

RESEARCH ARTICLE

Vocalisations of the bigeye *Pempheris adspersa*: characteristics, source level and active space

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ABSTRACT

Fish sounds are an important biological component of the underwater soundscape. Understanding species-specific sounds and their associated behaviour is critical for determining how animals use the biological component of the soundscape. Using both field and laboratory experiments, we describe the sound production of a nocturnal planktivore, *Pempheris adspersa* (New Zealand bigeye), and provide calculations for the potential effective distance of the sound for intraspecific communication. Bigeye vocalisations recorded in the field were confirmed as such by tank recordings. They can be described as popping sounds, with individual pops of short duration (7.9 ± 0.3 ms) and a peak frequency of 405 ± 12 Hz. Sound production varied during a 24 h period, with peak vocalisation activity occurring during the night, when the fish are most active. The source level of the bigeye vocalisation was 115.8 ± 0.2 dB re. $1 \mu\text{Pa}$ at 1 m, which is relatively quiet compared with other soniferous fish. Effective calling range, or active space, depended on both season and lunar phase, with a maximum calling distance of 31.6 m and a minimum of 0.6 m. The bigeyes' nocturnal behaviour, characteristics of their vocalisation, source level and the spatial scale of its active space reported in the current study demonstrate the potential for fish vocalisations to function effectively as contact calls for maintaining school cohesion in darkness.

KEY WORDS: Contact call, Active space, Ambient sound, Fish, Vocalisations

INTRODUCTION

Fish sounds are an important component of underwater marine soundscapes (Radford et al., 2011a; Simpson et al., 2008a,b, 2005). Identifying species-specific sounds and understanding their behavioural role provides a basis to interpret this biological component of underwater sound (Tricas and Boyle, 2014) and opens possibilities for the use of acoustic remote sensing to monitor fish populations and behaviour.

In coral reef habitats, the diversity of fish species is matched by a diversity of soniferous species, especially members from the families Pomacentridae (Myrberg et al., 1993; Parmentier et al., 2009, 2006), Holocentridae (Parmentier et al., 2011) and Chaetodontidae (Boyle and Tricas, 2010; Tricas et al., 2006). The types of vocalisations produced are almost as diverse as the number of species that produce sounds. These include a variety of chirps (Chen and Mok, 1988; Lobel and Kerr, 1999; Luh and Mok, 1986), grunts (Amorim, 2006;

Tricas et al., 2006) and pops (Mann and Lobel, 1998; McCauley and Cato, 2000). Daily patterns of sound production are also evident, with highest activity levels during crepuscular periods that correspond to increased behavioural activities, such as mating and territorial defence (Parmentier et al., 2010). Characterisation of species-specific sounds and their associated behaviour typically depends on field recording and the use of diver or camera observations. Using these methods, vocalisations have commonly been found to serve a communication function during inter- or intra-specific interactions (Bradbury and Vehrencamp, 1998; Kasumyan, 2008). For example, the bicolor damselfish *Pomacentrus partitus* produces a chirp sound as a 'keep-out' signal to intruders during agonistic territorial behaviour (Myrberg, 1997), and the male albino damselfish *Dascyllus albisella* produces chirp sounds during courtship behaviour (Mann and Lobel, 1998).

Other fish sounds are associated with nocturnal activity and it has been proposed that 'pop' sounds produced by species from the families Priacanthidae and Holocentridae may be used as a group cohesion cue to maintain school structure at night, and allow the fish to track prey aggregations (McCauley and Cato, 2000). More recently, it has been shown that larval grey snapper (*Lutjanus griseus*) produce sound only at night, and it has been suggested that these sounds could play a role in maintaining group cohesion (Staaterman et al., 2014). Determination of the behavioural context for these sounds is difficult, particularly as these nocturnal planktivores roam extensively and most often away from their home reef. As a first approach, it is useful to ask whether these 'pop' sounds have the appropriate characteristics to be used in group cohesion. At the very least, they must achieve a source level that gives rise to a suitable active space. The active (Janik, 2000) or communication (Clark et al., 2009) space is generally defined as the volume or space around an individual within which acoustic communication with other conspecifics can take place. In the marine environment, active or communication space has been studied in marine mammals but has largely been ignored in fishes because of difficulties in obtaining critical bioacoustical information (i.e. target source, vocalisation characteristics, source level and auditory sensitivity) in combination with the ambient habitat noise.

Measuring the source level (SL) of fish vocalisations presents inherent challenges and necessitates recording the vocalisations in a free non-reverberant sound field using calibrated recording systems (Urlick, 1983). As SL refers to sound pressure measurements at 1 m (dB re. $1 \mu\text{Pa}$ at 1 m), knowledge of the source distance to the hydrophone is critical for the conventional method of back-calculating received levels in the far field. However, if more than one hydrophone is used, SL can be calculated from the difference in sound level and time of arrival of sound at the different hydrophones (Cato, 1998). Using such a method, SL estimates of vocalisations in the wild are possible and the identity of the call can be verified by comparing (sound-truthing) its characteristics with those of captive

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List of symbols and abbreviations

AEP	auditory evoked potential
ANL	ambient noise level
DT	detection threshold
FFT	fast Fourier transform
f_c	centre frequency
f_{bw}	frequency bandwidth
f_{peak}	peak frequency
IQR	interquartile range
NL _{rms}	root mean square noise level
N_p	number of pulses
PP	pop period
PP _w	peak power
PP1	period between the first and second pop
PP2	period between the second and third pop
PSD	power spectral density
Q	damping co-efficient
r	range
RL	received level
RL _{rms}	root mean square received level
rms	root mean square
SD	sound duration
SE	signal excess
SL	source level
SL _{rms}	root mean square source level
TL _{sp}	spherical spreading transmission loss
3 dB BW	3 dB bandwidth
3 dB Lf	3 dB lower frequency
3 dB Uf	3 dB upper frequency
10 dB BW	10 dB bandwidth
10 dB Uf	10 dB upper frequency

fishes. Despite differences in background noise (i.e. multiple sound sources in the field and reflection of sound in tanks), field and tank recordings of species-specific calls can be sound-truthed by appropriate comparison of their acoustic parameters (Sprague et al., 2001).

The underwater soundscape around northeastern New Zealand has been well studied (Radford et al., 2008, 2010, 2011b). While there are a number of soniferous species, the overall contribution of fish noise to this soundscape is much less than in coral reef habitats. This lower species diversity may in fact lend itself to better characterisation of individual species' vocalisation within their natural setting. In particular, identifying nocturnal fish sounds, and characterisation of SL and active space of nocturnal species may shed light on the possible use of sound for group cohesion.

In temperate reefs around northeastern New Zealand, the endemic bigeye, *Pempheris adspersa* Griffin 1927, is a cryptic nocturnal planktivorous fish. Groups of bigeyes typically leave their daytime

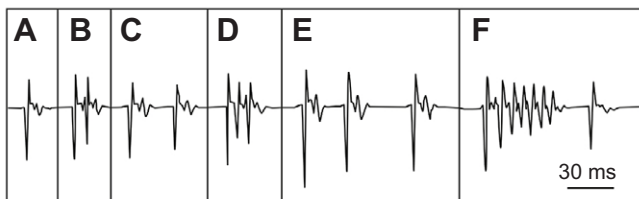


Fig. 1. Representative oscillogram of different bigeye call types held in captivity. (A) Single pop; (B) double pop fused; (C) double pop unfused; (D) triple pop fused; (E) triple pop unfused; and (F) seven pop fused and followed by a single unfused pop. Oscillogram was plotted after band-pass filtering sound between 50 and 1500 Hz.

shelters an hour after sunset to forage over the reef area throughout the night (Kingsford and MacDiarmid, 1988). Within an hour before sunrise, they return and take refuge within the same daytime shelter, usually a rocky overhang, crevice or cave. Although the vocal behaviour of *P. adspersa* has not been described, vocalisations have been reported for another species within the same genus, the silver sweeper *P. schwenkii* (Takayama et al., 2003). Therefore, the overriding objectives of the present study were to first ascertain the presence of vocalisation in *P. adspersa*, then characterise the nature and daily patterns of their sound production, and finally determine their source level and the active space of the sounds they produce.

RESULTS**Vocalisation repertoire and acoustic characteristics**

Bigeye vocalisations consist of a pulsed type sound that is commonly described aurally as a 'pop' (Fig. 1). The duration of the pop is very short (7.9 ± 0.3 ms) and is composed of either one or two cycles of the sound wave. Pops are produced either individually or in series to form calls comprising trains of up to

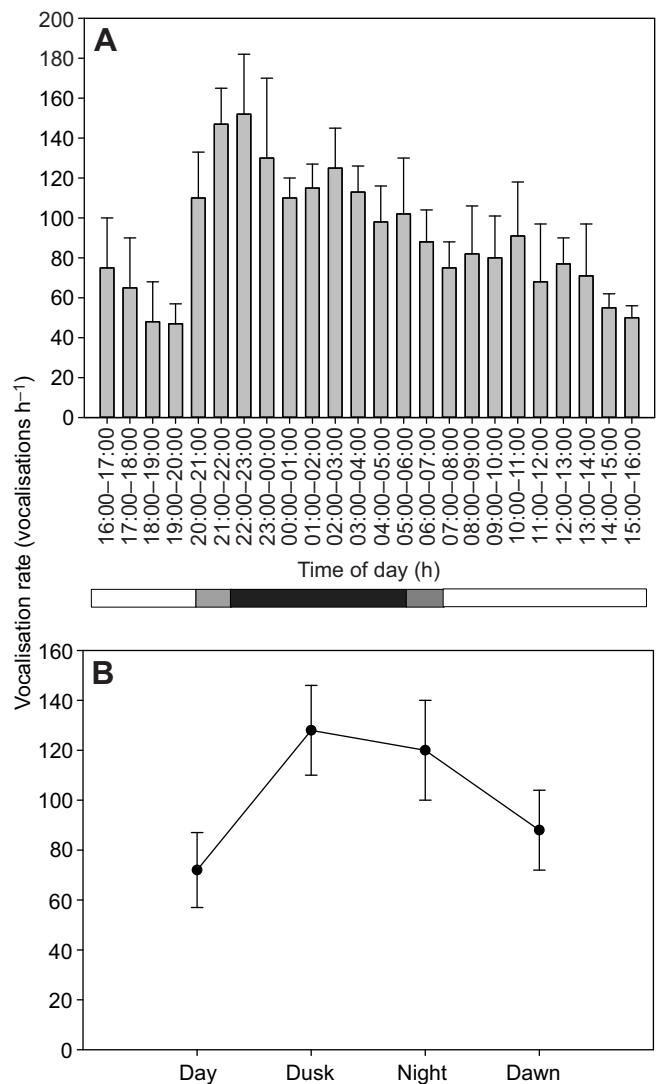


Fig. 2. Bigeye vocalisation rates. (A) Mean (+s.e.) hourly vocalisation rate of bigeyes in captivity ($N=6$ days, $N=20$ fish). The horizontal bar indicates hours of the day (white), night (black) and dawn/dusk (grey). (B) Comparison of mean (+s.e.) vocalisation rate among different periods of the entire 24 h of recording.

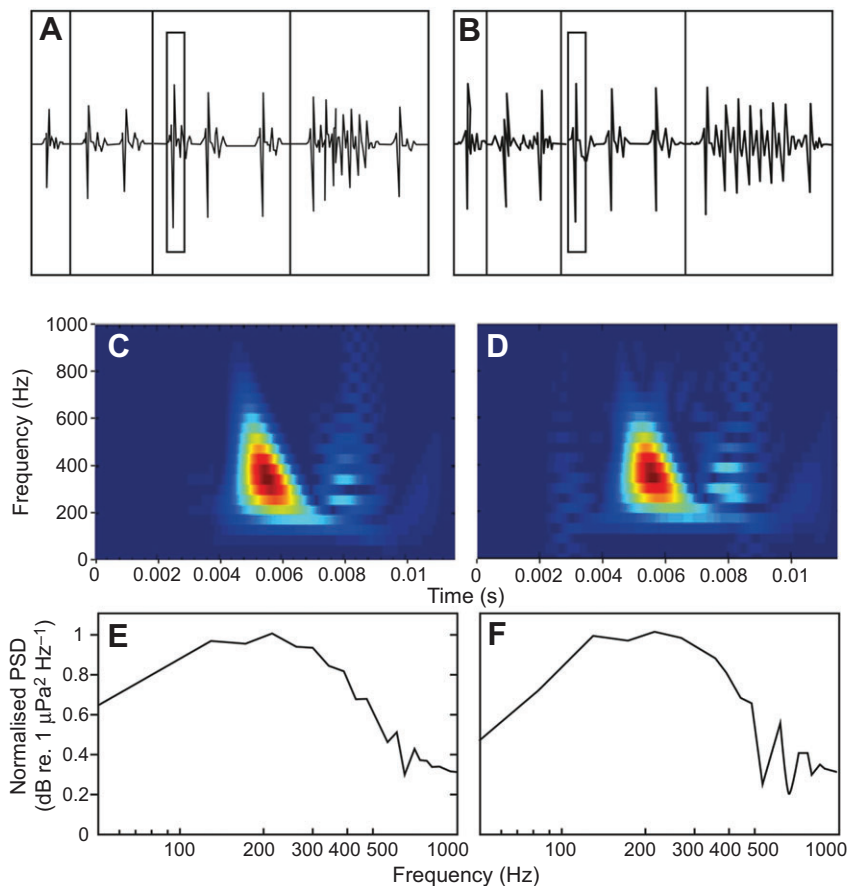


Fig. 3. Representative oscillogram, spectrogram and normalised power spectrum of selected bigeye calls. Calls are from captive (A,C,E) and North Reef (B,D,F) bigeye. Sounds were band-pass filtered between 90 and 700 Hz. Spectrograms and power spectra were computed using 512-point fast Fourier transform (FFT) for the boxed pulses. PSD, power spectral density.

seven pops (average of three pops). When forming trains of pops, the individual pops can either be fused together (fused) with one pop merging into the next (Fig. 1B,D,F) or separated (unfused) with each pop being distinct from the next in the train (Fig. 1C,E). Here, pops that were separated by a minimum time interval of 100 ms were considered as separate calls. The single pop had a mean sound duration (SD) of 7.9 ± 0.3 ms with a mean peak frequency (f_{peak}) of 305 ± 12 Hz. The mean 10 dB bandwidth (10 dB BW) of the sound was 906 ± 23 Hz encompassing the frequency range 74–980 Hz. The top 3 dB of the sound energy was in the 3 dB bandwidth (3 dB BW) of 510 ± 19 Hz spanning 149–659 Hz. The mean damping or tuning coefficient (Q value) was 0.82 ± 0.02 .

The double pop call had a mean SD of 9.9 ± 0.2 ms for fused calls and 29.5 ± 0.5 ms for unfused calls with a mean f_{peak} at 370 ± 10 and 308 ± 9 Hz, respectively. The mean pop period (PP) for a fused call was 8.2 ± 0.2 ms while for the unfused call it was 27.1 ± 0.5 ms. For triple pop calls, the mean SD for fused calls was 12.6 ± 0.3 ms and for unfused calls it was 58.7 ± 2.2 ms, with a mean f_{peak} at 404 ± 17 and 329 ± 15 Hz, respectively. The mean of the first pop period (PP1) for a fused call was 6.5 ± 0.1 ms while for the unfused call it was 20.8 ± 1.1 ms. The mean of the second pop period (PP2) was 5.4 ± 0.2 and 36.6 ± 1.2 ms, respectively.

Diel periodicity of vocalisation

Vocalisations occurred during the entire 24 h period (Fig. 2), where the vocalisation rate at night (126.4 ± 18.0 vocalisations h^{-1}) and dusk (116.8 ± 18.8 vocalisations h^{-1}) was significantly higher than that during the day (73.0 ± 13.3 vocalisations h^{-1}) (Friedman, $\chi^2_3 = 14.8$, $P = 0.002$).

Comparison of tank and field calls

The arrangement of pops in the recordings of bigeyes at North Reef, north-eastern New Zealand (see Materials and methods), was similar in most respects to those in recordings of captive fish. The majority of calls identified consisted of the three unfused pop train sound type (Fig. 1E). Band-pass filtering (9–700 Hz) of the vocalisations around their main frequency range showed that the overall waveform shape of several representative call types at North Reef was a close match to the tank recordings (Fig. 3A,B). Spectrograms and spectra from recordings of fish in captivity and at North Reef showed comparable time–frequency distribution (Fig. 3C,D) as well as frequency composition (Fig. 3E,F) of their dominant sound energy. The interquartile range (IQR) of the measurements of the acoustic parameters PP1 and f_{peak} showed overlapping values for captive and North Reef bigeye vocalisations (Fig. 4A,D), but this was not the case for the second pop period (PP2) and SD (Fig. 4B,C). The difference in the calls of captive and North Reef fish for the median values of PP1 (1.9 ms) was $<10\%$ of the lowest median value while the difference in f_{peak} (86 Hz) corresponded to the frequency resolution of the fast Fourier transform (FFT) used to plot the spectra.

Vocalisation source level

Root mean square source levels (SL_{rms}) were measured from 82 pops from calls that consisted of the triple pulse unfused type recorded at North Reef (Fig. 1E). Root mean square source level (SL_{rms}) was measured for the first pop of each call, which usually represented the highest amplitude within the call. The mean SL_{rms} of sound in octave band 1 [frequency bandwidth (f_{bw}) 89–178 Hz] was 100.2 ± 0.4 dB re. $1 \mu\text{Pa}$ at 1 m; band 2 (f_{bw} 178–355 Hz), 111.7 ± 0.3 dB re. $1 \mu\text{Pa}$ at

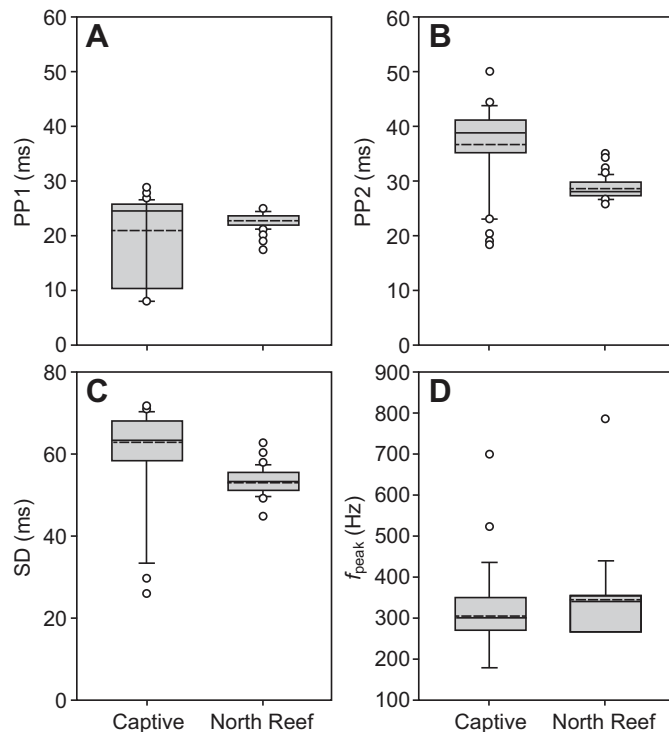


Fig. 4. Bigeye vocalisation parameters comparing captive ($N=42$) and wild (North Reef) recordings of the triple pop unfused call. Box outlines indicate the interquartile range (IQR), whiskers are ± 1.5 IQR and circles are outliers. Solid and dashed lines in the boxes are median and mean values, respectively. (A) Peak period between the first and second pop (PP1), (B) peak period between the second and third pop (PP2), (C) sound duration (SD) and (D) peak frequency (f_{peak}).

1 m; band 3 (f_{bw} 355–708 Hz), 113.1 ± 0.2 dB re. $1 \mu\text{Pa}$ at 1 m; and band 4 (f_{bw} 708–1410 Hz), 118.7 ± 0.7 dB re. $1 \mu\text{Pa}$ at 1 m (Fig. 5). When compared on a normalised dB scale, the relative composition of sound energy in octave bands 1, 2 and 3 compared well with similar call types from the captive fish recordings. Sound in band 4 was not comparable and showed higher energy content for the North Reef vocalisation, which can be attributed to the higher level of background noise at North Reef compared with the tank recordings. Consequently, sound level measurements in this band were not used in the subsequent analyses. With band 4 excluded, vocalisations were most energetic in band 3 followed by band 2 and band 1. The combined sound intensity in bands 1, 2 and 3 (band 123) produced a mean SL_{rms} of 115.8 ± 0.2 dB re. $1 \mu\text{Pa}$ at 1 m.

Habitat ambient noise and effective calling range

The noise level (NL_{rms}) in band 123 during the new moon was significantly louder than that during the full moon within every season [Mann–Whitney; summer (December), $U=14.1$, $P<0.001$; autumn (April), $U=9.2$, $P<0.001$; winter (June), $U=1142$, $P<0.001$; and spring (September), $U=8.0$, $P<0.001$]. Average ambient NL_{rms} was between 83 and 116 dB re. $1 \mu\text{Pa}$ during new moon periods (2 days either side of the lunar event) compared with 68–83 dB re. $1 \mu\text{Pa}$ during full moon periods. NL_{rms} was also significantly different between seasons for the same moon phase (Kruskal–Wallis; full moon, $H_3=213.5$, $P<0.001$; new moon, $H_3=197.4$, $P<0.001$). For both the full moon and new moon, ambient noise level (ANL) was highest in summer (83 dB re. $1 \mu\text{Pa}$ and 116 dB re. $1 \mu\text{Pa}$), whereas winter was the quietest for the new moon (82 dB re. $1 \mu\text{Pa}$) and autumn the quietest for the full moon (68 dB re. $1 \mu\text{Pa}$) (Fig. 6A–D). Because of

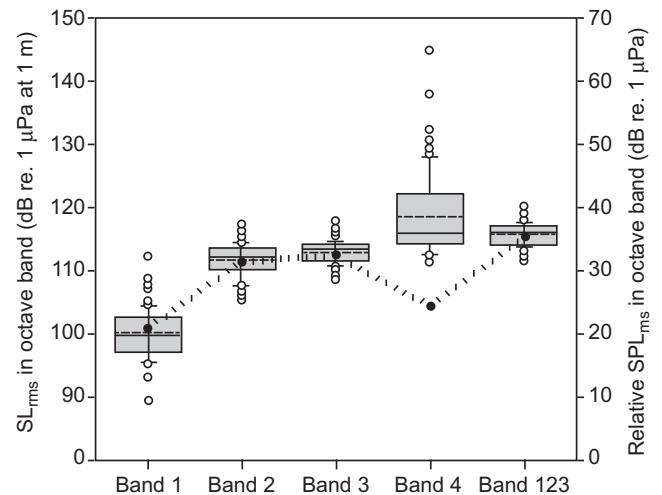


Fig. 5. Comparison of octave band source level measurements of a single sound pops within a bigeye call from the North Reef recordings ($N=82$). Box-plots show the root mean square source level (SL_{rms}) of sound in different octave bands. Box outlines indicate IQR, whiskers are ± 1.5 IQR and circles are outliers. Solid and dashed lines in the boxes are median and mean values, respectively. The mean octave band level for sound recorded in the tank is indicated by the dotted line across the box-plot. Wild and captive recordings are comparable using the relative dB scale on the right-hand y-axis.

the way effective calling range is calculated by incorporating the different levels of ambient background noise during different moon phases and seasons (see Materials and methods, Eqn 1), it directly influences the active space of the calls. Therefore, the effective calling range of sound in band 123 was greater during the full moon than during the new moon (Fig. 7). During full moon, the greatest calling range was observed in autumn and spring at 31.6 m and the shortest was in summer at 6.3 m (Fig. 7A). During new moon, the greatest calling range was observed in winter at 8.9 m, and the shortest was in summer at 0.6 m (Fig. 7B).

DISCUSSION

The present study has described for the first time the vocalisations of *P. adspersa*, the New Zealand bigeye, and the potential detection distances (active space) by conspecifics under ‘real world’ ambient noise regimes. The rapid decay of the pulsed sound and low Q (0.82 ± 0.02) indicated that the bigeye has a highly damped sound production mechanism typical of an extrinsic swim bladder muscle-generated sound (Fine et al., 2001, 2009; Radford et al., 2013). A high level of damping allows efficient temporal patterning of the pulses (Fine et al., 2004; Lindström and Lugli, 2000). This was evident from the variety of pulse combinations that comprised the various call types that were consistently observed for wild and captive fish. This may indicate the importance of the temporal character of the vocalisation for bigeye acoustic communication. The temporal and spectral characteristics of the bigeye sound differed from the vocalisation of another congeneric species, the silver sweeper *P. schwenkii*, found in tropical waters (Takayama et al., 2003). The silver sweeper produces a single sound type consisting of two to seven pulses with an average duration of 56 ms from the contraction of paired extrinsic sonic muscles that are attached to a double-chambered swim bladder, which is similar to the bigeye (Radford et al., 2013). Silver sweeper vocalisations cover a narrower frequency band-width (200 Hz) with three harmonically related frequency peaks. However, these results were obtained with the fish in air so are not directly comparable with the bigeye recordings

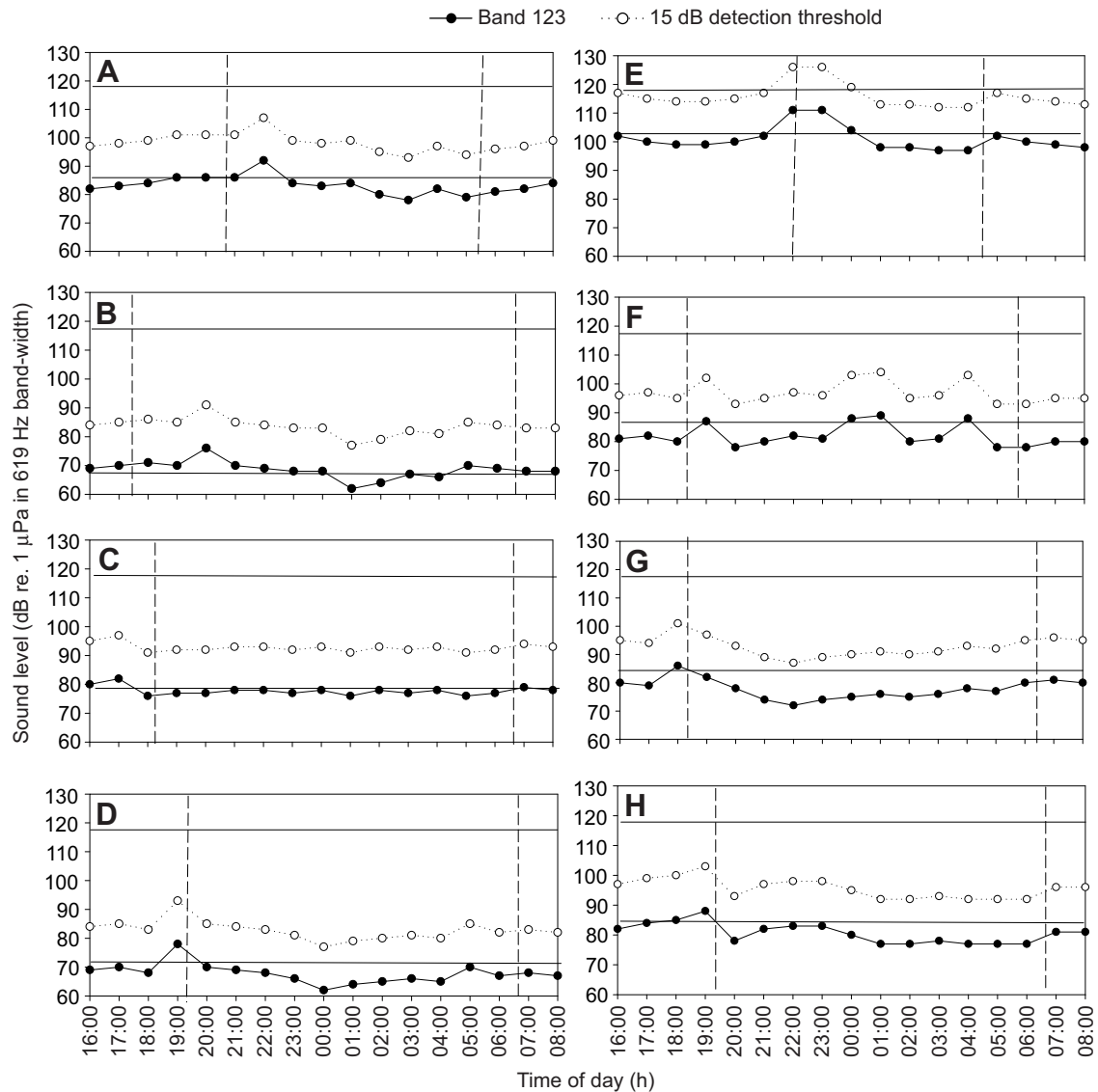


Fig. 6. Hourly octave sound level in band 123 and the 15 dB detection threshold during different seasons and lunar phases. Data were obtained during the full moon (A–D) and new moon (E–H) in summer (A,E), autumn (B,F), winter (C,G) and spring (D,H). Upper and lower solid horizontal lines indicate ambient noise level [ANL, mean root mean square noise level (NL_{rms}) + s.d.] and mean SL_{rms} , respectively. Vertical dashed lines indicate sunset and sunrise times.

reported in this study, which were taken both *in situ* and from captive fish in tanks.

Amongst coral reef fishes, the acoustic characteristics of their vocalisations are variable. Damselfishes (Pomacentridae) produce pulsatile sounds (one to 22 pulses) that have peak frequencies between 300 and 1000 Hz, pulse duration between 10 and 30 ms and pulse period between 8 and 120 ms (Amorim, 2006; Chen and Mok, 1988; Lobel and Kerr, 1999; Luh and Mok, 1986; Mann and Lobel, 1998; Myrberg et al., 1993; Parmentier et al., 2010, 2011). Squirrelfish (Holocentridae) and butterflyfish (Chaetodontidae) produce vocalisations with peak frequencies between 80 and 130 Hz (Parmentier et al., 2011) and 90 and 300 Hz (Boyle and Tricas, 2010; Tricas et al., 2006), respectively, with pulse duration in the range 30–60 ms. In terms of pulse number, pulse period and dominant frequency, the bigeye vocalisation characteristics were comparable to the lower range of the respective values for coral reef fishes. The pulse duration of the bigeye (<10 ms) was shorter although comparable with the ‘pop’ sounds recorded from nocturnal

planktivores by McCauley and Cato (2000) from the Great Barrier Reef, Australia. Despite the shortness of their temporal characteristics, bigeye pops were of sufficient duration that they could be resolved by the fish auditory system (Wysocki and Ladich, 2002, 2003). For example, it has been suggested that the minimum integration time for goldfish is 0.4 ms while for the majority of fish the minimum integration time may be slightly longer but within the range 1–10 ms (Wysocki and Ladich, 2002). The frequency resolution for the single pulse sound (7.9 ± 0.3 ms) and shortest pulse period (5.4 ± 0.2 ms) would be 126 and 185 Hz, respectively, which are shorter or close to the width of at least three critical bands (i.e. bands 2, 3 and 4) that encompass their vocalisation range (74–980 Hz). This would suggest that the bigeyes should also be able to resolve the spectral content of their vocalisation.

In captivity, the vocal activity of the bigeye peaked at dusk and remained relatively high throughout the night, which corresponds well with the nocturnally active nature of this species (Mooi, 2000). Therefore, it is possible that bigeye vocalisations are a significant

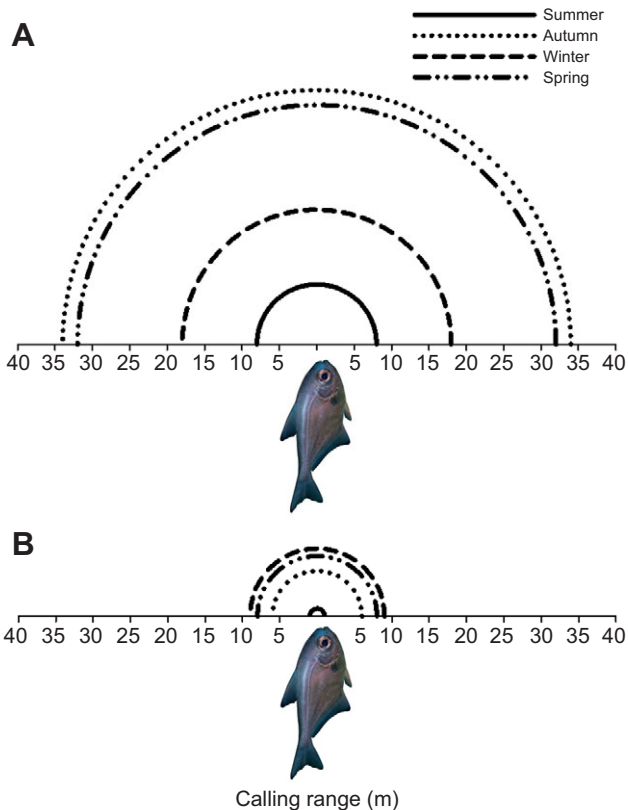


Fig. 7. Effective calling range of the bigeye vocalisation at North Reef during different seasons and lunar phases. (A) Full moon, (B) new moon.

component of nocturnal activity, and may function as a group cohesion cue or contact call, as has previously been suggested for some nocturnal coral reef planktivores (McCauley and Cato, 2000; Staaterman et al., 2014). In other animal groups such as mammals (Edds-Walton, 1997; Janik, 2000; Koda et al., 2008; Nakahara and Miyazaki, 2011; Sugiura, 2007) and birds (Cortopassi and Bradbury, 2006; Sharp and Hatchwell, 2006), the ability to maintain group cohesion using contact calls has been reported as biologically advantageous in a number of respects (Kondo and Watanabe, 2009). For example, calls could contain details about individuality and distance. However, to date there is no hard evidence that fish use vocalisations as contact calls.

Determining call SL_{rms} is imperative in the estimation of the range that sound produced by a sender could propagate and potentially be perceived by others. Measuring the SL_{rms} of a known fish species is challenging because audio-video recordings obtained with SCUBA are not suitable for analysis because of the interfering bubble noise from the diver (Cole et al., 2007; Radford et al., 2005). Consequently, 'silent' but less common methods such as remotely operated vehicles (ROVs) (Parsons et al., 2011; Sprague and Luczkovich, 2004) or divers on re-breather technology have been employed (Lobel, 2001). Sound recording using remote hydrophone arrays is also a viable option for estimating SL, and is particularly well suited to nocturnal recordings. Using a similar method to the current study, McCauley and Cato (2000) measured SL of three types of fish calls from the Great Barrier Reef and reported peak–peak SL for the 'pop' call to be 157 dB re. 1 μ Pa at 1 m, the 'trumpet' call to be 150 dB re. 1 μ Pa at 1 m and the 'banging' call to be 144–147 dB re. 1 μ Pa at 1 m, while Sprague and Luczkovich (2004) measured the SL of the 'purr' made by individual silver perch, *Bairdiella*

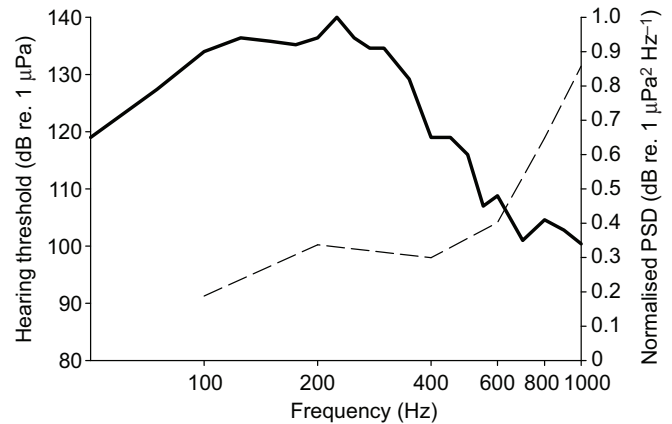


Fig. 8. Normalised power spectrum and audiogram of the bigeye vocalisation. The peak spectrum overlaps with the frequency band that the bigeye is most sensitive to. Audiogram data are from Radford et al. (2013). Dashed line is the hearing threshold and solid line the PSD.

chrysoira, from audio-video recordings using a ROV in the range 128–135 dB re. 1 μ Pa at 1 m. The SL of the bigeye (112–120 dB re. 1 μ Pa at 1 m) appeared relatively low in comparison with other studies. However, direct comparisons must be made with caution because of the differences in the frequency bandwidths, vocalisation duration and, most importantly, water depth from which the SL was measured.

The current study showed that the active space of fish vocalisations varies in relation to the ANL. At North Reef, the ANL varied considerably over different moon phases and seasons (Radford et al., 2008). The intensity of ambient noise was higher during the new moon than during the full moon, and peaked in summer. The smallest active space (radius <1 m) was thus observed during the summer new moon while the greatest active space was observed during the spring full moon (radius ~30 m). The spatial extent of these active space estimates argues that bigeye vocalisations could act as a contact call for maintaining school cohesion. Nonetheless, the active space for fish in general is modest in comparison to the active space of marine mammals. It has been reported that the spatial scale of the active spaces of dolphins and whales is of the order of several kilometres (>20 km), allowing them to maintain contact with each other over a large area of the ocean (Clark et al., 2009; Janik, 2000).

The ability of the bigeye to detect conspecific vocalisations within its active space will vary depending on the fish's hearing ability and the ANL of the environment. Using the auditory evoked potential (AEP) technique it has been shown that bigeyes are most sensitive to lower frequency sounds (100–400 Hz) (Radford et al., 2013), which is well within the dominant sound energy bandwidth of their vocalisation (Fig. 8). This highlights the fact that bigeyes have the capability to detect conspecific vocalisations and that the range of detection of conspecific calls within a school would be limited by ambient background noise.

In conclusion, the New Zealand bigeye produces a very distinct vocalisation that is different to that of its closest relative, the silver sweeper, which is widely found in tropical waters circumglobally. In our recordings, bigeye calls are the dominant vertebrate sound of the nocturnal soundscapes in a reef setting largely because of the relatively small proportion of soniferous fish found in New Zealand waters. The characteristics of the bigeye vocalisation, SL and the spatial scale of its active space reported in the current study

demonstrate the potential for fish vocalisations to function effectively as contact calls.

MATERIALS AND METHODS

Captive fish experiment

Capture and holding

Bigeyes from a single school were captured at a reef around the Outpost (36°17.421'S; 174°49.351'E), Leigh, New Zealand, by SCUBA divers using scoop nets to minimise injury. Captured fish were held in a flow-through filtered (200 µm) aerated seawater system (18°C and 34 ppt), and allowed to acclimatise to laboratory conditions for 4 weeks; they were fed *ad libitum* three times a week. The study was conducted under University of Auckland Animal Ethics Committee approval no. AEC727.

Characterising the bigeye vocalisation

Twenty fish measuring between 70 and 130 mm fork length were used throughout the experiments. Six non-consecutive continuous recordings each lasting 24 h were conducted in a plastic tank (1.65 m diameter; water depth 0.5 m). During sound recordings, fish were not fed and water flow and aeration were turned off to minimise extraneous noise. Experiments commenced at the same hour of the day (16:00 h) and were conducted between 30 December 2008 and 30 January 2009. Information for sunset and sunrise times was obtained from the astronomical database provided online by www.gaisma.com. Dusk and dawn times were defined as beginning 1 h before and lasting until 1 h after astronomical sunset and sunrise times.

For each experiment, sound was recorded continuously for 24 h with a calibrated HTI-96-MIN hydrophone (High Tech Inc., USA; sensitivity of -165 dB re. 1 V $1 \mu\text{Pa}^{-1}$ and a flat frequency response from 0.01 to 30 kHz) suspended in mid-water from the centre of the tank connected to a portable digital audio recorder (Sound Devices 722, WI, USA; sampling rate 44.1 kHz, 16 bit). Preliminary analysis showed that bigeye vocalisations contained frequency components less than the calculated minimum resonant frequency of 1662 Hz for the tank (Akamatsu et al., 2002) and indicated that fish vocalisation recordings were not distorted by the tank resonance.

Vocalisations were randomly selected from the total sound recording and analysed using RAVEN Pro 1.3 for Windows (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Cornell, NY, USA) and MATLAB® (Mathworks Inc., USA) with scripts specifically written for this work. Only sounds that could be clearly identified aurally and showed a clear visual representation in both oscillogram and spectrogram were considered for characterisation. Vocalisations or calls consisted of either a series of pops or a train of pops, where pops are made up of pulses. Acoustic measurements of the vocalisations were made after filtering the sound through a digital band-pass filter between 50 and 1200 Hz. The following sound parameters were measured; SD, the duration (ms) in which 90% of the sound energy is contained within a selection, defined by the limits of the parameter duration 90% in RAVEN; N_p , the number of pulses within a pop; f_{peak} , the frequency component with the highest amplitude in the entire sound; PP, the mean time (ms) elapsed between the peak amplitude of two consecutive pops; PP_w , the sound level at f_{peak} ; 10 dB Lf, the lower frequency limit with an amplitude of 10 dB less than the peak frequency; 10 dB Uf, the upper frequency limit with an amplitude of 10 dB less than the peak frequency; 10 dB BW, the range between the lower and upper frequency; 3 dB Lf, the lower frequency limit with an amplitude of 3 dB less than the peak frequency; 3 dB Uf, the upper frequency limit with an amplitude of 3 dB less than the peak frequency; 3 dB BW, the range between the lower and upper frequency; and Q , the damping coefficient. Sound duration was measured from spectrograms plotted using a 64-point FFT with 50% overlap, while PP_w was measured from oscillograms following band-pass filtering of the sound. Spectral parameters were measured from power spectra calculated using a windowed (Hann) 512-point FFT (filter bandwidth of 61.4 Hz; 50% overlap). Measurements of acoustic characteristics were conducted on the distinctive call categories based on number of pulses and nature, i.e. single pulse, double pulse (fused and unfused), triple pulse (fused and unfused) and multiple (>3) fused

pulses. Only calls of up to three pulses were characterised, as these are the most common calls produced, and the results show that the effective call space was mostly determined by the first and strongest pulse.

Diel patterns in vocalisation rates

The occurrence of vocalisation pops was counted from 10 s resolution time frames over the entire recording. The vocalisations were pooled among all individuals (20 fish) as they could not be traced to individual fish. Vocalisation rate was measured as the total count of vocalisations over each hour, and mean hourly vocalisation rates were calculated for different diurnal periods for data pooled across the six 24 h sampling events. Mean hourly vocalisation rates were calculated for the day (07:00 h–20:00 h), night (22:00 h–05:00 h), dusk (20:00 h–22:00 h) and dawn (05:00 h–07:00 h). These data failed normality and homogeneity tests. Therefore, the Friedman's test was used to test for statistical differences among the vocalisation rates for individual hours of the day and amongst the different periods as the same group of individuals was used throughout the experiment. Following a significant Friedman's test result, the *post hoc* multiple group comparisons were conducted with Tukey tests (Zar, 1999).

Field experiment

Recording and source level measurement

To determine the SL_{rms} of the bigeye vocalisation, a field experiment was conducted at North Reef, Leigh (36°15.45'S, 174°47.33'E), north-eastern New Zealand, in April 2011. During the recordings, the sea state was measured with the Beaufort scale at 0 or 0.5. The location was the same as for the habitat noise recordings (see below), which is a well-known habitat for bigeyes. Stereo recordings were conducted 1 m above the sea floor using two calibrated HTI-96-MIN hydrophones (High Tech Inc., USA) horizontally spaced 2 m apart. The hydrophones were each connected to a separate recording channel of a digital sound recorder (Edirol R09HR, Japan) encased in a waterproof housing. Recordings were made at 44.1 kHz (16 bit) continuously for 48 h.

Potential bigeye vocalisations were aurally selected from the entire record and were compared with the tank recordings in terms of their oscillogram, spectrogram, power spectra and acoustic characteristics. Only clear sounds detected at both hydrophones were used in SL measurements.

Calculation of SL using the differences in received level (RL) of the same sound arriving at two hydrophones and differences in the time of arrival of the sound was based on Cato (1998). Vocalisation root mean square RL (RL_{rms}) at both hydrophones was measured in four octave bands (i.e. bands 1–4) with their centre frequencies (f_c) at 125 Hz (f_{bw} 89–178 Hz), 250 Hz (f_{bw} 178–355 Hz), 500 Hz (f_{bw} 355–708 Hz) and 1000 Hz (f_{bw} 708–1410 Hz), respectively, using MATLAB® scripts modified from *octbank.m* by Christophe Couvreur. Time of arrival difference was measured from the cross-correlation of signals in both channels defined as the time at peak correlation using MATLAB® scripts specifically written for this purpose. SL_{rms} was measured over the integration time of 10 ms centred at the peak amplitude of the waveform, which was considered sufficient because fish in general are capable of resolving 10 ms or even shorter temporal resolution (Wysocki and Ladich, 2002).

Habitat ambient noise analyses

Habitat ambient noise was measured from the analyses of underwater sound recordings from North Reef over two moon phases (new moon and full moon) and four New Zealand austral seasons from December 2004 to October 2005 (Radford et al., 2008). Recordings were made using a calibrated omni-directional hydrophone (Sonatech BM216) connected to a DAT recorder (Sony TCD-D8, Japan) encased in a waterproof aluminium housing. A Unidata micrologger timer was used to program recordings of 5 min duration every hour on the hour over a period of 3 days centred on the day of the moon phase under consistent wind speed and sea conditions (sea state 2). Further details on these temporal recordings were described in Radford et al. (2008).

Octave analyses were used to characterise NL_{rms} during different seasons (summer, autumn, winter and spring), moon phases (full and new moon) and time of the day. Although the precise bandwidth of the auditory filters

for fish are unknown, it has been reported as being slightly larger than those found in other vertebrates (one-third octave band filters) (Fay, 1988) and is approximated by the octave band filter banks. Therefore, representing noise in octave bands was considered more meaningful and suitable to gauge the audibility of a signal in the presence of noise. The hourly NL_{rms} in bands 1, 2, 3 and 4 and total noise in these bands (band 123 f_{bw} 125–708 Hz) were obtained by averaging the measurements from four randomly selected 10 s sound samples taken from the hourly temporal recordings. Total noise in band 123 was plotted for the hours encompassing the time of sunset and sunrise (16:00 h to 08:00 h the following day) which included up to 5 h before and after the respective sun movement times. The average habitat ANL over this period was calculated as the mean of NL_{rms} plus 1 s.d.

The data did not conform to normality or homogeneity tests; therefore, the Mann–Whitney U -test was used to compare NL_{rms} between new moon and full moon periods within the same season, and the Kruskal–Wallis test was used to compare NL_{rms} among different seasons for the same moon phase (Zar, 1999).

Effective calling range estimation

For the purpose of this study, we assumed: (1) that signal detection is limited by the ambient noise; (2) that vocalisation SL does not vary in response to a varying ANL; and (3) equal omni-directional sensitivity of fish hearing. The sonar Eqn 1 used to describe the propagation of sound in the current study was modified from Clark et al. (2009):

$$SE = SL_{rms} - TL_{sp} - ANL - DT, \quad (1)$$

where SE is signal excess, which at $SE=0$ defines the 50% probability of signal detection (Clark et al., 2009; Urick, 1983); SL_{rms} is source level, defined as the root mean square sound pressure level at 1 m from the source; ANL is average habitat ANL, calculated as the mean hourly octave band level of noise (NL_{rms}) in the period described earlier plus the standard deviation; TL_{sp} is spherical spreading transmission loss, calculated as $20 \log[\text{range (m)}]$ (Mann, 2006); and DT is detection threshold, defined as the difference between signal and noise at the threshold sound level where signal can be perceived. There are no data on DT for fish; however, for sonar systems, as well as marine mammals, a DT of 10 dB is widely accepted (Clark et al., 2009; Kastelein et al., 2007). The current study used the DT value of 15 dB, which is considered an intermediate and rather conservative value (Kastelein et al., 2007). All of the sound intensity values (dB re. 1 μPa) and related sonar equation parameters were for a specified frequency band (octave bands) and were thus root mean square band level measurements. The effective calling range (r , Eqn 3) was derived from Eqn 2 when $SE=0$. The estimation of the active space for a single fish source was based on this r value. Increasing r indicates an increase in the radius of active space for call detection.

Solving for r in:

$$TL_{sp} = 20 \log r \quad (2)$$

gives r when $SE=0$. Thus:

$$r = 10^{(SL-ANL-DT/20)}. \quad (3)$$

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Competing interests

The authors declare no competing or financial interests.

Author contributions

S.G. and C.A.R. designed the experiments. S.G. conducted the experiments and analysed the results. S.G., C.A.R., J.C.M. and A.G.J. wrote the manuscript.

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