & Herrel, A. (2007). Sound production in the clownfish *Amphiprion clarkii*. *Science* **316,** 1006.

Popper, A. N. & Fay, R. R. (1999). The auditory periphery in fishes. In *Comparative Hearing: Fish and Amphibians* (Fay, R. R. & Popper, A. N., eds), pp. 43–100. New York, NY: Springer.

Randall, J. E. (2007). *Reef and Shore Fishes of the Hawaiian Islands*. Honolulu, HI: University of Hawai'i Sea Grant College Program.

Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution* **43,** 223–225.

Rice, A. N. & Lobel, P. S. (2003). The pharyngeal jaw apparatus of the Cichlidae and Pomacentridae: function in feeding and sound production. *Reviews in Fish Biology and Fisheries* **13,** 433–444.

Robertson, D. R. & Hoffman, S. G. (1977). The roles of female mate choice and predation in the mating systems of some tropical labroid fishes. *Zeitschrift für Tierpsychologie* **45,** 298–320.

Ross, R. M. (1983). Annual, semilunar, and diel reproductive rhythms in the Hawaiian labrid *Thalassoma duperrey*. *Marine Biology* **72,** 311–318.

Ross, R. M. (1984). Growth and sexual strategies in the fish *Thalassoma duperrey* (Labridae), a protogynous hermaphrodite. *Environmental Biology of Fishes* **4,** 253–259.

Schellart, N. A. M. & Popper, A. N. (1992). Functional aspects of the evolution of the auditory system of actinopterygian fish. In *The Evolutionary Biology of Hearing* (Webster, D. B., Fay, R. R. & Popper, A. N., eds), pp. 295–322. New York, NY: Springer-Verlag.

Streelman, J. T. & Karl, S. A. (1997). Reconstructing labroid evolution with single-copy nuclear DNA. *Proceedings of the Royal Society B* **264,** 1011–1020.

Tavolga, W. N. (1958). Underwater sounds produced by males of the blenniid fish, *Chasmodes bosquianus*. *Ecology* **39,** 759–760.

Tavolga, W. N. & Wodinsky, J. (1963). Auditory capacities in fishes: pure tone thresholds in nine species of marine teleosts. *Bulletin of the American Museum of Natural History* **126,** 179–239.

Walker, J. A. & Westneat, M. W. (1997). Labriform propulsion in fishes: kinematics of flapping aquatic flight in the bird wrasse *Gomphosus varius* (Labridae). *The Journal of Experimental Biology* **200,** 1549–1569.

Warner, R. R. (1982). Mating systems, sex change and sexual demography in the rainbow wrasse, *Thalassoma lucasanum*. *Copeia* **1982,** 653–661.

Warner, R. R., Robertson, D. R. & Leigh, E. G. Jr. (1975). Sex change and sexual selection. *Science* **190,** 633–638.

Westneat, M. W. & Alfaro, M. E. (2005). Phylogenetic relationships and evolutionary history of the reef fish family Labridae. *Molecular Phylogenetics and Evolution* **36,** 370–390.