PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 2000 **355**, 1289-1293
doi: 10.1098/rstb.2000.0686

THE ROYAL SOCIETY

doi 10.1098/rstb.2000.0686

Patterns of fish calling in a nearshore environment in the Great Barrier Reef

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Long-term sea-noise statistics have been obtained from a region of the central section of the Great Barrier Reef. Fish calling was a major contributor to sea-noise levels. Calling was either in choruses, where groups of fishes called *en masse*, or as isolated calls repeated *ad nauseam*. Four calling types predominated, with each displaying unique call characteristics and calling patterns through time and space. Analysis of call types offered information on the fish's calling physiology, behaviour and, through the call's interaction with the local environment, on the location of the caller. Call types ranged from less than 10 ms to several seconds long, and were comprised from one to nearly 40 pulses. The structure of each pulse was related to swim-bladder mechanics; normally swim-bladders were lightly damped. Fish calling was most common during the Australian summer with one call type also displaying lunar trends. All calls had daily patterns of sound production with highest activity levels generally at night. There was some spatial separation of zones of highest call rates, but sources avoided competition for the 'sound space' primarily by offsetting the time of chorus or maximum call rate. On some occasions, a call type attributed to nocturnal planktivorous fishes may have ensonified much of the Great Barrier Reef.

Keywords: fishes; acoustic; behaviour; chorus

1. INTRODUCTION

The production and interpretation of acoustic signals by marine animals is a common phenomenon (see Tavolga 1964; Moulton 1964; Hawkins & Myrberg 1983, for reviews). Biologically produced sounds have been shown to be produced in a variety of contexts, such as in reproductive displays, territorial defence, feeding sounds or echolocation. In addition to biologically produced signals, marine animals are continually subjected to physically produced sounds. Sources include wind-generated sea noise, rainfall, breaking surf, natural seismic noise, low-frequency swell noise or, for polar animals, ice movements. Such acoustic cues, either of biological or of physical origin, may be vital to many animals for navigation purposes, in mediating social and reproductive behaviour, for feeding activity, for predator avoidance or in perception of their environment.

Many studies have investigated the behavioural significance of sounds from tropical fishes (e.g. Myrberg *et al.* 1986). However, few workers report the time patterns, space patterns and levels of fish calling likely to be encountered in field situations.

2. MATERIAL AND METHODS

From 1987 to 1994 an experimental listening system was operated off Cowley Beach, near Innisfail, North Queensland, Australia, to describe long-term patterns in fish calling from a nearshore tropical environment. Measurements from small boats and autonomous recording packages supplemented the fixed system. A brief summary of the differences in fish call structure and fish calling patterns is presented, along with speculation on their implications.

The study region showing the location of the experimental hydrophone system is shown in figure 1. The fixed system comprised two calibrated General Instruments (USA) Z3B hydrophones, a custom-made calibration-tone generator, line amplifiers and rechargeable batteries mounted on the sea floor 2 km SSE of Kent Island, and cabling to the Island. A custom-made VHF radio link transmitted the signal to a control and listening hut at Cowley Beach. Additional to the sea-floor system, sea-noise recordings were made using calibrated Edmunds, Massa TR-1025C or Clevite (USA) CH17 hydrophones from small vessels or deployed custom-made housing systems. These were self-contained packages comprising an external hydrophone (Massa TR-1025C) and internal batteries, timers, pre-amplifiers and an analogue or digital tape deck (Sony WMD6C or TCD-D7, Japan). The response of all systems was periodically checked using pink- or white-noise input through the pre-amplifier–tape-deck combination. Sea-noise recordings were analysed by the following methods: counting call types through time; using Bruel & Kjaer (Denmark) 1/3 octave filters; spectral and time analysis using a Hewlett Packard (USA) HP 3582-A spectral analyser or a Data Physics (USA) DP430 signal-processing card in a PC; or digitizing the calls and analysing in the Matlab (The Math Works, Inc., USA) signal-processing environment.

3. RESULTS

Four fish sound types (sources) dominated sea-noise recordings. At least one of these sound types may be

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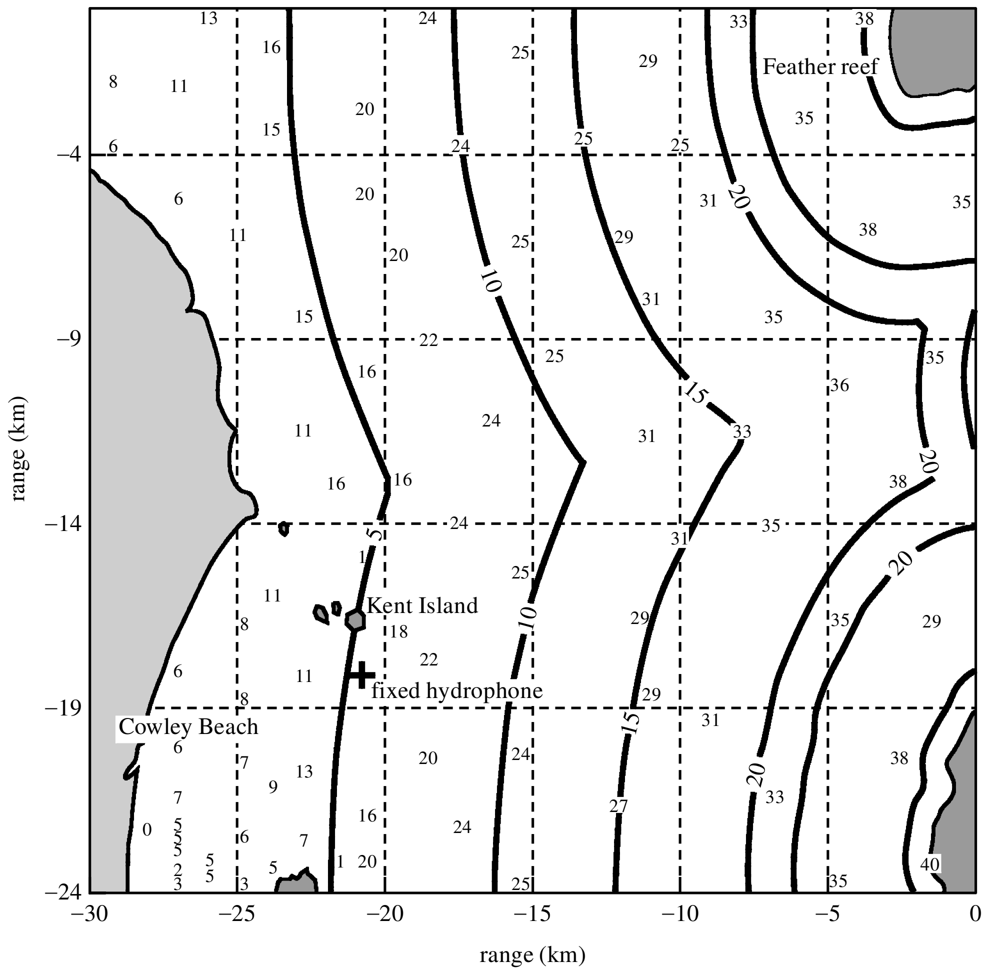

Figure 1. Location of study region showing position of fixed hydrophone system, spot depths (small font) and contours of the level above ambient in the 500 Hz 1/3 octave for a fish chorus ('pop' type). Coral reefs are evident to the east (north up) and the mainland to the west. The range scale has been arbitrarily centred on Feather Reef (17°32′ S, 146°23′ E).

produced by more than one species. Two sources always produced distinct calls separated in time but which regularly reached such high calling rates that they had a major impact on sea-noise levels. Two sources were predominantly heard in choruses, where schools of fishes called *en masse*. Fish chorus levels reached 35 dB above expected typical no-chorus background conditions. The sources were described as sounding like a 'pop' (chorus), 'trumpet' (chorus), 'drumming' (individual calls) and 'banging' (individual calls). The identification of species responsible for call types was based on gill-net catches, remotely operated vehicle observations, similarities to published spectrograms in the literature, comparisons of the morphology of sound-generating swim-bladders from fishes known to be present in the region with call characteristics, and fish habits matched to the calling habits. The 'pop' chorus was believed to be produced by nocturnally active planktivorous fishes of the families Priacanthidae and Holocentridae foraging in the water column. The 'trumpet' chorus was produced by schools of *Terapon theraps* (family Terapontidae). This fish was capable of producing at least three call types, the most common being the 'trumpet' but also a 'squawk' (as heard in sea-noise recordings) and an alarm call (heard from captive fishes). From sea-noise recordings the alarm call was only heard near bottom-set gill nets, possibly from fishes trapped in the net. The third call type, 'drumming', was believed to be produced by a member of the family Sciaenidae, while the species responsible for the fourth call, 'banging', was not identified but may have been a catfish.

The call types were considerably different, with representative waveforms shown in figure 2. The background noise is evident as the low-level signal between pulses and at the start and end of each trace. The calls are thus readily differentiated from the background, since they are more than ten times the amplitude. Characteristics of each call are given in table 1. Details of call structure were derived from analysis of waveforms which were characteristic of amplitude-modulated signals. The carrier frequency, evident in the cyclic rate within a pulse, was interpreted as the swimbladder resonant frequency, while the pulse repetition rate was interpreted as the rate of excitation of the swim-bladder (by muscular contraction). Individual spectra showed a broad peak at the swim-bladder resonance with sharper peaks at frequency intervals equal to the pulse repetition rate. Swim-bladder resonance values were derived from cycles within each swim-bladder-produced pulse, and damping was determined from the logarithmic decay rate of cycles in a 'clean' pulse (no overlapping calls or multipath arrivals of the same pulse). Source-level values were derived from the multipath arrival times and level differences of

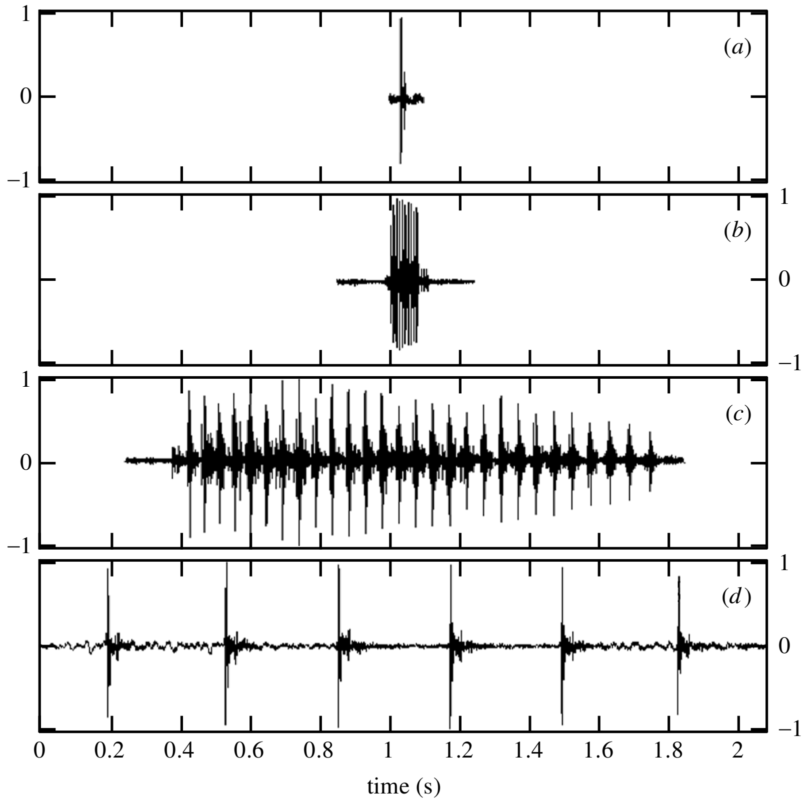

Figure 2. Waveforms of four calls: (*a*) 'pop', (*b*) 'trumpet', (*c*) 'drumming' and (*d*) 'banging'. Surface reflections were evident in all calls. The vertical axis (amplitude) has been normalized.

Table 1. *Details of call types with typical range or mean values of parameters given*

call	source	no. of pulses	total call length	pulse repetition rate (Hz)	swim-bladder resonance (Hz)[a]	pulse damping[b]	source level at 1 m
'pop'	nocturnal planktivores	1	< 10 ms	—	400–700	normally low, $Q = 5.8$	157 dB re 1 μPa p-p[c]
'trumpet'	*T. theraps*	9–16	79–105 ms	110–140	525–1129	normally low, $Q = 5.1$	150 dB re 1 μPa rms
'drumming'	possibly Sciaenidae	22–38	1–2.8 s	35	250–400	low	—
'banging'	unknown	5–13	1–2.7 s	4	280–420	low	144–147 dB re 1 μPa rms[d]

[a] Given as range of call spectral peak frequencies.
[b] Fishes were observed to vary damping, especially in alarm calls (not shown).
[c] p-p is peak to peak.
[d] Source level given as range of maximum individual pulse within a call.

individual pulses using the method described in Cato (1998). Usually the direct and surface-reflected arrivals without bottom reflection were used and distances were so short that spherical spreading loss would apply. Geographical and seasonal (same location) variability occurred in call characteristics, particularly for calls comprised of many pulses. This variability tracked local water temperatures.

4. DISCUSSION

A detailed analysis of calls offers information on the calling morphology and physiology of sound-production mechanisms. For example the *Terapon* sound-producing organ has been described by Schneider (1964) as comprising a two-chambered swim-bladder driven by laterally paired muscles attached to the anterodorsal surface of the anterior swim-bladder chamber, with these muscles extending to attach to the rear of the skull. Schneider described the chambers as separated by a narrow open tube surrounded by a sphincter muscle. The *Terapon* calls recorded in the field were made up of a series of pulses (figure 2), with each pulse considered to result from a single muscle contraction applied to the swim-bladder. Thus, muscle contraction rates equalled the pulse spacing. Pulse repetition rates of up to 200 Hz were measured in the *Terapon*, but for these higher-frequency rates it was not clear whether each pulse derived from the two laterally paired muscles contracting simultaneously or asynchronously, in which case a pulse rate double the possible muscle contraction rate could be obtained.

The spectral content of individual *Terapon* calls and choruses showed a broad peak (or peaks) related to the swim-bladder resonant frequency with sharp spectral peaks separated by the muscle contraction rate and extending into higher frequencies. For example, in the *Terapon* 'trumpet' call for fishes in 30 m of water, the swim-bladder resonant spectral peak was centred at around 920 Hz and extended over 600 and 800 Hz for the 3 and 6 dB down points, respectively. In contrast, sharp peaks separated by the muscle contraction rate of 122 Hz were observed, extending into higher frequencies.

It was found that the 'trumpet' and 'squawk' calls recorded from the *Terapon* differed in frequency content, with the 'trumpet' type having a single spectral peak and the 'squawk' type having several spectral peaks. There was evidence that this difference was due to the state of the passageway connecting the two swim-bladder chambers. With the sphincter muscle relaxed and the passageway open, the single spectral peak was believed to be produced by the entire swim-bladder oscillating with each muscle contraction. With the muscle constricted and the passageway blocked, spectral peaks related to the respective volumes of the anterior, posterior and total swim-bladder were believed to be produced.

In some *Terapon* time-averaged chorus spectra, the intensity measured at the pulse-rate frequency was often greater than that at the frequency of the swim-bladder spectral peak. This acted to enhance the call bandwidth into lower frequencies. This has been observed for other fish choruses analysed. Given that the fishes have precise control over the muscle contraction rate, whereas they have less control over the swim-bladder resonant frequency (this is a function of the depth, the swim-bladder volume, the swim-bladder wall characteristics and the applied damping), then it is possible that for some fishes the muscle contraction rate conveys more information than the swim-bladder resonant frequency. This may explain the mismatch between reported swim-bladder resonant frequencies and the lower, 'best hearing' frequency range of fishes.

The calls displayed in figure 2 differ considerably in total length and structure. The 'pop' call, at < 10 ms, was almost 300 times shorter than a 'drumming' or 'banging' call (table 1). One could speculate that this implies potential differences in the mechanics of the hearing systems used by the two fishes and the neural processing involved. The shorter signals would not allow temporal integration of nerve firings. The differences in call length imply differences in frequency analysis capabilities. A single call of 10 ms would give a minimum frequency discrimination of 100 Hz, whereas the calls lasting several seconds could potentially be analysed for components down to a few Hertz. The possibility that these longer low-frequency signals are adapted for sediment-borne transmission paths has also been suggested (e.g. D'Spain *et al*. 1997).

Each source displayed distinct calling patterns in time and space. All sources reached their highest calling rates or chorus levels during the Australian summer, with only the 'pop' chorus heard over the winter months. Lunar patterns were present in the 'pop' chorus with highest levels recorded over new-moon periods. All calls had marked daily and spatial patterns. Differences in the locations of aggregations of calling animals and/or the time of each source's optimal call rate or chorus time, separated the choruses so that competition for the 'acoustic space' over the 50–2500 Hz bandwidth was minimal. For example, a typical summer daily cycle of calling behaviour at the location of the fixed hydrophone system was as follows. Between 10.00 and 13.00 the 'banging' sound predominated, although some 'drumming' occurred. Towards the late afternoon the 'banging' call rate decreased while the 'drumming' call rate increased, reaching a peak at 18.30 or just on dusk. 'Drumming' calling then abruptly stopped soon after dusk, and on some occasions was followed by the 'popping' chorus produced by loose schools of nocturnal planktivores moving through the area. By 22.00 the planktivorous fishes had moved on, then around 23.00–24.00 schools of chorusing *Terapon* moved through. Between 01.00 and 03.00 these choruses had disbanded, and the 'banging' noise rate began to increase back to its 10.00–13.00 peak, along with the occasional 'drumming' call. Thus, although all four sources could, on occasion, be present at the same location throughout a 24 h period, temporal separation of the times of maximum call rate or chorus time assured that there was minimal competition for the 'sound space'. Despite this there were some interactions between call types. There were often instances in the daytime when 'drumming' and 'banging' call rates were at moderate levels. During these periods a 'drumming' call seemed to stimulate a 'banging' call, with call increment analysis revealing that 25% of the 'banging' calls interrupted or immediately followed 'drumming' calls.

Moving seaward from the coast, as shown in figure 1, it was found that the 'drumming' calling occurred between approximately the 10 and 22 m depth contours and was distributed throughout this region with the zone of maximum call rate centred along the 20 m depth contour. The 'banging' calling overlapped this range, but extended further seaward to about the 30 m depth contour, with the zone of maximum call rate approximately at the 22 m depth contour. Thus, although there was overlap in the areas where the calls were heard, the zones of maximum call rate were slightly offset, acting to reduce competition. The *Terapon* choruses were produced by schools of fishes. Measurements further south in 10 m water depth found schools to be of the order of several kilometres across with a chorus heard out to 5–8 km from its centre. These choruses were believed to be restricted to within the 30 m contour. The 'pop' choruses produced by the nocturnally active planktivores were more dispersed and widespread than the *Terapon* choruses. Although the fishes were believed to emanate predominantly from near the reef systems in the region, these choruses were regularly heard in large bands at up to 15 km from what were believed to be their parent reefs. Using several transects of chorus measurements extrapolated to a wider region, the extent of a 'pop' chorus is shown in figure 1 by the levels above background (calm conditions) in the 500 Hz 1/3 octave. These transect measurements showed the chorus to be active out to 5 km from the parent reef. On occasions these choruses were massive events, heard or detected from the 10 m contour and creating elevated sea-noise levels at their chorus spectral-peak frequency all the way across the region shown in figure 1. Given that similar choruses have been recorded many hundreds of kilometres north and south of this region, then it is possible that at certain times of the year a large proportion of the Great Barrier Reef system may be ensonified by these fishes.

The high source levels and the prodigious calling behaviour observed suggest acoustic cues are of major importance to the species concerned. At this stage we can only speculate on call function. Seasonal patterns suggest a reproductive-related function for the 'drumming', 'banging' and *Terapon* calling. The consistency of the 'pop' calling suggests other functions also, such as the possibility that calls are used to maintain loose school structure throughout the night and so allow the fishes to track planktonic prey aggregations.

This programme was funded by the Australian Defence Science and Technology Organisation.

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