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Fish Vocalisation:

Understanding its biological role from temporal and spatial characteristics

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A thesis submitted in partial fulfillment of the requirements for the degree of

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ABSTRACT

In the shallow coastal waters of New Zealand, sounds of biological origin dominate the lower frequency spectrum of the underwater soundscape. While the sounds of urchin and snapping shrimp have been well described, those of fish are poorly understood. Utilising sound recordings taken from a reef in the Cape Rodney to Okakari Point Marine Reserve, the present study described the vocalisations of two dominant fish vocalisations, the croak and the purr. These sounds dominated the soundscape at frequencies below 500 Hz and regularly formed choruses that lasted up to 3 hours after sunset during the new moon, indicating the presence of soniferous fishes in New Zealand coastal waters.

To help with the identification of soniferous fish species in field recordings, two local sound producing fish were studied in detail using 24 h sound recordings in captivity, the bigeye (Pempheris adspersa) and the bluefin gurnard (Chelidonichthys kumu). The bigeye produced a previously undescribed ‘pop’ vocalisation with a source level of 116 dB re 1 µPa @ 1m. The active space of their calls was estimated (radius of 0.6 – 31.6 m) which suggests that their call may serve a group cohesion function during nocturnal foraging.

The bluefin gurnard was acoustically prolific (19 sounds fish\(^{-1}\) h\(^{-1}\)) and had a larger acoustic repertoire than had been previously reported. In addition to the two types of grunt vocalisations, a distinctive nocturnal vocalisation consisting of two new types of growls was described. This indicates that bluefin gurnards could be a major contributor to the ambient sound of their off-shore soft bottom habitat and that field recordings in these areas may be a useful means of investigating gurnard biology and monitoring populations.

The present study has also described for the first time the bioacoustic environment of a fish aggregation device (FAD). Using a Malaysian FAD as a model, the present study showed that sounds in frequency bands typically dominated by various biological sources (500 Hz – 2000 Hz octave bands) could propagate up to 400 m during the day and to more than 1 km at dusk. Thus, suggesting FADs could be acting as a long range acoustic cue for fish. The results of this study have greatly enhanced our understanding of fish vocalisations and its significance in the underwater soundscape of New Zealand coastal waters. In addition, it has contributed to our general understanding of the contribution of the underwater soundscape to fish behaviour and orientation.
This PhD pursuit would not have been possible without the financial support given to me by the Universiti Kebangsaan Malaysia and The Ministry of Higher Education Malaysia.

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GLOSSARY OF ABBREVIATIONS

RMS  Root-Mean-Square
SEM  Standard error of means
FFT  Fast Fourier Transform
CROP Cape Rodney to Okakari Point
FAD  Fish Aggregation Device
SPL  Sound Pressure Level
SL   Source Level
dB   Decibel
FL   Fork Length
1.1 INTRODUCTION

This thesis is about the sounds (vocalisations) produced by teleost fishes. It reports findings on the acoustic characteristics and temporal occurrence of some New Zealand fish vocalisations from the wild as well as in captivity. Field recordings were also used to characterise the acoustic signature of a traditional Malaysian fish aggregation device. The overall aim was to better understand the significance of fish vocalisations and ambient sound in the underwater soundscape and the role they may play in group cohesion and acoustic orientation behaviour of fishes.

1.2 VOCALISATIONS OF TELEOST FISHES – THE WIDER CONTEXT

Vocalisations are sounds produced principally for the purpose of serving a biological function. Across vertebrates they are used in a wide variety of biological contexts, they mediate the dynamics of social interactions (Ladich 1997, Remage-Healey & Bass 2005, Vasconcelos et al. 2010) and promote the fitness of a species (Nottebohm 1972, Seyfarth & Cheney 2003, Ord et al. 2010, Vermeij 2010). Neurobiological studies show that the vocal basis for acoustic communication in fishes shares a common ancestral origin with other vertebrates, therefore fish and other vertebrates have, to some degree, similar vocal-acoustic behaviour and neural capacity to solve acoustic problems (Bass & McKibben 2003, Bass & Ladich 2008). Like song birds (Bentley et al. 1999, Avey et al. 2008), some fish species show seasonal neurophysiological regulation of vocal activity (Bass 2008, Rubow & Bass 2009) and plasticity of hearing sensitivity to vocalisations (Sisneros 2009). Within fish as a group it is further argued that both vocal and auditory systems co-evolved so that vocalisations and hearing sensitivity share the same underlying code for signal generation and recognition in such a way as to facilitate conspecific communication (Weeg et al. 2002, Sisneros 2007).
1.3 SOUND PRODUCTION MECHANISM

Unlike classical laryngeal (Kirchner 1993, Kogo et al. 1997) or syringeal (Goller & Suthers 1996, Suthers & Zollinger 2004) mechanisms of most vertebrates, vocalisations of soniferous fishes are the product of specialised morphological structures (sonic organs) which have evolved exclusively for acoustic signalling (Ladich & Fine 2006, Kasumyan 2009). Among vertebrates, fishes have evolved the largest diversity of sonic organs (Figure 1.1) (Ladich & Fine 2006). Sonic organs generally consist of: one, organs or rigid/bony body parts that are mechanically vibrated (Fine et al. 2001, Parmentier et al. 2008, Fine et al. 2009) or stridulated (Fine et al. 1997, Lechner et al. 2010); and two, specialised sonic muscles (Sprague 2000, Ladich 2001, Connaughton 2004) coupled with the swim bladder and are the most commonly utilised organ for sound production. These sonic muscles are controlled by a vocal motor system located between the caudal hindbrain and rostral spinal cord (Bass 1994, Ladich & Bass 1998, Bass et al. 2008, Chagnaud et al. 2011) or within the spinal cord (Ladich & Bass 2005).

The mechanism of sound production by swim bladders varies according to the nature of attachment of the sonic muscles. Intrinsic sonic muscles vibrate the swim bladder wall directly (Connaughton 2004, Onuki & Somiya 2004, Forbes et al. 2006) while extrinsic sonic muscles may generate a direct (Takayama et al. 2003, Onuki et al. 2010) or indirect swim bladder vibrating mechanism (Tavolga 1962, Ladich & Fine 2006, Parmentier et al. 2006a, Parmentier et al. 2006b). Classically, the swim bladder has been suggested to function as a monopole bubble resonator where vocalisations are dictated by the volumetric properties of the air within (Myrberg et al. 1993, Parmentier & Diogo 2006). More recently, it has been suggested that it can also function as a dipole vibrator where vocalisation characteristics are dictated by the rhythmic actions of sonic muscle contractions (Barimo & Fine 1998, Bradbury & Vehrencamp 1998, Fine et al. 2001, Fine et al. 2009). Compared to vocalisations produced by other vocal mechanisms, swim bladder vocalisations in general are loud, broadly tuned and directional (Barimo & Fine 1998, Sprague & Luczkovich 2004, Ladich & Fine 2006, Kasumyan 2008, Fine et al. 2009). To date, swim bladder vocalisations are evident in some species from the families, Batrachoididae (Fine et al. 2001, Rice & Bass 2009), Sciaenidae (Vance et al. 2002, Ramcharitar et al. 2006), Triglidae (Bayoumi 1970, Connaughton 2004, Amorim 2006), Zeidae (Onuki & Somiya 2004), Ophiididae (Parmentier et al. 2006a, Parmentier et al. 2010a), Gadiidae (Hawkins & Amorim...
Chapter One: General Introduction


1.4 ACOUSTIC CHARACTERISTICS OF VOCALISATION

Vocalisations of fishes are species specific, but are considered less diverse in comparison to vocalisations of other vertebrates and insects (Connaughton et al. 2000, Amorim 2006, Ramcharitar et al. 2006, Kasumyan 2008). Fish vocalisations are commonly described using aural descriptions based on onomatopoeic expressions such as grunts, growls, knocks, pops and many others (Amorim 2006, Kasumyan 2008). However aural descriptions can be ambiguous and not necessarily comparable across species. Nonetheless, aural knowledge can facilitate preliminary identification of generic fish vocalisations in underwater sound recordings (Anderson et al. 2008). Vocalisations are best described by the characteristics of their sound waves in both the temporal (e.g., duration and period) and spectral (e.g., peak frequency and bandwidth) domains.

In general, fish vocalisations consist of amplitude modulated sound pulse, or pulses, whose waveforms show rapid rise and/or decay. A distinctive amplitude maxima in one of the sound wave cycles is usually present within a pulse which determines the peak frequency of the sound (Kasumyan 2008). The temporal characteristic of vocalisations is a result of neural patterning by the vocal pattern generator and provides the communicative value of a call (Lindstrom & Lugli 2000, Wysocki & Ladich 2003, Bass & Ladich 2008). The spectral characteristics of vocalisations on the other hand corresponds to the morphometrics of the sonic organs (e.g., sonic muscle, swim bladder), therefore convey information of individual identity and in some cases mate quality (Connaughton et al. 2000, Amorim & Vasconcelos 2008, Amorim et al. 2009, Tellechea et al. 2010). Within a species, vocalisations may vary due to factors such as behavioural context (Hawkins & Amorim 2000, Amorim 2006, Ladich 2007), sex and sexual dimorphism (Fluet & Bass 1990, Fine 1997, Ueng et al. 2007), ecophysiological factors (Connaughton et al. 1997, Connaughton et al. 2000, Connaughton et al. 2002, Maruska & Mensinger 2009) and geographical separation (Mann & Lobel 1998, Parmentier et al. 2005).

In addition, the environment can act as a filter that changes the amplitude, temporal characteristics and frequency content of a sound as it propagates through the medium (Forrest
Given this environmental effect, fish vocalisations may appear varied in their natural setting depending on the distance of the source (Rogers & Cox 1988). Over short distances (i.e., <1 m to up to 5 m) from the signaller, there is little acoustic degradation thus, the temporal and spectral structure of vocalisations are retained (Fine & Lenhardt 1983, Mann & Lobel 1997, Mann 2006). During social interactions, vocalisations impart maximum call information providing the receiver with critical information such as, caller motivation, quality and identity (Myrberg et al. 1993). However, as perception range increases, vocalisations diverge from their original characteristics gradually losing all but their gross spectral properties or the ‘general impression’ of the sound. At long ranges, even though the communicative value is lost the ‘general impression’ of vocalisations may serve as a cue for fish to orientate and localise sound sources (soundscape orientation).

1.5 BIOLOGICAL FUNCTIONS OF FISH VOCALISATIONS

Figure 1.1: Overview of the main groups of sound generating (sonic) mechanisms in teleost fishes based on the classification proposed by Ladich and Fine (2006). The upper row shows swim bladder vibrating mechanisms. (A) Intrinsic sonic muscles (SM) attached to the walls of the swim bladder (SB) as found in the midshipman Porichthys notatus. (B) Extrinsic directly vibrating mechanism in the catfish Pimelodus sp. (C) Extrinsic indirectly vibrating mechanism in the catfish Synodontis sp.: the swim bladder is vibrated by a thin bony plate, the elastic spring (ES). The lower row shows pectoral mechanisms. (D) Pectoral spine (PS) stridulating mechanisms in many tropical catfishes. (E) Pectoral fin tendon plucking in croaking gouramis genus Trichopsis. Pectoral mechanisms also include vibrating the pectoral girdles by the cephalocleiavicular muscle (CM) in the sculpins (family Cottidae). Sounds might also be generated by rubbing of pharyngeal teeth (PT). The release of air bubbles (BR) through the anus in herrings is proposed to serve in communication. Cl, cleithrum; Co, coracoid; EM, epaxial muscles; ET, enhanced tendons; FP, friction process; FR, fin rays; MAS, superficial adductor muscle; TP4, transverse process of the fourth vertebrae; VC, vertebral column. (Adapted with permission from Bass and Ladich [2008]-Springer Science+Business Media)
1.5.1 Communication

Vocalisations are used for communication in a wide variety of biological contexts and are known to mediate the dynamics of social behaviours. The most commonly observed communicative use of vocalisations include agonistic interactions (Almada et al. 1996, Ladich 1997, 2006, Amorim & Neves 2008, Colleye et al. 2009, Vasconcelos et al. 2010), courtship (Lobel & Kerr 1999, Amorim et al. 2003, Amorim & Almada 2005, Amorim et al. 2008b, Boyle & Cox 2009) and spawning (Lobel 1992, Connaughton & Taylor 1995, 1996, Lobel 1996, Mann et al. 1997, Hawkins & Amorim 2000, Finstad & Nordeide 2004). This has led to the general argument that vocalisation of fishes are most relevant and useful only over very short ranges. Furthermore, vocalisations are considered as supplementary to communication cues of other sensory modalities such as vision (Lugli 1997, Amorim & Neves 2007, Bertucci et al. 2010) and olfaction (Lugli et al. 2004). The communicative aspect of vocalisations has become the paradigm of the majority of fish vocalisation research, whereas research on the use of vocalisations in other functions such as group cohesion and long range orientation is scarce.

1.5.2 Group Cohesion

Many animals use vocalisations as contact calls to maintain group cohesion within social groups (Cortopassi & Bradbury 2006, Carter et al. 2009, Kondo & Watanabe 2009, Soltis 2010) and to facilitate foraging activities (Boughman 1997, Townsend et al. 2010, Suzuki & Sugiura 2011). Pitcher (1983) defines a social group of fish as a shoal which has no implications for structure or function. On the other hand, a school have a structure that is measured in polarity and synchrony (Pitcher 1986). Nocturnal reef fishes that formed distinctive resting aggregations by the day occur in loose schools while foraging at night (Helfman 1986). It has been proposed that some nocturnal coral reef planktivores may use conspecific vocalisations to maintain loose school structure (McCauley & Cato 2000). Fish schools are formed by the collective behaviour of individuals dynamically establishing and maintaining a nearest-neighbour-distance (NND) with each other (Tien et al. 2004). For highly polarised schools, NND is established by sensing the visual (eyes) and hydrodynamic cues (lateral line) of the nearest neighbour (Pitcher 1979, Partridge & Pitcher 1980, Faucher et al. 2010). Here conspecific vocalisations are proposed as an alternative cue and NND corresponds to the audible range of vocalisations. Following suggestions by McCauley & Cato (2000), this would allow fish to maintain loose school structure throughout the night and allow the fish to track planktonic prey aggregations. This is a
plausible hypothesis, but one that is difficult to directly test experimentally. A less direct
approach is to quantify the audible range of the vocalisations by fish that demonstrate nocturnal
foraging behaviour. The range would infer a spatial area where vocalisation detection can occur,
which is known as the active space or communication space (Janik 2000, Clark et al. 2009).
Knowing the active space could provide a possible estimate of a vocalisation based NND where
it could serve as a basis for further field observations.

1.5.3 Acoustic Orientation

The use of vocalisations in mediating the orientation behaviour of fishes was forwarded
by the late Arthur Myrberg Jr., for which research is needed (Myrberg Jr 1981, Myrberg 1997b).
Orientation in this sense implies directed movement to the signaller from the act of
The spatial range of orientation is limited by the audibility of the vocalisations which in the case
of choruses may be up to a few km away. At such distances it is likely that orientation is on the
basis of detecting the vocalisation gross spectral composition or ‘general impression’. To be a
viable orientation cue in nature, vocalisations must be perceived among the cacophony or myriad
of other sound sources in the ambient underwater soundscape. Such an orientation is known as
‘soundscape orientation’ and has been observed in birds and frogs (Sinsch 2006, Slabbekoorn &
Bouton 2008) and proposed for fish (Simpson et al. 2008a, Fay 2009, Radford et al. 2011a). Fay
(2009) has proposed that the ambient soundscape may play an important role in the adaptation of
ears and the auditory systems of fishes. Furthermore, soundscape perception may provide fish
with important information about their environment (e.g., habitat) and specific events occurring
(e.g., feeding or predation). Soundscape orientation using vocalisations is achieved through the
fish’s ability to perform; one, auditory scene analysis; two, directional hearing; and three, sound
source localisation.

Auditory scene analyses implies having the neural ability to perform auditory source
segregation processing, which requires the fish to effectively tune the ears to discriminately
listen to specific sounds among many different sounds. Like other vertebrates, fishes are capable
and it is most robust when the spectral difference between sounds is large (Fay 2000, Bee 2008,
It has also been reported that fish are sensitive to conspecific vocalisations (Belanger et al. 2010, Lechner et al. 2010) and show explicit behavioural response when vocalisations are present in a myriad of sounds (Holt & Johnston 2010). This suggests that fish are likely to be able to detect vocalisations in the underwater soundscape and undertake appropriate behavioural responses.

Fish are also capable of directional hearing (Popper & Fay 2005, Rogers & Zeddies 2008, Sand & Bleckmann 2008). The underlying principle on how such tasks are achieved may be explained by one of the following models: one, vectorial analysis of particle motions model (Sand 1974a, b); two, several variations of the phase model (Schuijf 1975, Schuijf & Buwalda 1975, Buwalda et al. 1983); three, orbit model ((Demunck & Schellart 1987, Schellart & Demunck 1987); and four, model that incorporates some of the elements of the above models (Rogers et al. 1988). These models are based on the varying response of the otolith and the overlying sensory tissue to the particle motion properties of sound (acceleration). The displacement of the directionally sensitive hair cells translates the directionality of the sound’s particle motion. While vectorial analysis model only considers the direct sound stimulation on the ears, the phase and orbit model also consider the secondary stimulation induced by the redirection of sound by the swim bladder to the ears. In the latter, the 180° directional ambiguity can be solved by measuring the particle motion phase difference between the two stimulations.

For localisation of sound sources, the unifying guidance model was proposed (Kalmijn 1997, Popper & Fay 2005, Sand & Bleckmann 2008). This model suggests that localisation from a distance is achieved by continuously moving and sampling the particle acceleration sound field in a way that fish are guided to the source. More recently, it has been reported that fish have an auditory capacity that sharpens its directional hearing ability by tuning to the frequencies of signals of interests (Fay & Edds-Walton 2000, Weeg et al. 2002, Edds-Walton & Fay 2003, 2005, Lu et al. 2010). This indicates that fish vocalisations may elicit a sharper directional response of a receiver fish.

These physiological capabilities indicate that fish can perceive and potentially utilise vocalisations in the natural underwater soundscape in ways that may affect their behaviour not only at close proximity but also from beyond the sight of the signaller. Accordingly, this demands further understanding of the fish vocalisation characteristics in its context as...
components of the natural underwater soundscape. Of particular interest is the ambient underwater soundscape of habitats that appear to be favoured by and ‘attractive’ to fish. These include the underwater soundscape of reef habitat and fish aggregation devices (FAD).

Sounds from reefs appear to be attractive and used by some fishes and decapods in their orientation and migration to find suitable settlement habitat (Montgomery et al. 2001, Jeffs et al. 2003, Jeffs et al. 2005, Montgomery et al. 2006). Directional orientation and localisation behaviour of larval fish towards reef noise have been shown in field observations (Leis et al. 2003, Tolimieri et al. 2004, Leis & Lockett 2005). This indicates that reef noise which is dominated by biological sounds (e.g., snapping shrimp, urchin and fish) (Cato 1980, McCauley & Cato 2000, Radford et al. 2008a, Radford et al. 2008b) contain unique signals/cues that provide information that fish may use to evaluate and make appropriate behavioural decisions. The behavioural response of fish to manipulated reef noise playback has been demonstrated in the field by Radford et al. (2011) and Simpson et al. (2004, 2005, 2008a&b). Radford et al. (2011) investigated the orientation response of juvenile reef fishes to experimental reef patches that broadcast different types of habitat sound. The dominant frequencies of the habitat sounds being tested were different and reflected the dominant sound sources within the habitats (invertebrates vs fish). They have shown that fish were able to use the directional information in acoustic cues as well as interpret the content of acoustic signal in order to guide them to relevant habitat of choice.

Simpson et al (2005, 2008a&b) tested the preferences of various larval fish species to sounds containing different frequency ranges, for example sounds in the frequency range generally dominated by fish vocalisations or invertebrate sound. They found that fish show variable preferences to the two types of biological sounds presented. Pre settlement larval fish prefer invertebrate dominated noise while juvenile and adult fish prefer vocalisation dominated noise. These findings can be interpreted to suggest that one, reef noise contains signals that mediate the orientational behaviour of fishes and two, fish vocalisations in reef noise plays a significant role for the orientation behaviour of fishes. This emphasise the needs to investigate both the qualitative and quantitative characteristics of fish vocalisations as well as the overall contribution of fish vocalisations in reef noise in order to extend our understanding of its biological role.
An apparent demonstration of fish orientation to fish habitat can be observed from the aggregation behaviour of fish around man-made fish aggregation devices (FAD). Fish are attracted to and associate with FADs, a behaviour that is frequently exploited in fisheries to improve fishing efficiency (Fréon & Dagorn 2000, Girard et al. 2004). Extensive reviews describe the evolutionary mechanisms that may have driven the associative behaviour of fish with FADs (Fréon & Dagorn 2000, Castro et al. 2001) but do not address the proximal cues that allow fish to locate and orientate to FADs. An acoustic mechanism has been suggested for the attractive properties of FADs. Fish movement around FADs showed that some species can orient and return to a FAD from beyond visual range and regardless of current direction (Marsac & Cayré 1998, Dempster & Kingsford 2003). The bioacoustic environment of a working FAD particularly one that incorporates an artificial reef as part of its structure and populated by fishes is a suitable model to reflect the acoustical properties of a natural reef. The bioacoustic environment of FADs has never been studied before.

The perception of fish vocalisations (signal) in the underwater soundscape should be gauged in relation to noise since both sounds are simultaneously perceived. Furthermore, the acoustic communication and orientation of fishes are most likely limited by noise regimes in their environment (Wysocki & Ladich 2005). In considering fish vocalisations from field recordings, it is appropriate to evaluate power levels of the received signal relative to other sounds that compose the ambient noise. In addition, hearing involves processing sounds in frequency band-widths that corresponds to the critical bands of the respective animal auditory system (Madsen et al. 2006, Au & Hastings 2009a, Clark et al. 2009, Jensen et al. 2009). The exact critical band-widths of fish is unknown to date, but is widely assumed to be broader than those of mammals, for example one octave as opposed to one-third octave (Fay 1988, Wahlberg & Westerberg 2005, Au & Hastings 2009a). Auditory masking occurs when noise levels are similar or higher than signal level in the same critical bands, which prevents fish from hearing the signal (Wysocki & Ladich 2005, Clark et al. 2009, Codarin et al. 2009). Throughout this thesis fish vocalisations and noise power levels were repeatedly presented in octave bands to reflect critical bands of fish. In this way signal availability and perception is presented in a more meaningful way and approximates the hearing of fishes. Accordingly auditory source segregation is also most robust for sounds in different octave bands.
1.6 FIELD RECORDINGS OF FISH VOCALISATION

1.6.1 Temporal Pattern of Vocalisations

Fish vocalise during specific behavioural contexts which determines its temporal occurrence. Consequently, vocalisation periodicity can serve as proxies for specific behaviours occurring in nature. Depending on the type of behaviour and the fitness of the caller, vocalisation occurrence may show seasonal, lunar and diel periodicity. For example, spawning vocalisations of some marine teleosts are highly seasonal such as that reported in the family Sciaenidae (Connaughton & Taylor 1994, 1995, Lagardere & Mariani 2006), Gadiidae (Nordeide & Kjellsby 1999, Nordeide et al. 2008) and Batrachoididae (Amorim et al. 2006). Since spawning usually involves aggregations of many individuals, vocalisations merge and form loud choruses (Luczkovich et al. 1999, Mann et al. 2010). These choruses can increase the overall ambient noise level by several orders of magnitude higher than normal (Fish 1964, Fish & Cummings 1972, Cato 1978, Cato 1980). Seasonal vocalisation patterns can also relate to environmental conditions (Connaughton et al. 2000, Connaughton et al. 2002, Ripley & Foran 2007, Gillooly & Ophir 2010). Chorus may also exhibit lunar (Mann et al. 2009) and diel periodicity (Connaughton & Taylor 1995, Parsons et al. 2009).

The diel periodicity of individual fish vocalisation is less well understood. It may relate to common general activities of fish such as feeding, foraging, courting or territorial defence. Although, vocalisation correlates with behavioural activities that are regulated by the circadian system (Reebs 2002) it is not known if vocal behaviour is regulated by the same system. Across fish species, peaks in vocalisations has been reported to occur during the day (Amorim 2005), night (Locascio & Mann 2008, Sirovic et al. 2009) and crepuscular (Thorson & Fine 2002b, Boyle & Tricas 2010) periods. However, sometimes a strict diel pattern could not be determined (Anderson et al. 2008). In coral reef fish, vocalisations appear to be temporally patterned as a strategy for competing for the acoustic communication space (McCauley & Cato 2000).

Knowledge on the temporal pattern of fish vocalisations is important for understanding its contribution to the ambient noise of their habitat. Furthermore, such knowledge would be useful in the application of passive acoustic monitoring of fisheries.
1.6.2 Use of Fish Vocalisations in Passive Acoustics

Passive acoustics relies on listening to the vocalisations of fish with a hydrophone to infer their temporal and spatial distribution and behaviour (Mann et al. 2008). It shows potential applications in fisheries, whereby soniferous fishes of commercial value can be mapped from the occurrence of their vocalisations (Gannon 2008, Luczkovich et al. 2008a). The technique is non-destructive and can also serve as a monitoring tool for the general assessment of marine environments (Mooney et al. 2005, Lammers et al. 2008, Anagnostou et al. 2011). Understanding the vocalisation character of target fish is essential to the success of fish passive acoustics. Also, if the context of sound production is known then fish presence can be related to specific behaviours. Most commonly targeted are vocalisations during spawning (Luczkovich et al. 1999, Rountree et al. 2006, Luczkovich et al. 2008a), which provides information on breeding grounds of the targeted species.

Passive acoustics has been conducted on several croaker species (Luczkovich et al. 1999, Lowerre-Barbieri et al. 2008), cod (Nordeide & Kjellsby 1999), grouper (Mann et al. 2009, Nelson et al. 2011), rockfish (Sirovic et al. 2009) and toadfish (Fine & Thorson 2008), which has shown promising results. Due to its non-destructive nature and the rapid advancement in sound recording technology, it is anticipated that passive acoustics will gain popularity and find widespread applications. In New Zealand waters, suitable fish candidates for passive acoustic monitoring are unknown due to the lack of knowledge on the local fish species that vocalise.

1.7 THESIS STRUCTURE AND AIMS

There has been very little work conducted on New Zealand fish species that vocalise. The first aim of this thesis was to document the acoustic characteristics of some common fish vocalisations and their temporal occurrence/periodicity in New Zealand waters (Chapter 2, 3 and 4). To determine the vocalisation types present in New Zealand coastal waters, underwater sound recordings from Cape Rodney to Okakari Point Marine Reserve were analysed for fish vocalisations (Chapter 2). It is generally argued that fish vocalisations are important source of low frequency biological noise (<1000 Hz) especially, where they are common. However, since fish vocalisations in New Zealand waters have never been characterised, therefore its significance and contribution to ambient noise is unknown. The specific objective of chapter 2
was to describe the general characteristics of some putative fish vocalisations in the wild, evaluate their potential as sources for choruses and their contribution to the ambient reef noise.

The field recordings are complemented by, two subsequent chapters dedicated to validating the identities of the soniferous fishes (sound-truthing) responsible for the vocalisations in the field recordings and examining the context of their sound production. Vocalisations of selected fishes were recorded in captivity using unconventional continuous recording method to avoid possible under-sampling of sporadic vocalisation episodes. Chapter 3 investigates the vocalisation of a nocturnal reef planktivore the bigeye, *Pempheris adspersa* in captivity and in the wild. The underlying hypothesis for this chapter revolves around the group cohesion function of vocalisations suggested by McCauley & Cato (2000). The current study is the first attempt to explore the plausibility of the hypothesis. The specific objectives of this chapter were to describe the bigeye vocalisation characteristics, source level and estimate its active space.

Chapter 4 investigates the vocalisations of a sandy bottom habitat species - the bluefin gurnard, *Chelidonichthys kumu* - in captivity. Gurnards in general are well known for their vocal prowess where vocalisations of several other members of the Triglidae family have been reported (Amorim et al. 2004, Connaughton 2004, Amorim 2006). However, there is limited information on the vocalisations of the local gurnard *C. kumu* or the behavioural context for the vocalisations. As it is both recreationally and commercially valuable, the assessment of their wild population is important. There is a potential passive acoustic application for this species if their vocalisations are fully understood. The specific objectives of this chapter were to describe the species vocalisation characteristics, call repertoire, behavioural context and diel periodicity.

The second aim of this thesis was to evaluate the temporal and spatial characteristics of fish vocalisations in relation to non-communicative roles of schooling (chapter 3) and orientation (chapter 5). Chapter 5 examines the potential role of a fish aggregation device (FAD) to serve as a long range acoustic orientation cue for fish. Fish aggregation devices are widely recognised for their ability to attract and aggregate fish over spatial scales of meters to kilometres, but its acoustic role is unknown. The bioacoustic environment of a FAD could relate to natural fish habitats, therefore understanding its spatio-temporal properties may convey the understanding of similar properties of natural fish habitats, such as reefs. The specific objectives of chapter 5 were to characterise the bioacoustical environment of a FAD (using a Malaysian “unjam” FAD as
model) and to examine the spatio-temporal properties of sounds in the octave bands that represent the frequency range of fish vocalisations and invertebrate sounds in general.

Overall, the aim of this thesis was to begin to understand the character of New Zealand fish vocalisations, its significance in the underwater soundscape and its potential role in a number of behavioural contexts.
Chapter Two: Fish Vocalisations From a Temperate Reef

CHAPTER TWO:

FISH VOCALISATIONS AND CHORUSES FROM A NEW ZEALAND TEMPERATE REEF

2.1 INTRODUCTION

It has been shown that ambient reef noise provides cues that mediate the behaviour of marine animals (Radford et al. 2008b, Radford et al. 2010). For example, studies have shown that ambient reef noise can be used as an orientation and settlement cue by pelagic larval fish and decapods (Montgomery et al. 2001, Jeffs et al. 2003, Montgomery et al. 2006, Radford et al. 2007, Stanley et al. 2010, Radford et al. 2011a). In general, reef noise is dominated by biological sounds, particularly those produced by the snapping shrimp (Au & Banks 1998, Radford et al. 2008b), sea urchins (Castle & Kibblewhite 1975, Radford et al. 2008a) and vocalisations of fishes (Kennedy et al. 2010). Fish vocalisations are communication signals which are known to be biologically significant in ways that can influence the social behaviours of fishes (Bradbury & Vehrencamp 1998, Bass & Ladich 2008, Kasumyan 2009). However, not much is known of the acoustic composition of fish vocalisations in New Zealand waters and the extent of their contribution to ambient reef noise (Radford 2007).

Fish vocalisations, commonly described using onomatopoeic expressions such as grunts, growls, purrs, croaks, pops, squawks and many others (Amorim & Hawkins 2000, Amorim 2006, Maruska & Mensinger 2009, Speares & Johnston 2011), are sometimes distinguishable from reef noise recordings both aurally and by close visual inspection of oscillograms or spectrograms. Typically fish vocalisations consist of pulses of sound that have a finite duration (transient) lasting milliseconds up to a few seconds. The waveform of the pulse contains several subsequent cyclic changes in amplitude where there is usually a distinct maxima in one of the cycles (Kasumyan 2008). The frequency range for the majority of fish vocalisations lies below 3000 Hz (Hawkins 1986). Typical fish vocalisations are generated in two ways. Vibration of the swim bladder, tend to be relatively lower in frequency (< 1000 Hz) (Fine et al. 2001, Connaughton 2004, Ladich & Fine 2006), compared to those produced by stridulations of rigid
bony appendages (1000-3000 Hz) (Fine et al. 1997, Ladich & Fine 2006, Lechner et al. 2010). By way of comparison with other marine animals, the vocalisation repertoire of marine mammals consist of long whistles, clicks and burst pulse sound in frequency range $< 100$ Hz to $> 20,000$ Hz with modulation of peak frequencies (Au & Hastings 2009b). Invertebrates such as urchins produce sounds of short duration in the frequency range between 700 – 2000 Hz via the mechanical action of the aristotle lantern during feeding (Radford et al. 2008a). Snapping shrimp produce implosive sounds in the frequency range from 2000 Hz to 200000 Hz from the collapse of cavitation bubbles formed by rapid snapping of the enlarged chelae (Au & Banks 1998, Versluis et al. 2000).

It has been widely reported that fish vocalisations are characteristic of the underwater soundscape and make up a significant proportion of the biological sound below 1000 Hz (Cato 1980, 1992, McCauley & Cato 2000, Kennedy et al. 2010). When large numbers of individual fish emit sounds simultaneously, source levels are intensified thus creating a phenomenon known as a chorus (Fish 1964, Cato 1978, Tellechea et al. 2010, Tellechea et al. 2011). In contrast to the transient nature of individual calls, choruses appear as sustained background noise resulting from the continuous and overlapping sounds from a large number of sound sources (Knudsen et al. 1948, Cato 1976). The spectral characteristics of fish choruses are correlated with the characteristics of dominant fish vocalisation types, therefore fish choruses vary with the composition of the local fish population (Cato 1992, Kennedy et al. 2010). It has been reported that fish choruses could increase ambient noise levels by 35 dB (McCauley & Cato 2000) or even up to 50 dB (Fish & Cummings 1972), potentially insonifying surrounding waters within a few km radius. The occurrence of fish choruses have been reported to exhibit some degree of seasonal and diurnal variation. Choruses around crepuscular periods are most commonly reported (Fish 1964), although in some places, such as in the Timor Sea, choruses during midday have also been observed (Cato 1978, Cato 1980).

Fish choruses are likely to be apparent in biologically diverse habitats with healthy fish populations. However, in such habitats like temperate reefs around New Zealand, the acoustic space are dominated by the choruses of sea urchin *Evechinus chloroticus* (Castle & Kibblewhite 1975) and snapping shrimps *Alpheus sp.* (Radford 2007). These invertebrate choruses could increase the ambient noise levels by 20 and 25 dB on average in the frequency range between 700 - 15000 Hz (Radford et al. 2008b) and may mask potential fish choruses if their sounds...
overlap in frequency and time of occurrence. Not much is known about fish vocalisations or fish choruses associated with New Zealand’s temperate reefs (Radford 2007). In order to further explore the ecological function of reef noise, we need a better understanding of the characteristics of fish vocalisations and their contribution to reef noise.

This current study aims to determine the fish vocalisation component in reef noise for one location in northern eastern New Zealand. This will be achieved by;

1) characterising some of the fish vocalisations present at a reef in the Cape Rodney to Okakari Point (CROP) marine reserve,
2) identifying the spectral range of these fish vocalisations and its contribution as choruses in the ambient reef noise
3) evaluating the potential masking of fish chorus by invertebrate choruses.

2.2 METHODS

2.2.1 Temporal Recordings

Fish vocalisations and ambient reef noise was analysed from underwater sound recordings of North Reef within the CROP marine reserve, Leigh (36°15'45"S, 174°47'33"E), north-eastern New Zealand. The recordings were made over two moon phases (new moon and full moon) over the four New Zealand austral seasons from December 2004 to October 2005 by Radford (2007). 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 2 days on each side of the moon phase under consistent wind speed and sea condition (sea state 2). Further details on the temporal recordings was described in Radford (2007).

2.2.2 Data Analyses

Acoustic Characterisation

The occurrence of fish vocalisations throughout the temporal recordings was identified, counted and isolated by aural and visual examination using the software RAVEN Pro 1.3 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Cornell, NY, U.S.A.). The
categorisation of fish vocalisations was primarily based on comparison with known and published vocalisations in the literature and animal sound databases (e.g., Macaulay Library of Animal Sound, Cornell University) as well as with vocalisations of captive fish at the Leigh Marine Laboratory. Only clear vocalisations (at least 10 dB Signal to Noise Ratio (SNR)) without boat or rain noise were selected for categorisation which was based upon *a posteriori* classification of aurally distinguishable sound types, i.e.; croak and purr. Acoustic measurements of the vocalisations were made after filtering sound through a band-pass filter (50-1500 Hz).

The temporal limits of a vocalisation were manually defined from the oscillogram and the following sound parameters were measured from these selections; sound duration, SD (duration in which 90% of the sound energy is contained within a selection, defined by the limits of the parameter duration 90% in RAVEN); peak frequency, Pf (the frequency component with the highest amplitude in the entire sound); lower frequency, Lf (lower frequency limit which amplitude is 10 dB less than the peak frequency); upper frequency, Uf (upper frequency limit which amplitude is 10 dB less than the peak frequency), 10 dB bandwidth, BW (range between lower and upper frequency), 3 dB lower frequency, 3dBLf (lower frequency limit which amplitude is 3 dB less than the peak frequency); 3 dB upper frequency, 3dBUf (upper frequency limit which amplitude is 3 dB less than the peak frequency), 3 dB bandwidth, 3dBBW (range between lower and upper frequency) and damping coefficient, Q value (Q = Pf/3 dB bandwidth). Temporal parameters were measured from the spectrogram while spectral parameters were measured from power spectra calculated using a 512-point Fast Fourier Transform (filter bandwidth of 135 Hz) with a Hann window.

**Octave Analysis**

The octave analysis was used to analyse the frequency composition of each fish vocalisation and ambient reef noise. By comparing their RMS sound powers in respective octave bands (octave band level$_{rms}$; dB re 1 µPa octave bandwidth$^{-1}$), the frequency range where fish vocalisations dominate can be determined. This is shown in octave bands where there is a significant difference in octave band levels$_{rms}$ between fish vocalisations and ambient reef noise ($\delta$dB). This also indicates the sound energy contribution of fish vocalisations to the particular frequency range of the reef noise. Fish vocalisations and ambient reef noise was examined for the different seasons (summer, autumn, winter and spring), moon phases (full and new moon) and hours of the day. Sounds (from temporal recordings) in five octave bands, i.e., band, 1 - 5
with their centre frequencies at 125, 250, 500, 1000 and 2000 Hz respectively (Table 2.1) were
analysed with MATLAB® using digital octave band filters created with scripts modified from
octbank.m by Christophe Couvreur. The octave band levels_{rms} of sound segments containing an
individual fish vocalisation (also including reef noise) was measured. Next, a sound segment
containing only reef noise was sampled either before or after the individual fish vocalisation
from the same track and its octave band levels_{rms} was measured. This was done for all
vocalisation samples (n = 175). Both measurements were plotted together to visually examine
the bands in which the vocalisation were most dominant as indicated by a positive departure in
sound intensity from the ambient reef noise level. The difference in octave band levels_{rms}
between these two sound segments (δdB) was calculated for the octave bands and compared
with the data pooled from all seasons and moon phases.

A chorus was defined as the noise from many individuals that was continuously above
normal ambient noise over an extended period of 1 hour or more. (Cato 1978). For this study, a
chorus was assumed by the rise of noise intensity in the octave bands where animal sounds are
most dominant (Cato 1992). Fish choruses were designated to noise in band 2, corresponding to
the dominant frequency of fish vocalisation. Invertebrate choruses (urchin and snapping shrimp)
were designated to the combined noise level in bands 4 and 5 (band 4 & 5) corresponding to
their dominant frequency range (Au & Banks 1998, Radford et al. 2008a, Radford et al. 2008b).
Octave band levels_{rms} was measured with an averaging time of 1 s for consistency with noise
measurements averaging time by Cato (1978, 1992). The mean value of four random octave
band level_{rms} measurements from each hourly recording was taken as the hourly octave band
levels_{rms} of noise (NL_{rms}). The normal ambient reef noise level for the respective octave band
was calculated from the 24 h NL_{rms} as the mean value plus one standard deviation. This level is
also known as the chorus threshold level. A chorus was identified when NL_{rms} exceeded and was
sustained (longer than one hourly period) above the chorus threshold level. Chorus was
examined according to season and moon phase.
Table 2.1: Octave band filter characteristics

<table>
<thead>
<tr>
<th>Band</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Centre frequency, Fc / octave bandwidth, BW (Hz)</td>
<td>125 / 89</td>
<td>250 / 178</td>
<td>500 / 353</td>
<td>1000 / 702</td>
<td>2000 / 1410</td>
</tr>
<tr>
<td>Octave band frequency range (Hz)</td>
<td>89 - 178</td>
<td>178 - 355</td>
<td>355 - 708</td>
<td>708 - 1410</td>
<td>1410 - 2820</td>
</tr>
</tbody>
</table>

2.2.3 Statistical Analyses

The mean ± standard error of means (SEM) values were used in all measurements throughout this study unless stated otherwise. A linear discriminant analysis (LDA) based on the sound parameters, SD, Pf, BW and Q was used to validate the adequacy of the aural classification of the two vocalisation categories that were observed (Amorim et al. 2004). The octave bands were compared for their δdB values using the Kruskal - Wallis test with the data pooled from all seasons and moon phases. Where significant differences were identified, two post-hoc multiple comparison tests were made with Dunn tests (Zar 1999). Firstly, pairwise comparisons versus a control consisting a dataset of zero values (0 dB) were run to test for differences in the δdB values of octave bands. Secondly, pairwise comparisons were run to test for differences in δdB values among octave bands. The relationship between fish chorus (band 2) and invertebrate chorus (band 4 & 5) was tested with the Pearson product correlation analysis using the respective NLrms data. Statistical analyses were performed using Minitab R. 14 and Sigmaplot ver.11.

2.3 RESULTS

2.3.1 Sound Identification and Characteristics

In general, five types of fish vocalisations could be categorised from a total of 32 h of sound recordings. Aurally, these putative vocalisations can be categorised as croak, purr, knock, growl and drum. However, only two vocalisation categories (i.e., croak and purr) occurred regularly within daily recordings over seasons and moon phase with sufficient sound quality (SNR > 10 dB) hence, these were considered for further analyses.
The waveform of croaks \((n = 76)\) consisted of a distinctive pulse envelope containing trains of contiguous short pulses (Figure 2.1a). Mean PN was \(12.75 \pm 0.52\) pulses forming vocalisations with a mean SD of \(0.119 \pm 0.005\) s (Table 2.2). Croaks had a mean Pf of \(271 \pm 7\) Hz but may have more than one frequency peak that are not harmonically related (Figure 2.1c). The mean BW of croaks was \(465 \pm 13\) Hz with Q value of \(1.2 \pm 0.04\) (Table 2.2). The waveforms of purrs \((n = 99)\) consisted of trains of discrete pulses (Figure 2.2a). Mean PN of purrs was \(6.66 \pm 0.27\) pulses forming vocalisations with a mean SD of \(0.207 \pm 0.009\) s. Purrs had a mean Pf of \(284 \pm 4\) Hz (Figure 2.2c) and mean BW of \(398 \pm 8\) Hz (Table 2.2). The Q value of purr was of \(1.5 \pm 0.03\). The adequacy of the aural classification categories was supported by a significant LDA of all croaks and purrs combined (Wilks \(\lambda_{175} = 0.614\), \(P < 0.01\)). Approximately 81% of the total sounds were correctly classified by the LDA, Croak 82.9% and Purr 79.8% (Table 2.3) with the variable SD as the main contributors to the discriminant functions (Table 2.4).
Table 2.2: Acoustic features of croak and purr sounds. Values are means ± SEM. Value range for SD, PN and Pf is given in parentheses below. SD = sound duration; PN = number of pulses; Pf = peak frequency; Lf = 10 dB lower frequency; Uf = 10 dB upper frequency; BW = 10 dB band width; 3dBLf = 3 dB lower frequency; 3dBUf = 3 dB upper frequency; 3dBBW = 3 dB band width Q = damping coefficient.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Croak (mean ± SEM)</th>
<th>Purr (mean ± SEM)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n = 76</td>
<td>n = 99</td>
</tr>
<tr>
<td>SD</td>
<td>0.119 ± 0.005</td>
<td>0.207 ± 0.009</td>
</tr>
<tr>
<td></td>
<td>(0.048 - 0.197)</td>
<td>(0.053 - 0.437)</td>
</tr>
<tr>
<td>PN</td>
<td>12.75 ± 0.52</td>
<td>6.66 ± 0.27</td>
</tr>
<tr>
<td></td>
<td>(5 - 20)</td>
<td>(3 - 14)</td>
</tr>
<tr>
<td>Pf</td>
<td>271 ± 7</td>
<td>284 ± 4</td>
</tr>
<tr>
<td></td>
<td>(187 - 469)</td>
<td>(187 - 375)</td>
</tr>
<tr>
<td>Lf</td>
<td>80 ± 1</td>
<td>84 ± 1</td>
</tr>
<tr>
<td>Uf</td>
<td>545 ± 13</td>
<td>482 ± 7</td>
</tr>
<tr>
<td>BW</td>
<td>465 ± 13</td>
<td>398 ± 8</td>
</tr>
<tr>
<td>3dBLf</td>
<td>156 ± 4</td>
<td>177 ± 4</td>
</tr>
<tr>
<td>3dBUf</td>
<td>390 ± 8</td>
<td>376 ± 6</td>
</tr>
<tr>
<td>3dBBW</td>
<td>234 ± 8</td>
<td>199 ± 5</td>
</tr>
<tr>
<td>Q</td>
<td>1.22 ± 0.04</td>
<td>1.48 ± 0.03</td>
</tr>
</tbody>
</table>
Table 2.3: Classification of the two sound types by linear discriminant analysis. Columns show the reallocation of sounds in each group (sound type)

<table>
<thead>
<tr>
<th>True Group</th>
<th>Croak</th>
<th>Purr</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sound Type</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Croak</td>
<td>58</td>
<td>0</td>
</tr>
<tr>
<td>Purr</td>
<td>0</td>
<td>59</td>
</tr>
<tr>
<td>Total, n</td>
<td>76</td>
<td>99</td>
</tr>
<tr>
<td>n Correct</td>
<td>63</td>
<td>79</td>
</tr>
<tr>
<td>Proportion (%)</td>
<td>82.9</td>
<td>79.8</td>
</tr>
</tbody>
</table>

n = 175    n Correct = 142    Proportion Correct = 81.1%

Table 2.4: Linear discriminant functions for the validation of sound type classification.

<table>
<thead>
<tr>
<th>Discriminant functions</th>
<th>Croak</th>
<th>Purr</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variables</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>-35.390</td>
<td>-38.997</td>
</tr>
<tr>
<td>SD</td>
<td>35.675</td>
<td>51.350</td>
</tr>
<tr>
<td>Pf</td>
<td>-0.034</td>
<td>-0.018</td>
</tr>
<tr>
<td>BW</td>
<td>0.097</td>
<td>0.087</td>
</tr>
<tr>
<td>Q</td>
<td>25.202</td>
<td>25.643</td>
</tr>
</tbody>
</table>
Figure 2.1: Representative croak sound; a) oscillogram, b) spectrogram (512 pt FFT; Hann window), and c) smoothed power spectra of the croak sound (solid line) in comparison with reef noise (dashed line).
Figure 2.2: Representative purr sound; a) oscillogram, b) spectrogram (512 pt FFT; Hann window), and c) smoothed power spectra of the purr sound (solid line) in comparison with reef noise (dashed line).
2.3.2 Octave Band Characteristics

There was noticeably greater sound intensity compared with ambient sound in bands 1, 2 and 3 for sound segments containing both croak and purr sounds (Figure 2.3 and 2.4). The rise in these bands was consistent for all vocalisations recorded during different seasons and moon phases. The δdB in band 1, 2 and 3 for both croak (H₃ = 278.59, P < 0.001) and purr (H₅ = 358.23, P < 0.001) were significantly greater than control. For the croak, the biggest difference in comparison to ambient noise was observed in band 2 (mean = 11.1 ± 0.6 dB) followed by band 3 (mean = 8.1 ± 0.5 dB) and band 1 (4.7 ± 0.5 dB). Taken over the duration of the croak, the δdB in band 2 was significantly greater (H₄ = 220.86, P < 0.001) than all other bands except for band 3 (Figure 2.5a). For the purr, the biggest difference in comparison to ambient noise was also observed in band 2 (mean = 9.9 ± 0.4 dB) followed by band 3 (mean = 4.5 ± 0.4 dB) and band 1 (mean = 3.7 ± 0.4 dB). Taken over the duration of the purr, the δdB in band 2 was significantly greater (H₄ = 293.36, P < 0.001) than all other bands (Figure 2.5b).

Both vocalisation categories did not show any significant sound intensity rise in band 4 and 5 when compared to ambient when the vocalisations were not present. The δdB of band 4 and 5 were similar to control (Dunn test, P > 0.05). For the croak, the mean δdB in band 4 and 5 were 0.3 ± 0.3 dB and 0.1 ± 0.3 dB, respectively. For the purr, the mean δdB were -0.3 ± 0.1 dB and -0.1 ± 0.2 dB.
Figure 2.3: Mean sound level within five octave bands for recordings with (solid circle and line) and without (ambient reef noise only - hollow circle and dashed line) croak vocalisations. Figure 2.3a, c, e and g are during full moon of summer \((n = 55)\), autumn \((n = 85)\), winter \((n = 20)\), and spring \((n = 25)\) respectively. Figure 2.3b, d, f and h are during new moon of summer \((n = 15)\), autumn \((n = 65)\), winter \((n = 45)\), and spring \((n = 55)\) respectively.
Figure 2.4: Mean sound level within five octave bands for recordings with (solid circle and line) and without (ambient reef noise only - hollow circle and dashed line) purr vocalisations. Figure 2.4a, c, e and g are during full moon of summer ($n = 110$), autumn ($n = 65$), winter ($n = 35$), and spring ($n = 35$) respectively. Figure 2.4b, d, f and h are during new moon of summer ($n = 20$), autumn ($n = 80$), winter ($n = 45$), and spring ($n = 85$) respectively.
Figure 2.5: Box and whisker plot of δdB values in five octave bands 1-5 for, a) croak ($n = 73$), and b) purr ($n = 95$). Box outline indicates interquartile range (IQR). Whisker indicate $1.5\times$IQR values. Median = horizontal line in box; mean = dashed line in box. Dots indicate outliers (i.e., automatically generated showing only the 5th and 95th percentile respectively). An asterisk indicates the octave band has a δdB greater than control. Different letters indicate octave bands with significantly different δdB (Dunn’s tests; $P < 0.05$).
2.3.3 Fish Chorus

Sound in band 2 was used to represent croak and purr vocalisations since it contained the peak frequency of both sounds. Fish choruses were not observed during the full moon (Figure 2.6a-d) but were observed during the new moon of every season (Figure 2.7a-d). Choruses occurred after sunset and lasted between 2 to 4 hours. In summer and winter, the chorus started within an hour after sunset and lasted three hours with mean peak intensities of $105.0 \pm 0.2$ dB re 1 µPa (7 dB above ambient noise) and $81.4 \pm 0.5$ dB re 1 µPa (3 dB above ambient noise), respectively. In autumn, the chorus started five hours after sunset and lasted 4 hours, with a peak intensity of $85.4 \pm 0.9$ dB re 1 µPa (4 dB above ambient noise). In spring, the fish chorus in band 2 started three hours after sunset and lasted 2 hours, with a mean peak intensity of $82.4 \pm 0.6$ dB re 1 µPa (2 dB above ambient noise). Fish choruses were correlated with invertebrate choruses during the new moon of summer ($r = 0.49$, $P < 0.001$), winter ($r = 0.54$, $P < 0.001$) and spring ($r = 0.33$, $P < 0.001$) but was not correlated in autumn ($r = 0.2$, $P = 0.051$).
Figure 2.6: $\text{NL}_{\text{rms}}$ in octave band 2 (circle solid line) and total $\text{NL}_{\text{rms}}$ in octave band 4 & 5 (square dashed line) during full moon in, a) summer, b) autumn, c) winter, and d) spring. Horizontal lines indicate chorus thresholds (mean ± SD). Vertical dotted lines indicate sunrise and sunset times respectively.
Figure 2.7: \( \text{NL}_{\text{rms}} \) in octave band 2 (circle solid line) and total \( \text{NL}_{\text{rms}} \) in octave band 4 \& 5 (square dashed line) during new moon in, a) summer, b) autumn, c) winter, and d) spring. Horizontal lines indicate chorus thresholds (mean ± SD). Vertical dotted lines indicate sunrise and sunset times respectively. Arrows indicate fish chorus.
2.4 DISCUSSION

The current study showed that fish vocalisations are apparent at a New Zealand reef. At least five different aural categories were present although only two were regularly heard. Even though their identities could not be verified they were most likely fish vocalisations based on their general resemblance to known fish vocalisations. Numerous fish vocalisations have been characterised together with a wide range of onomatopoeic expressions to describe the type of sounds involved in the vocalisation (Myrberg et al. 1993, Bremner et al. 2002, Amorim et al. 2004, Finstad & Nordeide 2004, Amorim 2006, Amorim et al. 2006, Lagardere & Mariani 2006, Lin et al. 2007, Amorim et al. 2008a, Anderson et al. 2008, Maruska & Mensinger 2009).

Collectively, these descriptions convey the aural impression of generic fish vocalisations that can help to facilitate preliminary identification of fish vocalisations in wild recordings (Anderson et al. 2008). The aural descriptions of croaks and purrs have been extensively reported as part of the vocalisation repertoires for many fish species. Croaks have been described for members of the families Batrachoididae (Amorim et al. 2006, Amorim et al. 2008a), Osphronemidae (Henglmuller & Ladich 1999, Ladich 2007) and Sciaenidae (Ramcharitar et al. 2006). Purr type sounds have been attributed to members of the families Percidae (Johnston & Johnson 2000, Speares & Johnston 2011) and Sciaenidae (Luczkovich et al. 1999, Sprague 2000, Lin et al. 2007). However, while useful for preliminary identification, such descriptions are subjective which gives rise to considerable ambiguity within aural categories (Amorim 2006, Kasumyan 2008). Measurements of acoustical characteristics provide the basis for comparison of vocalisations across fish species, which is not possible from aural descriptions alone.

Waveforms of both croaks and purrs reported in the current study exhibited temporal and spectral characteristics that were typical of many reported fish vocalisations, and their measured acoustic parameters were not dissimilar to the majority of known fish vocalisations (Kasumyan 2008). The pulses (3-20) of the vocalisations varied in amplitude and were arranged in trains to form total sound durations of up to 0.197 s (croak) and 0.437 s (purr). Their low peak frequency (croak = 271 ± 7 Hz and purr = 284 ± 4 Hz) and Q (< 1.5) indicates rapid decay of the sound wave, which was suggestive of sound produced by highly damped swim bladder vibrations (Bradbury & Vehrencamp 1998, Ladich & Fine 2006). The low Q for both categories of fish vocalisations in the present study was similar in comparison to other known swim bladder sounds which include those of toadfishes (Batrachoididae) 1.8 (Fine et al. 2009), gurnards (Triglidae), 1.5 (Connaughton 2004), and croakers (Sciaenidae) 1.3 - 2.9 (Fine et al. 2004).
However, comparison of the croaks and purrs from this study with vocalisations of some local species, i.e., bluefin gurnard (*Chelidonichthys kumu*), bigeye (*Pempheris adspersa*) and John dory (*Zeus faber*) in captivity at the Leigh Marine Laboratory did not show either aural (grunts, growls, pops and bark) nor visual resemblance. Therefore, it was not possible to determine the identity of the fish responsible for these sounds and each sound type might be produced by more than one species. Despite being unable to identify the source for the vocalisations, the distinctive aural descriptions and acoustic characteristics suggests that both croaks and purrs in the current study were of biological origin and were most likely to be produced by fish. For the purpose of the current study, putative fish vocalisation was considered sufficient to evaluate the general character of fish vocalisations in the reef noise.

The present study has shown that the dominant sound energy of the croaks (80 - 545 Hz) and purrs (84 - 482 Hz) were contained in three octave bands (band 1, 2 and 3), with an energy peak in band 2. There was a significant increase in the sound level in this octave band for clear individual vocalisations compared to the ambient reef noise. Accordingly, these fish vocalisations were likely contributors to the overall ambient reef noise and a potential contributor to choruses in the frequency range of their dominant octave bands. It is common to find that during the choruses of fish, individual vocalisations are merged together and are difficult to separate from the background noise (Cato 1978, Luczkovich et al. 1999, D'Spain & Batchelor 2006). However, it might be expected that the gross spectral composition of a fish chorus is the reflection of the individual vocalisation spectral characteristics. In similar studies, where identification of individual fish vocalisations was not possible from the chorus recordings, the determination of the composition of the vocalisations within the choruses have been inferred from spectral characteristics of individual vocalisations available within the same locality or from captive fish (Cato 1978, Sprague & Luczkovich 2001, Gannon 2008). In passive acoustic surveys in North America, the choruses of several croaker species (Sciaenidae) were inferred from recorded sound of captive fish (Saucier & Baltz 1993, Luczkovich et al. 1999). In coral reefs of Australia, choruses consisting of ‘pop’ and ‘trumpet’ categories of fish vocalisations were inferred from individual sounds of fish trapped in nets and observations using remotely operated vehicle (McCauley & Cato 2000).

In New Zealand waters, choruses by sea urchins (Castle & Kibblewhite 1975, Radford et al. 2008a) and snapping shrimp (Radford et al. 2008b) have been reported. In addition this study
strongly suggests that fish choruses are a common feature of New Zealand reefs, reliably occurring during new moon after sunset for up to four hours across all seasons. The diel timing (after sunset) of fish choruses in this study was consistent with the timing of the majority of fish choruses observed elsewhere around the world (Cato 1978, Luczkovich et al. 1999, D'Spain & Batchelor 2006, Locascio & Mann 2008). The intensity and duration of the choruses observed in the current study was variable with the loudest observed in summer followed by autumn, winter and spring. The fish choruses in this study tended to be relatively quieter and shorter in duration to choruses observed elsewhere. In the Timor Sea, West Pacific, and East Indian Oceans near Australia, evening fish choruses were up to 30 dB above usual ambient noise (Cato 1978). In coastal waters of North America, choruses of the croaker (Sciaenidae) and toadfish (Batrachoididae) increased the ambient noise by up to 50 dB (Fish & Cummings 1972) and 20 dB (Fish 1964), respectively. In North Carolina, the average sound pressure level of evening choruses by a mix of species of sciaenids was up to 147 dB re 1 µPa in the frequency range 0-6000 Hz (9 dB above mean ± SD) (Luczkovich et al. 1999). For the majority of fish choruses mentioned above, the duration was between 4 - 8.7 h which was longer than the duration of choruses observed in this study (maximum 3 h). However, direct comparisons of chorus characteristics (i.e., intensity and chorus threshold) among different researchers should be made with caution due to the differences of frequency bands, in which the sound level was measured.

In the present study moon phase had an effect on fish vocalisations with choruses occurring during the new moon but not during the full moon. One interpretation was that vocalising during the darker nights of the new moon may incur less predation risk compared to the full moon. These findings do differ from some studies, where fish choruses were also observed during the full moon, although in such cases the choruses also coincided with spawning events (Luczkovich et al. 1999).

The magnitude of a fish chorus is highly dependent on the number of participating individuals whereby loud choruses commonly involve a large aggregation of individuals such as, during spawning. As a consequence, spawning choruses vary in intensity and depends on location and time of occurrence. Croakers (Sciaenidae) in particular demonstrate this behaviour, utilising the chorus effect of their courtship calls to enhance the attraction of potential mates to spawning aggregations (Connaughton & Taylor 1995, Lagardere & Mariani 2006, Luczkovich et al. 2008b, Tellechea et al. 2010). In New Zealand waters where sciaenids are not found,
comparable vocalisation behaviour among the approximately 270 coastal species of fish is unknown. Here, fish chorus were probably due to an increase in acoustic communications during various social interactions of the reef fish community. Extensive knowledge of the vocalisation repertoire of local species would be useful in further understanding the interpretation of these local fish choruses. Based on the characteristics of two putative vocalisation types analysed, the current study showed that fish choruses do occur in reefs in the temperate waters of New Zealand. However, they were quiet compared to elsewhere. Hence, it was also concluded that these choruses may not be as distinctive a feature of the reef soundscape as the choruses of urchins and snapping shrimps. It was also likely that sea conditions and shipping noise may mask the fish chorus due to the similar low frequency bands they share (Wenz 1962, Hawkins 1986).

Biological choruses by different animal sources within a habitat usually overlap in time and space. Consequently, masking is likely to occur and may exert considerable constraints on animals that utilise a particular sound or frequency range for communication (Wahlberg & Westerberg 2005, Clark et al. 2009, Codarin et al. 2009). The current study showed that the fish choruses and those produced by urchins and snapping shrimps occurred at the same time and that the acoustic intensities of the latter were noticeably greater compared to those of the fish. Urchin sounds are the result of the resonance of their test, triggered by the rasping action of the Aristotle lantern during feeding (Radford et al. 2008a). Therefore, the dominant frequencies of urchin sounds are inversely related to their test diameter, with the biggest urchin producing sounds as low as 700 Hz (Radford et al. 2008a). Snapping shrimp on the other hand produces an intense click sound that has a low-frequency peak between 2000 and 5000 Hz and energy extending out to 200 kHz (Au & Banks 1998, Versluis et al. 2000). Therefore, urchin and snapping shrimp choruses would only increase the ambient noise in band 4 and 5. Here it was shown that fish choruses occupy different octave bands (i.e., band 1 - 3 with a peak in band 2) than those of the invertebrates. This finding suggests that fish choruses at a reef may be audible to fish through a quiet spectral window during the invertebrate choruses. This is facilitated by the fact that fish in general are sensitive to a rather restricted range of frequencies < 100 Hz to 2000 Hz (Hawkins 1986), with greatest sensitivity at the lower frequencies covered by the octave bands 1, 2 and 3 (Fay 1988). Furthermore, it has been found that for some soniferous fishes, the frequency of best hearing correlates with the spectral characteristics of their vocalisations (Sisneros 2007, Lechner et al. 2010). The combination of spectral characteristic
disparities between vocalisations and other reef noise, as well as the small frequency range of hearing may help to reduce or avoid the possible effects of temporally overlapping choruses from other animal groups. The phenomenon may be interpreted as comparable to the ‘partitioning’ of the acoustic space and utilization of an acoustic communication window that has also been reported for fish living in noisy freshwater habitats (Lugli & Fine 2003). For example, the vocalisation frequencies of two species of stream gobies, Padogobius bonelli and Gobius nigricans (Lugli 2010), and darters, Etheostoma crossopterum and E. flabellare (Speares et al. 2011), have been shown to correlate with the quiet spectral window of their noisy stream habitat. Similarly in birds, the vocalisation frequencies of the green hylia (Hylia prasina) was inversely correlated to the spectral profile of the dominant insect generated noise within a habitat (Kirschel et al. 2009). It has been hypothesised in these cases that habitat noise may served as an environmental selection pressure on the acoustic signals of animals (Slabbekoorn & Smith 2002).

The current study has shown that fish vocalisations form dusk choruses during the new moon on a New Zealand reef across all seasons. The magnitude of the chorus was modest, and thus not as distinctive a feature of the reef soundscape as the choruses of urchins and snapping shrimps (Radford et al. 2008a, Radford et al. 2008b). The relatively low intensity of the fish chorus also suggests that fish choruses may not propagate the same distances as previously described for choruses of invertebrates. However, it does contribute to the overall noise level within the reef environment. The current study also showed that the fish chorus occupied a spectral window below the higher frequencies of the invertebrate chorus such that the communicative value of the fish vocalisations could be minimally affected by the more intense invertebrate noise.
Chapter Three: Vocalisations of the Bigeye

CHAPTER THREE:

VOCALISATION OF THE BIGEYE *Pempheris adspersa*:
CHARACTERISTICS, SOURCE LEVEL AND ACTIVE SPACE

3.1 INTRODUCTION

Reef habitats are known to sustain healthy populations of a wide variety of fish species (Bellwood & Wainwright 2002). In coral reefs, many resident fish species are reported to be soniferous which includes some members of the families Pomacentridae (Myrberg et al. 1993, Parmentier et al. 2006c, Parmentier et al. 2009), Holocentridae (Parmentier et al. 2011b) and Chaeotodontidae (Tricas et al. 2006, Boyle & Tricas 2010). It has been widely reported the types of vocalisations they produce are as diverse as the number of species concerned. These include a variety of chirps (Luh & Mok 1986, Chen & Mok 1988, Myrberg et al. 1993, Lobel & Kerr 1999), clicks, grunts (Amorim 2006, Tricas et al. 2006) and pops (Mann & Lobel 1998, McCauley & Cato 2000). Coral reef fishes show a variable diel sound production pattern. Most commonly, sound production rates of many coral reef fishes were reported to peak around crepuscular periods (McCauley & Cato 2000, Parmentier et al. 2010b), corresponding to an increase in behavioural activity during this period. At other times sound production appears to be biased, discriminately occurring during day or night time among species which is probably subjective to the activity state of the fish. On the other hand, vocalisations of fish from temperate reefs are less well known.

Vocalisations are widely reported to serve a communication function during various inter-individual interactions and are usually associated with specific behaviours (Bradbury & Vehrencamp 1998, Kasumyan 2009). For territorial defence, the bicolour damselfish *Pomacentrus partitus* produces a chirp sound as a “keep-out” signal to intruders as part of its agonistic behaviour (Myrberg 1997a). For courting, the male albino damselfish *Dascyllus*
albisella) produces chirp sounds during its courtship behaviour known as the ‘signal jump’ to
court potential mates for spawning (Mann & Lobel 1997, 1998). In addition, 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 loose school structure and allow
the fish to track prey aggregations (McCauley & Cato 2000). Whatever the context of
vocalisations may be, the receiver’s behavioural response is expected to be restricted to within
the range that vocalisations are audible. This range is also known as the active (Janik 2000) or
communication (Clark et al. 2009) space which can be 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 largely been studied in
marine mammals but is lacking for fishes. This may be in part due to difficulties in obtaining
critical bioacoustical information (i.e., vocalisation characteristics, source level and auditory
sensitivity) of a target fish in combination with the ambient noise of their habitat.

Measuring source levels (SL) of fish vocalisations presents inherent challenges and
necessitates recording of the sound in a free non-reverberant sound field using calibrated
recording systems (Urick 1983). Since SL refers to sound pressure measurements at 1 m (dB re 1
µPa @ 1m), 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 estimation of
vocalisations in the wild is possible if the identity of the call can be verified by comparing
(sound-truthing) its characteristics with those of captive fishes. Despite differences in their
background noise (i.e., multiple sound sources in the field and reflection of sound in tanks) field
and tank recordings can be corroborated by comparing their acoustic parameters (Sprague &

A family typical of reef fishes is the Pempheridae which consists of cryptic
planktivorous fish that undergo nocturnal migrations to forage (Gladfelter 1979, Golani &
Diamant 1991, Annese & Kingsford 2005). In temperate reefs around north eastern New
Zealand, the endemic bigeye, Pempheris adspersa, is one such example. Typically within an
hour after sunset, bigeyes leave their day time shelter in rocky crevices and beneath overhangs,
moving out to forage over the reef area throughout the night (MacDiarmid 1981, Kingsford &
MacDiarmid 1988). Within an hour before sunrise, they return and take refuge at the same
daytime shelter. Although, the vocal behaviour of *P. adspersa* is currently unknown,
vocalisations have been reported for another species within the same genus, *P. schwenkii*
(Takayama et al. 2003).

Fish sound is widely regarded a significant component of a reef soundscape. Nonetheless
the vocalisation of New Zealand reef fishes has never been described hence its contribution to
the reef soundscape is poorly understood. Knowledge on the characteristics of fish vocalisation,
SL and active space in general is useful for understanding the spatial scale of the vocalisations. It
may also shed some light on the possible use of vocalisation during certain behaviours of fish.
Thus the overriding objective of this chapter was to study the vocalisation characteristics, SL
and active space of the bigeye, *Pempheris adspersa* as a function of ambient noise levels. This
will be achieved by;

1) characterising bigeye vocalisations and their daily periodicity of production;
2) measuring the SL of bigeye vocalisations;
3) estimate the effective calling range and active space of bigeye vocalisations with respect
to the effects of temporal (seasonal and lunar) amplitude variation of their habitat noise.

3.2 METHODS

3.2.1 Captive Fish Experiment

Capture and Holding

Bigeyes from a single shoal were captured at a reef around the Outpost (36°17’23” S,
174°49’09” E) near Leigh, New Zealand by SCUBA divers using scoop nets and custom made
plastic nets to minimise injury. Captured fish were immediately transported in seawater to the
Leigh Marine Laboratory where they were housed in a circular polyethylene tank (opaque,
diameter1.6 m; depth 0.5 m) with flow-through filtered (200 µm) aerated sea water supply. The
tank was located in a quiet area outdoors to minimise extraneous noise. The fish were held under
ambient photoperiod and sea water temperature (18° C). They were allowed to acclimatise to
laboratory conditions for ten weeks prior to the experiments and were fed fish roe or sliced squid
three times a week.
Experimental setup

One group comprising 20 fish (i.e., 9 females (6 gravid) and 4 males as well as 7 smallest individuals that could not be sexually verified), measuring between 70 - 130 mm (FL) were used throughout the experiments. Diel vocalisation periodicity experiments were conducted using the same group of fishes. The experiments were designed to allow the captive fish to behave as naturally as possible by minimising human contact and could be observed using an underwater video camera. Six non-consecutive continuous recordings each lasting 24 h was conducted. During sound recordings, fish were not fed and water flow and aeration was turned off.

Experiments commenced at the same hour of the day (1600 h) and were conducted between 30 December 2009 and 30 January 2010 on fine days without rain. Information for the sunset and sunrise times was obtained from the sun data provided online by www.gaisma.com. Dusk and dawn time were defined as beginning one hour before and lasting until one hour after sunset and sunrise times.

Recording and analyses

For each experiment, sound was recorded at a sampling rate of 44.1 kHz (16 bit) continuously for 24 h with a HTI – 96 - MIN hydrophone (High Tech Inc. USA) with a sensitivity of -165 dB re 1V/1μPa and a flat frequency response from 0.01 to 30 kHz connected to a portable digital audio recorder (Sound Devices 722, Wisconsin, USA). The hydrophone was suspended in midwater from the centre of the tank. Preliminary assessment showed that bigeye vocalisations contain frequency components much less than the minimum resonant frequency of 1662 Hz calculated for the tank (Akamatsu et al. 2002). This 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, U.S.A.) 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. Acoustic measurements of the sounds were made after filtering the sound through a digital band-pass filter between 50 and 1200 Hz. The following sound parameters were measured for the basic single pulsed sound; sound duration (SD, 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); number of pulses (PN); peak frequency (Pf, the frequency component with the highest amplitude in the entire sound); 10 dB lower frequency (10dBLf, lower frequency limit which amplitude is 10 dB less than the peak frequency); 10 dB upper frequency (10dBUf, upper frequency limit which amplitude is 10 dB less than the peak frequency), 10dB bandwidth (10dBBW, range between lower and upper frequency); 3 dB lower frequency (3dBLf, lower frequency limit with an amplitude of 3 dB less than the peak frequency); 3 dB upper frequency (3dBUf, upper frequency limit with an amplitude of 3 dB less than the peak frequency), 3dB bandwidth (3dBBW, range between lower and upper frequency) and damping coefficient (Q, \( Q = \frac{Pf}{3 \text{dB BW}} \)). For calls with multiple pulses, the SD, Pf, PN and pulse period (PP, mean time (ms) elapsed between the peak amplitude of two consecutive pulses) was measured from the whole call. Sound duration was measured from spectrograms plotted using a 64-point Fast Fourier Transform (FFT) with 50% overlap while PP was measured from oscillograms following band-pass filtering of the sound (50 - 1500 Hz). Spectral parameters (which are in abbreviations in brackets here) 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 pooled from the distinct 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 up to 3 pulses were characterised.

For the diel periodicity experiment, the occurrence of vocalisation pulses was counted from 10 s resolution time frames divided from the entire recording. The vocalisations were pooled among all individuals (20 fish) since they could not be traced to individual fish from the recording. 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 period (0700 - 2000), night period (2200 - 0500), dusk (2000 - 2200) and dawn (0500 - 0700). The Friedmans test using total hourly counts of vocalisations was used to compare vocalisation rate among individual hours of the day and among the different periods since the same group of individuals were used throughout the experiment and non-normality of data distribution. Following a significant Friedmans test result, the post hoc multiple group comparisons were conducted with Tukey tests.
After the experiments ended, several fishes were euthanised using an overdose of fish anaesthetic (Aqui-S®) and dissected to identify possible sound production mechanisms under a stereo microscope. All fish capture, handling, and experimentation was conducted under guidelines of the University of Auckland Animal Ethics Committee approval, AEC727.

### 3.2.2 Field Experiment: Recording and Source Level (SL) Measurement

Underwater recordings to measure the SL of bigeye vocalisation in the field were conducted at North Reef, Leigh (36°15'45" S, 174°47'33" E) north-eastern New Zealand in April 2011. During the recordings the Beaufort sea state scale was measured at 0 or 0.5. The location was the same as the location of the temporal 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 by an aluminium bar. The hydrophones were each connected to a separate recording channel of a digital sound recorder (Edirol - R09HR, Japan) encased in a waterproof plexiglass housing together with a 12 V power supply. Simultaneous recordings were made at 44.1 kHz (16 BIT) continuously for 48 h, which preserved the difference in times of arrival of the same sound on different hydrophones, and stored in a 32 GB SDHC memory card.

The recording system was calibrated before and after every recording session. For all recordings, the gain on the recorder was fixed at a set level (level 20), which was calibrated by taking a series of 1 kHz pure tone (sine wave) recordings produced by a function generator (IEC F34, USA). The voltage (V<sub>rms</sub>) of the tone recordings were measured and compared with the hydrophone sensitivity (-164.6 dB re 1V/1µPa). Subsequently, a correction factor was calculated and applied to sound pressure measurements obtained with the hydrophones. 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 source level measurements.

Calculation of SL using the differences in received levels (RL) of a same sound arriving at two hydrophones and differences in time of arrival of the sound was based on Cato (1998). Vocalisation Root-Mean-Square RL (RL<sub>rms</sub>) at both hydrophones were measured in four octave bands i.e., Band 1 - 4 with their centre frequencies at 125, 250, 500 and 1000 Hz respectively.
(Table 3.1) 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. The RMS source level (SL_{rms}) were 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 & Ladich 2002). The level of self-noise of the recording system was determined from a control recording conducted in air in a quiet room at the Leigh Marine Laboratory. It was found that the level of self-noise from the recording system was much lower than the sea ambient noise in the relevant octave bands therefore, SL measurement was not limited by self-noise.

3.2.3 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 taken by Radford (2007) for another study. 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 2 days on each side of the moon phase under consistent wind speed and sea conditions (sea state 2). Further details on these temporal recordings were described in Radford (2007).

Octave analyses was used to characterise the ambient noise during different seasons (summer, autumn, winter and spring), moon phases (full and new moon) and hours of the day. Root-Mean-Square habitat noise level (NL_{rms}) in four octave bands, i.e., Band 1-4 with their centre frequencies at 125, 250, 500 and 1000 Hz respectively (Table 3.1) were measured with MATLAB® using digital octave band filters created with scripts modified from octbank.m by Christophe Couvreur. These bands were selected because they corresponded to the frequency range (band-width) of the bigeye vocalisation. Although the precise band-widths of the auditory filters for fish is 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 audibility of a signal in the presence of noise. Masking of signal by noise occurs within and not between octave bands except when the noise level is at very high intensity which would cause downward/upward communication masking in adjacent bands (Clark et al. 2009, Jensen et al. 2009). The hourly NL$_{\text{rms}}$ in band 1, 2 and 3, and total noise in these bands (band123) were obtained by averaging the measurements from four randomly selected 1 s sound samples of the hourly temporal recordings. Total noise in Band123 were plotted for the hours encompassing the time of sunset and sunrise (1600 hrs to 0800 hrs the following day) which included one to up to a five hours before and after the respective sun movement times. The average habitat ambient noise level (ANL) over this period was calculated as the mean of NL$_{\text{rms}}$ plus one standard deviation (mean NL$_{\text{rms}}$ + SD).

The Mann-Whitney U-test was used to compare NL$_{\text{rms}}$ between new moon and full moon within the same season. The Kruskal - Wallis test was used to compare NL$_{\text{rms}}$ among different seasons within the same moon phase. The mean ± standard error of means (SEM) values were used in all measurements throughout this study unless stated otherwise.

### Table 3.1: Octave band filter characteristics

<table>
<thead>
<tr>
<th>Band</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Centre frequency, Fc / octave band-width, BW (Hz)</td>
<td>125 / 89</td>
<td>250 / 178</td>
<td>500 / 353</td>
<td>1000 / 708</td>
</tr>
<tr>
<td>Octave band frequency range (Hz)</td>
<td>89 - 178</td>
<td>178 - 355</td>
<td>355 - 708</td>
<td>708 - 1410</td>
</tr>
</tbody>
</table>

### 3.2.4 Sonar Equation and Effective Calling Range Estimation

For the purpose of this study, it is assumed that; 1) signal detection is limited by the ambient noise; 2) vocalisation source level does not vary in response to a varying background noise level; and 3) equal omni-directional sensitivity of the fish hearing. The sonar equation used to describe the propagation of sound in the current study follows Equation 1, which is modified from Clark et al.(2009):
Sonar parameters used include; SE, signal excess, which at SE = 0 defines the 50% probability of signal detection (Urick 1983, Clark et al. 2009); $SL_{rms}$, source level, defined as the RMS sound pressure level at 1 m from the source; ANL, average habitat ambient noise level, calculated as the mean hourly octave band levels $NL_{rms}$ of noise (NL$_{rms}$) in the period described earlier plus the standard deviation; $TL_{sp}$, spherical spreading transmission loss, calculated as $20 \log (\text{range (m)})$; and DT, detection threshold, defined as the difference between signal and noise at the threshold sound level where signal can be perceived. Little is known about the DT for fish (Wahlberg & Westerberg 2005). The limited available data indicates considerable variation in the range from 5 to more than 20 dB (Chapman & Johnstone 1974, Fay 1988, Yan & Popper 1993, Mann & Lobel 1997, Wysocki & Ladich 2005). For sonar systems, as well as marine mammals, DT = 10 dB is usually used (Kastelein et al. 2007, Clark et al. 2009). The current study used the DT value of 15 dB which is considered an intermediate and rather conservative value. All of the sound intensity values (dB re 1 µPa) and related sonar equation parameters reported in this current study were for a specified frequency band (octave bands) and were thus RMS band level measurements. The effective calling range ($r$) was calculated as in Equation 3 that was derived from Equation 2 when SE = 0. The estimation of the active space for a single fish source was based on this $r$ value. Increasing range ($r$) indicates an increase in the radius of active space for call detection.

Solving for range, $r$ in:

$$TL_{sp} = 20 \log r \text{ gives, } r \text{ when } SE = 0; \quad \text{Equation 2}$$

Thus

$$r = 10^{(SL - ANL - DT/20)} \quad \text{Equation 3}$$
3.3 RESULTS

3.3.1 Vocalisation Repertoire and Acoustic Characteristics

Bigeye vocalisation consists of a pulsed type of sound that may be aurally described as a ‘pop’ (Figure 3.1a). The duration of the pop was very short (7.9 ± 0.3 ms) and was composed of either one or two cycles of the sound wave. Pops were produced either individually or in series to form calls comprising trains of up to seven pulses. Consequently, such calls especially those with shorter pulse period, sounded more like a ‘grunt’. When forming trains of pops, the individual pops can either be fused together (fused) with one pop merging into the subsequent pop (Figure 3.1b,d & f) or separated (unfused) with the pop being distinct from the subsequent pop (Figure 3.1c & e). Pops that are separated by a minimum time interval of 100 ms were considered as separate calls. For the single pulse call (pop), mean SD was 7.9 ± 0.3 ms with mean peak frequency of 405 ± 12 Hz (Table 3.2). The mean 10dBBW of the sound was 906 ± 23 Hz encompassing the frequency range 74-980 Hz. Top 3 dB of the sound energy was in the 3dBBW of 510 ± 19 Hz spanning between 149 - 659 Hz. The mean Q value which indicate tuning or damping coefficient was 0.82 ± 0.02.

For double pulse calls, the mean SD for fused calls was 9.9 ± 0.2 ms and for unfused calls was 29.5 ± 0.5 ms with their mean Pf at 370 ± 10 Hz and 308 ± 9 Hz, respectively. The mean 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 pulse calls, mean SD for fused calls was 12.6 ± 0.3 ms and for unfused calls was 58.7 ± 2.2, with their mean Pf at 404 ± 17 Hz and 3297 ± 15 Hz, respectively. The mean of the first pulse period for a fused call was 6.5 ± 0.1 ms while for the unfused call was 20.8 ± 1.1 ms. Mean of the second PP was 5.4 ± 0.2 ms and 36.6 ± 1.2 ms respectively.

The arrangement of pulses in the recordings of bigeyes at North Reef was similar in most respects to those of captive fish recordings. Many of the calls were clearly separated from each other with the majority of calls detected and identified consisting of the 3 unfused pulse train sound type (Figure 3.1e). Band-pass filtering (90 - 700 Hz) of the vocalisations around their main frequency range showed that overall waveform shapes of several representative call types at North Reef was a close match to the tank recordings (Figure 3.2a & b). Spectrograms and spectra from both recordings of fish in captivity and at North Reef showed comparable time-frequency distribution (Figure 3.2c & d) as well as frequency composition (Figure 3.2e & f) of
their dominant sound energy. The interquartile range (IQR) of the measurements of the acoustic parameters PP1 and Pf showed overlapping values for captive and North Reef bigeye vocalisations (Figure 3.3a & d), but this was not the case for PP2 and SD (Figure 3.3b & c). The differences in the calls of captive and North Reef fish for the median values of the PP1 (1.9 ms) were < 10% of the lowest median value while the difference in Pf (86 Hz) corresponded to the frequency resolution of the FFT used to plot the spectra. The overall variations of the measurements of acoustic parameters between captive and North Reef vocalisations were attributed to the differences in the nature of the recordings.

Figure 3.1: Representative oscillogram of the different call types of the bigeye in captivity. a) single pulse; b) double pulse fused; c) double pulse unfused; d) triple pulse fused; e) triple pulse unfused; and f) seven pulse fused and followed by a single unfused pulse. Oscillogram was plotted after band-pass filtering sound between 50 - 1500 Hz.
Table 3.2: Acoustic features of the bigeye vocalisations. Values are means ± SEM and range is given in parentheses below. For Pf, Lf and Uf the median value is given in parentheses on the right. SD = sound duration (ms); PN = number of pulses; PP1 & PP2 = pulse period 1&2 (ms); Pf = peak frequency (Hz); 10dBLf = 10 dB lower frequency limit (Hz); 10dBf = 10 dB upper frequency limit (Hz); 10dBBW = 10 dB band-width (Hz); 3dBLf = 3 dB lower frequency limit (Hz); 3dBf = 3 dB upper frequency limit (Hz); 3dBBW = 3 dB band-width (Hz); Q = damping coefficient.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Single pulse</th>
<th>Two pulse</th>
<th>Three pulse</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± SEM</td>
<td>Mean ± SEM</td>
<td>Mean ± SEM</td>
</tr>
<tr>
<td></td>
<td>(range)</td>
<td>(range)</td>
<td>(range)</td>
</tr>
<tr>
<td>n</td>
<td>68</td>
<td>86</td>
<td>68</td>
</tr>
<tr>
<td>SD (ms)</td>
<td>7.9 ± 0.3</td>
<td>9.9 ± 0.2</td>
<td>29.5 ± 0.5</td>
</tr>
<tr>
<td></td>
<td>(1.0 - 11.6)</td>
<td>(7.2 - 25.4)</td>
<td>(23.9 - 40.6)</td>
</tr>
<tr>
<td>PN</td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>405 ± 12</td>
<td>370 ± 10</td>
<td>308 ± 9</td>
</tr>
<tr>
<td>Pf</td>
<td>(258 - 603)</td>
<td>(176 - 603)</td>
<td>(258 - 603)</td>
</tr>
<tr>
<td></td>
<td>344</td>
<td>388</td>
<td>258</td>
</tr>
<tr>
<td>10dBLf</td>
<td>74 ± 1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>10dBf</td>
<td>980 ± 23</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>10dBBW</td>
<td>906 ± 23</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>3dBLf</td>
<td>149 ± 3</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>3dBf</td>
<td>659 ± 20</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>3dBBW</td>
<td>510 ± 19</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Q</td>
<td>0.82 ± 0.02</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>PP1</td>
<td>-</td>
<td>8.2 ± 0.2</td>
<td>27.1 ± 0.5</td>
</tr>
<tr>
<td>PP2</td>
<td>-</td>
<td>-</td>
<td>5.4 ± 0.2</td>
</tr>
<tr>
<td>meanPP</td>
<td>-</td>
<td>-</td>
<td>5.9 ± 0.1</td>
</tr>
<tr>
<td>PP1/PP2</td>
<td>-</td>
<td>-</td>
<td>1.23 ± 0.03</td>
</tr>
</tbody>
</table>
Chapter Three: Vocalisations of the Bigeye

Figure 3.2: Representative oscillogram, spectrogram and normalised power spectrum of selected calls from captive (a,c and e) and North Reef (b,d,f) vocalisation of bigeye. Sounds were band-pass filtered between 90 - 700 Hz. Spectrograms and power spectra were computed using 512 point FFT for the pulses marked by square inserts.
Figure 3.3: Parameter comparison between captive \((n = 42)\) and North Reef recordings \((n = 82)\) of the triple pulsed unfused call. Box outlines indicate the interquartile range (IQR), whisker bar = ± 1.5*IQR and circles are outliers. Solid and dashed lines in the boxes are median and mean values respectively. a) first PP (PP1) b) second PP (PP2) c) SD d) Pf
3.3.2 Diel Periodicity of Vocalisation

Vocalisation of captive fish occurred during all hours with significant variation in vocalisation rate among individual hours (Friedman, $\chi^2_{23} = 53.1, P < 0.001)$ (Figure 3.4). The vocalisation rate at night and dusk was significantly higher than the day (Friedman, $\chi^2_3 = 14.8, P = 0.002$). Vocalisation rate was similar among night, dusk and dawn (Tukey test, $P < 0.05$). Vocalisation rate was also similar between dawn and day as well as between dawn and night (Tukey test, $P < 0.05$) (Figure 3.5). Mean vocalisation rate during the periods were; day = $73.0 \pm 13.3$, dusk = $126.4 \pm 18.0$, night = $116.8 \pm 18.8$ and dawn = $78.5 \pm 19.6$ vocalisations h$^{-1}$. 
Figure 3.4: Hourly vocalisation rate of bigeyes in captivity ($n$ days = 6; $n$ fish = 20). White, black and grey horizontal bar indicate hours of day, night and dawn/dusk respectively.

Figure 3.5: Comparison of vocalisation rate among different periods of the 24 h period. Different letters indicate statistically significant differences between periods (Tukey test; $P < 0.05$)
3.3.3 Vocalisation Source Level

Root-mean-square source levels (SL$_{rms}$) were measured from 82 pulses from calls that consisted of the triple pulse unfused type recorded at North Reef (Figure 3.1e). Source level was measured for the first pulse of each call which usually represented the highest amplitude within a call. The mean SL$_{rms}$ of sound in band 1 was 100.2 ± 0.4 dB re 1 µPa @ 1m, band 2 111.7 ± 0.3 dB re 1 µPa @ 1m, band 3 113.1 ± 0.2 dB re 1 µPa @ 1m and band 4 118.7 ± 0.7 dB re 1 µPa @ 1m (Figure 3.6). 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 type from the captive fish recordings. Sound in band 4 was not comparable which showed higher energy content for the North Reef vocalisation. The mean sound energy in band 4 of the North Reef recording was 14 dB higher compared to captive recordings. The elevated sound intensity in band 4 was attributed to the high level of noise in this band at North Reef. Consequently, sound level measurement in this band was 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 band 1, 2 and 3 produced mean SL$_{rms}$ of 115.8 ± 0.2 dB re 1 µPa @ 1m.
Figure 3.6: Source level (SL$_{rms}$) measurement of single sound pulses within a call from the North Reef recordings ($n = 82$). Box-plots show SL$_{rms}$ of sound in different octave bands. Box outline indicate inter-quartile range (IQR), whisker bar $= \pm 1.5$IQR and circles are outliers. Solid line and dashed line in box are median and mean values respectively. Dotted line across the box-plot is mean octave band level for sound recorded in the tank. Both wild and tank recordings are comparable using the relative dB scale on the right axis.
3.3.4 Habitat Ambient Noise and Effective Calling Range

Noise level ($NL_{rms}$) in band 1, 2, and 3 during new moon was significantly louder than full moon within respective seasons [Mann-Whitney; $U = 0.000$, $P < 0.001$ (summer – December); $U = 0.0$, $P < 0.001$ (autumn – April); $U = 1142$, $P < 0.001$ (winter – June) and $U = 8.0$, $P < 0.001$ (spring – September)]. Average ambient noise levels were between 83 - 116 dB re 1 µPa during new moon periods (two days either side of lunar event) compared to 68 - 83 dB re 1 µPa during full moon periods (two days either side of lunar event). $NL_{rms}$ were also significantly different among seasons within the same moon phase (Kruskal-Wallis; $H_3 = 213.48$, $P < 0.001$ (full moon); $H_3 = 197.42$, $P < 0.001$ (new moon)). Tukey multiple comparison tests showed that all season pairs were significantly different ($P < 0.05$), except between autumn and spring during full moon and between winter and spring during new moon. For both full moon and new moons, ANL was highest in summer (83 dB re 1 µPa and 116 dB re 1 µPa, respectively) and lowest in winter (68 dB re 1 µPa and 82 dB re 1 µPa, respectively) (Figure 3.7a - d, 8a - d). Due to the way effective calling range was calculated, the relative difference of effective calling range between moon phases and season is correlated with patterns of background noise. Therefore, effective calling range of sound in band 1, 2, and 3 was greater during full moon compared to the new moon. During full moon, the greatest calling range was observed in autumn and spring at 31.6 m and the shortest in summer at 6.3 m (Figure 3. 9a). 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 (Figure 3. 9b).
Figure 3.7: Hourly octave sound level in band 123 (circle solid line) and the 15 dB detection threshold (dashed line) during full moon. a) summer, b) autumn, c) winter, and d) spring. Lower and upper solid horizontal lines indicate ANL (mean NL_{rms} + SD) and mean SL_{rms} respectively. Vertical dotted lines indicate sunset and sunrise times respectively.
Figure 3.8: Hourly octave sound level in band 123 (circle solid line) and the 15 dB detection threshold (dashed line) during new moon. a) summer, b) autumn, c) winter, and d) spring. Lower and upper solid horizontal lines indicate ANL (mean NL_{rms} + SD) and mean SL_{rms} respectively. Vertical dotted lines indicate sunset and sunrise times respectively.
Figure 3.9: Effective calling range of vocalisation by bigeyes in North Reef for different octave bands during different seasons and lunar phases. a) full moon, b) new moon
3.4 DISCUSSION

The current study has described for the first time the vocalisations of the bigeye. The rapid decay of the pulse sound wave and low Q (0.82 ± 0.02) indicated that the bigeye has a highly damped sound production mechanism typical of a swim bladder vibration (Fine et al. 2001, Fine et al. 2009). Comparable to a congeneric *P. schwenkii* (Takayama et al. 2003), the bigeye swim bladder is vibrated by a pair of cylindrical extrinsic sonic muscles that originated at the neurocranium and attached to a thickened membrane on the anterior-dorsal part of the swim bladder. A highly damped sound production system would allow for efficient temporal patterning of pulses (Lindstrom & Lugli 2000, Fine et al. 2004). This was evident from the variety of pulse combinations that form the various call types that were consistently observed at North Reef and in captive fish recording. This may indicate the importance of the vocalisation temporal character for bigeye acoustic communication. The temporal and spectral characteristics of the bigeye sound were different in comparison with the vocalisation of another species, the silver sweeper *Pempheris schwenkii*. Takayama et al. (2003) reported that *P. schwenkii* produced a single sound type consisting of 2 - 7 pulses with an average duration of 56 ms from the contraction of similar paired extrinsic sonic muscles that attached to a double chambered swim bladder. *Pempheris schwenkii* vocalisations covered a narrower frequency band-width (200 Hz) with three harmonically related frequency peaks (100 Hz fundamental frequency). However, these results were obtained with the fish in air so are not directly comparable with the bigeye recordings reported in this study.

Among coral reef fishes, the acoustic characteristics of their vocalisations are variable. Damselfishes (Pomacentridae) produce pulsatile sounds (1-22 pulses) that have peak frequencies between 300-1000 Hz, pulse duration between 10-30 ms and pulse period between 8 - 120 ms (Luh & Mok 1986, Chen & Mok 1988, Myrberg et al. 1993, Mann & Lobel 1997, 1998, Lobel & Kerr 1999, Amorim 2006, Colleye et al. 2009, Parmentier et al. 2010b). Squirrelfish (Holocentridae) and butterflyfish (Chaetodontidae) produce vocalisations with peak frequencies between 80-130 Hz and 90 - 300 Hz respectively (Tricas et al. 2006, Boyle & Tricas 2010, Parmentier et al. 2011a, Parmentier et al. 2011b). Their pulse duration were 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 planktivore ‘pop’ sounds recorded by McCauley & 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 & Ladich 2002, 2003). For example, it has been suggested that the minimum integration time for goldfish was 0.4 ms while for a majority of fish the minimum integration time may be slightly higher but likely within the range of 1 - 10 ms (Wysocki & 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 Hz and 185 Hz respectively, which are smaller or close to the width of at least three critical bands (i.e., band 2, 3 and 4) that encompass their vocalisation range (74 - 980 Hz). This would suggest that the bigeyes should also able to resolve the spectral content of their vocalisation.

In captivity, the vocalisation rate of bigeyes was quite high (91 vocalisation fish$^{-20}$ h$^{-1}$) but calling occurred intermittently rather than continuously and lasted no longer than a few seconds at a time. There was a significant increase in vocalisation rate during dusk and the night period compared to the day. Many fish species show an increase in vocal activity during crepuscular periods (dawn and dusk), which possibly corresponding to an increase in a specific activity around this time. Higher numbers of vocalisations can be heard at a nesting population of toadfish, *Opsanus beta* around sunset corresponding to an increase in the rate of their advertisement call (Thorson & Fine 2002b, Fine & Thorson 2008, Locascio & Mann 2008). Similarly, several sciaenid species show increasing vocal activity at dusk particularly during their reproductive season (Connaughton & Taylor 1995, Luczkovich et al. 1999, Locascio & Mann 2011). At a coral reef habitat, higher sound production rates of the damselfish *Dascyllus flavicaudus* during sunrise and sunset were associated with different types of activities (Parmentier et al. 2010b). The increase in sound production rate during sunrise was associated with mating or nest visiting activity while at sunset the sounds were associated with chasing and signal jumps. This indicates that an increase in sound production rate is associated with an equivalent increase in a certain type of activity.

In captivity, the vocal activity of the bigeye peaked at dusk and remained relatively high throughout the night which corresponds well with the nocturnal nature of this species (MacDiarmid 1981, Mooi 2000). It is thus speculated that vocalisations are an important feature that accompanies certain nocturnal activities. In the wild, the primary nocturnal activity of the bigeye is foraging although spawning could also occur during their reproductive season between November and February (Thompson 1981, Mooi 2000). Nonetheless, both foraging and
spawning behaviours in this species are poorly understood. The use of vocalisations during foraging of a schooling fish is not known. For a non-schooling fish such as the gurnard (Triglidae), it has been shown that vocalisations accompanied the aggressive behaviour during competitive feeding of patchy food source (Amorim & Hawkins 2000, 2005). Here it is suggested that the bigeyes vocalisations may function as a group cohesion cue or contact calls during foraging following similar suggestions for the function of vocalisations in some coral reef planktivores (McCauley & Cato 2000). In other animal groups such as mammals (Edds-Walton 1997, Janik 2000, Sugiura 2007, Koda et al. 2008, Janik 2009, Nakahara & Miyazaki 2011) and birds (Cortopassi & Bradbury 2006, Sharp & Hatchwell 2006), the ability to maintain group cohesion using contact calls has been reported as biologically advantageous in a number of respects (Kondo & Watanabe 2009). However, to date fish are not known to use vocalisations to function as contact calls.

Determining call SL 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 of a known fish species is challenging because audio-video recordings obtained with SCUBA are not suitable for analyses due to the interfering bubble noise from the diver (Radford et al. 2005, Cole et al. 2007). Consequently, ‘silent’ but less common methods such as remotely operated vehicles (ROV) (Sprague & Luczkovich 2004, Parsons et al. 2009) or divers on closed circuit rebreathers have been employed (Lobel 2001). Sound recording using hydrophone arrays is a common and acceptable practice for estimating SL. There have been a few studies using these various recording techniques that have reported varying SL measurements of individual species. Using a similar method to the current study, McCauley & Cato (2000) measured source levels of three types of fish calls from the Great Barrier Reef and reported the ‘pop’ call SL_{peak-peak} at 157 dB re 1 µPa @ 1m, the ‘trumpet’ call SL_{rms} at 150 dB re 1 µPa @ 1m and the ‘banging’ call SL_{rms} at 144-147 dB re 1 µPa @ 1m. Parsons et al. (2009) measured SL_{rms} of mulloway, Argyrosomus japonicas, in the Swan River, Australia as ~ 170 dB re 1 µPa @ 1m. Sprague & Luczkovich (2004) measured the SL_{rms} of the ‘purr’ made by individual silver perch, Bairdiella chrysoura, from audio-video recordings using a remotely operated vehicle (ROV) in the range 128-135 dB re 1 µPa @ 1m. The haddock, Melanogrammus aegelfinnus was reported to produce grunts with SL_{rms} of 114-120 dB re 1 µPa @ 1m (Wahlberg & Westerberg 2005). The SL_{rms} of the bigeye (112-120 dB re 1 µPa @ 1m) appeared relatively low in comparison to the above mentioned studies. However, direct comparisons must be made with caution due to the
differences in the band-widths and durations of the vocalisations from which the SL was measured.

Unlike marine mammals, which have the ability to manipulate their vocalisation SL (Goodson & Sturtivant 1996, Mohl et al. 2000, Atem et al. 2009), fish are unable to manipulate their SL. Fish vocalisations at their respective SL are generally assumed to be used for communication over short ranges and are thought to be limited in their ability to propagate over long distances. For the toadfish (Bathrachoididae) that lives in very shallow waters ( < 2m), their low frequency vocalisations may not propagate to more than 1 m or the most up to several meters (Fine & Lenhardt 1983, Lugli & Fine 2003, 2007). For the damselfish Dascyllus albisella, it has been shown that their ‘signal jump’ vocalisations could propagate to up to 12 m (Mann & Lobel 1997) before losing all of its initial acoustic characteristics. Mann & Lobel (1997) also showed that the acoustic characteristics of a call change varyingly during propagation. The acoustic parameter pulse period was least affected by propagation when compared to peak frequency and pulse duration. This may show that the pulse period may also be important to the communicative value of the bigeye call.

The current study showed that the active space of fish vocalisations vary in relation to the ambient noise level. At North Reef, the ambient noise level varied considerably over different moon phases and seasons. The intensity of ambient noise was higher during new moon compared to the full moon, and peaked in summer. The smallest active space (radius < 1 m) was thus observed during summer new moon while the greatest active space was observed during spring full moon (radius ~ 30 m) which coincides with peak settlement of wild bigeye. Consequently, in addition to the argument that bigeye vocalisations could act as a school cohesion cue for the bigger fish, it may also serve as a settlement cue for bigeye larvae attracting them to areas with a high conspescific population. The spatial extent of these active space estimates may argue 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 dolphins and whales active spaces are in the order of several kilometres to > 20 km allowing them to maintain contact with each other over a large area of the ocean (Janik 2000, Clark et al. 2009).
Actual detection of vocalisations within the estimated active space could be expected to vary due to masking by changes in the ambient noise level (i.e., varying sea state) as well as the presence of anthropogenic noise within the same band-width of their vocalisation. In addition, auditory sensitivity would have to be sufficient to detect the contact calls. Preliminary results on the auditory threshold of the bigeye using auditory evoked potentials (AEP) technique (Radford et al., unpublished data) indicate that the hearing of bigeye was most sensitive at the lower frequencies of their vocalisation range (i.e., 92 dB re 1 µPa @ 100 Hz, 100 dB re 1 µPa @ 200 Hz, 98 dB re 1 µPa @ 400 Hz and 105 dB re 1 µPa @ 600 Hz). However, AEP threshold values are known to be higher (by up to 30 dB) than behavioural threshold values (Kenyon et al. 1998, Wright et al. 2005, Wright et al. 2010). Furthermore, it has been reported that in the presence of noise, soniferous fish were more sensitive to conspecific vocalisations compared to pure tones (Maruska & Tricas 2009, Belanger et al. 2010). Both of these effects have the potential to bring the hearing threshold level lower than the habitat ambient noise, therefore supporting the assumption of this study that conspecific call detection within a shoal could be limited by ambient noise in bigeyes. In addition, comparison with vocalisation energy content in the octave bands (Figure 3.6) covered by the greatest hearing sensitivity range of the bigeye also suggests that they have the ability to detect the whole frequency range of their vocalisation. The ability to detect and process the complete frequency range of a vocalisation is critical for harnessing its communicative value (Wysocki & Ladich 2003).

Actual demonstration of the vocalisations as contact calls would require field observations of the bigeye nocturnal schooling and foraging behaviour. In addition, playback experiments that examine the behavioural response of schooling fish to conspecific vocalisation (i.e., unmasked and masked by noise) could confirm the role of the vocalisation as a contact call. Nevertheless, the characteristics of the bigeye vocalisation, SL and the spatial scale of its active space in field situations reported in the current study demonstrate the potential for vocalisations of this fish to function as a contact call. These results demonstrate the plausibility of contact calling in fishes particularly for nocturnal fishes.
CHAPTER FOUR:

VOCALISATION OF THE BLUEFIN GURNARD,
*Chelidonichthys kumu*: CALL REPERTOIRE, CONTEXT
AND DIEL PATTERN

4.1 INTRODUCTION

Many teleost fish are capable of producing species specific sounds using specialised sonic organs. Although the sound production mechanism in fish is not analogous to the laryngeal mechanism in other vertebrates, this behaviour is also commonly termed vocalisation (Ladich & Fine 2006, Fay 2009). Field recordings show that fish vocalisation is a major contributor to the biotic component of ambient underwater noise in many coastal areas often making a significant contribution in the frequency range between 100 - 1000 Hz (Cato 1980, Radford et al. 2010). Interpretation of ambient sound recordings requires identification of soniferous fishes through sound-truthing individual species in isolation, since identification in the wild can lead to confusion (Sprague & Luczkovich 2001). Given the diversity of fish species and the technical difficulties of sound recording isolated individuals in the wild, sound-truthing is most commonly conducted on captive fish despite the constraints that may impose on natural behaviour. These practical considerations mean that, the call repertoire, behavioural context and temporal patterns of vocalisation are less well known in fish than in other vertebrates (Bass & McKibben 2003).

Although, the vocal repertoire of a single species is generally limited to one or two types of sounds, some fish may have more extensive repertoires (Amorim 2006). Members of families within the teleosts with extensive vocal repertoires include the toadfishes (Batrachoididae) (Amorim et al. 2008a, Maruska & Mensinger 2009, Rice & Bass 2009), elephantfish (Mormyridae) (Crawford et al. 1986, Crawford et al. 1997) and gurnards (Triglidae)(Amorim & Hawkins 2000, Amorim et al. 2004, Connaughton 2004, Amorim & Hawkins 2005). The functional role behind this sound diversity in fish is less well understood (Amorim et al. 2008a, Sebastianutto et al. 2008, Simoes et al. 2008, Maruska & Mensinger 2009, Rice & Bass 2009). However, the vocal repertoire can vary temporally, often increasing during reproductive seasons.

As part of a temporal and spatial survey of ambient noise at various marine habitats around New Zealand, numerous 24 hour field recordings have been undertaken which include a wide range of fish vocalisation (Radford et al. 2008b, Radford et al. 2010). In order to evaluate the acoustic contributions from individual fish species it is necessary to characterise the vocalisation of the more acoustically active species. The bluefin gurnard (*Chelidonichthys kumu*) is a member of a family (Triglidae) that is well known for vocalisation. It is a commercially important demersal species that is common in many coastal waters with sand and mud seafloor in New Zealand and Australia, Indo-West Pacific, Japan and Korea (Heemstra 1986, Kendrick & Francis 2002). The aural descriptions for Triglid vocalisation in general are knocks, grunts and growls, which consist of pulsed sounds ranging in duration from 10 - 3000 ms and with peaks of sound energy between 250 and 600 Hz (Amorim 2006). A single study on the vocalisation of *C. kumu* recorded two types of dull grunts described as ‘gus’ and ‘pons’ with dominant frequencies ranging from 250 to 300 Hz (Bayoumi 1970). The sounds in this species are thought to be produced by the contractions of paired intrinsic sonic muscles that occupy the dorso-lateral surface of the swim bladder (Bayoumi 1970).

The vocalisation pattern and behavioural context of sound production for the bluefin gurnard is currently unknown. In other gurnard species, the grey (*Eutrigla gurnadus*), streaked (*Trigloporus lastoviza*), tub (*Trigla lucerna*), red gurnard (*Aspitrigla cuculus*), northern sea robin (*Prionotus carolinus*) and striped sea robin (*Prionotus evolans*) has been reported to produce agonistic vocalisation sounds (Amorim & Hawkins 2000, Amorim et al. 2004, Amorim & Hawkins 2005, Amorim 2006). During competitive feeding, the streaked gurnard, northern and striped sea robin only produced one type of sound (described as a growl, squawk and grunt respectively) as opposed to the grey gurnard which produced three types of sound (knocks, grunts and growl). In addition to the variable size of the sound repertoire among Triglid species, not much is known with regards to their diel patterns of vocalisation. The vocalisation activity of the grey gurnard was reported to vary daily with photoperiod and feeding activity but not with temperature or season (Amorim 2005). This lack of knowledge for members of the Triglidae conforms with our general lack of understanding of the diel periodicity of vocalisation in most soniferous fish species. It is most likely that bouts of vocalisation of fish are not randomly distributed in time. Therefore, determining temporal variability of vocalisation is best achieved
through continuous sampling, rather than through intermittent sampling designs. By using continuous acoustic sampling, this study aims to describe the vocalisation repertoire and the daily vocalisation pattern of C. kumu in captivity and investigate possible association with feeding.

This information can be used to help determine the diel pattern of activity in this species, assuming that vocalisation activity could be used as a proxy for the general state of activity. Additionally, this information would be useful in understanding the contribution of this species to sound in the underwater soundscape. A clear identification of the vocal repertoire of individual species and an understanding of their temporal pattern of vocalisation has the potential to be used for passive acoustic surveys of fish populations in the wild. Furthermore, if the behavioural context of sound production in fish species is also known, such as an association with feeding and reproductive behaviour, it would ultimately allow more detailed interpretation of ambient sound recordings (Mok & Gilmore 1983, Connaughton & Taylor 1995, Nordeide & Kjellsby 1999, Luczkovich et al. 2008a, Sirovic et al. 2009).

4.2 METHODS

4.2.1 Fish Capture and Holding

Bluefin gurnards were captured in Omaha Bay, North Island, New Zealand using bottom long lines (<10 m depth), set for only 30 min to minimize injury and stress. Captured fish were immediately transported in seawater to the Leigh Marine Laboratory where they were housed in a circular polyethylene tank (opaque, diameter 1.6 m; depth 0.6 m) with flow-through filtered (200 µm) aerated sea water supply and sand placed on the floor of the tank. The tank was located in a quiet area outdoors to minimise extraneous noise. The fish were held under ambient photoperiod and sea water temperature (18°C). They were allowed to acclimatize to laboratory conditions for six weeks prior to the experiments and were fed sliced pilchards three times a week. One group comprising three adult female fish with standard lengths (TL) measuring 397, 395 and 394 mm respectively were used throughout the experiments.

4.2.2 Experimental Setup

Two sets of experiments were conducted using the same group of fishes. The experiments were designed to allow the captive fish to behave as naturally as possible by
minimising human contact and could be observed using an underwater video camera. The first experiment (vocalisation activity) involved continuous recording sessions without providing any stimuli (including food) for vocalisations. This experiment was conducted for five non-consecutive days each lasting 24 h. The second experiment (feeding related vocalisation) involved introducing food to the fish as a stimulus for competitive feeding. This was done by feeding, without exceeding demand, through a feeding tube one piece of food at a time over duration of 15 min at two specified times (0000 and 1200 h). Observations using an underwater closed circuit camera confirmed food consumption during every feeding session. The feeding experiments were also conducted for five non-consecutive days each lasting 24 h. During both the experiments, water flow and aeration was turned off except over duration of one hour between 0900 to 1000 hrs. Recordings made during this time were not analysed.

Experiments commenced at the same hour of the day (1700 h) and were conducted from 16 November to 12 December 2008. Information for the sunset (2030 h) and sunrise (0555 h) times were obtained from the sun data provided online by www.gaisma.com. Dusk and dawn time were defined as beginning one hour before and lasting until one hour after sunset and sunrise times respectively.

4.2.3 Recording and Analysis

For each experiment, sound was recorded continuously for 24 h with a hydrophone (High Tech Inc. USA, HTI 960 min) with a sensitivity of -165 dB re 1V/1µPa and a flat frequency response from 0.01 to 30 kHz connected to a portable digital audio recorder (Sound Devices 722, Wisconsin, USA). Sound was sampled at 32 kHz sampling rate at 16 bit resolution. All time stamped recordings were analysed using RAVEN Pro 1.3 for Windows (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Cornell, NY, U.S.A.). The hydrophone was suspended in midwater from the centre of the tank. Preliminary assessment showed that bluefin gurnard vocalisation sounds contain frequency components much less than the minimum resonant frequency of 1441 Hz calculated for the tank. This indicated that fish vocalisation recordings were not distorted by the tank wall resonance with best signal-to-resonant ratio recording obtainable within 0.46 m of the hydrophone (Akamatsu et al. 2002).

4.2.4 Analysis of Vocalisation and Activity

Only vocalisations that could be clearly identified aurally and showed a clear visual representation in both oscillogram and spectrogram were considered for characterization. i.e.,
most likely the sounds recorded within 0.46 m of the hydrophone. Individual vocalisations were selected from recordings based upon *a posteriori* classification of aurally distinguishable sound categories, i.e.; grunts and growls. Acoustic measurements of the sounds were made after filtering the sound through a digital bandpass filter between 40 and 1200 Hz. The following sound parameters were measured; sound duration, SD (time elapsed between the start of the first pulse to the end of the last pulse measured in ms); pulse duration, PD (mean time elapsed between start and the end of a pulse measured in ms); number of pulses, PN; pulse period, PP (mean time elapsed between the peak amplitude of two consecutive pulses measured in ms); pulse interval, PI (mean time elapsed between the ending and the beginning of two consecutive pulses measured in ms); peak frequency, Pf (the frequency component with the highest amplitude in the entire sound); lower frequency, Lf (lower frequency limit which amplitude is 3 dB less than the peak frequency); upper frequency, Uf (upper frequency limit which amplitude is 3 dB less than the peak frequency), 3 dB bandwidth, 3dBWB (range between lower and upper frequency) and damping coefficient, Q (Q = Pf/3 dB bandwidth). All temporal parameters were measured from the oscillogram (averaged for all or up to ten pulses in long sounds) while spectral parameters were measured from spectrograms and power spectra calculated using a 750-point Fast Fourier Transform (filter bandwidth of 61.4 Hz) with a Hann window. The adequacy of the aural classification were validated using linear discriminant analysis (LDA) based on the extracted sound parameters except for the parameter 3dBBW since it was highly correlated with the frequency limit values.

For the diel vocalisation experiment, the occurrence of different vocalisation types was counted from 10 s resolution time frames divided from the entire recording. The sounds were pooled among all individuals since they could not be traced to individual fish from the recording. Vocalisation activity is represented by calculating the vocalisation rate (vocalisations fish$^{-1}$ day$^{-1}$ or h$^{-1}$) where values for single fish calculated by dividing the overall counts with the total number of fish ($n = 3$). The mean hourly vocalisation rate were compared among different periods of the day (day, dusk, night and dawn) with repeated measures analysis of variance (rmANOVA) since the same group of individuals were used throughout the experiment. Following a significant rmANOVA result, the *post hoc* multiple group comparisons were conducted with Tukey tests. Correlation analysis was used to compare the occurrence of grunt and growl vocalisations while the Mann-Whitney U test was used to compare the prevalence of the different type of sound between day and night.
For the feeding experiment, the occurrence of vocalisation was counted in 15 min time periods (vocalisations fish\(^{-1}\) 15min\(^{-1}\)) encompassing the duration of two hours before, during and two hours after feeding commenced. This duration was from 1000 to 1400 h for the noon feeding and 2200 to 0200 h for the midnight feeding respectively. The Friedman’s test was used to compare the mean amount of vocalisation among the 15 min time periods (n = 16) which include periods during feeding session (n = 1) and non-feeding sessions (n = 15). Association of vocalisation with feeding is assumed when a significant variation in the amount of vocalisation is observed throughout the observation duration (4h) centered at feeding. All statistical analyses were calculated using the software Minitab release 14.

4.3 RESULTS

4.3.1 Sound Characteristics and Vocalisation Repertoire

Sounds produced by the bluefin gurnard consisted of short and repeated low frequency pulses. Aurally, four different types of vocalisations can be distinguished from the recordings that could be grouped into two general categories, ‘grunts’ and ‘growls’ (Figure 4.1 - 4.4). The grunt consisted of two subtypes, ‘Gu-grunt’ and ‘Pon-grunt’, terms adapted from previous description by Bayoumi (1970)(Figure 4.1 & 4.2). The growl, which is reported for the first time for this species, also consisted of two subtypes, the ‘Short-growl’ and ‘Long-growl’ (Figure 4.3 & 4.4). The adequacy of the different aural categories was supported by LDA of a set of 318 randomly selected pulsed sounds in a train (n = 318, Kolmogorov-Smirnoff = 0.231, P < 0.01). Single pulsed sounds were excluded from the analyses due to the absence of the variable PP and PI. Approximately 83% of the total sounds were correctly classified by the LDA; Gu-grunt 74.4%, Pon-grunt 83.2%, Short-growl 79.7% and Long-growl 95.2%)(Table 4.1). The variables PN, PD and PRR were the main contributors to the discriminant functions (Table 4.2). SD for all vocalisation types were relatively long exceeding 2 s for grunts (Pon-grunt 2.27 ± 0.15 s and Gu-grunt 2.44 ± 0.14 s) and exceeding 1s for growls (Short-growl 1.66 ± 0.18 s and Long-growl 2.66 ± 0.20 s). The waveform of the pulse was consistent within sound types. Grunts had 3 to 8 wave cycles per pulse, whereas growls had 1 to 3 wave cycles per pulse. Mean PN were similar for Gu-grunt and Pon-grunt, but were less in number (mean = 11.0± 0.5 pulses) compared to growls (mean =28.2± 1.3 pulses). Consequently grunts had longer temporal characteristics of the pulses, as measured by PD, PP and PI (Table 4.3). Grunts had lower Pf1 (129 ± 1.3 Hz and 144
± 1.4 Hz) than growls (190 ± 5.4 Hz and 215 ± 5.8 Hz) but had a harmonic component (secondary peak frequency, Pf2) at approximately an octave higher than Pf1. It appeared that the harmonic was more pronounced in Pon-grunt with a smaller difference between peak levels (5 - 10 dB) as compared to a > 10 dB difference in Gu-grunt (Figure 4. 1a & b). The growls lack a harmonic component and had broader 3dBBW. The PRR for the Short-growl (26.2 ± 1.5 pulses s⁻¹) was twice as fast as the Long-growl (12.3 ± 0.7 pulses s⁻¹), and five times faster than the grunts (Gu-grunt 4.8 ± 0.1 pulses s⁻¹ and Pon-grunt 5.6 ± 0.2 pulses s⁻¹). Q values were relatively low with means of 1.3 ± 0 for growls and 2.0-2.2 ± 0 for grunts.

A majority of vocalisations were produced in series or trains with initial pulses having low amplitude which gradually increased and reached the maximum level by the fourth or fifth pulse for a short sound, but after the tenth pulse for longer sounds.
Table 4.1: Classification of vocalisation types to four categories by linear discriminant analysis. Columns show the reallocation of sounds in each group (sound type)

<table>
<thead>
<tr>
<th>True Group</th>
<th>Gu-Grunt</th>
<th>Long-Growl</th>
<th>Pon-Grunt</th>
<th>Short-Growl</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gu-Grunt</td>
<td>58</td>
<td>0</td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>Long-Growl</td>
<td>0</td>
<td>59</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Pon-Grunt</td>
<td>20</td>
<td>0</td>
<td>99</td>
<td>0</td>
</tr>
<tr>
<td>Short-Growl</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>47</td>
</tr>
<tr>
<td>Total, n</td>
<td>78</td>
<td>62</td>
<td>119</td>
<td>59</td>
</tr>
<tr>
<td>N Correct</td>
<td>58</td>
<td>59</td>
<td>99</td>
<td>47</td>
</tr>
<tr>
<td>Proportion (%)</td>
<td>74.4</td>
<td>95.2</td>
<td>83.2</td>
<td>79.7</td>
</tr>
</tbody>
</table>

n = 318    n Correct = 263    Proportion Correct = 82.7%

Table 4.2: Linear discriminant functions for the validation of vocalisation type classification

<table>
<thead>
<tr>
<th>Variables</th>
<th>Gu-Grunt</th>
<th>Long-Growl</th>
<th>Pon-Grunt</th>
<th>Short-Growl</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-95.56</td>
<td>-94.24</td>
<td>-98.78</td>
<td>-121.37</td>
</tr>
<tr>
<td>SD</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>PN</td>
<td>0.46</td>
<td>0.74</td>
<td>0.45</td>
<td>0.96</td>
</tr>
<tr>
<td>PD</td>
<td>0.45</td>
<td>0.29</td>
<td>0.32</td>
<td>0.26</td>
</tr>
<tr>
<td>PP</td>
<td>0.01</td>
<td>-0.08</td>
<td>-0.02</td>
<td>-0.08</td>
</tr>
<tr>
<td>PI</td>
<td>0.10</td>
<td>0.10</td>
<td>0.11</td>
<td>0.10</td>
</tr>
<tr>
<td>PRR</td>
<td>0.48</td>
<td>0.58</td>
<td>0.49</td>
<td>1.02</td>
</tr>
<tr>
<td>Pf1</td>
<td>-0.45</td>
<td>-0.41</td>
<td>-0.47</td>
<td>-0.43</td>
</tr>
<tr>
<td>Lf1</td>
<td>-0.32</td>
<td>-0.06</td>
<td>-0.33</td>
<td>0.04</td>
</tr>
<tr>
<td>Uf1</td>
<td>0.65</td>
<td>0.66</td>
<td>0.69</td>
<td>0.68</td>
</tr>
<tr>
<td>Q1</td>
<td>63.58</td>
<td>48.16</td>
<td>68.37</td>
<td>46.74</td>
</tr>
</tbody>
</table>
Table 4.3: Acoustic features measured in Gu-grunt, Pon-grunt, Short-growl and Long-growl vocalisations. Values are means ± SEM and range is given in parentheses below. For Pf, Lf and Uf the median value is given in parentheses on the right. SD = sound duration; PN = number of pulses; PD = pulse duration; PP = pulse period; PI = pulse interval; PRR = pulse repetition rate; Pf = peak frequency; Lf = lower frequency; Uf = upper frequency 3dBBW = 3 dB bandwidth; Q = damping coefficient.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Gu-grunt</th>
<th>Pon-grunt</th>
<th>Short-growl</th>
<th>Long-growl</th>
</tr>
</thead>
<tbody>
<tr>
<td>SD (s)</td>
<td>2.437 ± 0.135</td>
<td>2.271 ± 0.151</td>
<td>1.655 ± 0.178</td>
<td>2.663 ± 0.197</td>
</tr>
<tr>
<td></td>
<td>(0.397 - 8.137)</td>
<td>(0.050 - 11.856)</td>
<td>(0.288 - 6.815)</td>
<td>(0.376 - 8.660)</td>
</tr>
<tr>
<td>PN (pulses)</td>
<td>11.0 ± 0.5</td>
<td>11.1 ± 0.6</td>
<td>33.8 ± 2.1</td>
<td>28.2 ± 1.3</td>
</tr>
<tr>
<td></td>
<td>(4 - 29)</td>
<td>(1 - 39)</td>
<td>(6 - 88)</td>
<td>(7 - 56)</td>
</tr>
<tr>
<td>PD (s)</td>
<td>0.084 ± 0.003</td>
<td>0.056 ± 0.001</td>
<td>0.0153 ± 0.000</td>
<td>0.0323 ± 0.001</td>
</tr>
<tr>
<td></td>
<td>(0.038 - 0.139)</td>
<td>(0.027 - 0.105)</td>
<td>(0.009 - 0.035)</td>
<td>(0.011 - 0.057)</td>
</tr>
<tr>
<td>PP (s)</td>
<td>0.229 ± 0.005</td>
<td>0.214 ± 0.004</td>
<td>0.033 ± 0.002</td>
<td>0.080 ± 0.004</td>
</tr>
<tr>
<td></td>
<td>(0.105 - 0.372)</td>
<td>(0.109 - 0.434)</td>
<td>(0.008 - 0.112)</td>
<td>(0.026 - 0.195)</td>
</tr>
<tr>
<td>PI (s)</td>
<td>0.148 ± 0.005</td>
<td>0.157 ± 0.004</td>
<td>0.020 ± 0.001</td>
<td>0.050 ± 0.004</td>
</tr>
<tr>
<td></td>
<td>(0.042 - 0.257)</td>
<td>(0.062 - 0.353)</td>
<td>(0.008 - 0.050)</td>
<td>(0.013 - 0.174)</td>
</tr>
<tr>
<td>PRR (pulse s(^{-1}))</td>
<td>4.8 ± 0.1</td>
<td>5.6 ± 0.2</td>
<td>26.2 ± 1.5</td>
<td>12.3 ± 0.7</td>
</tr>
<tr>
<td></td>
<td>(3.1 - 10.1)</td>
<td>(2.8 - 20.0)</td>
<td>(7.7 - 59.3)</td>
<td>(5.0 - 36.6)</td>
</tr>
<tr>
<td>Pf 1 (Hz)</td>
<td>129 ± 1.3 (125)</td>
<td>144 ± 1.4 (156)</td>
<td>215 ± 5.8 (218)</td>
<td>190 ± 5.4 (187)</td>
</tr>
<tr>
<td></td>
<td>(95 - 156)</td>
<td>(125 - 156)</td>
<td>(125 - 313)</td>
<td>(125 - 313)</td>
</tr>
<tr>
<td>Lf 1 (Hz)</td>
<td>96 ± 1.5 (98)</td>
<td>110 ± 0.9 (109)</td>
<td>137 ± 3.2 (131)</td>
<td>123 ± 2.2 (121)</td>
</tr>
<tr>
<td></td>
<td>(52 - 118)</td>
<td>(76 - 130)</td>
<td>(94 - 210)</td>
<td>(82 - 181)</td>
</tr>
<tr>
<td>Uf 1 (Hz)</td>
<td>163 ± 1.0 (164)</td>
<td>177 ± 0.9 (176)</td>
<td>313 ± 6.0 (320)</td>
<td>276 ± 7.0 (263)</td>
</tr>
<tr>
<td></td>
<td>(143 - 187)</td>
<td>(153 - 193)</td>
<td>(192 - 393)</td>
<td>(190 - 407)</td>
</tr>
<tr>
<td>3dBBW (Hz)</td>
<td>67 ± 0.8</td>
<td>67 ± 0.6</td>
<td>176 ± 5.5</td>
<td>154 ± 6.4</td>
</tr>
<tr>
<td></td>
<td>(58 - 95)</td>
<td>(57 - 115)</td>
<td>(88 - 253)</td>
<td>(83 - 283)</td>
</tr>
<tr>
<td>Q1</td>
<td>2.0 ± 0.0</td>
<td>2.2 ± 0.0</td>
<td>1.3 ± 0.0</td>
<td>1.3 ± 0.0</td>
</tr>
<tr>
<td></td>
<td>(1.0 - 2.7)</td>
<td>(1.4 - 2.7)</td>
<td>(0.6 - 2.2)</td>
<td>(0.7 - 1.9)</td>
</tr>
<tr>
<td>Pf 2 (Hz)</td>
<td>276 ± 2.5 (281)</td>
<td>290 ± 1.8 (281)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>(250 - 313)</td>
<td>(250 - 314)</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
### Chapter Four: Vocalisations of the Bluefin Gurnard

<table>
<thead>
<tr>
<th></th>
<th>Lf 2 (Hz)</th>
<th>Uf 2 (Hz)</th>
<th>3dBBW 2 (Hz)</th>
<th>Q2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>234 ± 2.0 (230)</td>
<td>246 ± 1.9 (249)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(187 - 274)</td>
<td>(187 - 281)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>313 ± 2.1 (311)</td>
<td>326 ± 1.8 (322)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(281 - 346)</td>
<td>(283 - 365)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>79 ± 1.1</td>
<td>80 ± 0.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(55 - 99)</td>
<td>(58 - 125)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3.6 ± 0.1</td>
<td>3.7 ± 0.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(2.6 - 5.1)</td>
<td>(2.5 - 4.9)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 4.1: Representative Gu-grunt type vocalisation. a & b) Oscillograms (whole sound and enlarged section), c) spectrogram and d) power spectrum (750 point FFT; Hanning window; 64 Hz filter bandwidth). Amplitude and power are shown as relative units.
Figure 4.2: Representative Pon-grunt type vocalisation. a & b) Oscillograms (whole sound and enlarged section), c) spectrogram and d) power spectrum (750 point FFT; Hanning window; 64 Hz filter bandwidth). Amplitude and power are shown as relative units.
Figure 4.3: Representative Short–growl type vocalisation. a & b) Oscillograms (whole sound and enlarged section), c) spectrogram and d) power spectrum (750 point FFT; Hanning window; 64 Hz filter bandwidth). Amplitude and power are shown as relative units.
Figure 4.4: Representative Long–growl type vocalisation. a & b) Oscillograms (whole sound and enlarged section), c) spectrogram and d) power spectrum (750 point FFT; Hanning window; 64 Hz filter bandwidth). Amplitude and power are shown as relative units.
4.3.2 Diel Pattern

In total, 6368 sound (5464 grunts and 904 growls) were recorded from the group of three female bluefin gurnard over 5 d (i.e., 5 replicate 24 h periods). Temporal analyses were conducted on the two general sound categories (grunt and growl) rather than on individual vocalisation type. The bluefin gurnard was acoustically prolific producing calls with a mean of $424.5 \pm 46.3$ call fish$^{-1}$ day$^{-1}$ or $18.5 \pm 2.0$ call fish$^{-1}$ h$^{-1}$ with an average composition of 85.6% grunts ($364.3 \pm 42.5$ call fish$^{-1}$ day$^{-1}$ or $15.8 \pm 1.8$ call fish$^{-1}$ h$^{-1}$) and 14.4% growls ($60.3 \pm 11.8$ call fish$^{-1}$ day$^{-1}$ or $2.6 \pm 0.5$ call fish$^{-1}$ h$^{-1}$) respectively.

However, the proportions of the grunts to the growls was significantly different between day and night (Mann-Whitney; P< 0.001), primarily due to the large increase in growl vocalisation at night (Figure 4.5 & 4.6). Grunts tend to be produced periodically in groups, while growls were produced singly and intermittently. There was no significant correlation between the number of grunt vocalisations and the number of growl vocalisations within an hour (Pearson correlation, r =0.36; P > 0.08) indicating that vocalisation of one call type is independent of the other. There were significant differences in the mean vocalisation rate (i.e., number of sounds fish$^{-1}$ h$^{-1}$) among the different periods of the day for both grunt (rmANOVA F = 7.438, df = 3; P= 0.004) and growl vocalisation (rmANOVA F= 20.502, df = 3; P < 0.001). Tukey tests showed that the number of grunt vocalisation was significantly higher (P=0.003) at dawn compared to during the day, but not significantly different than other periods, i.e., night and dusk. There were no significant differences in the number of grunt vocalisation among other periods (day, night and dusk). For growls, the number of calls was significantly higher (P<0.005) at night compared to other periods, i.e., day, dusk and dawn. (Figure 4.7).

Occasional observation using closed circuit television camera showed that sounds were produced in a non-specific behavioural manner either during swimming or just lying on the sandy tank floor. However, strict validation on the context of sound production could not be verified in this study.
Figure 4.5: Diel variation in the proportion of grunt and growl type vocalisations. Grey vertical bar are growls and black vertical bar are grunts. Bar represents mean values observed in the hourly interval over five non-consecutive days of sampling. Crossed bar at 09-1000 h indicate no data due to activation of water flow.
Figure 4.6: Diel pattern of vocal activity showing mean hourly vocalisation rate (mean ± SEM; n = 5). Black bar represents grunt sounds and grey bar represents growl sounds. The single shaded vertical bar at 09-1000 h indicates the activation of water flow.
Figure 4.7: Comparison of vocalisation rate (mean ± SEM; n = 5) during different periods of the day. White square represent grunt vocalisations and white circle represent growl vocalisations. Different letters indicate statistically significant differences between individual means within either growls or grunts (Tukey test; P<0.05).
4.3.3 Feeding Related Sound

Friedman’s test showed that there was no significant difference in the amount of vocalisation in the 15 min periods containing feeding and non-feeding activity for either grunt or growl at any time of feed (noon and midnight) (Table 4.4). Feeding activity did not cause a significant rise in the amount of vocalisation of either type of sound in the 15 min feeding period (Figure 4.8).

Table 4.4: Result summary of the Friedman’s test comparing amount of vocalisations in the 15 min time periods with feeding and non-feeding activity.

<table>
<thead>
<tr>
<th></th>
<th>df=15</th>
<th>Chi-square</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grunt</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>noon</td>
<td>18.7</td>
<td>0.23</td>
<td></td>
</tr>
<tr>
<td>midnight</td>
<td>19.8</td>
<td>0.18</td>
<td></td>
</tr>
<tr>
<td>Growl</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>noon</td>
<td>17.3</td>
<td>0.30</td>
<td></td>
</tr>
<tr>
<td>midnight</td>
<td>16.8</td>
<td>0.33</td>
<td></td>
</tr>
</tbody>
</table>
Figure 4.8: Total vocalisation counted in consecutive 15 min periods from 2 h prior to feeding, during feeding and 2 h after feeding commenced. a) Grunts and b) Growls. Counts of vocalisations were conducted for 5 non-consecutive days. Solid line and symbol = midnight; dotted line and hollow symbol = noon feeding. Vertical arrow indicates time of feeding. Data represent the mean values ± SEM.
4.4 DISCUSSION

This current study has shown that the bluefin gurnard, have a larger acoustic repertoire than had been previously reported (Bayoumi 1970). Despite the low number of individuals \((n = 3)\) used in this study, sufficient vocalisations were produced to reveal new vocalisation types (growls). However, it must be noted that due to the exclusively female fish used in the current study (unavailability of males), the influence of sexual dimorphism on the species vocalisation could not be explored. Two new types of growl vocalisations which is consistent with at least five other Triglid species also known to growl (Amorim 2006). This current study also confirmed the presence of the two grunt type vocalisations, ‘Gu’ and ‘Pons’, previously described for \(C. kumu\) (Bayoumi 1970). However, for both of these grunt vocalisations, a slightly shorter pulse duration (0.03 - 0.14 s versus 0.2 s) and lower peak frequency (95 - 156 Hz versus 250 - 300 Hz) were found to that previously described. In addition, a harmonic component with a lower amplitude (5 - 25 dB lower) compared to the amplitude of the primary peak frequency (Pf1) or fundamental frequency was identified. Harmonics of grunt sounds has not been reported before in other Triglid species. The occurrence of harmonics is not typical for grunt type vocalisations but are more common for tonal type swim bladder sounds such as the boatwhistles and hoots produced by Batrachoidids (Kasumyan 2008). Nonetheless, harmonics can be generated when grunts are produced in trains as has also been observed in the vocalisation of the three-spined toadfish, \(Batracomoecus trispinosus\) (Rice & Bass 2009). The fundamental frequency of grunt vocalisations (129 ± 1.3 Hz and 144 ± 1.4 Hz) could be related to the contraction frequency of the sonic muscle (Kasumyan 2008). The growls were aurally distinguishable from grunts by having a lower amplitude, no harmonic, and a relatively broad frequency spectrum. The broadly tuned sound for both sound categories had low Q values indicating that the swim bladder is highly damped.

This current study also revealed that the growls were distinctively produced at night as what appear to be a form of nocturnal vocalisation. It is not clear from this study what activities this nocturnal sound may be associated with. We have discovered that combinations of different sound types within a category (i.e., grunt or growl) could also be combined to form a call that can last up to 11 s. This ability to mix and blend different sound types has also been reported for the Lusitanian toadfish, \(Holobatrachus didactylus\), and haddock, \(Melanogrammus aeglefinus\) (Hawkins & Amorim 2000, Amorim et al. 2008a).
Chelidonichthys kumu has a relatively large sound repertoire in comparison to other Triglid species, such as the European grey gurnard, Eutriglia gurnadus (three types of sound), tub gurnard, Trigla lucerna, (two types) and the streaked gurnard, Trigloporus lastoviza (two types) (Amorim & Hawkins 2000, 2005, Amorim 2006). The acoustic features of C. kumu vocalisation also showed some marked differences to these other Triglids. For example, sound duration for C. kumu (up to 11 s) were typically longer than the above species (up to 3 s) with lower peak frequency (129 - 215 Hz versus 510, 311 , 555 Hz in grey, tub and streaked gurnard respectively). In other fish families, large vocal repertoires have been reported in a few species such as the mormyrid fish, Pollimyrus adspersus, the Lusitanian toadfish, H. didactylus, and the three-spined toadfish, B. trispinosus, which all produce four or more different types of sound. (Crawford 1997, Amorim et al. 2008a, Maruska & Mensinger 2009, Rice & Bass 2009).

In this current study, C. kumu were highly vocal with sounds, particularly grunts, consistently being produced every hour (15.8 ± 6.4 grunts fish⁻¹ h⁻¹) throughout the 24 h period. Although grunts were more prevalent during dawn compared to day, there was a sustained vocalisation activity during day and night time with no significant difference between the two periods. In contrast, the grey gurnard in captivity showed a different diel pattern of vocal activity, where maximum acoustic activity occurred during the day, minimum activity at night, and intermediate at dawn/dusk (Amorim,2005). Crepuscular vocalisation peaks are not uncommon among marine fishes as had been previously reported for species in several families such as Sciaenidae, Pomacentridae and Batrachoididae (Connaughton & Taylor 1995, Thorson & Fine 2002b, Locascio & Mann 2008). In our study however, the crepuscular peak in the bluefin gurnard vocalisation is consistent with cathemeral activity patterns described in mammals in which the activity peaks or centred around sunrise and sunset but extends into both day and night phases (Curtis & Rasmussen 2006, Hill 2006, Tattersall 2008). This differs from bimodal activity patterns observed for many diurnal and nocturnal species where the crepuscular peaks mark either the beginning or the end of activity confined to either the light or dark phase. Accordingly, we suggest that the bluefin gurnard in captivity demonstrate cathemeral vocalisation behaviour. Cathemeral behaviour could be widespread across fish taxa especially for fish that are not visually dependent. In marine species, the toadfishes, Opsanus beta (Thorson & Fine 2002b) and B. trispinosus (Batrachoididae) (Rice & Bass 2009), weakfish Cynoscion regalis (Sciaenidae) (Luczkovich et al. 1999), red hind Ephinephelus guttatus (Serranidae) (Mann et al. 2010) and four rockfish species Sebastes sp. (Sirovic & Demer 2009) have been
reported to vocalise sporadically throughout the day and night. Similarly, two freshwater species, the gudgeon, *Gobio gobio*, and the bullhead, *Cottus gobio*, lack clear diel vocalisation patterns (Ladic 1988, 1989).

The bluefin gurnard vocalisations during this study were not found to be associated with feeding activity, unlike those of the grey (Amorim et al. 2004) and streaked gurnard species (Amorim & Hawkins 2000). Predominantly for a majority of soniferous fish species, vocalisation is a communication tool that accompanies specific social behaviours (Kasumyan 2009) such as to convey aggression during competition for territory or food (Ladich 2006), and self advertising during reproduction (Amorim & Vasconcelos 2008). Consequently, vocalisation activity has often been reported to correlate and increase with these behaviours. Although, the behavioural context of vocalisation for the captive bluefin gurnard could not be determined from this study, the magnitude of vocalisation in terms of its large vocal repertoire and call quantity may indicate that the fish could be in a breeding state. Triglids are known to be most acoustically active during breeding season (Moulton 1956, Amorim 2006) and the period of this study coincide with the general breeding season during late spring and early summer for the bluefin gurnard in the Hauraki Gulf from where the experimental fish were captured (Clearwater & Pankhurst 1994). For other species, the Gulf toadfish *O. beta*, Lusitanian toadfish *H. didactylus* (Batrachoididae) and the weakfish *C. regalis* (Sciaenidae), diel and seasonal variation in their sound production have been found to be associated with behavioural changes during spawning (Connaughton & Taylor 1995, Thorson & Fine 2002b, Amorim et al. 2006, Rice & Bass 2009).

Understanding the vocalisation repertoire and temporal periodicity of the bluefin gurnard could help in determining the identity of biological sound sources in the local underwater soundscape. The results of this study provided a preliminary insight into the potential contribution of the bluefin gurnard vocalisations to the biological noise of a nearby location (Pakiri Beach) known as gurnard habitat among local commercial fishers (Ghazali, S.M., pers. obs). A recent study on the ambient noise at this location showed that the proportion of total noise intensity was largest in the frequency band 100 - 800 Hz (Radford et al. 2010). This frequency band encompassed the peak frequency range of bluefin gurnard vocalisation repertoire (Pf1 = 129 - 215 Hz; Pf2 = 276 - 290 Hz) suggesting that the bluefin gurnard vocalisation as a viable source for this sound energy. This would also suggest that the bluefin gurnard as a potential candidate for the application passive acoustic survey of their population in the wild. Other commercial fish species elsewhere that have been identified as potential candidate for
passive acoustic monitoring elsewhere include cod, weakfish, rockfish and haddock (Luczkovich et al. 1999, Hawkins & Amorim 2000, Finstad & Nordeide 2004, Sirovic et al. 2009). The characteristics, magnitude and temporal pattern of the bluefin gurnard vocalisation showed that in areas where they are common, they are likely to be a major contributor to the ambient underwater soundscape.
CHAPTER FIVE:

THE BIOACOUSTIC ENVIRONMENT OF A FISH AGGREGATION DEVICE (FAD)

5.1 INTRODUCTION

Fish are attracted to, and associate with, aggregation devices (FADs). These behaviours are frequently exploited as a means to improve fishing efficiency (Fréon & Dagorn 2000). Extensive reviews describe the evolutionary mechanisms that may have driven the associative behaviour of fish with FADs (Fréon & Dagorn 2000, Castro et al. 2001) but do not address the proximal cues that allow fish to locate and orientate to FADs. For orientation, it is most likely that a combination of sensory modalities such as vision, olfaction and sound are involved. However, studies on fish movement around moored FADs have shown that some species can orient and return to the FAD from well beyond their visual range. For example, a translocation study of at least five Malaysian fishery target species have shown that fish could return to their respective FADs from up to 180 m away (Ibrahim et al. 1990). In addition, using acoustic telemetry, the yellowfin tuna, *Thunnus albacares*, around Oahu, Hawaii has been observed to repeatedly visit their release FAD after moving several kilometres away (Dagorn et al. 2007). Additional evidence shows that homing behaviour from distances beyond visual range cannot be solely attributed to chemical cues. For example, in an experiment designed to examine the possible role of chemical cues in homing behaviour, it was demonstrated that the dolphinfish, *Coryphaena hippurus*, and the kingfish, *Seriola lalandi*, were able to return to FADs in equal proportions from both across and down-current directions from up to 275 m away (Dempster & Kingsford 2003). Also yellowfin tuna in the Indian ocean were reported to orientate upstream from a FAD and made repeated movements to it from as far as 9.3 km away (Marsac & Cayré 1998). These studies clearly indicate that sensory modalities other than vision and olfaction must play a role in mediating long range fish movement around FADs.

Sound has previously been suggested as a potential cue for the navigation and orientation of fish to FADs (Dempster & Kingsford 2003, Dempster & Taquet 2004). Underwater sound
propagates equally in all directions from its source with little attenuation (Rogers & Cox 1988) thus would allow for a sound signal to be detectable over spatial scales of metres to kilometres from its source. Although sound is a potentially important sensory cue involved in fish aggregation, studies of the acoustic characteristics of FADs are scarce (Dempster & Taquet 2004). The only study to date on the underwater sound characteristics of a FAD was inconclusive. Babaran et al., (2008) reported that ‘payao’ (Filipino FAD) generated underwater sound (dominant frequency = 49 Hz) from the vibration of the anchor rope, the intensity of which increased with water depth. This frequency was considered to lie outside the main auditory sensitivity of the jack mackerel, *Trachurus japonicus*, (500-1000 Hz) and other fishes and hence it was concluded that it was not likely to be audible to fish (Babaran et al. 2008). Furthermore, below 100 Hz, the underwater soundscape would typically be dominated by shipping traffic noise (Wenz 1962) that could mask the payao sound. In contrast to these conclusions, the potential for sound to be acting as an orientation cue for FADs is suggested by some aspects of the traditional use of FADs in Malaysian fisheries (Moulton 1963).

The application of FADs in Malaysian fisheries has been a long standing traditional practice. The FADs are locally known as unjam, which typically consisting of palm fronds attached to ropes suspended vertically in mid-water by bamboo or plastic drums and moored in position. An important component of a traditional unjam fishery is the engagement of a ‘juruselam’ (diver) who listens to underwater fish sounds around unjams to determine fish types and quantity prior to catching (Moulton 1963). Such basic passive acoustic survey provided *a priori* information about the fish stock that would influence subsequent catching effort. Although the traditional practice is gradually being replaced by modern active acoustic (sonar) methods, the former practice shows that there is significant acoustic information generated by the unjam environment. At present, the majority of unjam fall under the administration of the Fisheries Development Authority of Malaysia (LKIM) who recently improved this design by integrating artificial reefs on the seafloor beneath the unjam. The aim was to create stable fish habitats as well as to deter bottom trawling near unjams.

To our knowledge, the detailed nature of underwater sound around an operational FAD has never been studied. Here we use the unjam as a model to investigate the spatio-temporal acoustic environment of a FAD in order to evaluate the availability of sound cues for fish in the surrounding waters.
5.2 METHODS

5.2.1 Unjam Description and Study Site

The unjam used in the study is registered as Jali Rhu 10 (JR10) located in the east coast state of Terengganu, Malaysia. Its surveyed location is at 05° 38.920' N and 102° 54.172' E in water depth of 23 m over a sandy seabed. The nearest mainland coast is at Penarek and an offshore island (Redang) were approximately 9 km and 13 km away respectively. There was no other FAD or reef within 3 km radius in the direction of our propagation experiments (Figure 5.1).

The unjam consisted of two main components. The first was a series of palm fronds suspended in the water column (pelagic) using a polypropylene rope tethered to a buoy on the surface and moored to a large concrete block at the seafloor (Figure 5. 2). The second component is the artificial reef (benthic) composed of 1000 units of cube-shaped concrete frames (1 m$^3$ each) placed on the seafloor beneath the suspended palm fronds. Consequently, this study defines the unjam comprising both these pelagic and benthic components acting together as a single FAD unit. During the LKIM fish census surveys from April to June 2006, an estimated 58 fish species from 27 families were observed regularly within 50 m of the 27 unjam off the Terengganu coast (LKIM internal report, unpublished). In the current study, an abundance of fish at the JR10 unjam was confirmed by several reconnaissance dives using SCUBA before and after conducting the sound recording experiments.
Chapter Five: Bioacoustic Environment of a FAD

Figure 5.1: Map showing the study area with enlargement showing locations of other LKIM unjam (solid black dots) relative to the study unjam (JR10). Lines connecting day and dusk (solid black box) indicate approximate propagation experiment tracks.

Figure 5.2: General overview of the JR10 unjam components.
5.2.2 Recording system and experimental design

Temporal experiment

A single 24 h temporal recording was conducted using a custom made temporal hydrophone system beginning at 1100 hrs on 1 August 2009 and ending at the same time the next day. The temporal hydrophone consisted of a calibrated hydrophone (HTI - 96 min; sensitivity -165.6 dB re 1 V with a flat frequency response between 10 Hz to 30 kHz), a digital recorder (Edirol R09, Roland, Japan) and a 12 V battery power supply encased in a waterproof aluminium housing. The system recorded continuously at 44.1 kHz sampling rate with 16 bit resolution to a 16 GB SDHC memory card. The buoyant temporal hydrophone was suspended 5 m above the artificial reef by tethering to an artificial reef block that was 10 m from the attachment point for the rope holding the palm fronds. Sea condition was identified as sea state 3 throughout the 24 h recording period.

Spatial experiment

Two sets of horizontal spatial experiments were conducted on 16 August 2009. Sea condition during these experiments was identified as sea state 2. The first set of recordings was conducted in the afternoon from 1400 - 1600 hrs (day experiment) and the second set from 1800 – 2000 hrs (dusk experiment). Each recording system consisted of a floating water-tight plastic barrel which contained a digital sound recorder (Edirol R09, Roland, Japan) connected to a calibrated hydrophone (HTI min-96, High Tech Inc, USA; sensitivity -165.5 dB re 1 V with a flat frequency response between 10 Hz to 30 kHz) suspended at 10 m water depth. In order to measure the distance that sound propagates from the unjam, simultaneous recordings of the underwater sound using two of the above hydrophone systems was conducted. Initially both hydrophones recorded for 3 min at the unjam. Subsequently, while one hydrophone remain fixed (stationary) at the unjam by tethering the barrel unit to the surface float of the unjam, the second (roving) hydrophone was allowed to drift away from the unjam with the wind and current direction. There were no other unjams closer to the roving hydrophone than JR10 throughout the recording. Both hydrophones recorded continuously and were synchronised to the nearest second. The position of the roving hydrophone was recorded using a GPS unit (Garmin EtrexH, USA) every minute from the research vessel which drifted 30 m down-wind of the floating hydrophone. Our assumption was that the roving hydrophone recorded the underwater sound of the unjam at different distances away and changes in sound intensity were measured by
comparing the measurements between the two hydrophones. The experiments ended when the roving hydrophone drifted 1200 m away from the unjam.

For all recordings, the gain on the recorder was fixed at a set level. This setting was calibrated by taking a series of recordings of a pure tone 1 kHz sine wave produced by a signal generator. The voltage ($V_{\text{rms}}$) of the tone recording was measured and compared with the hydrophone sensitivity data. Subsequently, a correction factor was calculated and applied to sound pressure measurements obtained with the hydrophones.

**Control recording**

To represent the local underwater soundscape without the presence of the unjam, a five-minute control recording was made prior to the beginning of the day experiment at a location ($5^\circ 38.946' \text{ N and } 102^\circ 52.905' \text{ E}$), 3 km northwest of the study unjam. The recording setup used was the same as for the propagation experiments. No other boat was observed in the vicinity during the control recording.

### 5.2.3 Sound Analyses

Preliminary visualization and editing of the recordings were made using RAVEN Pro 1.3 (Cornell Bioacoustics) where only recordings without boat noise were used. For quantitative analysis, the recordings were analysed and plotted using octave band and power spectrum (PSD) using MATLAB® with scripts modified from octbank.m by Christophe Couvreur and scripts specifically written for this work. Although more commonly used, spectrum level plots (1 Hz band) has little relevance to the manner marine animals perceive sound because it does not incorporate the critical bands of the auditory system. Thus, presenting the sound power in the relevant critical band ($N^{\text{th}}$ octave band level) is potentially more meaningful in the context of sound perception by approximating the auditory filter of marine animals (Madsen et al. 2006, Au & Hastings 2009a). Although the precise bandwidths of the auditory filters for fish is unknown, it has been reported as being slightly larger than those found in other vertebrates (one-third octave band filters) (Fay 1988) which makes the octave band analysis a suitable method for representing the sound. Five octave bands between the centre frequencies 125 Hz and 2000 Hz were selected which encompass the frequency range of best hearing for the majority of fishes (Table 5.1).
For the temporal experiment, the sound was divided into hourly bins followed by random sampling of five 60 s clips from within each hour. The sound pressure levels (SPL$_{rms}$) of the 60 s clips were measured and averaged ($n=5$) for the hour. These SPL$_{rms}$ were pooled into four periods of time of day (night, dawn, day and dusk). Distinctions of these periods were based on sun transit data for the study site provided by the website, www.gaisma.com.

For the spatial experiments, time synchronisation allowed for the comparison of sound pressure level measurements at the unjam (stationary hydrophone) and at a fixed distance away (roving hydrophone). Sound level measurements at specified distances was calculated from the integration of 50 s of acoustic data. Signal loss, SgL (dB re 1 µPa/bandwidth) is defined as the difference in sound pressure level (SPL$_{rms}$) measurements between the roving and the stationary hydrophone and calculated as follows:

$$SgL = SPL_{rms \text{ Roving}} - SPL_{rms \text{ Stationary}}$$

Masking can occur when ambient or background noise contains energy (similar or higher) in the same frequency band as the signal such that it is inaudible (Clark et al. 2009). In the absence of marine life, underwater ambient noise levels are dependent on shipping activity, wind force and sea state (Wenz 1962). The theoretical noise levels for these conditions during temporal and spatial recordings was calculated for the respective octave bands using equations modified from methods by Urick (1986) and Knudsen (1948) (Lurton 2002). This calculated value is considered as the estimation for the idealistic sound level of the ambient noise in the absence of the unjam. These estimated sound levels were used in the verification of the unjam signal and to estimate masking of the unjam signal as it is reduced to ambient noise level.

### Table 5.1: Octave band filter characteristics

<table>
<thead>
<tr>
<th>Band</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nominal centre frequency, Fc / octave bandwidth, BW (Hz)</td>
<td>125 / 89</td>
<td>250 / 178</td>
<td>500 / 353</td>
<td>1000 / 702</td>
<td>2000 / 1410</td>
</tr>
<tr>
<td>Octave band frequency range (Hz)</td>
<td>89 - 178</td>
<td>178 - 355</td>
<td>355 - 708</td>
<td>708 - 1410</td>
<td>1410 - 2820</td>
</tr>
</tbody>
</table>
5.2.4 Statistical analyses

For the temporal experiment, the non-parametric Kruskal-Wallis test was used to compare measured sound pressure levels at different times of the day (night, dawn, day and dusk, \( n = 4 \)) for all octave bands. Where significant differences were identified, it was followed by the Dunn’s pairwise multiple comparison procedure to test for differences in sound pressure levels between times.

For the spatial experiment, the relationship between propagation loss and hydrophone separation, i.e., distance were analysed using linear regression. In order to justify the linearity between signal loss and distance, the hydrophone separation data was firstly log transformed to fit the assumption of geometric spreading loss of sound levels with distance. The resulting regression equation would estimate the relationship of signal loss with distance. The regression lines were then plotted against estimated cylindrical and spherical spreading loss for comparison. All data were analysed using Sigmaplot Ver.11 software and presented as statistical means ± SEM.

5.3 RESULTS

5.3.1 Underwater sound characteristics of the unjam

Power spectra analysis shows that there was a rise in sound energy between the frequency band 500 Hz and 2000 Hz at the unjam compared to the control location (Figure 5.3a). The sound intensity (SPL\(_{\text{rms}}\)) within this frequency bandwidth were 100.2 dB re 1 µPa and 117.5 dB re 1 µPa at the unjam during day and dusk respectively compared to 93 dB re 1 µPa at the control location. There was a noticeable energy peak at 750 Hz in the unjam recording at dusk but this was not obvious during the day. Octave band analysis also showed a marked rise of sound intensity in the octave bands 3, 4 and 5 (Figure 5.3b). The biggest rise was observed in octave band 4 with sound intensity of 116.0 dB re 1 µPa (dusk) and 97.1 dB re 1 µPa (day) at the unjam compared to 87.0 dB re 1µPa at the control location. The smallest increase in sound intensity was in octave band 3 with 109.7 dB re 1 µPa (dusk) and 93.0 dB re 1 µPa (day) at the unjam compared to 88.1 dB re 1 µPa at the control location (day). Overall, the underwater sound intensity was 5 to 29 dB re 1 µPa higher at the unjam compared to the control in the three octave bands. Sound intensity at the control location approximated the calculated theoretical ambient
noise level in the three octave bands. The level difference was 0.6, -3.6 and -2.0 dB re 1µPa in the octave bands 3, 4 and 5 respectively.

Figure 5.3: Comparison between underwater sound at the unjam and control site. (a) Spectrum level plot comparing the control site (light grey line), unjam during day (dark grey line) and unjam during dusk (black line). (b) Octave band level plot comparing the control site (light grey triangle), unjam during day (dark grey square), unjam during dusk (black diamond) and estimated theoretical ambient noise level (black circle).

5.3.2 Daily pattern of the unjam sound

There were statistically significant differences in the sound intensity among the times of the day for octave band 3 to 5 (Figure 5.4). Dunn’s multiple comparison test showed that the sound intensity during the day was significantly lower (P<0.05) compared to other periods. However, there were no significant differences in sound intensity among dusk, night and dawn. There was a steep rise in sound intensity which peaks at dusk in all bands. For band 3 (H=77.12, 3 d.f., P<0.001), dusk sound intensity peaked at 118.9 ± 1.5 dB re 1 µPa, followed by night
(113.0 ± 0.5 dB re 1 µPa), dawn (108.5 ± 2.4 dB re 1 µPa) and lowest during the day (98.5 ± 0.8 dB re 1µPa). For band 4 (H=73.13, 3 d.f., P<0.001), dusk sound intensity peaked at 121.2 ± 1.6 dB re 1 µPa, followed by night (115.5 ± 0.4 dB re 1 µPa), dawn (113.4 ± 2.6 dB re 1 µPa) and lowest during the day (101.4 ± 0.9 dB re 1 µPa). For band 5 (H=77.12, 3 d.f., P<0.001), sound intensity during dusk measured 106.8 ± 1.5 dB re 1 µPa, followed by night (101.4 ± 0.3 dB re 1 µPa), dawn (101.1 ± 2.1 dB re 1 µPa) and lowest during the day (92.2 ± 0.5 dB re 1 µPa). Sound intensity during dusk was approximately 14 – 20 dB re 1µPa higher compared to during the day.

Comparing against the estimated ambient noise level for sea state 3, in all octave bands, the unjam sound intensity was 10 to 30 dB higher than background noise during night, dawn and dusk. However, during the day, the sound intensity was only 1- 10 dB higher than the background noise.
Figure 5.4: Daily pattern of underwater sound intensity in different octave bands a) band 3, b) band 4 and c) band 5. Times with significantly different sound pressure levels (SPL\textsubscript{rms}) within each octave band (P < 0.05) are indicated by different letters (results from Dunn’s tests). The horizontal line indicates estimated theoretical ambient sea noise levels (sea state 3).
5.3.4 Spatial pattern of the unjam sound

Day experiment

Sound intensity at the stationary hydrophone remained relatively low at 6-8 dB re 1 µPa higher than the estimated ambient noise (87.5 - 90.5 dB re 1 µPa). Mean sound intensity during the experiment was 93.3 ± 0.3 dB re 1 µPa in octave band 3, 97.6 ± 0.2 dB re 1 µPa in octave band 4 and 96.4 ± 0.3 dB re 1 µPa in octave band 5 (Figure 5. 5a, c, e). Sound level measurements at the roving hydrophone showed an immediate signal loss with distance from the unjam in all octave bands. Linear regression showed a significant relationship between signal loss and the distance from the source for all octave bands (Figure 5. 5b, d, f). For band 3, the acoustic signal dropped below background noise at approximately 400 m from the FAD. Signal loss was significantly related to distance from the FAD ($R^2 = 0.306$, $P = 0.002$) and decreased at a rate of 3.45 dB log distance$^{-1}$ (-1.0 dB with the doubling of distance). For band 4, the signal also dropped below ambient background noise at approximately 400 m away from the FAD and signal loss was significantly related with distance ($R^2 = 0.576$, $P < 0.001$) decreasing at a rate of 3.08 dB log distance$^{-1}$ (-0.9dB with the doubling of distance). For band 5, the signal fell below ambient background noise at only 100 m from the FAD. Signal loss was significantly related with distance ($R^2 = 0.604$, $P < 0.001$) at a rate of 3.87 dB log distance$^{-1}$ (-1.2 dB with the doubling of distance). Signal loss in all octave bands did not follow typical geometric spreading loss for a point source which was neither cylindrical, i.e., -3dB with doubling of distance or spherical, i.e.,-6dB with doubling of distance (Urick 1983).
Figure 5.5: Day experiment. 5.5a,c & e) Scatterplot of consecutive paired sound level measurements at stationary hydrophone (black dots) and at roving hydrophone (white dots) for octave bands 3-5. The horizontal line indicates estimated ambient sea noise levels (sea state 2). Figure 5.5b, d, f): Plots of signal loss as a factor of distance. Solid line indicates regression line while dashed (cylindrical) and dotted (spherical) lines indicate geometrical spreading model.
Dusk experiment

Sound intensity at the stationary hydrophone showed considerable variation, but were above estimated ambient background noise throughout the experiment (Figure 5.6a, c, e). Mean sound intensities during the experiment were 101.7 ± 1.4 dB re 1 µPa in octave band 3, 109.0 ± 1.3 dB re 1 µPa in octave band 4 and 102.1 ± 1.0 dB re 1 µPa in octave band 5. In all octave bands, sound intensity at the unjam initially dropped approximately 10 dB before increasing to respective maxima. Loss of acoustic signal from the unjam was not apparent until about 300-400 m away from the unjam but the loss increased thereafter. Consequently, linear regression analysis was calculated from this distance onwards where a consistent trend in signal loss was observed (Figure 5.6b,d,f). For band 3, signal loss began at 410 m away from the unjam and was significantly related to distance (R²= 0.731, P < 0.001) decreasing at a rate of 4.45 dB log distance⁻¹ (-1.3 dB with the doubling of distance). For band 4, signal loss began at 384 m away and was significantly related to distance (R²= 0.826, P < 0.001) decreasing at a rate of 6.57 dB log distance⁻¹ (-2.0 dB with the doubling of distance). For band 5, signal loss was apparent at 290 m away and showed significant relationship with distance (R²= 0.729, P < 0.001), decreasing at a rate of 7.26 dB log distance⁻¹ (-2.2 dB with the doubling of distance). Sound intensity measured at the roving hydrophone was also above the calculated background noise throughout the experiment. As in the day experiment, signal loss in all octave bands did not follow either cylindrical or spherical spreading.
Figure 5.6: Dusk experiment: 5.6 a,c & e) Scatterplot of paired sound level measurements at stationary hydrophone (black dots) and at roving hydrophone (white dots) for octave bands 3-5. The horizontal line indicates calculated ambient sea noise levels (sea state 2). Figure 5.6 b, d, f): Plots of signal loss as a factor of distance. Solid line indicates regression line while dashed (cylindrical) and dotted (spherical) lines indicate geometrical spreading model.
5.4 DISCUSSION

5.4.1 Spatio-Temporal Characteristics of the Unjam

The underwater sound of the unjam is characterised by a distinctive peak in sound energy in the frequency band 500 to 2000 Hz. Correspondingly, the sound energy in the octave bands (band 3, 4 and 5) within this bandwidth were also higher at the unjam compared to the control. In these bands, sound levels at the control approximated the theoretical ambient noise (without biological noise) which is in agreement with Urick (1983). This indicated that the higher sound energy recorded at the unjam compared to the control, and that might be expected from theoretical calculations of ambient noise, was due to the unjam. Furthermore, the characteristics of the bandwidth of the sound conform to what have been identified as biological sound sources from other studies (Cato 1980, Au & Banks 1998, Radford et al. 2008a). For example, many fish species (Cato 1976, Cato 1978) and invertebrates such as, sea urchin (Radford et al. 2008a) and snapping shrimp (Au & Banks 1998) are known to produce sound in the marine environment. Vocalisation sounds of fishes are predominantly in the lower end of the range of hearing typically in the frequency range between 100 to 1000 Hz (Amorim 2006, Kasumyan 2008). Some of the known soniferous fish that were observed at the unjam include the sweetlip (Diagramma pictum; Haemulidae), trevally (Caranx sexfasciatus; Carangidae), seargent major (Abudefduf saxitalis; Pomacentridae) and tigerfish (Terapon jarbua; Terapontidae). Although individual fish calls could not be isolated from the recordings, it is known that fish sounds often dominate the underwater soundscape and could increase the ambient noise level by up to 35 dB re 1 µPa when present in large numbers such as during spawning aggregations (Connaughton & Taylor 1995, Luczkovich et al. 1999, McCauley & Cato 2000). In tropical waters near Australia, sounds of fish choruses are thought to be responsible for the 500 and 800 Hz spectral peaks which increased ambient noise spectral level by up to 30 dB (Cato 1978).

Sea urchins (Diadema spp.) inhabit the concrete artificial reef structure of the unjam and were notably abundant (S.M Ghazali and C.A Radford, pers. obs.). In New Zealand, noise from sea urchins (Evechinus chloroticus) grazing on rocky reefs have been identified as an important source of biological sound in the range of 700 to 2000 Hz (Radford et al. 2008b). The urchin feeding sound is amplified by the urchin’s calcareous test acting as a Helmholtz resonator with the peak frequency and amplitude related to urchin test diameter and relative abundance respectively (Radford et al. 2008a). Another sea urchin species, Diadema setosum was also
known to produce sound with spectral characteristics similar to the 1600-2000 Hz spectral peaks observed in tropical waters near Australia (Cato 1978). Above 2000 Hz, the dominant biological sounds are most commonly due to the cavitation sounds of air bubbles produced by the snapping action of the snapping shrimp chelae (Au & Banks 1998). Our observations of the abundant aquatic life at the unjam and the characteristics of the sound accord with the view that the unjam sound source is most likely to be of biological origin. The seafloor surrounding the unjam consists of an expansive area of sand seafloor which is habitat generally not associated with soniferous organisms (Radford et al. 2010)

Our study showed that the underwater sound intensity of the unjam varies at different times of the day. Signals were 10 – 20 dB louder during crepuscular periods and night compared to during day. The daily pattern of sound levels recorded at the unjam was comparable to other habitats, such as coral (Cato 1978) and temperate reefs (Radford et al. 2008b) in regards to the dawn and dusk peaks in sound level resulting from biological choruses. At an Australian coral reef, fish calling is a major contributor to sea noise levels with daily sound patterns showing highest intensity at night (McCauley & Cato 2000). The temporal pattern of biological choruses (dawn and dusk) in New Zealand reefs is suspected to correlate with the higher settlement to habitat rate of fish and crustacean larvae during these times (Radford et al. 2008b). A similar suggestion can be made with respect to fish abundance and their movement in relation to unjams where day and night variability of fish abundance has been observed (LKIM internal report, unpublished).

Our spatial experiments have shown that sound in octave band 3, 4 and 5 show significant signal loss with distance. However, we have noted that acoustic signal loss did not follow either spherical or cylindrical spreading models for a point sound source. Signal loss occurred at rates between 0.9 to 2.2 dB with the doubling of distance, which was less than would be predicted by conventional sound spreading models. During the day when source sound level was low, signal loss occurred immediately in the vicinity of the unjam and was reduced to ambient noise level at 400 m in octave bands 3 and 4, and at 100 m away in band 5. However, during dusk, sound levels were constant beyond the unjam up to a certain distance before signal loss commenced ranging from 290 m to 410 m for the different octave bands. Additionally, the unjam signal remained above ambient noise until beyond 1000 m due to the higher source levels. This indicated that the unjam is not a typical point source but could potentially be a more extensive sound source (line or planar) which might be expected to have a different sound spreading
pattern. Unlike point sources, spreading losses for both line and planar sound sources are smaller and correlate with source dimensions (Lurton 2002). In our study, the dimension of a potential line source, i.e., ≈ 25 m could be inferred to the length of the vertical distribution of sound sources along the unjam’s pelagic component (palm fronds and rope). In addition, the dimension of a potential planar source, i.e., ≈ 1000 m$^2$ could be inferred to the horizontal distribution area of sound sources over the benthic artificial reef component (S.M Ghazali and C.A Radford, pers. obs). During the dusk experiment, increase in bioacoustical activity over the artificial reef area may have elevated the effect of a planar sound source which formed the zone of constant sound level.

### 5.4.2 Potential acoustic attraction of the unjam

With the exception of clupeiform species that can detect ultrasound (Mann et al. 2001), the frequency range of the maximum auditory sensitivity for a majority of fish is between 100-1000 Hz with the upper frequency limit at 2000 Hz (Fay 1988, Au & Hastings 2009b). Our study has demonstrated that an unjam produces a distinct underwater sound with a frequency range and sound level that encompasses the hearing range of the majority of fish. In this regards, our findings differed to that of Babaran et al. (2008) albeit design differences between the unjam and the payao. The difference between the sounds, i.e., peak frequency (750 Hz vs. 49 Hz) and signal bandwidth of the unjam (this study) and the payao (Babaran et al. 2008) we attribute to the bioacoustical activity of the fauna inhabiting the unjam which is lacking in the payao study.

Sounds of biological origin can play a functional role in the communication, interception and orientation of fish (Myrberg 1997b). The larvae of the coral-reef damselfish *Chromis atripectoralis* can distinguish between a sound with potential biological significance and one devoid of biological significance (Leis et al. 2002). This ability was determined from their swimming response to playback of nocturnal reef sound indicating that sounds of biological origin could mediate the directional swimming behaviour of fish. It is, however, likely that the effect of sounds will be different among species depending on the nature of the sound, their motivation and circumstance. For example, the fish larvae of some reef species use reef sound to orient to and settle on reefs (Leis & Lockett 2005, Montgomery et al. 2006, Simpson et al. 2008b), and predators may be guided to prey by intercepting fish vocalisation sounds (Myrberg 1997b). These examples indicate the potential for unjam sound to influence fish behaviour.
Our study has shown that the acoustic signal of the unjam is strongest during crepuscular periods and night time. Assuming that detection thresholds of fish are limited by the sound level of ambient-noise, during the day the unjam signal is detectable by fish above ambient background noise from 100 to 400 m away. During dusk, the signal could potentially be detected by fish from more than 1000 m away. Past fish displacement experiments elsewhere have shown that during daytime, fish could return to a FAD from up to 180 m (Ibrahim et al. 1990) and 275 m away (Dempster & Kingsford 2003). Assuming that these previously studied FADs have the same underwater sound characteristics as in the current study, the FAD sound could still be detectable at these ranges, even when the signal level is at its lowest during the day. The propagation properties of the unjam signal signifies the existence of a horizontal sound pressure gradient of the signal centred at the unjam. In the far field, fish that have swim bladder that is in close proximity or coupled to the ears by the Weberian apparatus (otophysan) could sense this sound pressure gradient (Higgs et al. 2003) and use it for localization or orientation to the unjam (Rogers & Cox 1988). For fishes that have swim bladders but do not possess such couplings to the ears, localization of the FAD using particle motion component of the sound may be suggested by the sound localization mechanism model based on the phase difference between the direct and indirect reradiated signal from the swim bladder (Demunck & Schellart 1987) and elliptical orbits of hair cells with respect to the otoliths (Schellart & Demunck 1987). However, it must be noted that actual sound detection using either component of the sound is dependent on the hearing threshold of the respective sound components. In addition, variation in ambient noise due to sea surface condition and shipping (Wenz 1962, Lurton 2002) would also change the transmission range and detectable distance. The significance of these findings are that they demonstrate for the first time, the potential acoustic function of a FAD as a long range attraction and orientation cue for fish. The current findings may help in understanding the dynamics of fish association around FADs which in turn will have implications for their use in fisheries.
6.1 FISH VOCALISATIONS IN NEW ZEALAND WATERS

6.1.1 Field Recordings and Sound-truthing

In the shallow coastal waters of New Zealand, sounds of biological origin dominate the lower frequency spectrum of the underwater soundscape (Radford et al. 2008b, Radford et al. 2010). Although the waters are known to be biologically diverse, only sounds produced by the snapping shrimp (Radford et al. 2008b) and urchin (Castle & Kibblewhite 1975, Radford et al. 2008a) have been described thus far. Despite the fact that approximately 270 fish species inhabit the coastal waters around New Zealand, their vocalisations have never been documented. This is rather surprising because worldwide more than 800 fish species from 109 families are known to be soniferous with new vocalisations reported regularly (Tricas et al. 2006, Anderson et al. 2008, Kennedy et al. 2010). Therefore, it is expected that the coastal waters here also contain considerable number of soniferous fish. Several reasons may explain the lack of information on this subject; One, low vocalising rate and source level of vocalisations; two, severe masking by environmental noise; three, the sporadic (both temporal and spatial) nature of their occurrence; and four, relatively little research effort into near-shore underwater acoustics.

The current study found at least eight aural types of fish vocalisation from recordings in captivity and in the field (Table 6.1) (Chapter 2, 3 & 4). Studies in captivity clearly show that different species may produce distinct vocalisations even within a single aural category. This also indicates that vocalisations within the same aural category could be produced by more than one species.

Two putative fish vocalisations, croaks and purrs were described based from temporal records made at a temperate reef at the Cape Rodney to Okakari Point Marine Reserve (Chapter 2). The sounds were described as putative because their identity could not be verified. However, based on their aural and visual (waveform) character that resemble the general character of...
known fish vocalisations, they were most likely sounds produced by fish. Croaks and purrs were the most prevalent vocalisations among several other less common vocalisations (i.e., knocks, drums, grunts and growls). They could be heard both during the new and full moons across all the austral seasons. During the new moon of all seasons, these sounds formed choruses in the frequency range 178-355 Hz (band 2@ 250 Hz octave band) corresponding to the vocalisation’s dominant frequency. Fish choruses commenced after sunset around the same time as the invertebrate choruses and lasted up to 3 h. However, the fish choruses here (up to 9 dB above normal ambient noise) were not as loud or as prolonged as choruses reported elsewhere, which can be up to 30-50 dB above normal ambient noise and lasting up to 8 h (Fish 1964, Fish & Cummings 1972, Cato 1978, Luczkovich et al. 2000, Locascio & Mann 2008). Furthermore, they were not as loud as the choruses of snapping shrimps or urchins, therefore may not emanate to the distance proposed for the invertebrate choruses (Radford 2007, Radford et al. 2008b).

Overall, the temperate reefs in the current study are comparable to coral reefs in terms of the number of fish vocalisation types. Lammers et al. (2008) reported five types of fish sounds from a coral reef off Hawaii, while McCauley & Cato (2000) reported four dominant types of fish sound from Australia. However, the number of fish vocalisations encountered in sound recordings in the wild is subject to the recording duty cycle and recording time. Therefore, short intermittent sound recordings (2 - 5 min every hour) used in the above studies (including the current study) was likely to underestimate the actual number of calls and call types. For example, in continuous sound recordings each lasting 7 - 60 h, a passive acoustics survey along the Hudson River in North America found fifty seven types of fish vocalisations (Anderson et al. 2008). Four were identified to respective species, while the remaining fifty three were described as potential fish vocalisations.

To avoid under sampling temporally sporadic vocalisations continuous recordings were undertaken during sound-truthing of captive fish. Using this approach, the current study identified the vocal repertoire of three local fish species namely the bigeye (Pempheris adspersa), bluefin gurnard (Chelidonychthys kumu) and john dory (Zeus faber), although the latter is not described in the thesis. Vocalisations of the bigeye were described for the first time (Chapter 3) and constitute a single basic type of acoustic pulse which wasaurally described as a ‘pop’. Pops may be produced singly or in multiples and temporally patterned to form various calls. When multiple pops are fused to produce a call, that call may sound more like a grunt.
Chapter Six: General Discussion

Generally the vocal repertoire of fishes is limited to one or two types of sounds (Amorim 2006) as shown for the bigeye. However, this may not be the case for some fish species. This thesis has also reviewed the vocalisations of the bluefin gurnard (Chapter 4). It confirmed the variation of the grunt type vocalisations first reported for the species over 40 years ago based on Japanese species (Bayoumi 1970). In addition, the current study also discovered that the vocal repertoire of the bluefin gurnard was actually more extensive and includes two variations of a growl type vocalisation, identified here as the short and long growl. More interestingly growls were mainly produced during the night, which indicates a selective vocal behaviour not seen in other fishes to date. The functional role of multiple sound repertoire of a species is not well understood even though it has been observed in a few fish families, such as the Batrachoididae (Amorim et al. 2008a, Maruska & Mensinger 2009, Rice & Bass 2009), Mormyridae (Crawford et al. 1986, Crawford et al. 1997) and Triglidae (Amorim & Hawkins 2000, Amorim et al. 2004, Connaughton 2004, Amorim & Hawkins 2005). The vocal repertoire of a species can also vary temporally, often expanded during reproductive seasons (Hawkins & Amorim 2000, Amorim 2006, Ueng et al. 2007, Kasumyan 2009).

6.1.2 Rate and Diel Pattern

In captivity both bigeyes (91 vocalisation fish\(^{20} \text{h}^{-1}\)) and gurnards (16 vocalisation fish\(^{1} \text{h}^{-1}\)) were prolific sound producers with sporadic vocalisations occurring within every hourly period. However, the overall distribution throughout the 24 h period differed across these two species. Bigeyes showed peak vocal activity during dusk and night periods, while the bluefin gurnard peaks occurred at dawn and dusk. The diel pattern of fish vocal activity is reported to be variable. Grey gurnard in captivity showed maximum vocal activity during the day, minimum activity at night, and intermediate during dawn/dusk (Amorim & Hawkins 2005). Some species from Sciaenidae (Connaughton & Taylor 1995), Pomacentridae (Locascio & Mann 2008) and Batrachoididae (Thorson & Fine 2002b) are active during crepuscular periods. Other species, such as the toadfishes, Opsanus beta (Batrachoididae) (Thorson & Fine 2002a) and Batrachomoeus trispinosus (Batrachoididae) (Rice & Bass 2009), weakfish Cynoscion regalis (Sciaenidae) (Luczkovich et al. 1999), red hind Ephinephelus guttatus (Serranidae) (Mann et al. 2010), four rockfish species Sebastes sp. (Sirovic & Demer 2009) as well as two freshwater species, the gudgeon, Gobio gobio L., and the bullhead, Cottus gobio L., (Ladich 1988, 1989)
lack clear diel vocalisation patterns and vocalise sporadically throughout the day and night. Since vocal activity corresponds to certain behaviours, it may be a proxy to the general activity of animals (Parmentier et al. 2010b). Some fish show plasticity in their general activity patterns where they may switch between diurnality and nocturnality (Helfman 1986, Reebs 2002). This plasticity also applies to fish with a circadian system. Strict activity rhythms may breakdown during biological processes, such as during migration and spawning (Reebs 2002). Alternatively there is the cethemeral activity pattern that is widely used to describe activities of mammals in which the activity peaks centre around sunrise and sunset, but extend into both day and night (Curtis & Rasmussen 2006, Hill 2006, Tattersall 2008). The current study compared the vocal activity of the bluefin gurnard to the cethemeral activity patterns. Although the notion requires further behavioural study, a conclusion from the current study was that some fish activity may exhibit this alternative diel activity pattern.

6.1.3 Source Level

Information on the source level (SL) of individual fish vocalisations is scarce. This is due to the fact that SL cannot be measured in tanks due to the effects of sound reflections and tank reverberation (Akamatsu et al. 2002), as well as difficulties in controlling fish behaviour in the open water. Despite such difficulties there have been some attempts that measured fish SL in the open water via two different approaches. Firstly, by using ‘silent/quiet’ diving equipment to approach fish in their natural habitat and to record (i.e., audio and video) their vocalisations from a known or estimated distance. This way the identity of the source can be verified with confidence. Secondly, by using audio recordings from calibrated hydrophone arrays where source distance is not critical (Cato 1998, Parsons et al. 2009). However, the identity of the source must be verified from sound-truthing the target fish (Chapter 3). It must be noted that for both methods the vocal behaviour of the target fish is beyond the control of the researcher so the chance of recording any vocalisations is random.

To date, there is a limited yet wide range of SL values for different types of fish. Parsons et al. (2009) measured source level of mulloway, Argyrosomus japonicas in the Swan River Australia as 170 dB re 1 µPa @ 1m. Sprague & Luczkovich (2004) measured the SL_{rms} of individual silver perch, Bairdiella chrysoura ‘purr’ in the range 128-135 dB re 1 µPa @ 1m. The haddock, Melanogrammus aegelfinnus was reported to produce grunts with SL_{rms} of 114-120 dB
re 1 µPa @ 1m (Wahlberg & Westerberg 2005). McCauley & Cato (2000) measured SL of 3 types of fish calls from the Great Barrier Reef and reported the ‘trumpet’ call $SL_{rms}$ as 150 dB re 1 µPa @ 1m, the ‘banging’ call $SL_{rms}$ as 144-147 dB re 1 µPa @ 1m and the ‘pop’ call $SL_{peak-peak}$ as 157 dB re 1 µPa @ 1m. The $SL_{rms}$ of the bigeye (Chapter 3) which was in the range 112-120 dB re 1 µPa @ 1m and appeared relatively low in comparison to previous fish studies, especially to the loud planktivore ‘pop’ sounds reported by McCauley & Cato (2000). The same study also reported that ‘pops’ formed loud choruses that emanate up to 15 km away from the parent reef of the fish. Loud choruses have also been reported for sciaenids during their spawning season (Luczkovich et al. 1999). Sciaenid choruses during spawning function as advertisement calls aimed at attracting potential mates from a distance, therefore benefit from being loud. In comparison with the current study, the relatively low SL of bigeye vocalisations was not likely to form loud choruses or propagate over large distances. The low SL of the bigeye vocalisations would be better suited to serve as contact calls since group cohesion contact calls should only be sufficiently loud enough to be heard in the immediate vicinity by members of the group or shoal, and not so loud to increase the risk of signal interception by predators.

6.1.4 Characteristics

All fish vocalisations described in this thesis were produced by the sonic muscle/swim bladder mechanism. For recordings of captive fish (i.e., bigeye and gurnard), this was obvious from dissections and general anatomical investigations. For croaks and purrs from the field recordings, this was inferred from the characteristics of their sound wave and associated acoustic parameters. Of particular interest was the Q value (peak frequency/3dB band-width) which is a measure of tuning efficiency. All vocalisations have low Q values (< 2) that indicate broad tuning corresponding to sound produced by a highly damped sound generating mechanism, such as the swim bladder. A highly damped sound generating mechanism is critical for the production of vocalisations with fine temporal patterning of pulses within a call (Connaughton 2004, Fine et al. 2004, Fine et al. 2009). All vocalisations in the current study were pulsatile sounds, each with its distinctive temporal patterning of the sound wave. An excellent example was shown in the vocalisations of the bigeye, where very fine temporal patterning can be observed in the shortness of the vocalisation pulse duration (i.e., 7.9 ± 0.3 ms) and pulse periods (i.e., 5.4 ± 0.2 ms). There was considerable variation among vocalisations in terms of their pulse structure and temporal characteristics. The longest single call was produced by the bluefin gurnard (long growl) lasting
more than 2000 ms while the shortest was a single pop (8 ms) produced by the bigeye. The dominant frequencies of fish vocalisations were below 500 Hz with their 3 dB bandwidths encompassed in three octave bands (i.e., 125, 250 and 500 Hz octave).

6.1.5 Vocalisations amid other Biological Sounds

In general the frequency range of fish vocalisations reported in this thesis was lower than the frequency range of the urchins (700 - 2000 Hz; 1000 Hz octave) and snapping shrimps (2000 Hz - 22000; 2000 Hz octave). The spectral disparity between the sound of these animals indicate that masking was likely to be minimal and that within the reef, the louder invertebrate noise may not be detrimental to the presence of fish vocalisations in the underwater soundscape. Spectral adaptation or partitioning in the frequency domain has never been reported for marine fishes.

Soniferous animals must compete for acoustic space in order to communicate acoustically (Sueur et al. 2010). This involves competition among different animal groups and congeners that form the background noise of the habitat. Habitat noise may serve as an environmental selection pressure on the acoustic signals of animals (Slabbekoorn & Smith 2002). The spectral adaptation of acoustic signals to habitat noise has been demonstrated in birds (Slabbekoorn & Smith 2002, Blumstein & Turner 2005, Baker 2006, Halfwerk & Slabbekoorn 2009, Kirschel et al. 2009, Nemeth & Brumm 2010) and insects (Forrest 1994, Sueur et al. 2010). Evidence is emerging that may indicate a similar adaptation in fishes. Freshwater gobies (Padogobius bonelli and Gobius nigricans) (Lugli & Fine 2003, Lugli 2010) and darters (Etheostoma crossopterum and E. flabellare) (Speares et al. 2011) that live in noisy stream habitats utilise an acoustic window of their habitat noise to communicate acoustically. In addition, it has also been reported that hearing abilities are also adapted to habitat noise where spectral sensitivity inversely correlates with peak frequency of the habitat noise (Wysocki & Ladich 2005, Wysocki 2006, Wysocki et al. 2007, Amoser & Ladich 2010), which could further facilitate acoustic communication. In the marine environment, instead of sound ‘partitioning’ in the frequency domain, McCauley & Cato (2000) reported that coral reef species partition their sound production in time and space. Different fish species from the Great Barrier Reef were heard vocalising at different times of the day and at different places with minimal overlap. For vocalisations that overlap in their frequency characteristics, this is a useful strategy to minimise masking.
Table 6.1: Summary of all the vocalisation types encountered during the preparation of this thesis

| Vocalisation type     | Identity       | Recorded from                | Status  
|-----------------------|----------------|------------------------------|---------
| Grunt 1 (‘Gu’ & ‘Pon’) | Bluefin gurnard | Captivity                    | Described |
| Grunt 2               | Bigeye         | Captivity & North Reef       | Described |
| Grunt 3               | Unknown        | North Reef                   | Undescribed |
| Growl 1 (Short & Long)| Bluefin gurnard | Captivity                    | Described |
| Growl 2               | Unknown        | North Reef                   | Undescribed |
| Pop                   | Bigeye         | Captivity & North Reef       | Described |
| Croak                 | Unknown        | North Reef                   | Described |
| Purr                  | Unknown        | North Reef                   | Described |
| Drumming              | Unknown        | North Reef                   | Undescribed |
| Knock                 | Unknown        | North Reef                   | Undescribed |
| Bark                  | John dory      | Captivity                    | Undescribed |

1 status refers to the current knowledge of the vocalisation. Described means that the vocalisation has been at least characterised in the current study.

6.2 COMMUNICATION AND OTHER ROLES OF VOCALISATIONS

Communication occurs when a signal produced by a signaller results in a change in the behaviour of the receiver (Moller 2006). Furthermore, communication entails benefits to the signaller although most of the time it is also beneficial to the receiver. Like other vertebrates,
vocalisations principally serve a communication function in fishes (Bass & Ladich 2008), such as advertisement or courtship calls. Courtship is an important stage in the reproductive behaviour of fish which precedes spawning (Connaughton & Taylor 1996, Mann et al. 1997, Boyle & Cox 2009). Calls of a courting male contain information on its readiness and fitness to fertilise eggs (Connaughton et al. 2002, Amorim et al. 2003, Amorim et al. 2010). Following a successful courting session by males, mating pairs are established and spawning commenced. Another example, is the agonistic calls produced by many fishes during aggressive behaviours, such as territorial defence or competing for a limited food source (Ladich 1994, Myrberg 1997a, Henglmuller & Ladich 1999, Amorim & Hawkins 2000, Ladich 2006, Amorim & Neves 2008, Kasumyan 2009, Vasconcelos et al. 2010). In contrast to the unilateral communication of courtship calls, disputing individuals usually exchange agonistic calls that contain information of each other’s fitness and motivation (Ladich 1998, Colleye et al. 2009). Such communication between individuals may inform decisions to cease confrontations, therefore avoiding possible physical injury or death by both parties.

Alternatively, Myrberg (1981, 1997) suggested that an information transfer in which the beneficiary is clearly not the sender should not be called communication but interception. Interception is mostly a spinoff from communication and forms the basis of behaviours relating to guided movement and orientation in space. One such ecologically important behaviour is the orientation of larval fish to suitable settlement habitat (Montgomery et al. 2001, Simpson et al. 2004b, Montgomery et al. 2006). The attraction of larval and juvenile fishes to ambient reef noise has been demonstrated in the field by various researchers (Tolimieri et al. 2000, Tolimieri et al. 2004, Leis & Lockett 2005). Fish vocalisations may make a significant contribution to this attraction. It has been recently shown that some fish preferred reef noise that is dominated by fish vocalisations (Simpson et al. 2008a, Radford et al. 2011a). However, these experiments do not directly demonstrate long distance orientation and it remains unknown what the effective range of the orientation is. At long ranges, orientation to fish vocalisations is expected to be on the basis of detecting the gross spectral composition or general impression of the vocalisations. Detecting vocalisations in the soundscape may allow location of breeding grounds by conspecifics (Luczkovich et al. 1999) and also food/prey by congeners (Myrberg 1997b, Luczkovich et al. 2000).
6.2.1 Possible Group Cohesion Function for Fish Vocalisation

Among the various soniferous reef fishes, an assortment of acoustic communication may take place within the reef (Mann & Lobel 1997, Myrberg 1997a, Lobel & Kerr 1999, Lagardere et al. 2005). McCauley & Cato (2000) have suggested that some coral reef planktivores may use their vocalisations to maintain loose schools (i.e., group cohesion cue) during nocturnal foraging to track conspecifics and prey aggregations. However, this has never been experimentally demonstrated. The current study examined the vocalisations of an obligate reef dweller, the bigeye against the background noise of the reef soundscape (Chapter 3) with the aim to describe the active space of their vocalisations. It was shown that the active space of the bigeye calls corresponds with the variability in reef noise intensity during different seasons and moon phases. For example, the active space of the vocalisations was greater during full moon compared to the new moon.

Active space has a potential application in the group cohesion hypothesis to infer a hypothetical inter-individual spacing of individuals in a shoal or school. It should also be noted that shoals and schools subscribes to different definitions (Pitcher 1983, Pitcher 1986). The terms are used here to simply denote the grouping of fish and focus more on the structure of the group rather than the social context. Schooling fish remain connected with each other by maintaining a particular distance between nearest neighbours (Burgess & Shaw 1981). This is achieved by establishing a spatial attraction and repulsion zone from continuous hierarchical assessments of the presence or absence of neighbours (Tien et al. 2004). For a highly organised and polarised school structure where such distance is only up to few body lengths, hydrodynamic (lateral line) and visual cues play an important role in maintaining the small inter-individual spacing (Partridge et al. 1980, Partridge & Pitcher 1980, Burgess & Shaw 1981, Faucher et al. 2010). In contrast, disorganised or loose schools have significantly bigger inter-individual spacing and fish often swim beyond the effective range of hydrodynamic cues. Furthermore, it has been observed that individuals or small groups of a large foraging shoal may occasionally disperse to feed but would return and regroup later on (Pitcher 1986, Pitcher et al. 1988). This has been observed for the bigeyes (MacDiarmid 1981) and other Pempherid species (Gladfelter 1979, Golani & Diamant 1991).

The current study showed that bigeye vocalisations could be exploited to serve as a group cohesion cue. By listening to vocalisations of neighbours, contact with the school can be
maintained up to a range limited by the audibility of the vocalisation. The effective range of this cue would be predicted to be inversely related to levels of ambient noise. The current study showed that the habitat ambient noise level varied considerably over different moon phases and seasons. The intensity of ambient noise was higher during the new moon compared to the full moon and peaks in summer. The shortest effective call range (< 1 m) was observed during summer new moon while the longest effective range was observed during spring full moon (~ 30 m). This varying spatial extent of bigeyes active space may further support the idea that these vocalisations act as a contact calls.

It is known that in the organisation of fish schools, cohesion and size are functions of predation pressure and availability of food patches (Magurran & Pitcher, 1983, Krause et al., 1998). It has also been shown in the zebrafish (Danio rerio) that group cohesion can change in response to manipulations of the environment (Miller & Gerlai, 2007) and the inter-individual distance within a shoal may oscillate with a period between 5 and 15 s (Miller & Gerlai, 2008). However the proximate mechanism that would allow for inter-individual distance expansion beyond hydrodynamic and visual sensing for shoaling fish in general is unknown. Here it is suggested that for soniferous fishes contact calls could mediate loose shoal cohesion and shoal size expansion.

It is of interest that prey (zooplankton) abundance and density also varies with moon phase. Generally, prey density in the water column is highest during new moon and lowest during full moon corresponding to the variable extent of predatory pressures during these periods (Alldredge & King, 1980, Gliwicz, 1986). Although actual predation rate is a function of prey density and visual detection (Holzman & Genin, 2003), bigger shoals may improve the chance of prey encounters by foraging in groups as well as reducing the time of finding patches of food (Pitcher et al., 1982). Unlike foraging shoals of some reef species that migrate over distances (i.e., hundreds of m to a few km) beyond the reef to track denser prey aggregations (Marnane & Bellwood, 2002, Annese & Kingsford, 2005), the bigeye nocturnal forage is limited to the immediate area of the reef (i.e., within 80-100 m from their day time shelter) (MacDiarmid, 1981). Therefore, the need to increase foraging and feeding efficiency within the limited time and space is more pronounced. The current study demonstrates that the larger active space during full moon could allow bigeyes to expand their inter-individual distances and forage as a loose school to track and capture low density prey aggregations within the reef more
efficiently. Conversely, the reduced active space during new moon may not be detrimental to foraging since prey is more abundant with densities several orders of magnitudes higher (Alldredge & King 1980, Gliwicz 1986). Furthermore, it has been reported that despite different prey densities during new and full moons, similar amount of prey were consumed by the bigeyes (MacDiarmid 1981), which is consistent with the shoal cohesion mechanism proposed in the current study.

6.2.2 Acoustic Orientation of Fish to FAD

An example of long range orientation in fish is demonstrated by the movement dynamics of fish around fish aggregation device (FAD). It has been reported that several pelagic species (e.g., tuna) maintain a spatial association with FADs from distances up to a few km away (Castro et al. 1999, Dagorn et al. 2000, Taquet et al. 2007). For example, tuna were observed to regularly make returned movements to its home FAD or between a network of FADs (Marsac & Cayré 1998, Ohta & Kakuma 2005, Dagorn et al. 2007). Two key translocation experiments have demonstrated the directional and orientational swimming of fish to FADs. The first was by Ibrahim et al. (1990) who showed at least five Malaysian fishery target species could return to their respective FADs from up to 180 m away (Ibrahim et al. 1990). Second was by Dempster & Kingsford (2003) who demonstrated that the dolphinfish, Coryphaena hippurus, and the kingfish, Seriola lalandi, were able to return to their home FADs in equal proportions from both across and down-current directions from up to 275 m away. Sound was suggested as the potential orientation cue (Dempster & Taquet 2004) yet a potential FAD’s signal has never been identified. Therefore, the spatio-temporal bioacoustic environment of FADs is unknown.

Using one particular type of FAD (Malaysian FAD known as ‘unjam’) as a model, the current study provided the first evidence that a FAD generates an underwater sound signature that propagates large distances from the sources (Chapter 5). The spectral characteristics of the sound is comparable to reef noise where it has dominant energies in octave bands dominated by sounds or choruses of biological sources (i.e., fish, urchin and snapping shrimp). The sound intensity showed diel variability and was loudest at dusk and lowest during the day. This diel pattern was reflected in the spatial distribution of the sound in the surrounding waters. The FAD sound propagated further during dusk (> 1 km) compared to during the day (<400 m). The FAD sound propagation experienced a reduced transmission loss not described by the conventional
models (spherical or cylindrical) for a point source. It was thus suggested that FAD may act as a planar sound source and was further supported by the existence of the zone of constant sound intensity near the FAD during dusk (Radford et al. 2011b).

The zone of constant sound intensity corresponds to the horizontal dimension of the FAD, therefore the immediate sound transmission loss from the center of the FAD becomes a function of its horizontal dimensions (Lurton 2002). It is proposed that affects the sound propagation from the FAD in three ways: one, within the FAD’s margin, noise intensity is constant; two, at the margin and immediate vicinity or adjacent waters, spreading loss is gradual but comparatively less than cylindrical spreading; and three, beyond this, the FAD becomes a point source and spreading loss follow a cylindrical (shallow water) model. Overall, this suggests that biological choruses are equally loud inside the immediate area of the FAD. Beyond the FAD’s margin, the FAD noise propagates further than a theoretical point source centered at the reef.

The propagation characteristics intersect with the hearing capabilities and behaviour of the fish to determine the effective attraction range of the FAD. The recordings also show that this will vary with the time of day, sea conditions and level of shipping traffic. The estimated attraction ranges from the current study appear to support the range of spatial movement of fish observed around FADs (Dagorn et al. 2007, Moreno et al. 2007). This is the first evidence that show at least one type of FAD is capable of providing acoustic cues into the surrounding waters that may be used by fish to detect and orientate to FAD from long distances.

6.3 FUTURE DIRECTIONS

The thesis used a range of approaches to understand the nature of fish vocalisations fish in the underwater soundscape and their potential biological role. Findings from the current study provide baseline information for future fish bioacoustics research in New Zealand. There is a huge potential for discovering new soniferous fish species and vocalisations particularly among the estimated 124 endemic species (marine and freshwater) (Froese & Pauly 2010). Understanding fish vocalisations from different geographical areas and across fish phylogeny will allow a better understanding of the evolution of fish vocalisation, and the adaptations of fish to their acoustic environment. Furthermore, only by first understanding the acoustic
characteristics of fish vocalisation can the effects of anthropogenic noise on their acoustic communication be gauged. Further research is thus suggested in the following areas.

6.3.1 Fish Vocalisations from Different Coastal Habitat

Knowledge on fish vocalisations especially from biologically rich marine habitats is important to better understand the characteristics of their contribution to ambient noise. The current study showed there were at least eight different types of fish vocalisations in New Zealand coastal waters. The majority of vocalisation types described here were recorded from a temperate reef habitat, except for the vocalisations of the gurnards (open sandy bottom). It has been reported for coral reefs that ambient noise relates with the habitats and communities of marine organisms that the reef supports (Kennedy et al. 2010). The same study showed that the acoustic profile of different Panamian coral reefs and the surrounding waters were associated with fish density, biomass and diversity. This indicates the strong relationship that fish vocalisation types have on the acoustic character of its habitat.

For the ambient noise of New Zealand coastal waters, Radford et al. (2010) have reported that coasts with different marine habitats have distinctive underwater noise characteristics. Habitats that are dominated by urchins and snapping shrimps have noise where the biggest proportion of sound energy is in the frequency band of their sound (801-2500 Hz and 2501-20000 Hz, respectively). The study also showed that for other habitats (i.e., macroalgal dominated and open sandy beach) the highest proportion of sound energy was in the frequency band 100-800 Hz. From the current study, it has been shown that this band encompassed the frequency range of fish vocalisations. Therefore, it is important to determine the individual vocalisations and identity of soniferous fish that contribute to these peak sound energies at these habitats.

With the latest advances of digital recording and data storage technology, a comprehensive sound recording approach can be conducted across a range of marine habitats.

- Simultaneous multi-channel sound recording from an array of hydrophones (Chapter 3, (Cato 1998, Parsons et al. 2009)).
Continuous audio and video recording with or without auto detection function to detect fish vocalisations (Chapter 3&4, (Mooney et al. 2005, Lammers et al. 2008)).

Data obtained from the above method could be used to: one, calculate source level of the fish vocalisations; two, localise relative position of vocalising fish if three or more hydrophones are used; three, describe temporal pattern of vocalisations more accurately; and four identify the vocalising fish.

6.3.2 Contact Calling in the Bigeye

The current study reported the vocalisations of the bigeye for the first time, and showed that the time of peak vocalising activity correlates with their nocturnal foraging activity in nature. The active space of vocalisations was also estimated to indicate a hypothetical scenario where individuals in a school may extend their inter-individual spacing by listening to each others call. This scenario was based on the general description of the nocturnal behaviour in the field by bigeyes and closely related species (Gladfelter 1979, MacDiarmid 1981, Golani & Diamant 1991) and loose schooling structure reported for other planktovires (Helfman 1986, McCauley & Cato 2000). However, the actual inter-individual spacing during their nocturnal foray has never been measured. To test if the contact call hypothesis and the contact call function several key pieces of information are needed.

1) Inter-individual spacing of bigeyes in a foraging school.
2) Schooling structure/organisation during different seasons and moon phases.
3) In-situ vocalisations during foraging
4) Behavioural response of a group or individual fish to conspecific vocalisations

Data for 1, 2 and 3 can be obtained from in-situ observations or audio-video records of the nocturnal schooling behaviour. The best way to record them is by divers using closed circuit re-breathers so that the foraging school can be approached and observed silently. To obtain data for 4 requires a playback experiment conducted in the field or in a large (ideally anechoic) tank. Prior to the experiment, the acoustical properties of the tank (e.g., wall resonance, standing wave) must be taken into account so that some knowledge of the sound field can be established.
During playbacks of various sounds including conspecific vocalisations, changes in the overall inter-individual spacing and group density is monitored and quantified.

6.3.3 Determining the Acoustic Behaviour during Spawning in the Bluefin Gurnards

Attempts were made during the current study to measure the source level of the bluefin gurnard vocalisations in the wild. Even though the instrumental setup and design was adequate (i.e., using a hydrophone array), vocalisations in nature could not be recorded from wild population nor could they be elicited from caged individuals. It may well be the case for the former that the wild gurnard population at the study site (i.e., Omaha Bay) is too small hence the probability of obtaining random recording is very low. As for the latter caged individuals simply did not vocalise even though they were left for 24 h. Thus there is need for further research on the source levels and behavioural context of bluefin gurnard vocalisations.

It is usually in the interest of passive acoustics to target sounds of spawning fishes to identify their spawning grounds. Promising results have been reported in delimiting spawning grounds of several sciaenid species (Saucier & Baltz 1993, Luczkovich et al. 1999, Luczkovich et al. 2008b). It has been suggested in several gurnard species that vocal activity was maximum during its spawning season (Moulton 1956, Amorim 2006), although this has never been experimentally observed. For efficient passive acoustic monitoring of wild bluefin gurnard, the behavioural context of its large vocal repertoire needs to be thoroughly described, particularly those associated with spawning. The current study indicates that the vocal repertoire of the bluefin gurnard is extensive with high vocalisation activity during the reported spawning season in this region (Chapter 4). Spawning of the bluefin gurnard is reported to occur in deeper waters (>70m) year-round but peaks in late spring and early summer (Clearwater & Pankhurst 1994, Kendrick & Walker 2004) but is largely poorly understood. Systematic observation of the gurnard spawning behaviour could be conducted in captivity where vocalisations of both male and female associated with every step of the behaviour must be identified and described. Similar work has been done for other species, such as haddock (Hawkins & Amorim 2000) and cod (Finstad & Nordeide 2004).
6.3.4 Fish Aggregation Device Acoustics

The unjam generated substantial sound power in band 3 which was attributed to fish vocalisations. Therefore, characterizing the vocalisation of individual fish species inhabiting the unjam is needed to corroborate the source of these sounds. This would involve conducting systematic sound-truthing study on all of the estimated 58 fish species in captivity using similar methods as in Chapter 3 and 4. In addition to spectral characteristics, information on the diel pattern of sound production for each species can also be compared to the diel pattern of the unjam.

Current knowledge on the propagation properties of FAD and reef noise is scarce. It is now known that FADs (Chapter 5) and reefs (Radford et al. 2011b) are planar type sound source rather than a point source. In general, they are more ‘powerful’ sound broadcasters than a point source with similar source level. There are various types and designs of FADs worldwide (Friedlander et al. 1994, Higashi 1994, Dempster & Taquet 2004) yet their bioacoustic environment is poorly understood. Since the sound characteristics of marine habitats depend on the assemblage of their respective biological communities, it may be the case that different FADs will have different sound characteristics. This is evident in natural habitats where variations in the ambient noise of different coastal habitats (Radford et al. 2010) and coral reefs has been reported to occur over relatively small spatial scales (Kennedy et al. 2010). It is thus suggested that further investigation on the sound characteristics of various FAD designs is undertaken using similar approaches as outlined in chapter 5 of the current study. Improvisation can be made by using a directional hydrophone or a hydrophone array with a known directional sensitivity. This would be useful when recording sounds in an area where multiple FADs are present as is usually the case for most coastal water FADs in some countries (e.g., Malaysia).

6.4 CONCLUSION

Overall the current study has described the characters of some fish vocalisations in the coastal waters of New Zealand and explored its significance from a non-communicative perspective. It has been shown that fish vocalisations here could be described by various aural descriptions that are already widely used for fish vocalisations elsewhere. However, their acoustic structures were different and therefore, were most likely to be new vocalisations reported for the first time in some local fish species. At a temperate reef, fish vocalisations were
the major contributor to the sound energy below 500 Hz and formed choruses in the respective range of their dominant frequencies during the new moon. Fish choruses at a New Zealand temperate reef were modest in magnitude compared to those observed for urchins and snapping shrimps, hence are not as a distinctive feature of the reef soundscape. Nonetheless, fish vocalisations are minimally masked by the invertebrate sound, therefore have a sizeable active space. Within the limits of the active space, vocalisations can serve a cue for spatial orientation to other listening fish. Individual vocalisation active space of the bigeye indicates that it could be potentially utilised as a schooling cohesion cue for conspecifics during nocturnal foraging. It was shown for the first time here that fish choruses from a FAD could emanate long distances and could provide a cue that allows fish to perform long range orientation to FADs. The FAD results may shed some light on the acoustic function of a natural reef. In conclusion, the results of the current study have greatly enhanced our understanding of fish vocalisations and its significance in the underwater soundscape of New Zealand coastal waters. In addition, it has contributed to our general understanding of the contribution of the underwater soundscape to fish orientation and behaviour.
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