

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

Robert D. McCauley and Douglas H. Cato

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Patterns of fish calling in a nearshore

onvirenment in the Great Barrier Beef **Fatterns of fish calling in a nearshore

environment in the Great Barrier Reef**

Robert D. McCauley1* **and Douglas H. Cato**²

¹*Department of Marine Biology, James Cook University,Townsville, Queensland 4811, Australia* ¹Department of Marine Biology, James Cook University, Townsville, Queensland 4811, Australia
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Long-term sea-noise statistics have been obtained from a region of the central section of the Great Barrier
Long-term sea-noise statistics have been obtained from a region of the central section of the Great Barrier
Reef. 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 fi 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 fi 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 ea 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 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 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, 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 me long, and were comprised from one to nearly 40 pulses. The structure of each pulse was related to swimbladder mechanics; normally swim-bladders were lightly damped. Fish calling was most common during the Australian summer 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 wit 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 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 may have ensonified much of the Great Barrier Reef.

Keywords: fishes; acoustic; behaviour; chorus

1. INTRODUCTION

The production and interpretation of acoustic signals by **EXECTED TRACES 1988**
The production and interpretation of acoustic signals by
marine animals is a common phenomenon (see Tavolga
1964: Moulton 1964: Hawkins & Myrberg 1983, for 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 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 repro-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 reproreviews). Biologically produced sounds have been shown
to be produced in a variety of contexts, such as in repro-
ductive displays, territorial defence, feeding sounds or
echological in addition to biologically produced si 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 phys ductive 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 se echolocation. In addition to biologically produced signals, marine animals are continually subjected to physically produced sounds. Sources include wind-generated sea 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 moveproduced sounds. Sources include wind-generated sea
noise, rainfall, breaking surf, natural seismic noise, low-
frequency swell noise or, for polar animals, ice move-
ments. Such acoustic cues, either of biological or of noise, rainfall, breaking surf, natural seismic noise, low-
frequency swell noise or, for polar animals, ice move-
ments. Such acoustic cues, either of biological or of
physical origin may be vital to many animals for navi frequency swell noise or, for polar animals, ice move-
ments. Such acoustic cues, either of biological or of
physical origin, may be vital to many animals for naviga-
tion purposes in mediating social and reproductive ments. Such acoustic cues, either of biological or of
physical origin, may be vital to many animals for naviga-
tion purposes, in mediating social and reproductive
behaviour for feeding activity for predator avoidance or 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. tion purposes, in mediating social and reproductive haviour, for feeding activity, for predator avoidance or
perception of their environment.
Many studies have investigated the behavioural signifi-
nee of sounds from tronical fishes (e.g. Myrberg et al.

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, a cance 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 1986). However, few workers r
space patterns and levels of t
encountered in field situations. **2. MATERIAL AND METHODS**

2. MATERIAL AND METHODS
From 1987 to 1994 an experimental listening system was oper-From 1987 to 1994 an experimental listening system was operated off Cowley Beach, near Innisfail, North Queensland, ated 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 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
encoulation on their implications fixed system. A brief summary of
structure and fish calling pattern
speculation on their implications.
The study region showing the speculation on their implications.
The study region showing the location of the experimental

hydrophone system is shown in figure 1. The fixed system 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
hydrophone: a system mode solibration tone generator 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
annihitary and rechargeable betteries mounted on t 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 customamplifiers 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 but at Coular Baneb Additio 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,
see poise, recordings, were mode, 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 TP 1025C ar Clauite (USA) CH17 b 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 outom made bousing 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
wave self-contained perhapse commission on automal Massa TR-1025C or Clevite (USA) CHI7 hydrophones from
small vessels or deployed custom-made housing systems. These
were self-contained packages comprising an external hydrophone
(Masse TR 1025C) and internal batteries time 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 and an analogue or digital tape deck (Sony WMD6C or TCDusing pink- or white-noise input through the pre-amplifier-tapedeck combination. Sea-noise recordings were analysed by the 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
 R_{nu} , R_{ion} (Denmark) 1/2 act 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 Haulatt Bosband (USA) HP 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 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 Ins. USA) signal processi analyser or a Data Physics (USA) DP430 signal-processii
in a PC; or digitizing the calls and analysing in the Matla
MathWorks, Inc., USA) signal-processing environment. 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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Technology, Curtin University, GPO Box U 1987, Perth
Australia 6845, Australia (r.mccauley@cmst.curtin.edu.au).

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 evi Figure 1. Location of study region showing position of fixed hydrophone system, spot depths (small font) a
level above ambient in the 500 Hz 1/3 octave for a fish chorus ('pop' type). Coral reefs are evident to the ea
mai

produced by more than one species. Two sources always
produced distinct calls separated in time but which 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 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 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 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 abov 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 po-chorus background conditions. The 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 'non' (chor called *en masse*. Fish chorus levels reached 35dB above
expected typical no-chorus background conditions. The
sources were described as sounding like a 'pop' (chorus),
'trumpet', (chorus), 'drumming', (individual, calls), 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 speci 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 c '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, similariti 'banging' (individual calls). The identification of species
responsible for call types was based on gill-net catches,
remotely operated vehicle observations, similarities to 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 fr remotely operated vehicle observations, similarities to
published spectrograms in the literature, comparisons of the morphology of sound-generating swim-bladders from ca
fishes known to be present in the region with call c the morphology of sound-generating swim-bladders from
fishes known to be present in the region with call characthe morphology of sound-generating swim-bladders from
fishes known to be present in the region with call charac-
teristics, and fish habits matched to the calling habits.
The 'pop' chorus was believed to be produced by noc 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 noctur-
nally active planktivorous fishes of the families P teristics, and fish habits matched to the calling habits.
The 'pop' chorus was believed to be produced by noctur-
nally active planktivorous fishes of the families Pria-
canthidae and Holocentridae foraging in the water The 'pop' chorus was believed to be produced by noctur-
nally active planktivorous fishes of the families Pria-
canthidae and Holocentridae foraging in the water nally active planktivorous fishes of the families Priacanthidae and Holocentridae foraging in the water
column. The 'trumpet' chorus was produced by schools of
Ternhan therabs (family Terapontidae) This fish was canable *Terapon the capacity* 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 tunes, 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 'squauk' (as bea 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 seaof 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 wa 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 hottom-set gill nets possibly from fish hoise 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 *Phil. Trans. R. Soc. Lond.* B (2000)

trapped in the net. The third call type, 'drumming', was
trapped in the net. The third call type, 'drumming', was
believed to be produced by a member of the family Sciaetrapped in the net. The third call type, 'drumming', was
believed to be produced by a member of the family Sciae-
nidae, while the species responsible for the fourth call trapped in the net. The third call type, 'drumming', was
believed to be produced by a member of the family Sciae-
nidae, while the species responsible for the fourth call,
'banging', was not identified but may have been a 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 repre-Suarging', 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 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 sentative 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 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 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 struct 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 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 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 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 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 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 muscula 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 a 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, peak 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 appear a 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 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 damning 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 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 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 arri-
vals of the same pulse). Source-level values were de was determined from the logarithmic decay rate of cycles
in a 'clean' pulse (no overlapping calls or multipath arri-
vals of the same pulse). Source-level values were derived
from the multipath arrival times and level diff 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

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time (s)
Figure 2. Waveforms of four calls: (*a*) 'pop', (*b*) 'trumpet', (*c*) 'drumming' and (*d*) 'banging'. Surface reflections were evident in Figure 2. Waveforms of four calls: (a) 'pop', (b) 'trumpet', (c) all calls. The vertical axis (amplitude) has been normalized. 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		< 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 μ Pa rms
'drumming'	possibly Sciaenidae	$22 - 38$	$1 - 2.8s$	35	$250 - 400$	low	
'banging'	unknown	$5 - 13$	$1-2.7s$	4	$280 - 420$	low	144–147dB re $1 \mu Pa$ 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 puls

 $\text{``Source level given as range of maximum individual pulse within a ca}$
individual pulses using the method described in Cato
(1998) I Isually the direct and surface-reflected arrivals 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 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 Geogr (1998). Usually the direct and surface-reflected arrivals
without bottom reflection were used and distances were so
short that spherical spreading loss would apply. Geogra-
phical and seasonal (same location) variability o without bottom reflection were used and distances were so
short that spherical spreading loss would apply. Geogra-
phical and seasonal (same location) variability occurred
in call characteristics, particularly for calls co 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 phical and seasonal (same location) variability occurred
in call characteristics, particularly for calls comprised of
many pulses. This variability tracked local water temperatures.

4. DISCUSSION

4. DISCUSSION
A detailed analysis of calls offers information on the
lling morphology and physiology of sound-production 4. **DISCUSSION**
A detailed analysis of calls offers information on the
calling morphology and physiology of sound-production
mechanisms. For example the *Teraton* sound-producing A detailed analysis of calls offers information on the calling morphology and physiology of sound-production
mechanisms. For example the *Terapon* sound-producing mechanisms. For example the *Terapon* sound-producing
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l.
organ has been described by Schneider (1964) as
comprising a two-chambered swim-bladder driven by organ has been described by Schneider (1964) as
comprising a two-chambered swim-bladder driven by
laterally paired muscles attached to the anterodorsal 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 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 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 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 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 Terator calls recorded in the field were made up of a Schneider described the chambers as separated by a narrow open tube surrounded by a sphincter muscle.
The *Terap on* calls recorded in the field were made up of a series of pulses (figure 2) with each pulse considered to 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 *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 equ 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 20 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 *Terahan* but for these highe 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 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

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derived from the two laterally paired muscles
contracting simultaneously or asynchronously in which derived from the two laterally paired muscles
contracting simultaneously or asynchronously, in which
case a pulse rate double the possible muscle contraction 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 contracting simultaneously or asynchronously, in which
case a pulse rate double the possible muscle contraction
rate could be obtained. See a pulse rate double the possible muscle contraction
te could be obtained.
The spectral content of individual *Terapon* calls and
oruses showed a broad neak (or neaks) related to the

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 choruses showed a broad peak (or peaks) related to the
swim-bladder resonant frequency with sharp spectral 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 swim-bladder resonant frequency with sharp spectral
peaks separated by the muscle contraction rate and
extending into higher frequencies. For example, in the
Terahon 'trumpet' call for fishes in 30 m of water the 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 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 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 around 920Hz and extended over 600 and 800Hz for
the 3 and 6dB down points, respectively. In contrast,
sharp peaks separated by the muscle contraction rate of
122Hz were observed extending into higher frequencies sharp peaks separated by the muscle contraction rate of 122 Hz were observed, extending into higher frequencies. France peaks separated by the muscle contraction rate of 2 Hz were observed, extending into higher frequencies.
It was found that the 'trumpet' and 'squawk' calls corded from the *Tembon* differed in frequency content

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 a 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 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 s 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 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 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 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 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 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 nassageway blocked spectral peaks related to th 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 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 the passageway blocked, spectral peaks rel
respective volumes of the anterior, posterio
swim-bladder were believed to be produced.
In some *Tembon* time-averaged chorus pective volumes of the anterior, posterior and total
im-bladder were believed to be produced.
In some *Terapon* time-averaged chorus spectra, the
rensity measured at the pulse-rate frequency was often

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 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 oth 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 pre 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 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 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 denth the swimcontrol over the muscle contraction rate, whereas they
have less control over the swim-bladder resonant
frequency (this is a function of the depth, the swimhave 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 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 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 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 swiminformation 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 This may explain the mismatch bet
bladder resonant frequencies an
hearing' frequency range of fishes.
The calls displayed in figure 2.0 adder resonant frequencies and the lower, 'best
aring' frequency range of fishes.
The calls displayed in figure 2 differ considerably in
callerath and structure The 'pop' call at < 10 ms was

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' The calls displayed in figure 2 differ considerably in total length and structure. The 'pop' call, at $\lt 10 \text{ ms}$, was almost 300 times shorter than a 'drumming' or 'banging' call (table 1). One could speculate that this total length and structure. The 'pop' call, at $\lt 10 \text{ ms}$, 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 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 potential differences in the mechanics of the hearing involved. The shorter signals would not allow temporal 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 canabilit 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 frequenc 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 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 composingle call of 10 ms would give a minimum frequency discrimination of 100 Hz, whereas the calls lasting
several seconds could potentially be analysed for compo-
nents down to a few Hertz. The possibility that these
longer low-frequency signals are adapted for sedimentseveral seconds could potentially be analysed for components down to a few Hertz. The possibility that these longer low-frequency signals are adapted for sediment-
horne transmission paths has also been suggested (e.g. nents 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) longer low-frequency signals are adapted for sediment-
borne transmission paths has also been suggested (e.g.
D'Spain *et al.* 1997). rne transmission paths has also been suggested (e.g.
Spain *et al.* 1997).
Each source displayed distinct calling patterns in time
d space. All sources reached their highest calling rates

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 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 *Phil. Trans. R. Soc. Lond.* B (2000)

intensity measured at the pulse-rate frequency was often
intensity measured at the pulse-rate frequency was often
intensity measured at the pulse-rate frequency was often
intensity measured at the pulse-rate frequency was the 'pop' chorus heard over the winter months. Lunar
natterns were present in the 'pop' chorus with highest 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 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 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 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 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, senarated the choruses so that competition for 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 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 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 by and calling '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 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 'drumcalling behaviour at the location of the fixed hydrophone
system was as follows. Between 10.00 and 13.00 the
'banging' sound predominated, although some 'drumsystem was as follows. Between 10.00 and 13.00 the

"banging" sound predominated, although some 'drum-

ming' occurred. Towards the late afternoon the 'banging'

call rate decreased while the 'drumming' call rate banging' sound predominated, although some 'drumming' occurred. Towards the late afternoon the 'banging'
call rate decreased while the 'drumming' call rate
increased reaching a neak at 18.30 or just on dusk '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. `Drum-
ming' calling then abruntly stopped soon after dusk, a call rate decreased while the 'drumming' call rate
increased, reaching a peak at 18.30 or just on dusk. 'Drum-
ming' calling then abruptly stopped soon after dusk, and
on some occasions was followed by the 'popping' chorus 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 ming' 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 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 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 *Terahan* moved through Between 01.00 and 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 dishanded and the 'banging' 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' 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 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 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 s 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 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 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 ca 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 types. There were often instances in the daytime when 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 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 '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 o 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 stimulate a 'banging' call, with call in
revealing that 25% of the 'banging' calls.
immediately followed 'drumming' calls.
Moving seaward from the coast as sho wealing that 25% of the 'banging' calls interrupted or
mediately followed 'drumming' calls.
Moving seaward from the coast, as shown in figure 1, it
as found that the 'drumming' calling occurred between

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 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 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 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 overlanned this range, but extended 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 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 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 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 beard, the zones of maximum 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 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 *Teraton* choruses were produced by schools of 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 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 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 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 3 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 noctur choruses were believed to be restricted to within the 30 m
contour. The 'pop' choruses produced by the nocturnally 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 *Terahan* choruses. Although the fishes wer 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 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 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 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 extranolated to a wider region, the 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 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 oct 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 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 occ 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

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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 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 kilolevels 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 kilo-
metres north and south of this region, then it is possib 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 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 metres 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 fishes. 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

The high source levels and the prodigious calling importance to the species concerned. At this stage we can 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' 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 *Terahan* calling. The consistency of t 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 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 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 fishe 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 prev aggregations possibility that calls are used to maintain loose school structure throughout the night and so allow the fishes to track planktonic prey aggregations.

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