THE EFFECTS OF PHYSICAL, BIOLOGICAL AND ANTHROPOGENIC NOISE ON THE OCCURRENCE OF DOLPHINS IN THE PACIFIC REGION OF THE PANAMA CANAL

Inez Campbell C.

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews

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The effects of physical, biological and anthropogenic noise on the occurrence of dolphins in the Pacific region of the Panama Canal

Inez Campbell C.

A thesis submitted to the University of St. Andrews
for the degree of Doctor of Philosophy

Scottish Oceans Institute
Sea Mammal Research Unit
School of Biology

University of
St Andrews

600
YEARS

Submitted:
January 2014

A dolphin surfaces in the region of the Panama Canal,

Pacific of Panama.

I, Inez Campbell, hereby certify that this thesis, which is approximately 45,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in January 2009 and as a candidate for the degree of Doctor of Philosophy in the School of Biology in January 2010; the higher study for which this is a record was carried out in the University of St Andrews between 2009 and 2013.

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ABSTRACT

The main aim of this thesis was to investigate the occurrence of dolphins in Pacific waters adjacent to the Panama Canal in the context of biological, temporal and spatial factors. Acoustic data were collected at 101 sites at a range of distances and depths from the shipping region. Data were collected between March 2010 and April 2011 in a diurnal cycle over a total of 114 recording days. Received sound levels were split into 1/3 Octave bandwidths to study variation in sound pressure levels and then converted to spectrum density levels to show the sound components of the background noise in this region. Generalised Linear Models were used to relate dolphin whistle detections to temporal, spatial, environmental and acoustic variables.

The major sources of background noise were biological noise from soniferous fish and snapping shrimp and anthropogenic noise from vessels characterised by mid to high frequencies produced by artisanal fishing boats. There was monthly and diurnal variation with some locations characterised by loud sounds in the mid to high frequencies at night.

Whistle characteristics analysis revealed that the frequencies and range of the whistles were different to those previously reported under similar conditions. Whistles varied diurnally and in the presence of fish chorus and fishing boats. The study highlights a strong correlation between fish choruses and whistle detection.

Temporal and spatial models showed that whistle detections varied monthly and in relation to fish noise and small vessel engine noise. Dolphins were distributed throughout most of the study area; however, whistle detections varied with distance from the coast.

The results provide new knowledge about background noise composition in this region and provide the first information on the ecology of dolphin whistles in relation to this background noise, especially to fish chorus.

ACKNOWLEDGEMENTS

These four years of PhD experience have been a roller coaster of ups and downs, of laughter and tears, and of triumph and anxiety. The challenges have been priceless and unforgettable; but moments like the first time I heard a whistle being recorded in my own dataset made it all worthwhile. This has also been a journey of self-discovery through which I learned I could go bit farther than I thought I could, and be quite stronger than I thought I was. I persevered in achieving this goal mainly for my love of dolphin and whales and I truly hope this work contributes in the making of a better world for their existence.

I now thank all those who have given me their support and without whom this PhD could have been fulfilled. I thank my funders: SENACYT-IFARHU for granting me this scholarship, The Rufford Small Grants Foundation for their support to acquire acoustic and other sensitive equipment for my fieldwork period; and to the Scottish Oceans Institute for helping me acquire essential sensitive acoustic equipment. Thank you to the Panama Canal Authority for granting permission to deploy hydrophones in the authorized areas.

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This work is dedicated to the loving memory of my Mother. To you Mom, because you always believed in me; I embraced this quest because you once told me I could be like the Phoenix Eagle and that I could spread my wings wide and start from scratch in search of my dream. I know that you have been with me and guiding me from heaven on every step of this journey. Thank you!

CHAPTER 1

GENERAL INTRODUCTION

Many species of marine mammals are at risk of being affected by human activities. These impacts range from alteration and exploitation of their habitats, to depletion of their selected prey, direct removals through bycatch and hunting, to contamination of coastal waters, ship strikes and noise produced by different sources of sound. These potential threats can often be made worse by synergistic effects.

1.1 THREATS TO CETACEANS

1.1.1. Habitat degradation

With the increase of large development projects in coastal areas of the world, whether it is to accommodate the growing population, commercialization or to increase tourism income, the consequence is degradation of the habitat that species depend on for shelter and food. In many tropical coastal areas, particularly in the developing world, population growth and therefore pressure on the environment is an important problem because of an increase in inhabitants moving to live closer to their source of food: fish (Lundin and Linden, 1993; Lotze *et al.*, 2006). As a consequence, mangroves are destroyed to build homes, seagrass and reefs are wiped due to artisanal fishing practices (by walking over reefs and intertidal zones) and therefore the chain “nursery-fish-predator” is broken. Elsewhere in the world, other coastal areas are exploited for marine aquaculture and fish farming (Reeves and Reijnders, 2002; Read and Fernandes, 2003). The consequences of these activities include net installations that take up coastal space, (which can add another problem if nets break loose and drift in the water column); waste products of fish and fish food, and therefore, chemical contamination.

Tropical coastal areas are attracting an increasing amount of tourism and this demand has increased the development of large projects to build marinas and beach resorts, and for snorkeling and diving (Davenport and Davenport, 2006). At a small scale, the effect of tourism on coastal environments is detrimental when tourists walk over rocky intertidal zones, stand on reefs when snorkeling, play with animals in the rocky pools, or collect specimens. Marina constructions bring vessel noise and engine contamination into coastal waters (Diez *et al.*, 2002; Schiff *et al.*, 2007) and beach resorts and hotels release waste close to the shore (Kocasoy, 1989; Baldwin, 2000). Together, these effects may threaten or destroy habitat for coastal cetaceans, including damaging or destroying prey resources.

1.1.2. Chemical pollution

Additional to the above mentioned chemical threat in coastal waters caused by vessel discharge and coastal development flow, is the potentially devastating effect of oil spills. Immediate impacts are typically most noticeable in direct effects on marine mammals, birds and fish, but the most important impacts of an oil spill are the delayed and long term indirect effects (Peterson, 2001; Williams *et al.*, 2011).

1.1.3. Hunting and other deliberate removals

Whaling activities date back to many years ago and have had a major impact on most species of large whales, however after protection measures were established several populations are recovering. Whaling takes place as aboriginal subsistence whaling, whaling under special permit or commercial whaling under objection of the moratorium. Commercial whaling today is mostly limited to a few hundreds of minke whales (<600) taken annually in the Southern Ocean, the North Atlantic and the Northwest Pacific (www.iwc.int/home).

Small cetacean hunting takes place in a number of countries; pilot whales are killed annually in the Faroe Islands (Denmark) as part of their traditional drive fishery (Ottensmeyer and Whitehead, 2003); in Taiji, (Japan) whaling is mainly focused on the killings of pilot whales and many species of dolphins (Butterworth *et al.*, 2013), in the Solomon Islands mainly bottlenose dolphins, spotted and spinner dolphins hunted by local villagers (Brownell *et al.*, 2008). Drive hunting consists of many boats herding animals into a bay or a beach using engine noise and sometimes surrounding them with large nets, with the purpose of killing them for their meat or taking them for dolphinariums around the world. It is estimated that up to 20,000 small cetaceans are caught each year using these methods (Brownell *et al.*, 2008; Butterworth *et al.*, 2013). Some species are also hunted by harpoon.

1.1.4. Bycatch

One of the top pressures on cetacean populations is bycatch in fisheries (Reeves and Reijnders, 2002; Read, 2008). Approximately 300,000 cetaceans die from bycatch each year (Read *et al.*, 2006). One of the most recognized bycatch problems was that of dolphins in the tuna purse seine fishery in the eastern tropical Pacific Ocean (Gerrodette and Forcada, 2005). Annual mortalities seem to have ranged between 200,000 and 500,000 during the years 1960-1972 before new netting techniques were implemented (Northridge, 2009). However, the present concern involves direct interaction between small cetaceans and fishing gear, where dolphins actually follow, seek and/or come into contact with set nets, drift nets or long lines with the end result of becoming entangled or entrapped (Read *et al.*, 2006; Read, 2008). Bycatch threats are particularly serious when an endemic species such as the Franciscana dolphin which is caught in coastal fisheries off Uruguay, Argentina and Brazil (Secchi *et al.*, 2004); as well as the Vaquita, endemic to the Gulf of California and almost being driven to extinction with a population of less than 500 (D'Agrosa *et al.*, 2000; Rojas-Bracho *et al.*, 2006) and given the status of critically endangered by the red list of the IUCN (www.iucnredlist.org).

1.1.5. Noise pollution

Noise pollution in the ocean from human related activities can be generated by: sonars (Barlow and Gisiner, 2006), the use of marine explosives (Ketten, 1995), geophysical surveys (Gordon *et al.*, 2003), oil and gas drilling (Myrberg, 1990), marine dredging (Richardson *et al.*, 1995a), pile-driving (Bailey *et al.*, 2010; Thompson *et al.*, 2010), and shipping noise (Richardson *et al.*, 1995a; Southall *et al.*, 2007; Jensen *et al.*, 2009; Simard *et al.*, 2010). Shipping noise is a major topic of this study and is fully discussed below.

As mentioned above, many of these threats are interconnected. Major coastal developments such as marinas and resorts damage cetacean habitat and generate chemical contamination through growing tourism, which may contribute to local prey depletion. Prey depletion occurs more generally because of over-fishing and overfishing may lead to increased bycatch of small cetaceans. Excessive vessel traffic caused by tourism and fisheries increases the risk of collisions and noise pollution.

1.2 SOUNDS IN THE UNDERWATER ENVIRONMENT

1.2.1 Basic terminology

Sound is a mechanical wave motion characterized by the periodic compression and expansion which is permitted by the elasticity of the medium in which it travels (e.g. gas or liquid). Sound cannot be measured directly as pressure. In modern acoustics this is achieved taking advantage of the phenomenon known as transduction, the conversion of electricity into sound and vice versa (Hunt and Balckstock, 1982). The basic properties of sound waves, considering the simplest example of a sinusoidal oscillation, can be resumed by the relation:

$c=f*\lambda$

Where c is the sound speed (m/s), f is the frequency (number of cycles per second or Hertz) and λ is the wavelength (distance between successive wave forms) (Fig. 1.1).

The period (T) of a tonal sound is defined as the time between two maximum peaks in the wave. Since f is the number of cycles passing in one second, we have:

$T= 1/f$

Figure 1.1, shows an example of a period of 1/3 for a 3 Hz Frequency.

Another important component of sound is Amplitude. The peak-to-peak amplitude reflects the change in pressure from the positive peak of the waveform to the negative peak, and in this way the cycle reflects pressure changes from high pressure to low pressure.

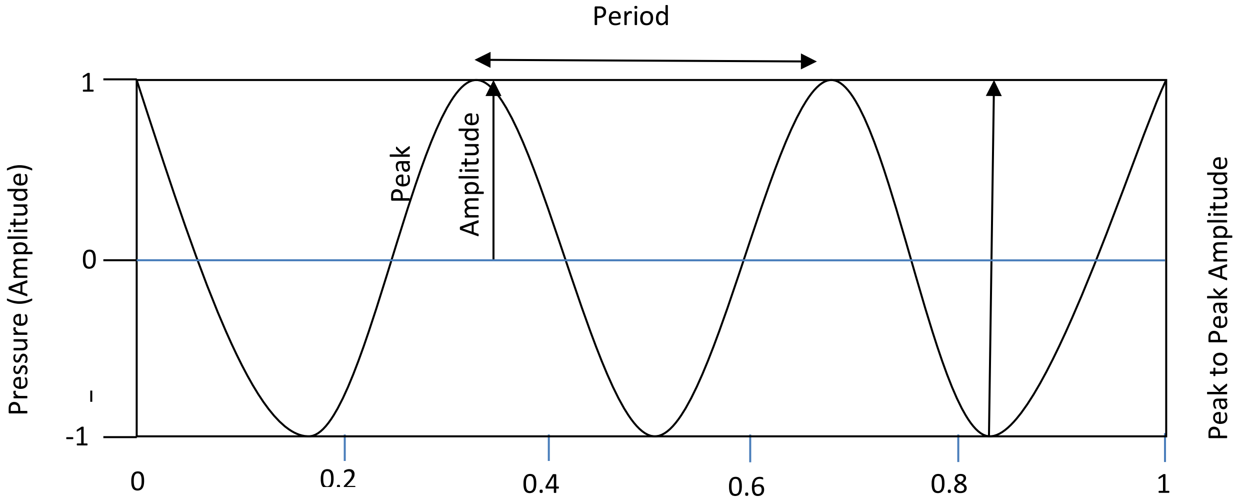

Fig. 1.1 A sound wave represented as a cosine waveform showing its basic properties: period, frequency, amplitude (Erbe, 2010).

1.2.1.1 Sound pressure and intensity

A travelling sound pressure wave has the property of carrying energy in its propagation direction with intensity *I*. *Sound pressure* is the sound force per unit area, measured in Pascals (Pa). In the International System of Units (SI) pressure is expressed in

1 Pascal (Pa) = 1 Newton/m^2

and it is therefore convenient to use the Pascal unit in mathematical calculations. However, for convenience, measurements of sound pressure levels in the sea are expressed in decibels (dB) relative to 1 micro Pascal (dB//µPa). The use of the dB unit in acoustics is convenient because of the need to work with a very broad range of energy.

The sound intensity is defined as the energy passing through a unit area per second. For a continuous sound wave, intensity is related to pressure by:

$$I = \frac{p^2}{c\rho}$$

where I is the intensity (W/m^2), p is the pressure (Pa), ρ is the water density (kg/m^3) and c is the speed of sound (m/s).

Using the existent relation between pressure and intensity (Simmonds *et al.*, 2003; Bradley and Stern, 2008), sound pressure level is defined as:

SPL (dB) = 20 log $\left(\frac{P}{Pref}\right) dB\ re\ 1\mu Pa$

where P is the measured pressure and P_{ref} is the reference value pressure (1µPa).

Then, sound intensity level is defined as:

SIL (dB) = 10 log $\left(\frac{I}{Iref}\right) dB\ re\ 1\mu Pa$

where I is the measured intensity and I_{ref} is the reference value intensity.

Because sound intensity is proportional to the square of sound pressure, Sound Pressure Level (SPL) and Sound Intensity Level (SIL) are equal when they are quoted in dB with the appropriate multiplier for the logarithmic scale and reference values (Richardson *et al.*, 1995b; Bradley and Stern, 2008):

SPL (dB) = 20 log $\left(\frac{P}{Pref}\right) dB\ re\ 1\mu Pa$ **= 10 log** $\left(\frac{I}{Iref}\right) dB\ re\ 1\mu Pa$ **= SIL (dB)**

1.2.1.2. Frequency

As described above, the waveform of a pure tone is sinusoidal and all its power is at a specific frequency. Most sounds have energy distributed over a range of frequencies, these are broadband sounds. To view how sound pressure is distributed through the different frequencies, a sound pressure density spectrum graph is plotted. The spectrum level is the sound intensity level within a 1 Hz frequency band. The plot of spectrum level shows the distribution of power per unit frequency in a signal versus a range of frequencies from a continuously distributed sound. The mean square pressure density spectrum is calculated by dividing the mean square pressure for each band by the frequency width, measured in µPa^2/Hz (Richardson *et al.*, 1995b; Bradley and Stern, 2008).

To illustrate better each frequency band of a sound, a proportional bandwidth filter is applied so that the sound is broken into narrower ranges of frequencies with lower and upper frequency limits. Scales of octave and one-third octave bands have been adopted (Fig 1.2). An octave band has an upper frequency twice the value of its lower limit. A one-third octave band is 1/3 of an octave wide, meaning its upper frequency limit is 2 $^{1/3}$ Hz times the lower limit. One third octave band analysis allows for a better description of the frequency content of sound sources than its overall level (Gelfand, 2009).

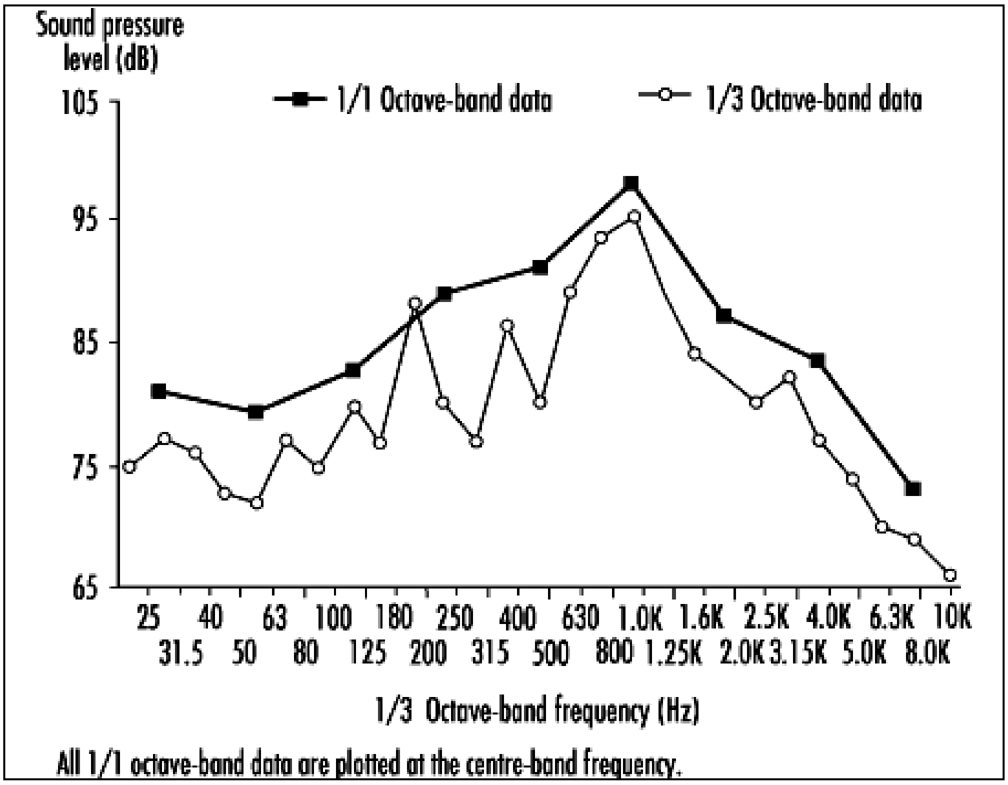

Figure 1.2. SPL measurements taken near a piston pump, used here to illustrate how the 1/3 octave band data provide more information than the octave band data. The octave band shows a total of nine data points compared to 27 data points when using 1/3 octave band measurements. (Taken from "Engineering Noise Control" in Encyclopedia of Occupational Health and Safety, Author: Driscoll, Dennis P. Accessed online at: http://www.ilo.org/oshenc/part-vi/noise/item/753-engineering-noise-control?tmpl=component&print=1)

The bandwidth of a 1/3 octave band is 23% of its center frequency and this is shown in Table 1.1 for the adopted standard center frequencies for 1/3 octave bands (Au and Hastings, 2008). The lower and upper limits are calculated by multiplying the centre frequency by 0.891 and 1.122, respectively.

Octave bands			**1/3 Octave bands**		
Lower limit (Hz)	**Center frequency (Hz)**	**Upper Limit (Hz)**	**Lower limit (Hz)**	**Center frequency (Hz)**	**Upper Limit (Hz)**
11.0	**16**	22.0	14.3	**16**	18.0
			17.8	**20**	22.4
			22.3	**25**	28.1
22.0	**31.5**	44.0	28.1	**31.5**	35.3
			35.6	**40**	44.9
			44.6	**50**	56.1
44.5	**63**	89.1	56.1	**63**	70.7
			71.3	**80**	89.8
			89.1	**100**	112.2
88.4	**125**	176.8	111.4	**125**	140.3
			142.6	**160**	179.5
			178.2	**200**	224.4
176.8	**250**	353.5	222.8	**250**	280.5
			280.7	**315**	353.4
			356.4	**400**	448.8
353.5	**500**	707	445.5	**500**	561.0
			561.3	**630**	706.9
			712.8	**800**	897.6
707	**1000**	1414	891.0	**1000**	1,122.0
			1113.75	**1250.00**	1402.50
			1425.60	**1600.00**	1795.20
1414	**2000**	2828	1782.00	**2000.00**	2244.00
			2227.50	**2500.00**	2805.00
			2806.65	**3150.00**	3534.30
2828	**4000**	5656	3564.00	**4000.00**	4488.00
			4455.00	**5000.00**	5610.00
			5613.30	**6300.00**	7068.60
5656	**8000**	11312	7128.00	**8000.00**	8976.00
			8910.00	**10000.00**	11220.00
			10888.02	**12220.00**	13710.84
11312	**16000**	22624	14256.00	**16000.00**	17952.00
			17820.00	**20000.00**	22440.00

Table 1.1. Standard levels of octave and one-third octave band center frequencies. Lower and upper limits were calculated using the equation from Richardson *et al.*, 1995.

Prior to describing sources of sound, a clarification must be made regarding Source Levels (SL) and Received Levels (RL). Source level (SL) refers to sound measured at a specific distance from the source, which is usually 1 metre and referenced to 1µPa (e.g. 60 dB re 1µPa @ 1m). Received level (RL) is the sound measured at the receiver's current position. When SL is known, it can allow Transmission Loss (TL) to be calculated from RL with the simple formula: TL= SL-RL. Transmission loss is the loss of intensity of a sound as it travels through a medium, which under specific conditions can occur as spherical spreading or cylindrical spreading.

Different sources of sound intensity are received in different frequency bands and for a more detailed analysis of the frequency distribution of sound (power) the RL measurements in 1/3 octave bands are converted into spectral density levels. Spectrum levels will show to be lower in value than 1/3 octave levels for all frequencies within that 1/3 octave, which represent sound power in bands whose widths are 23% of the center frequency (Fig. 1.3) (Richardson *et al.*, 1995b; MacGillivray *et al.*, 2011). The bandwidth conversion from the received levels is calculated by the following equation:

Spectrum Density Level = $\boldsymbol{N - 10\, log\, \Delta\ f\,;}$

Where **N** is sound intensity in dB at a particular centre frequency and Δ f is the difference between the lower and upper frequency limits. The units are dB re 1µPa^2/Hz (Au and Hastings, 2008a).

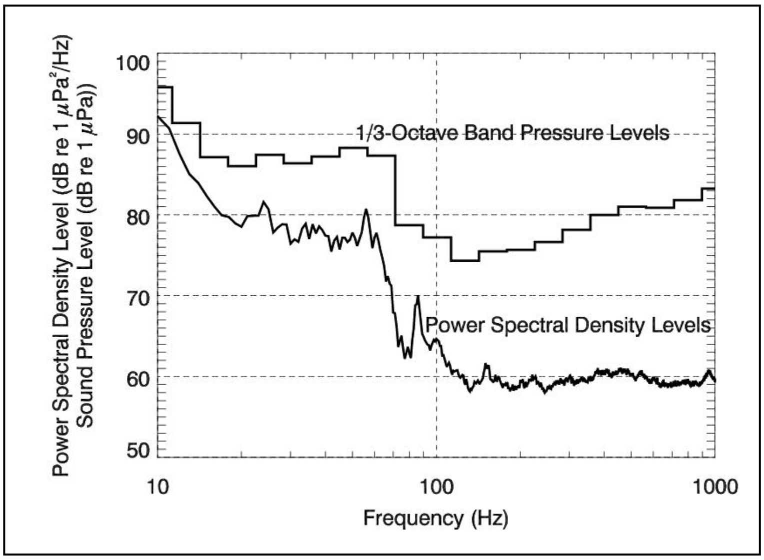

Figure 1.3. Example of an ambient noise power spectral density plot and corresponding 1/3 octave band levels (MacGillivray *et al.*, 2011).

1.2.2. Sources of sound in the ocean

Sound in the ocean is characterized by three major categories: water motion, marine life, and ship and man-made noises (Knudsen *et al*. 1948). Water motion includes surf and waves, rain, tides and wind speed with the latter identified as the major contributor to ocean background noises. In nature, sound sources are complex with energy peaks spread over a range of frequencies in time (i.e., transient or continuous sounds). Ambient (or background) noise is normally defined in the underwater environment as sounds where individual sources are generally difficult to categorize and are mostly identified as water motion, biological sound sources and ship traffic noises (Knudsen *et al.*, 1948; Hildebrand, 2009).

The work of Knudsen *et al*. (1948) was updated later by Wenz (1962) with new data and compared differences in sound source contributions at different depths; most importantly he introduced the concept of conversion of pressure levels to different bandwidths producing the well-known “Wenz curves” (Figure 1.4), which plot generalized ambient noise spectra attributable to various sources (mainly shipping traffic and sea conditions) and allow prediction of ambient noise levels for a given condition and frequency band.

Further, Urick (1984) compiled a report which summarises the knowledge on the topic. In his work he included a description of shallow water noise levels, noise under the ice cover and other generalized deep-water noise spectra. The most relevant contribution brought by this report is the description of sources as a function of frequency band, from infrasonic bands of 1 Hertz up to ultrasonic bands above 50 kHz (Urick, 1984). This latter detail along with details of variability of noise in shallow water for the different sources, will be most useful in this thesis since a wide range of frequencies have been considered to analyze the background noise of this shallow region. The relevant sources of sound will be discussed in detail in Chapter 3. Sources of sound in the ocean can be divided into three main categories: environmental, biological and anthropogenic. Some of these sounds occur continuously, others are intermittent (Bradley and Stern, 2008).

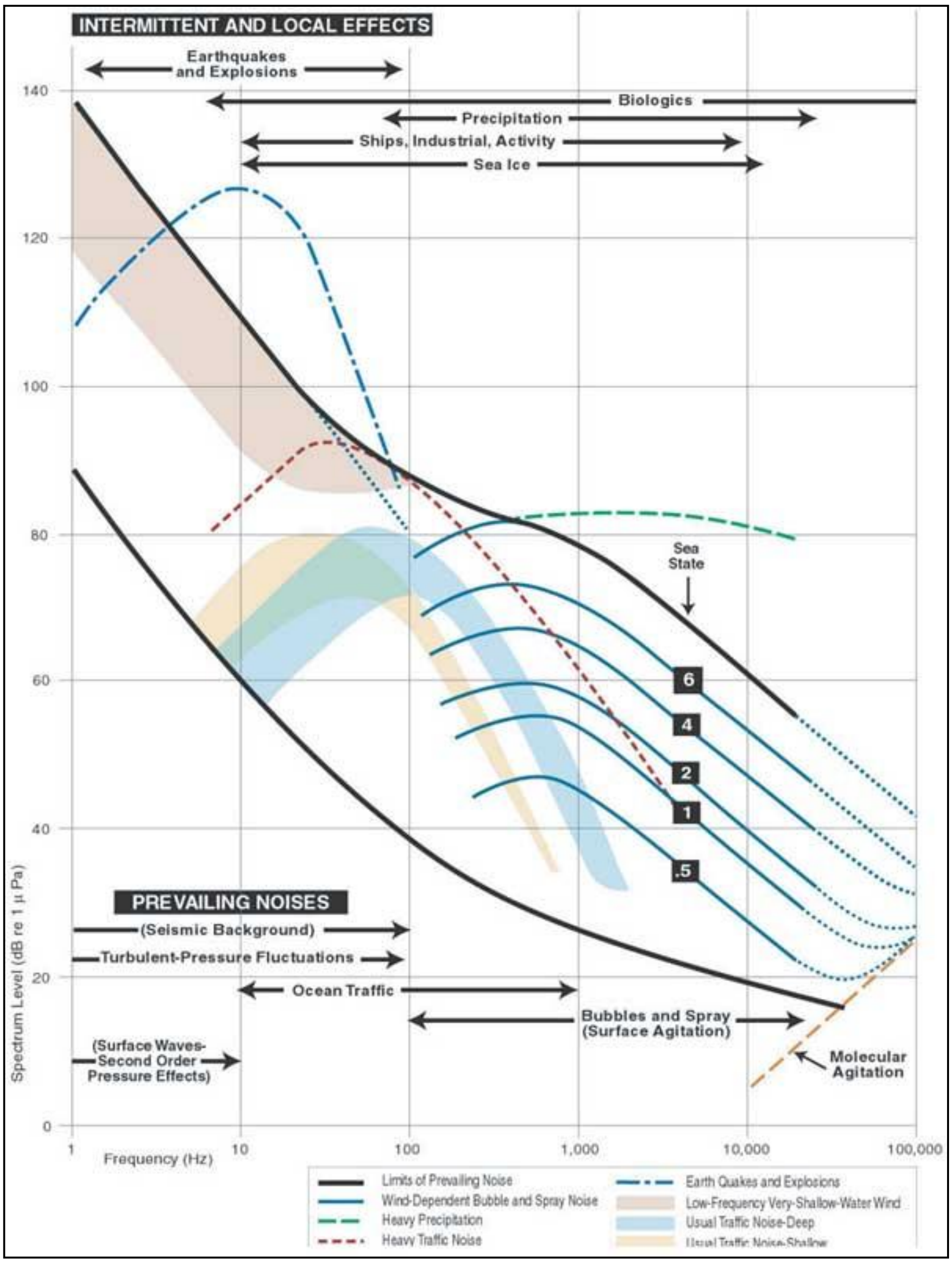

Figure 1.4 Wenz curves . Spectrum levels of the most common sound sources in the ocean, converted to current standard units (dB re 1µPa). (Reprinted with permission from National Research Council. 2003. Ocean Noise and Marine Mammals. National Academy Press, Washington, D.C. – as adapted from Wenz, 1962). [Online: www.dosits.org, 9-11-11]

1.2.2.1 Environmental sound

Sound in the ocean is mainly attributed to wind noise caused primarily by wave action. Wenz (1962) established that wind is the major contributor to noise between 100 Hz and 30 kHz, and for different conditions he established these empirical “rule of fives” which apply to measurements up to 20 kHz (Richardson *et al.*, 1995c):

a) Between 500Hz and 5 kHz there is a 5dB decrease in spectrum levels per octave with increasing frequency;
b) Between 5 and 75 km/h there is a 5dB increase in spectrum levels with each doubling of wind speed;
c) In deep water, the spectrum level at 1 kHz is 51 dB re 1µPa^2/Hz when the wind speed is 9km/h;
d) In shallow water, the spectrum level at 1 kHz is 56 dB re 1µPa^2/Hz when the wind speed is 9km/h.

Noises due to precipitation are also an important environmental sound source in the ocean at frequencies above 500 Hz. Fortunately such background disturbances are easy to distinguish taking advantages of their unique spectral characteristics (Nystuen, 1986; Nystuen *et al.*, 2010). Indeed size and speed of the rain droplets are the main factors affecting rain noise (Urick, 1984; Au and Hastings, 2008). For example, when heavy rainfall is present (30mm/h), these drops will generate sound at frequencies below 1 kHz and above 40 kHz and wind has no effect (Ma *et al.*, 2005). However, when rain and wind occur at the same time they are difficult to differentiate in a spectrogram.

Surf action is another source of noise present in coastal areas. Wilson *et al.* (1985) found that the breaking of waves in shallow water at 8.5 km from the coast causes sound levels to increase 5dB above the Knudsen curves (Knudsen *et al*. 1948) in the frequency range 300-700 Hz (Wilson *et al.*, 1985).

Seismic sources, mainly from tectonic or volcanic action can contribute greatly to ambient noise in the low frequencies. The sound is the result of energy travelling as compressed waves as a result of ocean bottom drastic movements (Wenz, 1962).

1.2.2.2 Biological sound

Biological sounds, namely sounds produced by living organisms, are usually the main interest in most of the studies seeking to find relationships between normal conditions and the effect of threats to the environment. In this thesis three sources of biological sound are discussed in detail: snapping shrimp, fish chorus and dolphin vocalizations.

These sounds vary with frequency, diurnal cycle, season and location (Wenz, 1962; Urick, 1984).

Snapping shrimp (Family Alpheidae) is the most common source of continuous biological noise in tropical shallow waters and is the least desirable source recorded when studies of ambient noise are being conducted because it interferes with clear signals of other sounds that match the same frequency (Au and Hastings, 2008). The sound level is reported to be higher at night than at daytime (Knudsen *et al.*, 1948; Urick, 1984). The typical snapping shrimp producing sound is of the family *Alpheidae* and it produces its sound by closing its claws and creating an extreme broadband signal with components of up to 200 kHz (Hildebrand, 2009).

Fish Noise (e.g. Family Sciaenidae): is one of the most complex sounds to differentiate because of the large number of species of fish. Different fish species produce sound in different ways and therefore in different frequency ranges, and this makes fish sound one of the main sources of biological sound (Mann, 2012). The most common types of fish sound are produced via the swim bladder and specialized muscles:

a) Contraction of the sonic muscles that run along the swim bladder;
b) Stridulation of bones;
c) Clapping jaws using a specialized sonic ligament;
d) Stroking tendons in the fourth and fifth pectoral fins;
e) Articulation of dorsal and ventral teeth in the pharynx.

When fish produce sound in any of these forms the acoustic characteristics will follow from the mechanism of sound production (Mann, 2012). For example, a croaker that contracts drumming muscles attached to the swim bladder generates sound that resembles the knocking of a woodpecker (Knudsen *et al.*, 1948).

Dolphin sounds (Family Delphinidae): dolphins produce echolocation clicks, whistles and burst pulses. Dolphin sounds are carefully discussed in the next section 1.3.

1.2.2.3. Anthropogenic noise

Since anthropogenic noise is one of the main subjects of this thesis, this is defined in section 1.1.5., while shipping noise is described in section 1.3.2 and in Chapter 3.

1.3 EFFECTS OF NOISE ON DOLPHINS

1.3.1 Cetacean vocalizations

The features of cetacean hearing can be characterized as: absolute threshold (level of sound alone); individual variation (individual auditory sensitivity); motivation (behaviour related); masking (in the presence of background noise); localization (direction of the sound); and frequency and intensity discrimination (the ability to tell apart sounds of different frequencies and levels) (Au *et al.*, 2000).

Cetaceans make sounds to communicate, providing information about position, prey, status, reproductive behaviour, territory, danger, among other things (Richardson *et al.*, 1995d). Odontocetes use echolocation to detect and localise objects such as prey, other animals and obstacles.

Types and frequencies of vocalizations vary among different groups of cetacean species, among species within each group, and from individual to individual due to changes in tone, duration, combination of sounds, and frequencies (Tyack, 1986; Richardson *et al.*, 1995d; Wang *et al.*, 1995; Janik and Slater, 1998; Janik, 2000c). In general, baleen whales produce low-frequency sounds (lower than 1 kHz) but they can reach as high as 25 kHz. The variety of sounds produced by odontocetes was first described in 1948 (McBride and Hebb, 1948) and they are still classified mainly as continuous tonal whistles, broadband clicks of short duration for echolocation, and pulsed sounds such as cries, groans and barks (Au and Hastings, 2008; Janik, 2009).

Dolphin whistles are narrow-band frequency modulated sounds of long duration and have been defined as social sounds (Au *et al.*, 2000; Sayigh *et al.*, 2007; Au and Hastings, 2008; Janik, 2009; Jensen *et al.*, 2012). The frequency can range from 1 kHz to 20 kHz and the pattern can be unmodulated, trilled, ascending, descending, ascending-descending, descending-ascending, or slowly wavering (Richardson *et al.*, 1995d; Buck, 2000; Bazua-Duran and Au, 2002; Bazua-Duran, 2004). They may be emitted once or repeated, or a series of sounds of several types, broken into segments or one whistle. Dolphins may also use higher frequency sounds for echolocation (between 20 kHz and 150 kHz) (Richardson *et al.*, 1995d; Herzing, 1996; Lammers *et al.*, 2003; Southall *et al.*, 2007; Au and Hastings, 2008; Janik, 2009). They are most sensitive to sound at frequencies above 10 kHz (Dotinga and Oude, 2007).

It is generally understood that whistles are social group calls and clicks are used for echolocation, while burst pulse signals can be for both social interactions and echolocation tasks (Au *et al.*, 2000; Sayigh *et al.*, 2007; Oswald *et al.*, 2008; Janik, 2009; Jensen *et al.*, 2012). *Tursiops truncatus* echolocation clicks and pulsed sounds are characterized by centroid frequencies from 33kHz to 109 kHz (Wahlberg et al. 2011), and peak to peak source levels of up to 220 dB re 1µPa at 1m (Au and Hastings, 2008), and depending on the activity, can be repeated at rates of 1-1000 clicks per second, generally occurring in trains that contain a few to hundreds of clicks (Herzing, 1996). Each pulse is mostly between 50-200 microseconds in duration (Richardson *et al.,* 1995, Au *et al.,* 2000). When dolphins encounter the need to overcome noises in order to use echolocation, they can emit higher frequency signals with intensities greater than 220dB re 1 µPa. Thus the sound frequency of clicks emitted by odontocetes can vary with the source level of the click (Richardson *et al.*, 1995d). For example, the false killer whale can make echolocation signals at different frequencies, with the center frequency of each click increasing as a function in increasing source level (Au *et al.*, 1995).

1.3.2. Shipping noise

As briefly mentioned above, noise pollution from shipping noise is one of the potential threats to cetaceans. The sound produced by vessels cannot be categorized into one particular frequency range because it is composed of a mixture of tonal sounds and broadband sounds with energy spread over a range of frequencies. The tonal components of the sound are related to propeller blade rate and the broadband components mainly to propeller cavitation. Thus, the frequency of the sound produced is mostly related to the size of a vessel (Table 1.2). Small vessels with smaller propellers produce cavitation noise at higher frequencies, whereas larger vessels (i.e., container ships and tankers) have slow-speed diesel engines and have more energy at lower frequencies. Richardson *et al.*, 1995a).

Type of Vessel	**Approximate Length**	**Approximate Frequency**	**Approximate source level**
Supertanker ship	340 meters	<10 Hz	187-232 dB re 1 µPa @ 1m
Container ship	270 meters	7- 8 Hz	181-198 dB re 1µPa @ 1m
Smaller tanker/freighter	135 meters	10-50 Hz	170 dB re 1 µPa @ 1m
Fishing trawler	30 meters	100- 250 Hz	158 dB re 1 µPa @ 1m
Small fishing boat	10 meters	300 - 7000 Hz	175 dB re 1µPa @ 1m

Table 1.2. Reported noise contributions generated by different types of vessels (Richardson *et al.*, 1995a; Hildebrand, 2004b).

Shipping noise produces bands of noise at low frequencies over long periods of time (Stafford *et al.*, 1999). Audiograms presented by Au *et al.* (2000) show that small cetaceans are not able to detect low frequency sounds as well as they do sounds above 1 kHz, and that hearing sensitivity gradually improves as frequency increases above 1 kHz. Most dolphins have their best hearing sensitivity between 20 and 90 kHz (Nachtigall *et al.*, 2000). Hearing sensitivity measurements vary both within and between species. Ships generally create noise by propeller action, propulsion machinery and hydraulic flow over the hull. Propeller cavitation sounds account for 80-85 percent of radiated noise (Arveson and Vendittis, 2000; Hildebrand, 2004a; Southall and Scholik-Schlomer, 2008). At low speed, the noise is almost completely generated by the engine's generator; at high speeds, the sources come from main engine, blade rate and propeller cavitation.

1.3.3 Shipping noise and dolphins

Alteration or disturbance of the acoustic environment could modify dolphin choice of habitat and alter dolphin vocal behaviour (Thomas, 2007). Shipping is the principal source of underwater noise at low frequencies (Dotinga and Oude, 2007); and commercial shipping is a major source of noise at frequencies of 5 to 500 Hz (Hildebrand, 2004a). The International Maritime Organisation (IMO) and many recent research studies have recognized that shipping noise is possibly one of the biggest threats to marine mammals (Au and Perryman, 1982; Croll *et al*., 2001; Erbe, 2002; Barlow and Gisiner, 2006; Southall and Scholik-Schlomer, 2008).

It has been difficult to document accurately the reaction of cetaceans to noise disturbance because there have not been controlled experiments in the wild. However, there are many studies on the effect of different vessel noise on the behaviour of cetaceans in general (Greene and Moore, 1995; Richardson *et al.*, 1995; Lesage and Barrette, 1999; Croll *et al.*, 2001; Erbe, 2002; Evans, 2003; Barlow and Gisiner, 2006; Bejder *et al.*, 2006; Taubitz, 2007; Weilgart, 2007; Holt *et al.*, 2009). Commonly, the reactions have been defined as cessation of feeding, resting, or social interaction, and onset of alertness or avoidance. It also depends on the activity at the time of disturbance. For example, for dolphins, when resting they tend to avoid boats, when foraging they tend to ignore boats and when socializing they may approach boats (Constantine *et al.*, 2004). Overall, noise from human activities, whether shipping noise or construction noise, may cause pronounced short-term behavioural reactions and temporary local displacement of certain species of cetaceans (Richardson *et al.,* 1995).

Vessel traffic is an activity that is known to cause changes in cetacean feeding behavior (Williams *et al.*, 2006) as well as dispersal of cetaceans, at least in the short term (Lusseau, 2005; Bejder *et al.*, 2006; Nowacek *et al.*, 2007). Habitat displacement may force animals in local populations to search out other areas for feeding and reproduction and may affect their survival rate (Evans, 2003). Dolphins have been observed avoiding noisy areas and boats (Harzen, 1998). However, cetaceans can develop tolerance, habituation and sensitization, which may allow certain animals to stay in “noisy” habitats (Richardson *et al.,* 1995, Evans, 2003), such as being close to fishing vessels (Leatherwood, 1975).

1.4. The Panama Canal

The Panama Canal is one of the most heavily transited shipping routes in the world (Panama Canal, 2009) and the traffic is due to increase further after 2014 on the completion of the construction of a third set of locks allowing a greater amount of ships to go through. However, there are no baseline data to characterize the background noise profile and establish if the noise has increased since the construction of the Panama Canal or if the noise contribution will increase once the expansion program begins.

The Environmental Impact Assessment for the expansion program (Panama Canal, 2012) stated that it did not address the effects that the expansion program would have on cetacean populations based on the fact that sightings in nearby waters to the entrance are temporary and incidental. In a personal email to the Panama Canal authority, a staff member stated there would be no threat to cetaceans because they considered the expansion would change the size of ships crossing but not the volume of transits.

In the light of this lack of knowledge regarding cetacean populations in this region, and lack of knowledge regarding how noise is characterized in the nearby region of the entrance to the canal, I sought to answer the question of how the noise caused by the shipping operations may be affecting cetaceans, in particular dolphins, in this area. The first challenge was to establish the noise profile at an appropriate temporal and spatial scale (See Chapter 3).

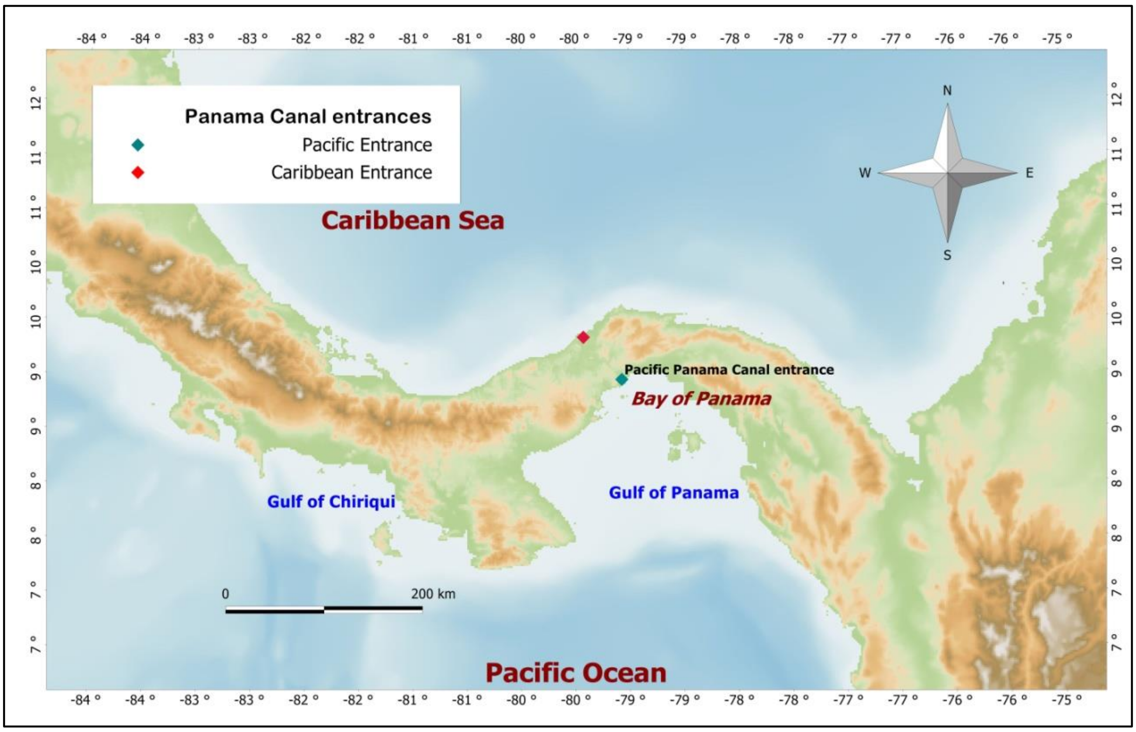

Figure 1.5. Map of Panama, Central America. Red diamond marks the North/Caribbean entrance, and the blue diamond marks the South/Pacific entrance.

The Panama Canal is one of the most heavily transited shipping routes in the world but there are no baseline data to characterize the background noise profile. It is approximately 80 km long joining the Atlantic (Caribbean) and the Pacific Oceans through the narrowest part of the Isthmus (Fig. 1.5). The ships are transported through a system of locks where they are elevated or lowered, using fresh water from the Gatun Lake. The Panama Canal operates 24 hrs a day, 365 days of the year (www.pancanal.com/eng/). The only aquatic mammal that lives in these waters is the West Indian Manatee (*Trichechus manatus*), introduced during the construction to control the algae growth in the lake (Muschett, 2008). The Canal receives vessels at the Miraflores Locks at the Pacific entrance and at the Gatun Locks at the Caribbean entrance. A breakwater protects the anchorage area on the Caribbean side. On the Pacific side, the Panama Canal Authority has designated special areas of anchorage for the different type of vessels. These areas are restricted but are close to the shore. Populations of dolphins have been sighted at both ends of the entrances to the Panama Canal.

Figure 1.6. The waiting area on the Pacific side for ships to go through the Panama Canal. In further chapters it will be referred to as the anchorage area. (Photo by Inez Campbell C.)

Heavy shipping traffic is present near both of the entrances of the Panama Canal (Fig. 1.6). The first ship went through the Panama Canal in 1914. Since then, more than a million ships have transited through the Canal (Panama Canal, 2009) an annual average of 14,600 transits. Nautical charts mark the routes that ships have to transit from the locks and after exiting the locks, but after they have left these shipping lanes there is no control over which way they go into the open ocean towards their destination. It was not until recently that the Panamanian Maritime Authority, in conjunction with the Smithsonian Tropical Research Institute, carried out a preliminary study to determine if there is conflict between the migratory routes of the humpback whales into this area and the vessels that approach this side of the Panama Canal (http://www.bbc.co.uk/news/science-environment-18720380). The canal lock operations are one of the best examples of industrial activities that contribute to underwater noise. Activities such as regular dredging produce noise in the frequency range from 50 to 500 Hz.

The usual types of vessels that go through the canal are: bulk carriers, vehicle carriers, container cargo ships, general cargo ships, passenger ships, refrigerated cargo ships, tank ships, and other types such as naval vessels, barges, dredges, tugs, and small vessels (Panama Canal, 2009). Sound level generally increases with ship size and speed (Evans, 2003) and propeller depth (Arveson and Vendittis, 2000). A brief description of the noise generated according to vessel size is given in Table 1.1.

The Panama Canal is undergoing the construction of a third set of locks, to allow bigger ships to go through the canal, and to allow for less waiting time for vessels. This construction generates high levels of noise in the underwater environment, because it includes explosions and dredging (Panama Canal, 2007). This, as well as increased shipping traffic, has the potential to disturb or exclude cetaceans from the area. The Environmental Impact Assessment carried out for this project highlights a lack of information; no study has been carried out regarding the impacts of noise on marine mammals in the region during the construction because there was no information about their presence and abundance in the area (Panama Canal, 2007). Unfortunately, there are no baseline data on cetacean populations since the Panama Canal construction took place from 1904 - 1914.

The types of sound that have been generated during this construction range from the sound emitted by dredging machinery to explosion sounds, and the effects will vary according to the different species of dolphins and whales present (Richardson *et al.,* 1995a). The immediate entrance area of the canal is supposedly far away from the migration routes of whales, but does include the foraging habitat of dolphins (Fishermen survey, personal observations, see Chapter 2). According to the construction plan, the Pacific side dredging will extend up to 13.3 km from the last lock into the sea and the marine dumping sites have been assigned to areas at the end of this distance near islands where dolphins have been sighted.

Regardless of whether vessel activity disperses or attracts cetaceans it may affect behaviour in other ways (Erbe, 2002; Lusseau and Bejder, 2007). The dolphins found in this study near the Pacific entrance of the Panama Canal may have habituated to the low frequency ship noise in the anchorage areas, but other forms of engine noise (small engine boats) could still pose a problem. A few studies have documented reactions to the vessel noise of small fishing boats. Janik (1996) and Bejder *et al.* (2006) studied behavioural reactions to boat approaches in similar scenarios to that of this study, and found differences in response depending on the vessel activity and number of encounters.

1.5. CETACEAN DISTRIBUTION AND MANAGEMENT

Knowledge of the status of cetacean populations and their patterns of distribution play a key role in implementing conservation plans in coastal areas (Thompson *et al.*, 2000; Reeves *et al.*, 2003; Simmonds *et al.*, 2003; Southall *et al.*, 2007). More specifically, the relationship between a species and its habitat is essential to understand critical areas for conservation and to help formulate effective measures to mitigate threats to populations. Short-term studies (e.g., a few months duration or coverage of seasons within a year or two) and long-term studies (e.g., covering longer periods of time, even decades) each have their benefits depending on the conservation interest of the research outcome to both the scientist and the stakeholder (Steklis and Steklis, 2009). Long-term studies designed to monitor trends may only have sufficient power to demonstrate significant declines when it is too late to implement effective mitigation measures (Taylor and Gerrodette, 1993). Nevertheless, long-term studies are typically needed after short-term conservation assessments to monitor a population's response to environmental variability and anthropogenic activities (Bowen *et al.*, 2010). One example of many is the long-term study of the bottlenose dolphin *Tursiops truncatus* population in Sarasota, Florida. The short-term study tested the use of tags to find out between 1970-1971 if the same dolphins in this area lived there year round ((Irvine and Wells, 1972; Irvine *et al.*, 1981). Since then, long-term research has developed around the objective of studying the dynamics, social structure, foraging behavior, habitat use, anthropogenic threats, acoustic research and testing field techniques, among others (Wells, 1991; Barros and Wells, 1998; Buckstaff, 2004; Sayigh *et al.*, 2007; Bowen *et al.*, 2010).

Anthropogenic sound has the potential to impact the relationship between cetaceans and their environment especially when it occupies the space they use to communicate with conspecifics (Richardson *et al.*, 1995a; Gannon *et al.*, 2005; Lusseau, 2005; Clark *et al.*, 2009). Areas where cetaceans overlap with high densities of ship traffic are potentially of great concern because this may interfere with their normal activities of reproduction and feeding (Ross, 2005; Hatch *et al.*, 2008). Responses to noise disturbance are varied and include changes in vocalization (Buckstaff, 2004; Weilgart, 2007), displacement (May-Collado *et al.*, 2007), avoidance (Lusseau, 2005), changes of breathing patterns (Hastie *et al.*, 2003), changes in foraging behavior (Williams *et al.*, 2006), and changes in distribution for short or long periods of time (Lusseau and Bejder, 2007).

1.5.1. Factors influencing cetacean distribution

There is a wide range of different factors that define the distribution and habitats of cetaceans in the different environments that they occupy (Shane *et al*., 1986).

Environmental factors. Cetacean distribution is influenced by many characteristics of the environment including water temperature, salinity, chlorophyll concentration, precipitation, wind speed, water productivity depth, bathymetry and distance to coastline (Gaskin, 1968; Selzer and Payne, 1988; Reilly, 1990; Jaquet and Whitehead, 1996; Gordon *et al.*, 1997; Hastie *et al.*, 2005; Kaschner *et al.*, 2006; Gomez de Segura *et al.*, 2008). Together these can define seasonal, diurnal and spatial variation.

Anthropogenic factors**.** There are many ways in which humans can affect the environment occupied by a cetacean species and potentially affect distribution. These include: bycatch (Hall *et al.*, 2000); vessel traffic and collisions (Waerebeek *et al.*, 2007); contamination from chemicals (Tanabe *et al.*, 1983); and noise from vessels (Lusseau, 2005). This study investigates the latter factor.

Prey availability. All species of cetacean show temporal and geographical variation in foraging distribution depending where food resources are found (Shane *et al.*, 1986;

Hanson and Defran, 1993; Barros and Wells, 1998; Allen *et al.*, 2001; Hastie *et al.*, 2003a; Gannon and Waples, 2004; Griffin and Griffin, 2004; Hastie *et al.*, 2004).

There are certain environmental features that may influence cetacean distribution more than others (Kaschner *et al.*, 2006; Perrin *et al.*, 2009). For example, Jaquet and Gendron (2002) found that prey distribution rather than primary productivity or high underwater relief was the most significant descriptor of sperm whale habitat. Smith *et al.* (1986) suggested that chlorophyll is a habitat indicator of distribution for certain marine mammals. Garaffo *et al.* (2007) found that distance to shore was the most important variable to define habitat use by dusky dolphins.

1.5.3. Cetacean distribution in Panama

The dolphin species most commonly found in the area of this study is the common bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821). Cetaceans are known to inhabit the waters of the Pacific coast of Panama, but there is a lack of published scientific literature on the abundance and distribution of species in this area; information comes mainly from unpublished reports (Vidal, 1992). The most complete information in terms of cetacean sightings is in NOAA reports which include abundance estimates in the wider Eastern Tropical Pacific region (Jackson *et al.*, 2004a; Ferguson *et al.*, 2006; Rankin *et al.*, 2008). There are also studies of the distribution of pantropical spotted dolphins in the Gulf of Chiriqui (Garcia and Dawson, 2003); humpback whales migrating to Pacific Panamanian waters (Acevedo *et al.*, 2007; Rasmussen *et al.*, 2007; Best, 2008); and bottlenose dolphins on the Caribbean side of Panama in Bocas del Toro (May-Collado *et al.*, 2007). Information from other open sources has been used to obtain data about dolphin observations in the Panamanian Exclusive Economic Zone (EEZ); i.e. Ocean Biogeographic Information System (OBIS). Other than these reports mentioned above, there is no published literature on delphinid population distribution in this region to provide a background to the questions posed in this study relating to whether shipping noise has any effect on the occurrence of dolphins in the region of the Panama Canal.

1.6. RESEARCH AIMS AND OBJECTIVES

Knowledge of the diversity, distribution and abundance of delphinids in this region of Panama is poor. Due to the lack of any baseline data, this study aimed, firstly, to provide a profile of ambient sound in the area, then to characterize the sounds obtained from the dolphins in the area, and then to investigate the relationship between dolphin call rates as measured by a moored recorder and various factors that may affect their temporal and spatial distribution, especially that of shipping noise.

The temporal objectives were to study variation of background noise and dolphin occurrence in a diurnal cycle (day and night), monthly variation and seasonal variation (dry and wet seasons), by collecting data day and night and collecting data represented by most of the months of the year and at both seasons. The spatial objectives studied the variation of background noise and dolphin occurrence in relation to depth, distance to anchorage area, distance to entrance buoys into the Panama Canal and distance to coast. Data were collected at different distances based upon these spatial scales and at different depths.

The main expected outcomes were to produce the first robust data and results regarding the acoustic behaviour of dolphins in this area in relation to the environment, and for these to form the baseline for further work to be initiated to answer the many questions that this research has raised.

1.7. THESIS STRUCTURE

- **Chapter 2**: **General Methodology**

  This Chapter describes the methods, equipment, techniques and statistical analysis employed to investigate the objectives of each of the following chapters. Geographical information regarding Panama is used to explain the role of the seasons and climate as factors used to model occurrence.

- **Chapter 3: The acoustic environment in the region of the Panama Canal**

  The chapter investigates the dominant sources of ambient sound in the areas close to the Pacific entrance to the Panama Canal. Extracting the 1/3 Octave bandwidths, acoustic analysis was performed to characterize the background sounds of the area, identifying the vessel noise contribution, physical sources, and that of biological origin.

- **Chapter 4: Characterization of dolphin whistles in the region of the Panama Canal**

  This chapter describes the first study to characterize the dolphin whistles in this region of the Panama Canal using a preliminary quantitative analysis. The first steps in a qualitative analysis are undertaken to show the diversity of whistles and whether they are related to any pattern in the environment. The patterns extracted from these data show how whistle characteristics help explain the relationship between dolphin whistles and biological cues. One of the important relationships highlighted here is that of the co-occurrence of whistle sounds and fish sound.

- **Chapter 5: Modelling variation in temporal occurrence of dolphins in the Bay of Panama**

  Temporal variation was studied by using generalized linear models to explain the relationships between the occurrence of dolphins and temporal variables, such as season, month, time of day, as well as biological variables and acoustic variables. This information will help the understanding of the characteristics of the occurrence of dolphins according to these features of the environment.

- **Chapter 6: Modelling spatial variation in occurrence of dolphins in the Bay of Panama**

  Spatial variation was studied by using generalized linear models to explain the relationships between the occurrence of dolphins and spatial variables, such as depth, distance to coastline, to anchorage, and shipping lanes; as well as biological variables and acoustic variables. This information will be useful in order to understand the habitat use of dolphins within this region.

- **Chapter 7: General Discussion**

  This chapter integrates the conclusions obtained from each of the chapters in a comprehensive discussion of the main question: how is shipping noise affecting the distribution of dolphins in relation to biological, temporal and spatial variables.

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CHAPTER 2

GENERAL METHODOLOGY:

DATA COLLECTION AND GENERAL ANALYSIS

2.1 STUDY SITE DESCRIPTION

2.1.1. Climatological and oceanographic characteristics

This study took place in Pacific waters off the coast of Panama (Central America) (Fig. 1.3) that belong to the Eastern Tropical Pacific (ETP) region that extends from Mexico to Peru and includes 28 million km^2 of ocean (Pennington *et al.*, 2006). Cold surface currents and warm pools define the ETP, where the North and South Equatorial currents run to the west and the North Equatorial Counter Current (NECC) runs towards the east (Kessler, 2006). The equatorial cold tongue, bringing cold and weak salinity waters, runs from the equator westward and is affected by the Humboldt Current with high seasonal surface temperatures. These currents influence the wide variation in surface temperature near the Costa Rica dome, where an oceanic upwelling occurs. In contrast, the changes in temperature off the coasts of Tehuantepec to Panama are the result of seasonal variations in wind due to three low-elevation gaps (~300m) in the Central American Cordillera (Fiedler and Reilly, 1994; Rodriguez-Rubio *et al.*, 2003; Chaigneau *et al.*, 2006; Pennington *et al.*, 2006)(Fig 2.1). This passage of wind-jets from the Atlantic region to the Pacific region causes hydrography variations in salinity, oxygen and thermocline layers of the ETP; the NECC transforms into the eastern Pacific warm pool as a result of seasonal net heat flux and weak wind mixing. More locally these winds define the Panama Bight, which extends from the Isthmus of Panama to southwest of Colombia and defines a complex system of seasonal variability in oceanic and meteorological conditions, as well as local upwelling and occasional El Niño events (Stevenson, 1970; Chaigneau *et al.*, 2006; Kessler, 2006)

In the Isthmus of Panama, three main climate conditions mark seasonal variations and biological resource availability: the Inter-tropical Convergence Zone (ITCZ), coastal upwelling and El Niño Southern Oscillation (ENSO) effect (D'Croz and O'Dea, 2007). North winds separate the ITCZ from the isthmus, while the south winds push the ITCZ towards the isthmus. The rainy season starts in mid-April to May and extends into November. The dry season, which generally extends from January to April, is the result of a southward migration of the ITCZ. It is characterised by the high intensity of winds from the north.

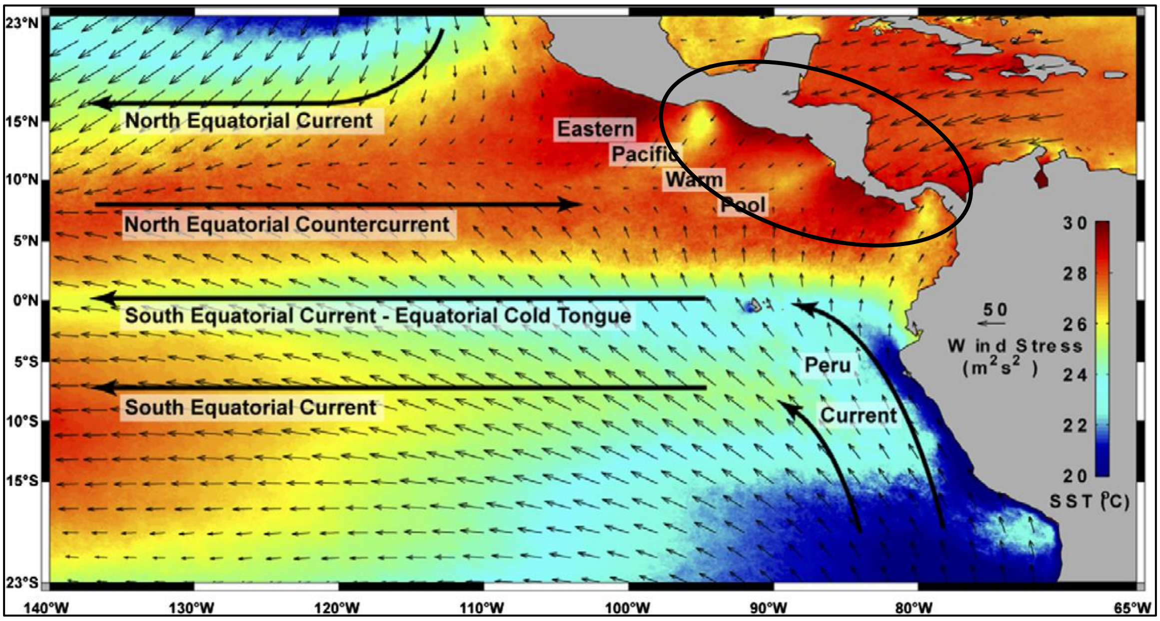

Figure 2.1 Average sea surface temperature and direction of major currents in the eastern tropical Pacific, defined by the confluence of the North and South Equatorial currents, subtropical gyres and the ETP warm pool. Heavy black lines show major currents and thin black arrows denote wind stress. The area within the circle refers to the Central American Cordillera from Tehuantepec to Panama. (Figure and description from Pennington *et al.*, 2006).

These wind jets are produced in the Gulf of Mexico and the trade winds from the Caribbean pass through mountain passes generally reaching their greatest speed in the months of February and March (D'Croz and Robertson, 1997). Along the Pacific coast these winds cause coastal upwelling, which is characterized by cold water rising up to the surface from a depth of approximately 150 meters (Gonzalez and D'Croz, 2007). This occurs in the Gulf of Panama during the dry season (Fig. 1.5). The most evident oceanographic consequence of this phenomenon is the reduction in sea surface temperature, which in the most extreme cases declines to 15°C (D'Croz and O'Dea, 2007; Gonzalez and D'Croz, 2007). The waters off Panama form a moderately productive area but represent one of the highest productivity levels of the region (692mg C m^2 day^{-1}), especially during the upwelling season (Pennington *et al.*, 2006). McClain *et al*. (2002) describe exceptional phytoplankton growth in the 1997-1998 ENSO event using ocean colour observations. Pelagic primary production of phytoplankton and zooplankton supports large fish populations and pelagic fisheries that may catch half a million metric tons per year, mostly anchovies. The high fish abundance attracts abundant tuna, dolphins and seabirds to the Bay of Panama (D'Croz and O'Dea, 2007). When the upwelling season is over, the Gulf of Panama reverts to being a warm pool (27°C) and consequently becomes nutrient poor and low in chlorophyll (D'Croz and Robertson, 1997; McClain et al., 2002; D'Croz and O'Dea, 2007; Gonzalez and D'Croz, 2007).

This upwelling also influences water salinity; the Gulf of Panama has the lowest salinity of the area (29 ppt) but it reaches its highest values during the dry season (greater than 34 ppt) (D'Croz and Robertson, 1997; D'Croz and O'Dea, 2007). This area has the highest silicate values (32.1 µmol 1^{-1}) measured in non-El Niño effect years (Pennington *et al.*, 2006). However, upwelling only occurs in the Gulf of Panama and not in the Gulf of Chiriquí (Fig.1.3). The most noticeable effects of upwelling are shown in the Bay of Panama, where this study took place (Fig.2.2).

El Niño Southern Oscillation (ENSO) is another seasonal event that causes changes in the Eastern Tropical Pacific Ocean off Panama. ENSO is an important source of inter-annual variation in the ETP (Pennington *et al.*, 2006). This occurs every 4 to 9 years, causing substantial temperature changes in surface waters that in turn can cause serious drought or extreme flooding because of large changes in atmospheric pressure across the South Pacific.

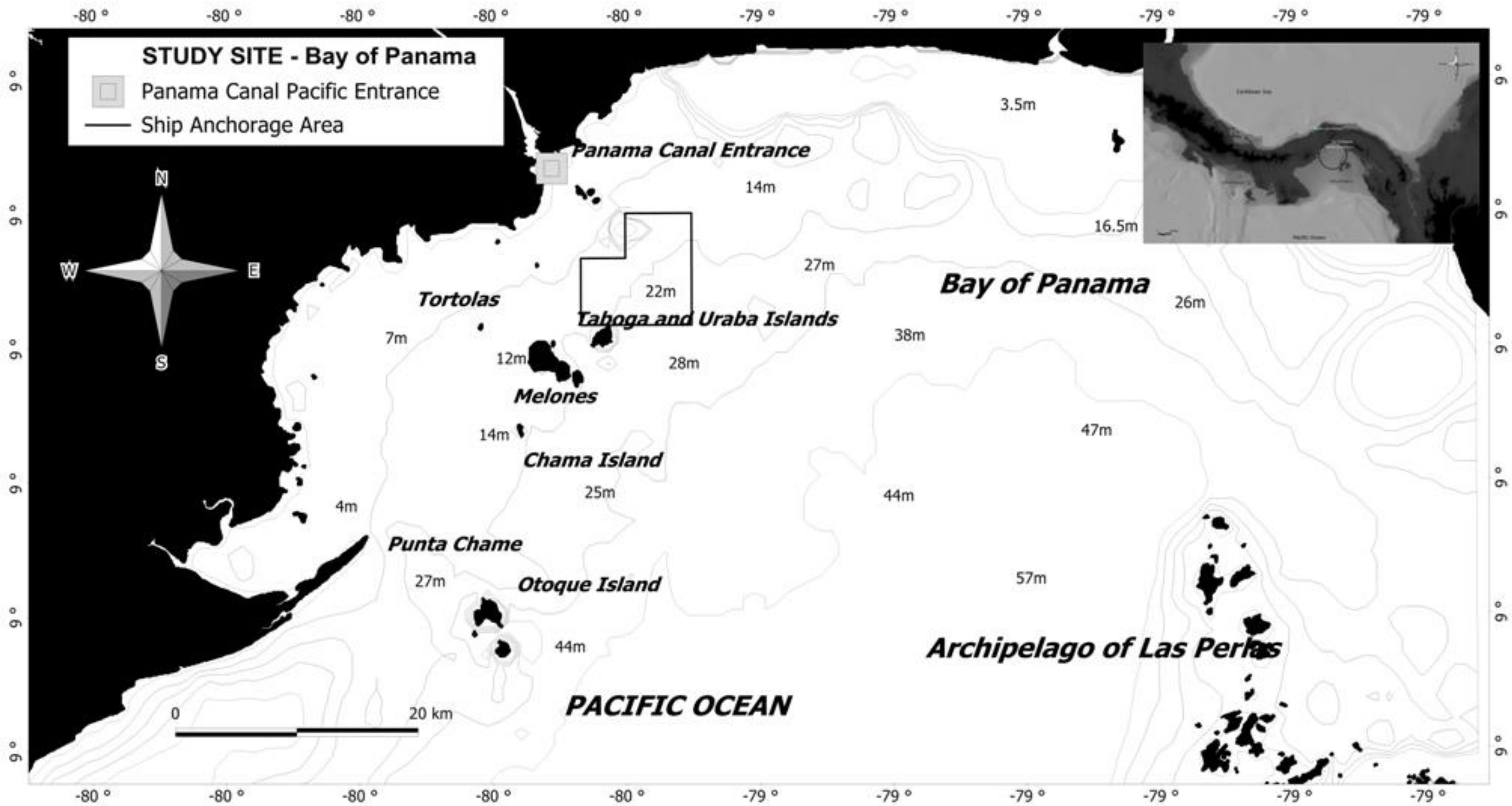

Fig.2.2 Map of study site showing the Bay of Panama within the Gulf of Panama in the Pacific side of the Isthmus. The rectangular shape demarks an area in which sampling was prohibited, imposed by the Panama Canal Authority because this is where vessels anchor to wait to enter the Canal.

Although Panama is in the Northern Hemisphere and therefore seasons should be named accordingly, climatological characteristics create dry and wet seasons. The dry season runs from December through March, and the wet season, characterized by rainy months, runs from April to November. The dry season is characterized by upwelling events causing colder waters and high biological productivity while the wet season has lower productivity (Lachniet *et al.*, 2004).

The study took place on the Pacific side of the Panama Canal on the southeast coast of the Isthmus of Panama and within a region extending both east and west of the Canal entrance (Fig. 2.2). Sampling of this region took place using a grid of randomised locations that covered approximately 900 km^2 within coordinates 8.98030°N 79.48879°W, 8.72689°N 79.50597°W, 8.65143°N 79.73569°W and 8.84196°N 79.68224°W (Fig. 2.3).

2.2. DATA COLLECTION

2.2.1 Passive Acoustic Monitoring (PAM)

Passive acoustic monitoring methods (PAM) are now frequently used in the study of cetacean populations (Oswald *et al.*, 2003; Oswald *et al.*, 2004; Barlow and Taylor, 2005; Wang *et al.*, 2006; Marques *et al.*, 2008), including to assess the effects of anthropogenic sound on cetaceans (Erbe, 2002; Barlow and Gisiner, 2006; Akamatsu *et al.*, 2008; Holt *et al.*, 2009; May-Collado and Wartzok, 2009; Kimura *et al.*, 2012). PAM is increasingly used as a tool for recording the presence of cetaceans and it has a number of advantages over visual monitoring (Richardson *et al.*, 1995b; Au and Hastings, 2008). The main features of PAM are:

(a) PAM devices can be left unattended for long periods of time and, in contrast to visual observations, they can operate at night as well as during the day, and under any weather conditions. The technologically advanced storage media in PAM devices give them the potential to store a large amount of data. However, this involves a delay period in data recovery and analysis.

(b) PAM devices can be deployed in several modes such as stationary platforms or by being towed behind a vessel, sometimes in conjunction with visual monitoring, as well as in drifting radio-linked sonobuoys deployed and monitored from ships, aircraft or land.

(c) PAM is most useful for cetaceans that vocalise frequently and regularly.

(d) One of the disadvantages is that only a limited number of cetacean species can be identified from their vocalisations. In particular, it is not possible reliably to distinguish acoustically among many species of small delphinids.

(e) PAM can be configured to estimate the location of vocalising animals. For some species, e.g. sperm whales (Lewis *et al.*, 2007), PAM may be capable of determining location at great distances.

The design of the system will depend on the question asked, the frequency ranges of the sounds of interest, the type of animals targeted and the depth at which animals produce sounds (Barlow and Gisiner, 2006). The design also depends on whether we want to study diversity, abundance, and/or behaviour.

2.2.1.1. Survey Design

Autonomous-recording stationary systems are effective for studying relative abundance of small cetaceans by detecting and recording clicks and whistles in a 24hr cycle in areas where visual methods are inefficient or infeasible, such as where density is low or in shipping channels (McDonald and Fox, 1999; Stafford *et al.*, 1999; Wang *et al.*, 2005; Akamatsu *et al.*, 2008; Kimura *et al.*, 2012) . In this study, hydrophones were used in stationary deployments for these reasons and because the Panama Canal authorities do not allow the free transit of boats in the anchorage area of the ships waiting to go through the canal. This area is heavily used in an erratic manner by both large and small vessels which would have interrupted line transect surveying with a towed hydrophone behind the boat. However, acoustic data were also collected at sampling stations with a boat-based hydrophone to enable more locations in the study site to be covered.

Thus, the survey design was based on point sampling, which is more appropriate than line transect sampling for large study areas with patchy environments and when free transit is difficult (Buckland *et al.*, 2009).

The survey design to select the sites to sample with both types of hydrophones was calculated using software Distance 6.0 (Thomas *et al*., 2009) to randomly generate the points that were to be used for deployment of hydrophones. The design considered the temporal and spatial objectives of the study to ensure an adequate sample size. Points were selected taking into account the need for replication; randomization; and sampling coverage. On a temporal scale, the recorders collected data monthly to include both dry and wet seasons and over periods of at least five days and nights to include a diurnal cycle. On a spatial scale, the bottom-based hydrophone was deployed and left *in situ* in different sites as far as possible according to the restrictions of the Panama Canal Authorities and depth. Because of these restrictions of depth and space, the survey with the boat-based hydrophone was incorporated in the sampling method to allow the coverage of more sites. The ability to collect data on environmental variables at the appropriate temporal and spatial scale is described below in section 2.2.2.1.

The point sampler function within software Distance generates a grid layer from the input sample area (latitude and longitude) and the specified distance between grid points. This resulted in a grid of approximately 200 points roughly 2km apart. The survey design was centred around the anchorage area and two gradients running perpendicular to one another within the study area were taken into consideration (Fig 2.3). One ran roughly southwest to northeast across the expected noise gradient associated with shipping and the other ran northwest to southeast across the continental shelf towards the Las Perlas archipelago (Fig 2.3).

Before every sampling trip, five of these points were selected at random from each of two different regions (northeast or southwest of the anchorage area). Five points were selected to allow logistical flexibility because once at the site the conditions might prove impossible for the deployment of the stationary hydrophone. Such conditions could include heavy traffic (i.e. dredge routes), very shallow areas, or a rocky-uneven seabed bottom. In addition, ten points were selected at random from the same two regions to select sites to sample with the boat-based hydrophone (Fig. 2.3).

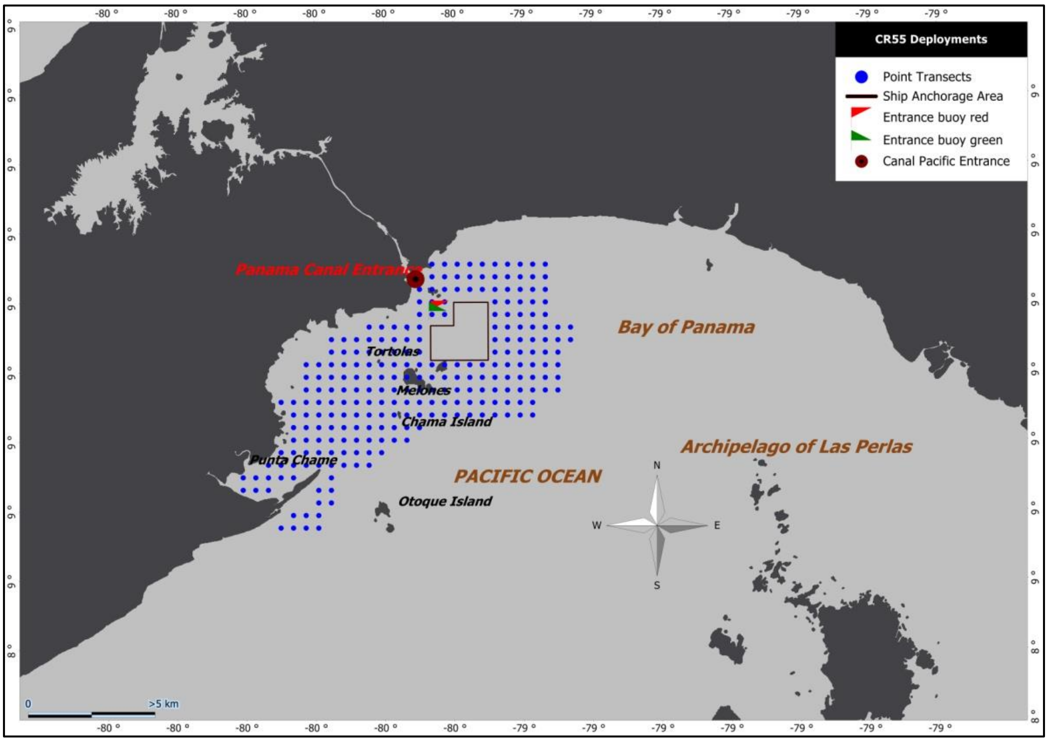

Fig. 2.3 Map showing the grid of points to be sampled as generated from the survey design component of software Distance for the area around the anchorage outside the Canal entrance.

2.2.1.2 Stationary Hydrophone: DSG

The stationary hydrophone used was a Digital Spectrogram (DSG) Recording System (Loggerhead Instruments, USA). It was lowered to the sea bed and was scheduled to be left *in situ* for several days (at least 5 days). This hydrophone had the capacity to sample at rates from 2Hz to 80 kHz, using a 16 bit resolution. The system was calibrated with a hydrophone sensitivity of -186 dB re 1V/µPa, which meant that the maximum power signal that could be received without clipping was 180-190 dB re 1µPa. The calibration plot for this system is given in Appendix Figure A.2. Data were saved directly to a 16GB SD card, downloaded to a laptop when the recorder was recovered and converted into audio (.wav) files for analysis. Each deployment schedule included continuous recordings on a duty cycle of 2.5 minutes every 10 minutes sampling at 50 kHz. This schedule was selected to balance the period of recording possible based on the storage capacity, life of the batteries and the objective to record over several days to investigate diurnal variability (§1.6). The settings for the schedule were set via software from the hydrophone manufacturer (Loggerhead/DSGschedule) and done from a small laptop on the boat at the site. This hydrophone was deployed at 15 sites (Fig. 2.4).

Deployment of any acoustic device into the ocean is a challenging task and sometimes it takes trial and error until a system works according to the particular conditions of the site in terms of weather, dredging activities, local fisheries, ship traffic, and bottom substrate (Dudzinski *et al.*, 2011). The hydrophone system was attached to a heavy concrete base and deployed from a small boat at a pre-planned location. The base was heavy enough to lie still on the seabed bottom to avoid any drifting caused by current and therefore avoid additional noise caused by movement of the equipment. A red marker buoy was attached to this base with a short rope for the purpose of aiding divers in case a search was needed (which it was on one occasion). This base was attached to 100m of rope which had an anchor attached to the other end and small buoy balls to prevent the rope from sinking in the soft bottom. The positions of both anchor locations were fixed with a GPS and the mooring was eventually recovered by dragging the intervening location with a grapnel to grab the 100m rope (Appendix Figure A.1); this arrangement was necessary because of the likelihood that equipment with surface markers would be stolen and because acoustic releases proved to be unreliable. No data were collected with the stationary hydrophone during the month of November because severe weather caused the loss of this equipment. The deployment of this hydrophone was restricted in certain circumstances, including the area prohibited by the Panama Canal authorities, in areas of very soft bottom type, and in areas where it was known that fishing (trawling) activities took place. A boat-based hydrophone was used to obtain data from these places.

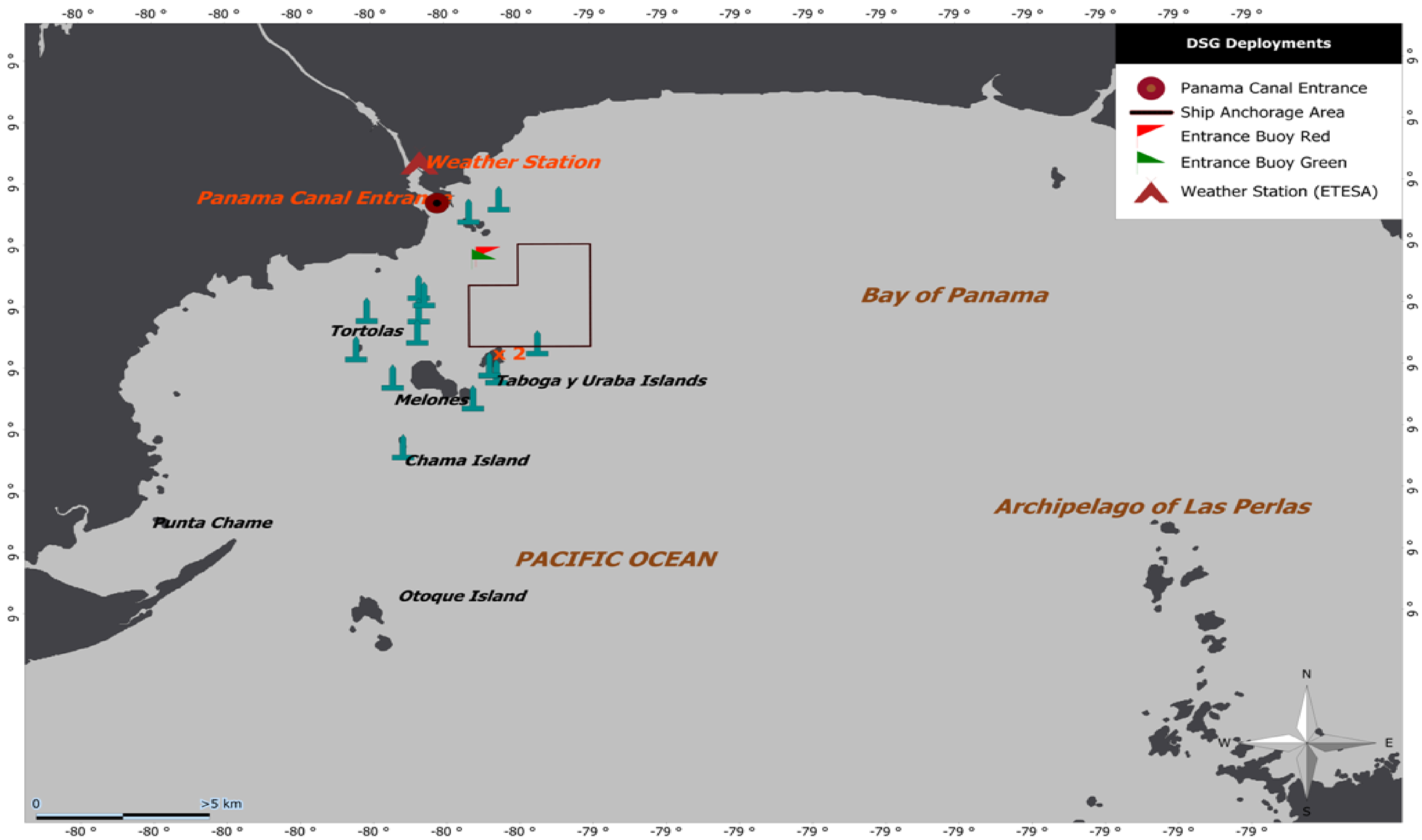

Figure 2.4. Locations where the stationary hydrophone was deployed in the Bay of Panama. There were 15 locations, of which two were deployed in the same site, marked “x2” in this map (in red). The location of the entrance buoys and the anchorage site were used to generate the covariates distance from buoy and distance from anchorage for modelling (see Chapters 5 and 6). The weather station shows how far from the deployments the wind speed and precipitation readings were taken.

2.2.1.2 Boat-based hydrophone: CR55

The boat-based hydrophone used was a CR55 Hydrophone combined with an FR2 recording system (Cetacean Research Technology, USA). The hydrophone was attached to a 100m cable and was deployed in the middle of the water column at each site to avoid bottom friction noise and wave motion noise at the surface; i.e. if the site selected had a total seabed depth of 30 meters, the hydrophone was held at 15 m from the surface. In addition, to avoid current noise, there was a weight attached to the end of the hydrophone to avoid drifting in the water column. The cable was hung from a rod that extended outside the axis of the boat to minimize any noise that could originate from friction with the boat's surface (Appendix Figure A.3).

The recordings took place at a depth range between 9 and 30 m. There was an option in this system to change the sampling frequency to 48 kHz, 44 kHz, and some were mistakenly set to 22 kHz; the quantization bit length was set to 16 bits. The overall sensitivity of this equipment was specified by the manufacturer to -165 dB re 1V/µPa, which means that the maximum recordable signal would be between 169 and 186 dB re 1µPa. A calibration plot for this system is given in Appendix Figure A.4. The boat-based hydrophone was omnidirectional below 10 kHz. Data were saved on a PCMCIA Ultra II 4GB Flash card. Recordings from this unit were automatically recorded in audio (.wav) format. Data collected with this hydrophone consisted of recordings of 20 to 30 min in a designated location, before moving on to another location(s) (during the same day). I was able to cover more sites with this hydrophone (86 sites) but only during daylight hours and for short periods of time at each location (Fig 2.5). For example, recordings were possible as far as the Otoque Islands and the Las Perlas Archipelago, which were outside the original sampling grid (Fig. 2.3) but presented an opportunity to test a farther off distance from the main shipping region; however, these were not analysed because of the high contamination of snapping shrimp noise and also strong currents, especially in the former. The boat was anchored and engines were off while recordings took place. Notes were taken when other vessels transited within a radius of approximately 2km.

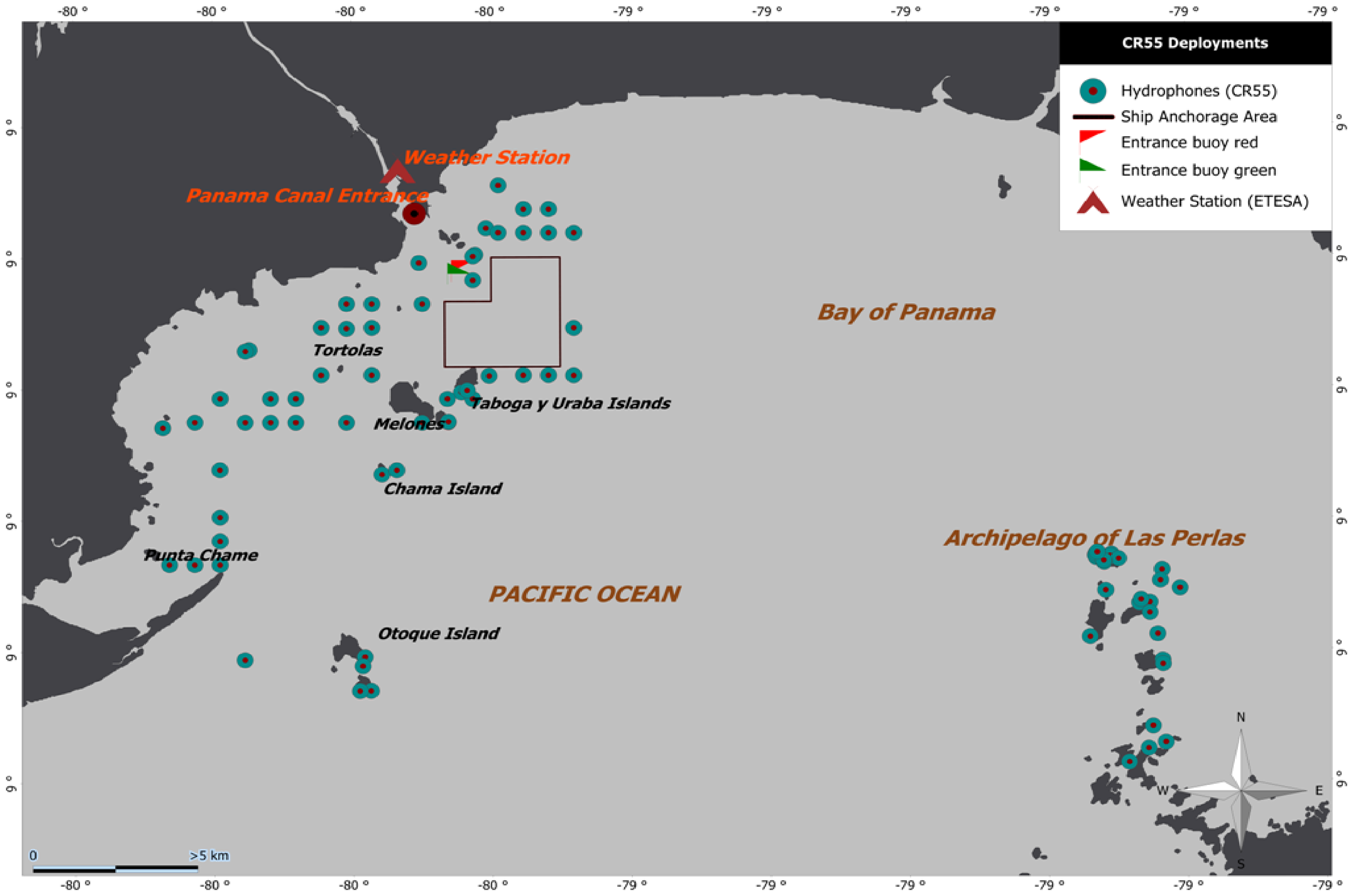

Figure 2.5 Locations where acoustic data were collected with the boat-based hydrophone (CR55). The buoys location and anchorage site were markers used to use its distance for modelling as a covariate. The weather station shows how far from the deployments wind speed and precipitation readings were taken.

2.2.2 Other data

2.2.2.1 Environmental Data

At each deployment site, for both recording systems, a Yellow Springs Instrument (YSI) Professional Plus 2030 instrument (YSI incorporated, USA) was used to measure salinity (range 0-70 ppt, accuracy of ±0.1 ppt), conductivity (range 0-200 ms/cm, accuracy of ±1.0us/cm), temperature (range 0-55°C, accuracy of ±0.2°C), barometric pressure (range 500-800 mmHg, accuracy ±5 mmHg) and dissolved oxygen (DO) (range 0-50 mg/L, accuracy ±0.2 mg/L). Water depth was measured using the boat's echo-sounder, a Garmin Fishfinder140 (Copyright 1996-2012 Garmin Ltd). The echo-sounder had a maximum depth range of 300 m, which was greater than the depth of the study area.

Daily average wind speed and daily average rainfall information was obtained from ETESA (Empresa de Transmision Electrica, S.A.) Hydrometeorology Program (ETESA 2012). Appendix Table A.6 shows daily average wind speed and precipitation per deployment site of the bottom-based hydrophone. Wind speed and precipitation data for the recordings with the CR55 are given in Appendix Tables A.6 - A.18. The instruments that registered this information were located at a stationary station 6-40 km from the sampling points (8.966667°N 79.56667°W) (Figs 2.4 and 2.5).

Ideally, these data should have been collected *in situ* where the hydrophones were deployed. However, it was not possible to incorporate this in the field. The use of these data instead of *in situ* data limited the ability of the study to investigate temporal and spatial variation because of the coarser resolution of the data and because the data were collected several kilometres from where the recordings were made.

2.2.2.2. Visual and fishermen surveys

Although visual observation was not the main detection method for this study, notes were taken on each occasion a dolphin sighting took place. Table 2.1 summarizes notes taken while at the field regarding dolphin sightings and positive confirmation of *Tursiops* *truncatus*. Additional data were also collected from fishermen who carried out their activities in the same areas where the recordings took place.

Dolphin sightings					
Nearby site	**Coordinates**	**Date**	***Tursiops truncatus***	**Unconfir-med**	**Notes**
P168	N 8.74 W 79.57	27/04/2010	X		**Recording with CR55. Confirmed species.**
P191	N 8.84 W 79.54	30/04/2010	X		**Deploying DSG. Confirmed species.**
P225	N 8.79 W 79.52	01/06/2010	X		**Retrieving DSG. Confirmed species.**
P266	N 8.93 W 79.50	11/06/2010		X	**Retrieving DSG. Unconfirmed species.**
P138	N 8,81 W 79.61	12/08/2010	X		**Retrieving DSG. Confirmed species.**
P295	N 8.80 W 79.45	15/09/2010	X		**Recording with CR55. Confirmed species.**
P306	N 8.80 W 79.44	15/09/2010	X		**Recording with CR55. Confirmed species.**
P284	N 8.81 W 79.47	15/09/2010	X		**Recording with CR55. Confirmed species.**
P244	N 8.79 W 79.51	21/12/2010	X		**Recording with CR55. Confirmed species.**
P172	N 8.81 W 79.58	08/02/2011	X		**Retrieving DSG. Confirmed species.**
P264	N 8.82 W 79.50	22/02/2011		X	**Retrieving DSG. Unconfirmed species.**
N079	N 8.80 W 79.58	14/03/2011	X		**Recording with CR55. Confirmed species.**
P64	N 8.70 W 79.70	16/03/2011	X		**The largest group found throughout the field season. Confirmed species.**
P66	N 8.73 W 79.70	16/03/2011	X		**Presumably the same group as previous. Confirmed species**
P287	N 8.95 W 79.47	30/03/2011	X		**Recording with CR55. Confirmed species.**

Table 2.1 Notes taken at the field confirming the dolphin species mostly identified was *Tursiops truncatus*. The observations were made while on effort on the boat (deploying, retrieving or recording with the hydrophones).

A group of 19 fishermen from a local fishing community, who frequented the study site, was surveyed in order to obtain additional (anecdotal) information to complement observed sightings of dolphins and whales. They were given illustrations of the most commonly seen dolphins and whales of the area for them to identify. Questions were related to frequency of fishing activity and the areas covered. Table 2.2 summarizes questions and answers from this survey.

Results of the survey show that most fishermen identified bottlenose dolphins as the most common cetacean sighted during their fishing activities and while travelling to the place where they fish. The months they saw dolphins were mostly between December and June; nevertheless, it is important to note that they are unable to go out to sea in their small fishing boats in October and November because of rough seas and heavy storms. When asked how many dolphins they see in a single trip, the majority (16/19) answered at least one and mostly less than five. These fishermen usually spend the night out fishing because their target fish (i.e. corvina, snappers) are easier to catch at night.

They reported that the times dolphins are mostly seen are in the early hours and at night. Some of them also mentioned that dolphins follow their boats because they discard waste from fish if they perform cleaning activities on board.

Survey to Local Artisanal Fishermen						
N=19	***Bottlenose dolphin***	***Common Dolphin***	***Spotted Dolphin***	***Spinner Dolphin***	***Risso's Dolphin***	***Humpback Whales***
Description of cetacean seen	16		2		1	In season
Month of sighting while fishing	*Dec-Jan*	*Feb-Mar*	*Apr-May*	*Jun-Jul*	*Aug-Sept*	*Oct-Nov*
	8	15	11	7	6	
Amount of animals seen	*At least one*	*1 to 5*	*1 to 10*	*More than 10*		
	16	14	3	1		In season
Time spent out at sea	*At least 4 hours*	*Between 4-8 hrs*	*More than 8hrs*	*Overnight*		
		4	5	10		
Fishing Activity	Net Fishing	Line Fishing				
	15	4				
Type of fish	Any fish	Corvina	Snapper			
	19	10	18			

Table 2.2 Responses from artisanal fishermen to surveys conducted to obtain information additional to sightings. The survey contained questions related to their type of fishing activity, type of fish, and type of technique. They all use the same kind of small artisanal fishing boat with one outboard engine, usually between 50-80HP. They were also asked to select the image of the cetacean they were likely to see the most and the estimated number in a trip. The fishermen responded to the question of which months they go out to sea and how long they spent at sea. The number in each of the boxes corresponds to the number of fishermen that answered that particular question; i.e. 16 fishermen answered Bottlenose dolphin is the most commonly seen species.

2.3. DATA PROCESSING

2.3.1 Acoustic data processing

For the purposes of this thesis, I have adopted the acoustic terminology published by Knudsen *et al.* (1948). Background noise or ambient noise is the sound normally present in water, usually from many sources such as water motion, sounds of diverse marine life and unwanted ship and vessel sounds. Underwater noise describes unwanted underwater sounds that impair acoustic recording devices from recording the desired signals of study.

2.3.1.1 Data processing of background noise

Audio data obtained from the hydrophones were analysed using Pamguard Beta Core software v.1.10.04 (Passive Acoustic Monitoring Guardian, www.pamguard.org). One feature of this program is the pre-defined detectors (i.e. whistle detectors, click detectors) that convert electrical signals from wave format sound into useful digital measurements. For this project, a noise detector was used and audio files were run to obtain received levels (RL) from a series of 1/3 Octave Bands centred at frequencies from 2 Hz up to 20,000 Hz. Recordings were sampled at 50 kHz with the DSG and 48kHz, 44kHz and 22kHz with the CR55 hydrophone; therefore, each of these groups of audio files was analysed separately. In total, the sound energy level from each unit of recording was broken up into 41 1/3 Octave Bands (except audio files obtained from recordings sampled at 22 kHz). In Chapter 3, nine of these were selected to investigate the variations in received levels at temporal and spatial scales. These centre frequencies were 20Hz, 160Hz, 400Hz, 1,000Hz, 1,600Hz, 5,000Hz, 10,000Hz, 16,000Hz and 20,000Hz. In Chapters 5 and 6, these same centre frequencies were used to investigate the effect of the RL at these frequencies on the presence or count of whistles.

2.3.1.2 Data processing of whistles

Dolphin whistles were characterized by breaking down the whistle contour into its qualitative and quantitative characteristics (Richardson *et al*., 1995d; Au and Hastings, 2008b). A contour of a whistle was defined as the fundamental frequency versus time on a spectrogram. Qualitative methods involved a description of the parts of the contour of a whistle in terms of the frequency modulation, whereas quantitative methods included the determination of various parameters of the whistle. The methods followed in this study were similar to those used by many researchers who have characterized whistle contours from whistle-producing odontocetes (Wang *et al.*, 1995; Rendell *et al.*, 1999; Bazua-Duran and Au, 2002; Lammers *et al.*, 2003; Oswald *et al.*, 2003; Oswald *et al.*, 2004; Camargo *et al.*, 2006; Azevedo *et al.*, 2007a; Oswald *et al.*, 2007; Hawkins, 2010; Hernandez *et al.*, 2010; Seabra de Lima *et al.*, 2012; Vaughn-Hirshorn *et al.*, 2012). These characteristics are described in Chapter 4.

The quantitative parameters of the whistles were extracted using the open source acoustic analysis software Pamguard (Passive Acoustic Monitoring Guardianship, Version 1.10.04 Beta), with a whistle and moan detector (available from www.ifaw.org/). The whistle and moan detector plug-ins were configured and automated detections were recorded and exported to a blank Access database table (Yack *et al.*, 2009). The detector sweeps the spectrogram in search of high intensity sounds and areas exceeding the background noise are selected. Consecutive peaks are joined resulting in a time-frequency contour. A whistle is considered a whistle event by Pamguard when the number of whistles exceeds some minimum value within a set time period (i.e. 1 sec). A problem to highlight here is that single whistles are often counted as multiple whistles in the presence of rapid and large amplitude changes or marked frequency steps in the signal (Yack *et al.*, 2009). As described below, most of the whistles detected by Pamguard were found to be “false-positives”. This may have been in part due to high frequency noise (from fishing boats) dominating the spectrograms during some of the recordings and being taken by Pamguard as a whistle when joining high intensity peaks.

The quantitative parameters used in this study were duration of the whistle, minimum and maximum duration of whistles, minimum and maximum frequency, and frequency range. Lammers *et al*. (2003) also presented characterization of whistles using only these parameters.

To eliminate false positive detections, in each case where Pamguard had recorded detections, each spectrogram was inspected visually and each of the audio files was listened to. For the bottom-based hydrophone, a random sample of 40% of these files was retained for analysis. Subsequently, 40% of the audio files in which Pamguard did not detect whistles (false negatives) were randomly selected for manual analysis to identify whistles missed by the program. Therefore, 40% of the audio files of each deployment were thoroughly analysed manually, whether or not these were files where Pamguard detected whistles; i.e., 40% of false positive and 40% false negative files were retained for analysis. In the same way, 40% of audio files with false positive detections and 40% of audio files with false negative detections were considered for analysis from the boat-based hydrophone.

Some authors have preferred manual analysis of spectrograms to program-based procedures (Dos Santos *et al.*, 2005). The qualitative description used in Chapter 3 was the result of a manual visual identification of different types of contours looking at spectrograms produced using Adobe Audition 3.0 (Copyright © 1992-2007 Adobe Systems Incorporated). Spectrograms were analysed using a Blackman-Harris window, which allowed for the widest frequency band viewing and least noise, in a 10 second window frame at a resolution of 512 bits.

Although this additional analysis incurred extra time, it allowed for a closer visual and acoustic analysis of whistles and other sounds occurring at the same time, which were noted as additional observations.

2.3.1.3 Biological sounds

Biological sounds (i.e. soniferous fish and snapping shrimp) were identified when listening to the audio files and during analysis of spectrograms with Adobe Audition 3.0 (Adobe Systems Incorporated,©1992-2007), using a Blackmann-Harris window function with a resolution of 512 bands and a viewing range of 10 seconds. The sound produced by snapping shrimp is stereotypical and hard to confuse with any other sound (See 1.2.3.2). These sounds were confirmed with sounds of tropical snapping shrimp obtained from the Macaulay Library (ML). The different fish sounds were also confirmed with recordings of known sounds of various species from Macaulay Library (ML). This library contains a large number of audio files of different type of soniferous fish. Fish sounds have low variation among species and often produce similar sounds within the same family (Sprague *et al.*, 2000; Mann, 2012), in part because of their specific mechanism of producing sound (stridulation, clapping jaws, or twitching the sonic muscles of the swim bladder). To confirm the fish sounds in the audio files, a comparison was made by listening to fish sounds contained in the archives of the Macaulay Library by selecting audio files belonging to the same family (mainly Family Sciaenidae) and, when possible, the same genus of the fish found in this study area (Allen and Robertson, 1994; Robertson and Allen, 2008).

2.4. DATA ANALYSIS

The statistical package R 2.13.1 (Development Core Team, 2011) was used for all statistical analysis and modelling.

2.4.1 Statistical Modelling

Statistical modelling involves the design of a mathematical model that helps us quantify a probability distribution of a set of data in order to make further generalisations about those data (Fowler *et al.*, 1998). The statistical modelling in this thesis used regression methods: Generalised Linear Models (GLMs) and Generalised Additive Models (GAMs), described below. In Chapter 3, I use these models to investigate how much the variation in ambient sound in this region, using measured sound received levels at different 1/3 Octave bands, can be explained by temporal, environmental and spatial variables. In chapters 5 and 6, I investigate which biological, spatial, temporal, environmental and anthropogenic factors influence the relative abundance of dolphins in time and space in the study area.

Regarding the latter modelling more generally, predictive models of species distribution are empirical models that use environmental variables and related species information to derive a statistical relationship that serves to predict distribution in space and/or time (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Kaschner *et al.*, 2006; Garaffo *et al.*, 2007). The type of data can include counts, presence-absence, presence only, and abundance of species. Each of these cases requires a different approach when modelling and the environmental variables selected must be appropriate in order to describe the effect on the species distribution. The use of several environmental variables to create models of cetacean distributions has been widely described (Hui, 1979; Selzer and Payne, 1988; Jaquet and Whitehead, 1996; Guisan and Zimmermann, 2000; Hastie *et al.*, 2005; Ferguson *et al.*, 2006; Kaschner *et al.*, 2006; Garaffo *et al.*, 2007; Cañadas and Hammond, 2008; Gomez de Segura *et al.*, 2008; Embling *et al.*, 2010). Thus, modelling is used to help understand the relationship between explanatory variables and the response variables. The aims of this study were to find an explanation of the data rather than to generate a prediction.

Combining ideas from Redfern et al. (2006) and Guisan & Zimmermann (2000), the general steps for statistical modelling can be described as follows: (a) defining the purpose of the model and the question to pursue; (b) based on the objective, collection and organisation of appropriate data in the appropriate format, including selection of spatial and temporal variables; (c) running appropriate tests, such as correlation tests between variables to investigate collinearity that influence model fitting and interpretation; (d) determination of the error distribution of the response variable and appropriate link function between data and the model; (e) selection of variables to include in models using appropriate model selection tools (e.g. AIC, QAIC) and finally; (f) model evaluation using model diagnostics to investigate the fit of the model to the data. These are described further in the following sections.

Simple linear regression is used to establish the relationship between two variables to be able to predict a value for ***y*** (response variable) from a given value of ***x*** (predictor or explanatory variable). A number of assumptions are made, including that ***x*** is measured without error, that measurements of ***x*** are independent, that the relationship between ***y*** and ***x*** is best fitted by a straight line (***y=a+bx***), that the residuals of ***y*** about the fitted line (error structure) are normally distributed, and that variance in ***y*** is not a function of ***x*** (Dytham, 2011).

The error structure of a response variable may not be normal; for example, count data are Poisson distributed and presence/absence data are binomially distributed. In these cases, Generalised Linear Models (GLMs) can be used, which can accommodate different error structures of response variables (Nelder and Wedderburn, 1972). GLMs include a link function between the data and the model that describes the relationship between the mean of the response variable and that of a linear combination of predictor variables (Faraway, 2006).

A generalised additive model (GAM) is a GLM consisting of a linear predictor that includes smooth functions of covariates (Hastie and Tibshirani, 1986; Wood, 2006). GAMs were developed by Hastie and Tibshirani (1986) as likelihood-based regression models to analyze distribution data. Wood (2006) defines a GAM as “a generalized linear model with a linear predictor involving a sum of smooth functions of covariates that may follow any exponential family distribution.”

Regression smoothers are functions that generate predicted values of a dependent variable and its first derivative without making assumptions about the relationship between the dependent and independent variables (Shipley and Hunt, 1996). The smooth functions produced can be used as a data description, for prediction, or to suggest covariate transformations (Hastie and Tibshirani, 1986).

Errors can occur when a low proportion of the variance in the data is explained by a model, but also if the model is over-fitted (Guisan and Thuiller, 2005). Over-fitting can happen as a consequence of modelling a variable that is significant by itself but not in combination with other predictors. Conversely, under-fitting can happen by omitting to use a variable that is only significant when combined with other variables (Pearce and Ferrier, 2000b). These problems can be avoided by testing all possible combinations of independent and dependent variables and using an appropriate model selection measure to select the most appropriate model (see below).

In Chapters 5 and 6, I used a Poisson error distribution for the response variable when it was whistle count, and a binomial error distribution when the response variable was presence/absence of whistles (1 or 0, respectively). For the Poisson models of counts, data from the DSG (2.5 mins) were multiplied by 0.8 to make the sampling unit the same length as the CR55 data (2 mins).

In Chapters 5 and 6, after running models with a Poisson error distribution for count data, the variance was shown to be much greater than the mean, indicating overdispersion in the data. Under these circumstances, the likelihood specified for this model is no longer valid and a quasi-likelihood was adopted, in which a quasi-Poisson error distribution is assumed and dispersion is a free parameter estimated by the model (Faraway, 2006). Models with a binomial error distribution for presence/absence data also showed over-dispersion; therefore a quasi-binomial model was used for these data.

2.4.1.1 Variables

The complete list of variables used in this thesis is shown in Table 2.2.

2.4.1.1.1 Response variables

Chapter 3: Received Level data

Received levels from nine bandwidths were selected to investigate temporal and spatial variation. Preliminary analysis showed that a Normal distribution was appropriate for the error structure of these response variables.

Chapters 5 and 6: Count data

Count data represent the number of times an event occurs in a unit of time or space, but independent of the time since the last event (Dytham, 2011). As described above, the Poisson distribution was used to model this type of discrete random variable. In this study, the response variable was counts of whistles.

The assumptions of the Poisson distribution are:

a. Mean number of occurrences is small in relation to the maximum possible;
b. Occurrences are random;
c. Occurrences of one event must be independent of other events.

Whistles tend to occur in clusters (Janik *et al.*, 2013) indicating serial correlation occurs over time and the assumptions that events are random and independent are violated. The sampling unit (an audio file) for modelling was a 2.5 minute period of time. Serial correlation in counts within audio files causes over-dispersion of counts among sampling units; this was taken into account by assuming a Quasi-Poisson error distribution for counts during the modelling process (see Chapter 5). Serial correlation in the data among sampling units (audio files) is likely to be present in data obtained from the boat-based hydrophone in which several consecutive 2 minute sampling units occurred in 20-30 minute blocks. Serial correlation in data from the boat-based and stationary hydrophone was investigated by fitting an Autocorrelation Function (ACF) and plotting the results. These results are presented and discussed in Chapter 5.

Chapters 5 and 6: Presence/Absence data

Data that are described by a possibility of one of only two outcomes in a trial are known as binomial data and the Binomial distribution is used to model this type of discrete random variable. It is assumed that each trial is independent. In this study, the response variable was the probability of whistles being present (1) or absent (0).

2.4.1.1.2 Predictor variables

The following predictor (explanatory) variables were included in analysis:

a. ***Temporal***: month, season, and hour. Season is defined as 1 or 2 (dry season or wet season, respectively). Month and hour were converted to circular variables because they form cycles in which 1 follows 12 (month) or 1 follows 24 (hour).
b. ***Spatial***: depth, distance from coastline, distance from anchoring area (where ships are anchored), latitude, longitude, distance to the main buoys (where ships transit in or out of the channel at constant speed).
c. ***Environmental***: temperature, salinity, wind speed, rainfall, dissolved oxygen, and conductivity.
d. ***Biological***: presence of fish, represented by listening for fish chorus sound (See §2.3.1.3).
e. ***Acoustic:*** received levels represented in the following 1/3 octave bands centre on frequencies: 20Hz, 160Hz, 400Hz, 1,000Hz, 1,600Hz, 5,000Hz, 10,000Hz, 16,000Hz and 20,000Hz. (Missing values of RL for recordings sampled at 20,000Hz were substituted with NA in models).

The acoustic variables are important potential predictors in this study. The frequencies of these bands (defined by received levels) were selected for analysis on the basis of the objectives of each chapter and on the background noise present within these frequencies (described in Chapter 3). For example, according to the literature, fish sounds are considered to be biological sounds that are measured between 400Hz and 1 kHz (Au and Hastings, 2008b); hence these frequencies were used for modelling the influence of fish sounds on dolphin relative abundance.

VARIABLE NAME	*ABBREVIATION*	*VARIABLE TYPE AND CHAPTER*	*VARIABLE CATEGORY*
Received Levels at Frequency 20 Hz	**f20Hz**	**Response (Ch.3) & Predictor (Ch.5 & 6)**	**Acoustical**
Received Levels at Frequency 160 Hz	**f160Hz**	**Response (Ch.3) & Predictor (Ch.5 & 6)**	**Acoustical**
Received Levels at Frequency 400 Hz	**f400Hz**	**Response (Ch.3) & Predictor (Ch.5 & 6)**	**Acoustical**
Received Levels at Frequency 1000 Hz	**f1000Hz**	**Response (Ch.3) & Predictor (Ch.5 & 6)**	**Acoustical**
Received Levels at Frequency 1600 Hz	**f1600Hz**	**Response (Ch.3) & Predictor (Ch.5 & 6)**	**Acoustical**
Received Levels at Frequency 5000 Hz	**f5000Hz**	**Response (Ch.3) & Predictor (Ch.5 & 6)**	**Acoustical**
Received Levels at Frequency 10000 Hz	**f10000Hz**	**Response (Ch.3) & Predictor (Ch.5 & 6)**	**Acoustical**
Received Levels at Frequency 16000 Hz	**f16000Hz**	**Response (Ch.3) & Predictor (Ch.5 & 6)**	**Acoustical**
Received Levels at Frequency 20000 Hz	**f20000Hz**	**Response (Ch.3) & Predictor (Ch.5 & 6)**	**Acoustical**
Whistles	**wh**	**Response (Ch. 5 & 6)**	***Count***
Whistles and Clicks	**whclk**	**Response (Ch. 5 & 6)**	***Count***
Presence/Absence	**presabs**	**Response (Ch. 5 & 6)**	***Binomial***
Month (circular month)	**circmo**	**Predictor (Ch.3, 5 & 6)**	**Temporal**
Season	**season**	**Predictor (Ch.3, 5 & 6)**	**Temporal**
Hour (Hour block)	**hrblck**	**Predictor (Ch.3, 5 & 6)**	**Temporal**
Depth	**depth**	**Predictor (Ch.3, 5 & 6)**	**Spatial**
Latitude	**lat**	**Predictor (Ch.3, 5 & 6)**	**Spatial**
Longitude	**lon**	**Predictor (Ch.3, 5 & 6)**	**Spatial**
Distance from coastline	**dcoast**	**Predictor (Ch.3, 5 & 6)**	**Spatial**
Distance from anchoring area	**danch**	**Predictor (Ch.3, 5 & 6)**	**Spatial**
Distance from buoys	**dbuoy**	**Predictor (Ch.3, 5 & 6)**	**Spatial**
Fish Noise	**fn**	**Predictor (Ch.3, 5 & 6)**	**Biological**
Wind Speed	**ws**	**Predictor (Ch.3, 5 & 6)**	**Environmental**
Precipitation	**prec**	**Predictor (Ch.3, 5 & 6)**	**Environmental**
Temperature	**temp**	**Predictor (Ch.3, 5 & 6)**	**Environmental**
Salinity	**sal**	**Predictor (Ch.3, 5 & 6)**	**Environmental**
Dissolved Oxygen	**do**	**Predictor (Ch.3, 5 & 6)**	**Environmental**
Conductivity	**cond**	**Predictor (Ch.3, 5 & 6)**	**Environmental**
Barometric Pressure	**press**	**Predictor (Ch.3, 5 & 6)**	**Environmental**

Table 2.2 List of response and predictor (explanatory) variables used in the models. The abbreviation used within the models is described for future reference in Tables and Figures.

2.4.1.2 Selection of best model

The standard quantity used to select the best model from a set of candidate models is Akaike's Information Criterion (AIC). The AIC is defined as:

$$\text{AIC} = -2 \text{ maximum log likelihood} + 2p$$

where p is the number of parameters in the model (Faraway, 2006).

However, the consequence of using quasi-likelihood models (§2.4.2.1) is that AIC cannot be calculated. However, an equivalent quasi-AIC (QAIC) incorporating the estimated dispersion parameter can be calculated. In QAIC, the number of model parameters is increased by 1 to account for estimating the overdispersion parameter.

I used the dredge function (Kamil, 2012) for model selection based on QAIC. Dredge runs all possible models with all combinations of variables given in the global (saturated) model and presents them in rank order; in this case determined by QAIC.

Before accepting the best model based on QAIC, I obtained the variance inflation factor (vif) to confirm there was no multicollinearity between the variables in the model (§2.4.2.1.).

2.4.1.3 Model Evaluation

Model Diagnostics

Model diagnostics were used to explore how well a model fitted the data (goodness of fit), including checking the assumptions of the model regarding distribution of residual variance. The following diagnostic plots were inspected for each model considered.

- The plots of **Fitted vs Observed** values of data points and **Residuals vs Fitted** values are two of the most important diagnostics to detect model lack of fit and unequal distribution of variance (Faraway, 2006).
- **Q-Q plots** (quantile-quantile plots) are a useful way to visualise the distribution of model residuals. They show the model residuals plotted against the observed data represented as quantiles of their probability distributions. Departure of data points from a 1:1 line show lack of normality of the residuals (Faraway, 2006).
- **Scale-Location**: A plot of the square root of the absolute value of the standardized residuals against fitted values. This helps detect skewness in the distribution of the variance if there was a trend in dispersion (Dalgaard, 2008).
- **Leverage**: This plot shows extreme values that have a large influence on model fit (Faraway, 2006). This plot is useful for identifying possible errors in the data but data points with high leverage may represent data values of biological importance.
- **Cook's distance:** This statistic is a measure of how model fit changes when a single data point is removed. Cook's distances can be shown on a plot of residuals against leverage as a way of highlighting influential observations (Faraway, 2006). Values of Cook's distance > 1 may require further consideration.

2.4.2 Pre-Modelling Analysis: Exploratory Data Analysis (EDA)

Before attempting to run the models, it is important to assess the patterns in the raw data. Exploratory Data Analysis (EDA) includes a set of graphical plots that help find patterns in data (Dytham, 2011). It is based on robust and nonparametric methods and therefore it is less sensitive to nonlinearity. In addition to calculating summary statistics to obtain the mean, variance, standard deviation and range of data, a series of commonly used plots are produced such as histograms and boxplots to show distribution of data and scatterplots to show correlation between variables. Detailed summary statistics of all data, including environmental variables and acoustic data obtained with both hydrophones, are presented in Appendix Tables A.2 - A.18 because of the large quantity of information. Some summary statistics are given in Chapter 5.

2.4.2.1 Correlation analysis of the variables

A Pearson's Rank Correlation test was carried out between each response variable and each predictor variable (Appendix Table A.19a-b). In Chapter 3, the relationship between Received Level as a response variable in the 1/3 octave band and each of the predictor variables was investigated. As an example, the relationships between the RL for frequency band 17.8Hz-22.4Hz (centred on 20Hz) and each of the predictor variables are shown in Figures 2.6 - 2.8. Relationships for the other frequency bands are shown in Appendix Figs A.5-A.12. The plots in Figs. 2.6 - 2.8 show three outliers corresponding to low received levels of 65 and 67 dB re 1μPa. These data were obtained from a deployment that failed to record continuously during all the days specified in the scheduled setting and therefore this might be the origin of the unusual readings. In Chapters 5 and 6, as described in section 2.3.1.1., the RL in nine frequency bands were used as covariates. Figures 2.9 - 2.13 show scatterplots of whistle count against all covariates considered in the models in Chapters 5 and 6.

In addition, all the explanatory variables (environmental, biological, temporal, spatial, and acoustic) were tested for correlation between each other so that including highly correlated explanatory variables in the models could be avoided. The values obtained are given in Tables A.19a and A.19b. Any r-value between 0.5 and 1.0 or between -1.0 and -0.5 was taken as a strong correlation and these two variables would not be included in the same model. If there was an important biological reason to include one of these variables showing correlation, only one of that pair was included in the first model containing most of the variables. The next section explains steps to avoid multicollinearity in these cases.

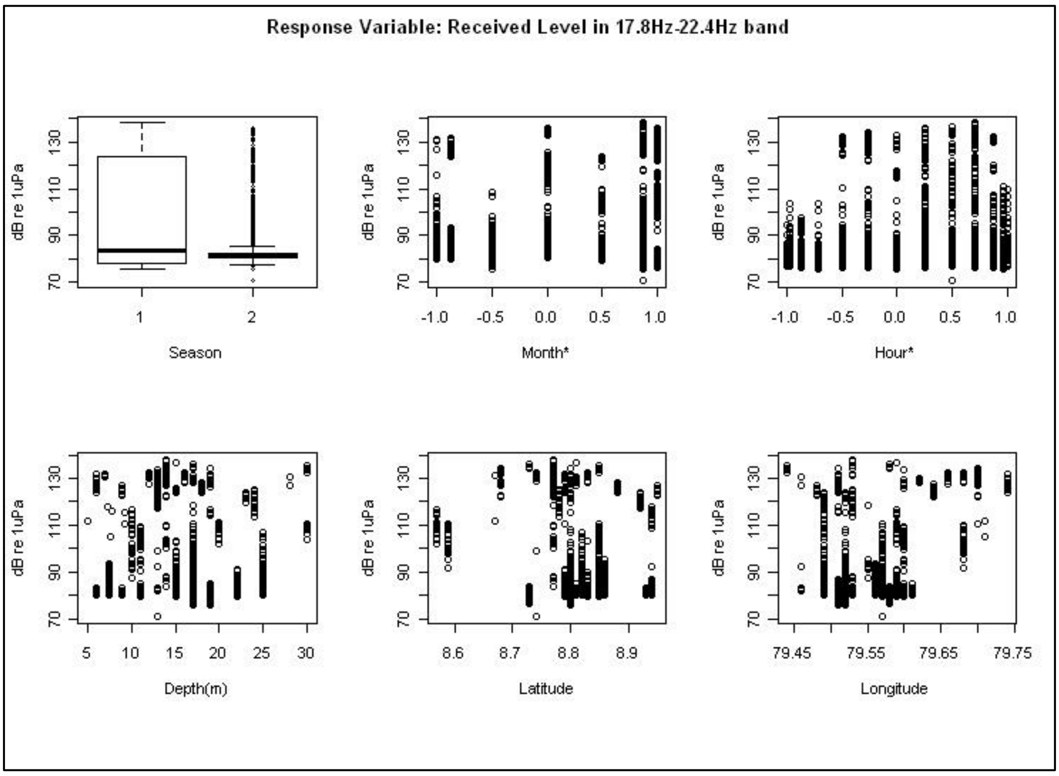

Fig. 2.6 Scatterplots showing the correlation between the response variable "Received Level (dB re 1µPa)" for the 17.8Hz-22.4Hz band (y-axis) against Season (Dry=1, Wet=2), Month (circular month= sine of month as a proportion of a year), Hour (circular hour=sine of hour as a proportion of a day), Depth (m), Latitude and Longitude (x-axis.

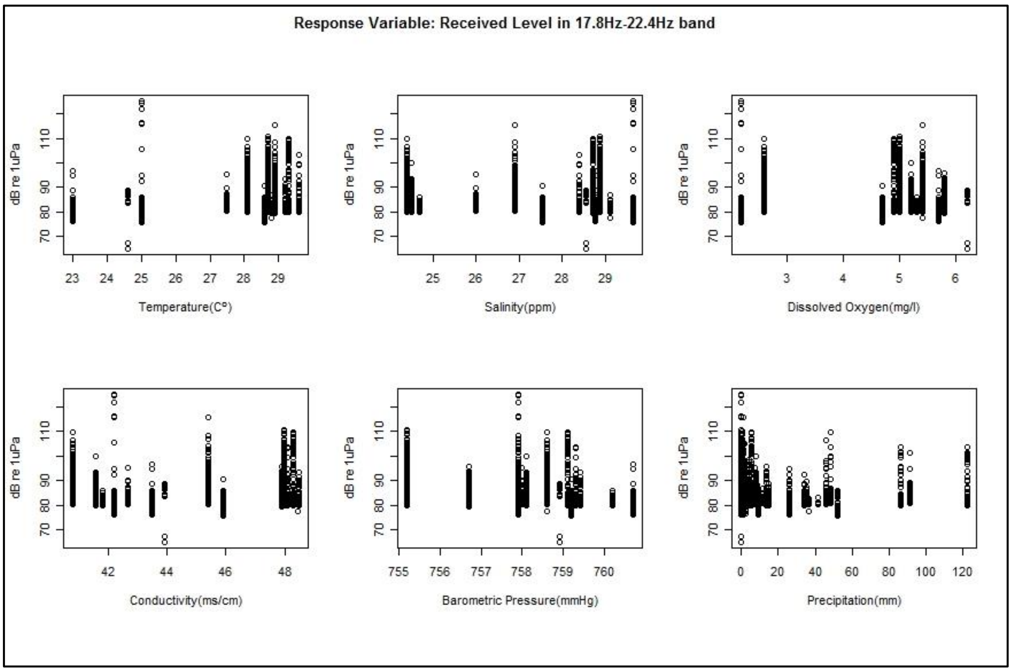

Fig. 2.7 Scatterplots showing the correlation between the response variable "Received Level (dB re 1µPa)" for the 17.8Hz-22.4Hz band against Temperature (Cº), Salinity (ppm), Dissolved Oxygen (mg/l), Conductivity (mg/cm), Barometric pressure (mmHg) and Precipitation (mm).

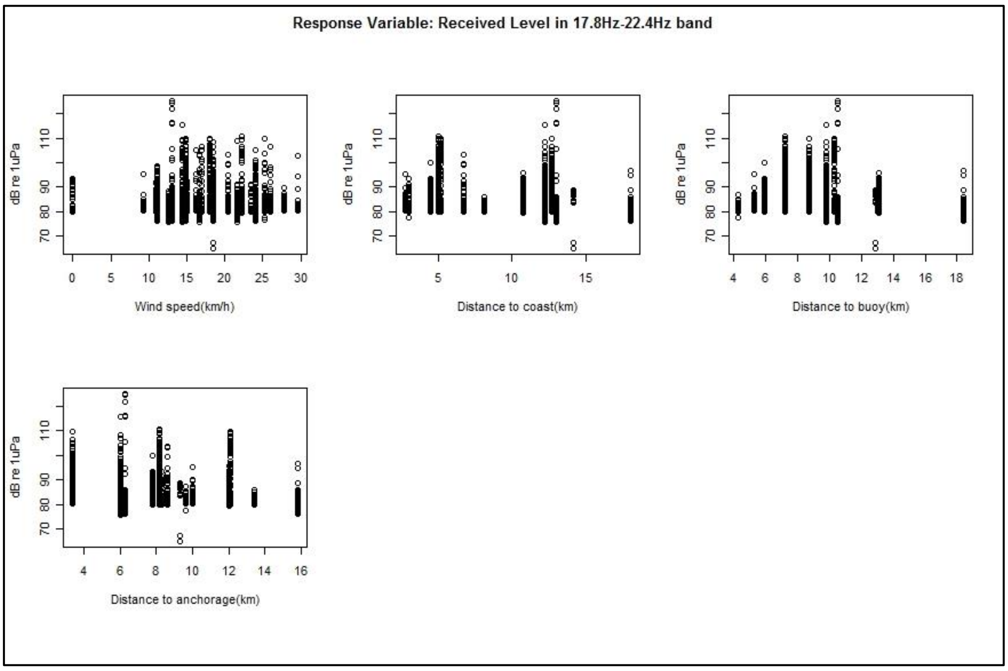

Fig. 2.8 Scatterplots showing the correlation between the response variable "Received Level (dB re 1uPa)" for the 17.8Hz-22.4Hz band against Wind Speed (km/h), Distance to coast (km), Distance to buoy (km) and Distance to anchorage (km).

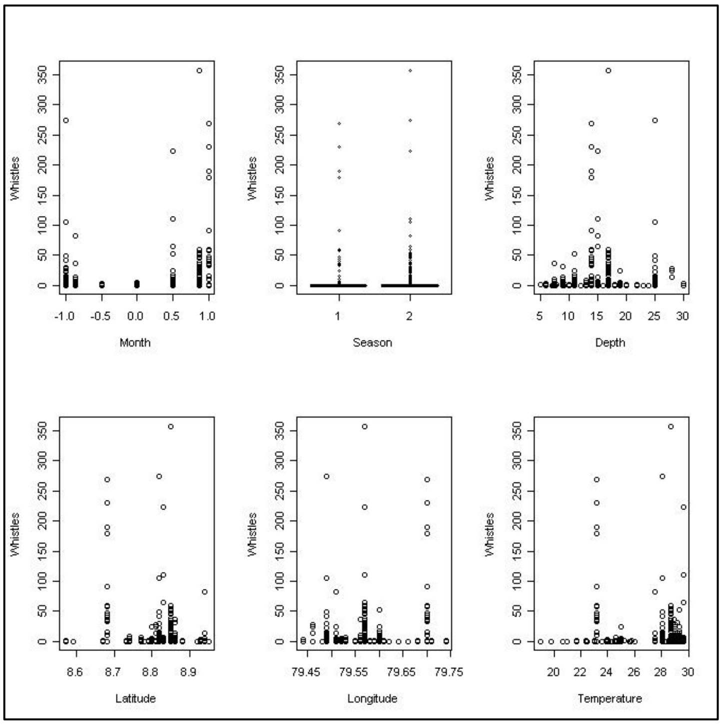

Fig. 2.9 Scatterplots showing the correlation between the response variable “Whistles” against Month, Season, Depth (m), Latitude, Longitude and Temperature (Cº).

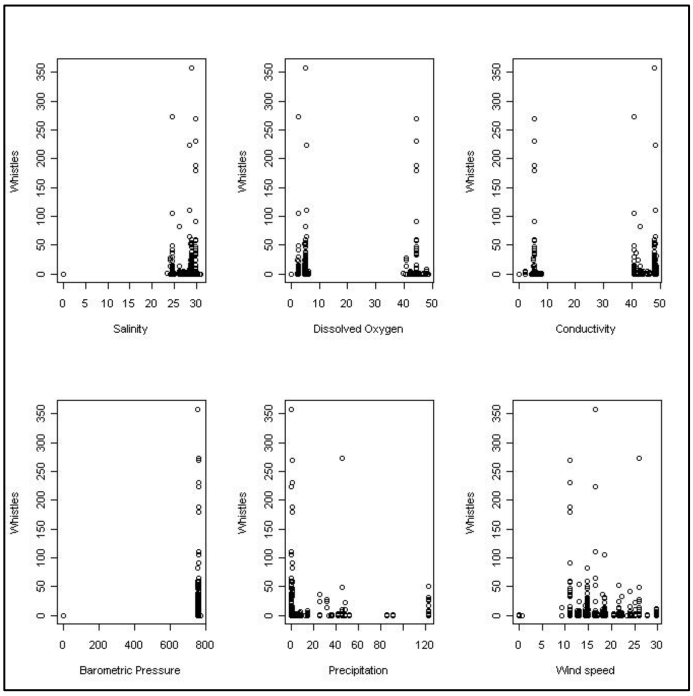

Fig. 2.10 Scatterplots showing the correlation between the response variable “Whistles” against Salinity, Dissolved Oxygen, Conductivity, Barometric Pressure, Precipitation and Wind speed.

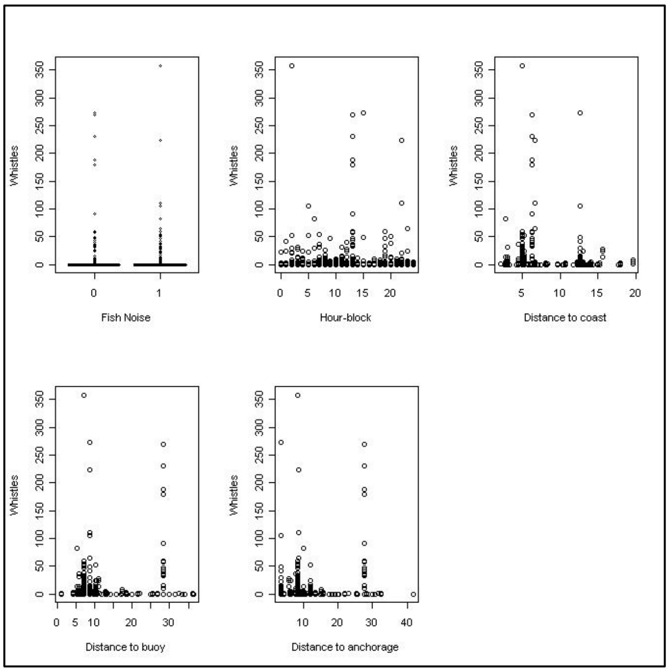

Fig. 2. 11 Scatterplots showing the correlation between the response variable "Whistles" against Fish Noise, Hour, Distance to coast (km), Distance to buoy (km), Distance to anchorage (km).

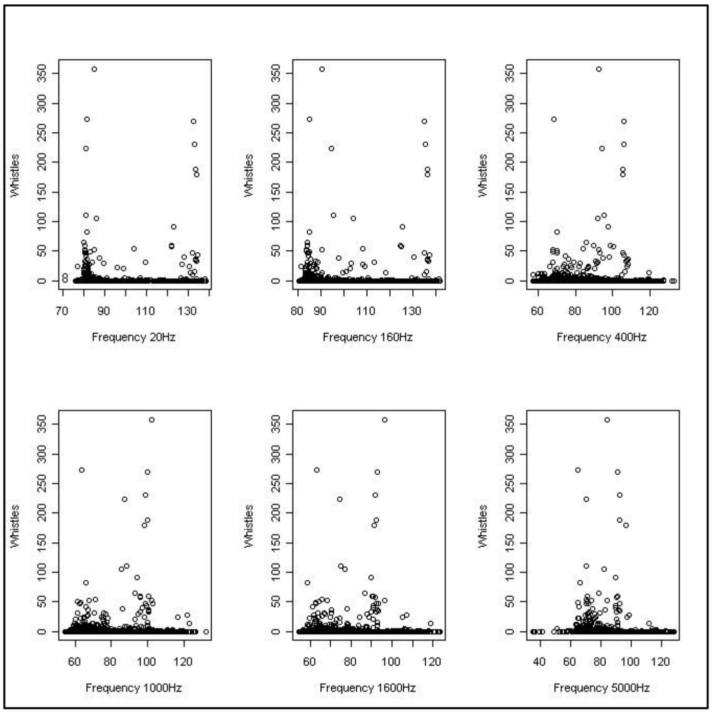

Fig. 2.12 Scatterplots showing the correlation between the response variable "Whistles" against centre frequency 20 Hz, 160 Hz, 400 Hz, 1,000 Hz, 1,600Hz, and 5,000Hz.

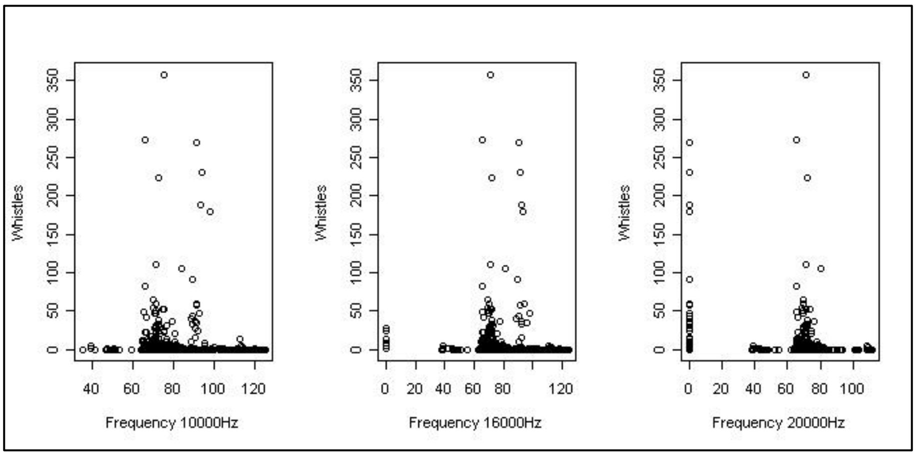

Fig. 2. 13 Scatterplots showing the correlation between the response variable "Whistles" against centre frequency 10,000Hz, 16,000 Hz, and 20,000 Hz.

2.4.2.2. Multicollinearity: Variance Inflation Factor

Multicollinearity is the situation in which two or more of the independent (explanatory) variables are correlated, meaning that a particular variable may be correlated with some linear combination of two or more other variables, while not necessarily correlated with any of the other variables alone. Some correlated variables were included in some of the models when they were considered biologically important. To investigate multicollinearity of these variables included in the model, a Variance Inflation Factor (VIF) was calculated for each term in a fitted model. The VIF is a measure of how much the variance increases if the predictor variables are correlated. If the VIF for a variable was greater than 5, that model was not considered further.

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CHAPTER 3

The underwater acoustic environment of the Panama Canal region

A profile of background noise

ABSTRACT

Noise generated from ships could threaten marine organisms that depend on natural sounds especially in coastal environments. An average of 14,500 ships transit the region of the Panama Canal each year but the background noise generated by this activity is unknown; an assessment is the first step to identify if the noise contribution may impose a threat to marine life. Acoustic data were collected at 101 sites located at various distances and depths from the designated shipping region to investigate temporal and spatial variation in background noise. Data collection spanned an entire annual cycle (2010-2011) with a total of 114 recording days. Analysis of received sound levels was carried out using nine 1/3 Octave bands. The highest sound pressure levels of 86 (SD=5) dB re 1µPa were found at the 1/3 octave band centred on 160 Hz and the maximum reported received level was 141dB re 1µPa at the 1/3 octave band centred on 1000Hz. There was no significant diurnal variation in sound pressure levels among frequencies; however there was a trend for sound pressure level to be greater at night than during the day at centre frequencies of 400Hz, 1000Hz and 1600Hz. Inspection of spectrograms suggested that the diurnal variation was of biological origin. There was no significant seasonal variation although there was a wide range in sound pressure level between centre frequencies of 400Hz and 5000Hz between the wet and the dry season. The data suggest that ambient sound in the vicinity of the Panama Canal is characterised by shipping activity and biological activity, potentially also by wind and waves, whereas sound levels in frequency bands between 5000-16000 Hz is mainly defined by local vessel

traffic activities. Overall, the area showed consistency in sound pressure levels for most frequency bands of background sound when compared to other studies in shallow waters. This study presents a first description of the ambient sound in this region, one of the busiest commercial shipping areas in the world.

3.1 INTRODUCTION

Ambient noise in the ocean is the integration of many individual sources of differing intensity and at widely varying ranges from the point at which measurements are made (Nystuen et al., 2010) (See Chapter 2). These sources include biological sounds such as those produced by fish, crustaceans or marine mammals; sounds from physical sources (weather) caused by waves, wind, tides, ice or rain; and anthropogenic sound from ships, small vessels and many different forms of industry, including sources on land and in the air (Knudsen *et al.*, 1948; Urick, 1984; Dahl *et al.*, 2007; Poikonen and Madekivi, 2010; Reeder *et al.*, 2011). Variation in ambient sound can also be a function of depth (Wenz, 1962; Perrone, 1970; Poikonen, 2011), pH (Brewer and Hester, 2009; Udovydchenkov *et al.*, 2010), salinity (Poikonen and Madekivi, 2010), breaking surf (Wilson *et al.*, 1985), tidal fluctuations (Wenz, 1962), and temperature (Ainslie, 2011).

Rain is one of the main physical sources of sound underwater, especially at mid to high frequencies (Nystuen, 2001). Rainfall creates noise at frequencies between 1 kHz and 50 kHz (Barry and Nystuen, 2004) depending on the size of the droplets and on its impact velocity with the water surface (Medwin *et al.*, 1992; Au and Hastings, 2008b). In contrast, wind blowing at >6 knots is expected to be the dominant sound source at 20 Hz and 20 kHz (Wenz, 1962; Burgess and Kewley, 1983; Nystuen *et al.*, 2010; Reeder *et al.*, 2011). In shallow waters (<200m), wind speed is the primary source of variation in ambient noise (Richardson *et al.*, 1995c) and, at frequencies above 500Hz, can be 5-10dB greater than in deeper waters (Urick, 1984).

Biological sounds, especially broadband impulses produced by snapping shrimp can dominate ambient sound at frequencies as high as 100 kHz in warm shallow waters (Love and Proudfoot, 1946; Johnson *et al.*, 1947; Latha *et al.*, 2005; Chitre *et al.*, 2006; Radford *et al.*, 2008). Most sounds produced by fish are of low-mid frequency (<1 kHz, Au and

Hastings, 2010). Different species of fish make distinct sounds at different sound source levels and in some species, spawning and breeding seasons can impose seasonal changes (Fish and Cummings, 1972; Mann and Grothues, 2009). Some of the most common fish to create sound are within the groups of grunt fishes, jacks, catfishes, toadfishes, parrotfishes, snappers, croakers, and drums. Ainslie (2011a) speculated that the distribution of fish with swim bladders in the water column could cause significant variation in underwater sound transmission because of the capability of swim bladders to attenuate sound transmission from low frequency sources. Marine mammals are also a source of biological sound (Richardson *et al*., 1995). In general, baleen whales produce intense, low-frequency sounds (lower than 1 kHz) but their vocalizations can reach 25 kHz (Au *et al.*, 2000). Toothed whales produce sounds mainly between 1 kHz and 25 kHz, but they also use higher frequency (up to 150 kHz) sounds for echolocation (Oswald *et al.*, 2008). Shipping traffic is the main source of anthropogenic noise at low frequencies and in some regions it could be the principal sound source (Wenz, 1962; Hildebrand, 2004a; Ross, 2005; Dotinga and Oude, 2007). The International Maritime Organisation (IMO) and several recent studies have recognized that shipping noise is a possible threat to some marine mammals and marine ecosystems in general (Au and Perryman, 1982a; Croll *et al.*, 2001; Erbe, 2002; Barlow and Gisiner, 2006; McDonald *et al.*, 2006; Thomas, 2007; Hatch *et al.*, 2008; Southall and Scholik-Schlomer, 2008; Andre *et al.*, 2011; Chapman and Price, 2011; Merchant *et al.*, 2012). According to Zakarauskas *et al.* (1990), shallow water ambient noise is more likely to be caused by local vessel and ship traffic, whereas distant shipping is the main cause in deep water. The areas sampled in this study are classed as shallow water because the maximum depth of the seabed is 50 m (Fig.2.2).

There is a high volume of ship traffic near both of the entrances of the Panama Canal. Large vessels that use the canal are constrained in size by the dimensions of the locks (34 meters wide, 320 meters long and 26 meters deep) but this includes most types of shipping. These vessels are present within the shipping lanes associated with the Panama Canal (Panama Canal, 2012) and this is possibly the greatest concentration of active shipping anywhere in the world. Nevertheless, there are no official established routes for ships that enter and exit the canal to follow and, as a consequence, there is concern about vessels colliding with cetaceans. Recently, a preliminary study was carried out by the local government attempting to establish how the non-specific routes used by large commercial vessels entering and exiting the channel sometimes overlap with those of humpback whales migrating into the area (Ameer and Linden, 2008; Black, 2012). For the purpose of this study, I attempted to obtain specific AIS tracks of the ships approaching the area of the study where the hydrophones where located and on the date they were recording. Unfortunately the Panama Canal Authority was unable to supply this information and it was not possible to investigate the relationship between ship tracks and background noise.

Large vessels generate low frequency noise which may interfere with communication in some species of whale. It has also been documented that whale/dolphin watching activities result in stress or injury due to speed boats getting too close to the groups, but less attention is paid to the disturbance caused by noise from these small boats affecting their communication (Richardson *et al.*, 1995a; Ameer and Linden, 2008).

Ships generally create noise by propeller action, propulsion machinery and hydraulic flow over the hull. In general, large vessels produce sounds in the frequency range of 5 - 500Hz, up to 200 dB re 1µPa at 1m, whereas small to mid-size vessels produce sounds in the range of 100Hz - 5kHz, up to 175 dB re 1µPa at 1m (Richardson *et al.*, 1995a). At low speed, the noise is almost completely generated by the engine but at high speeds, the sources come from the main engine, blade rate and propeller cavitation. Propeller cavitation is produced when ships are accelerating or traveling at high speed and the sounds account for 80-85% of radiated noise (Arveson and Vendittis, 2000; Hildebrand, 2004b; Southall and Scholik-Schlomer, 2008. The noise level generally increases with ship size and speed (Evans, 2003) and propeller depth (Arveson and Vendittis, 2000). In the region of the Panama Canal entrances, I expect the sound spectrum from ships to be mainly consistent with large vessels moving at slow speeds, which occurs upon passing the buoys to enter the channel. I tested the hypothesis that received levels (RL) in the low frequency bands would vary with distance from shipping areas (distance to anchorage) and with distance from entrance buoys.

The increase of shipping noise in the world’s oceans has been a topic of increased awareness in the past two decades. It is a matter of growing concern that shipping noise is contributing to detrimental changes in marine environments, especially for marine mammals, whose sounds may be masked by background noise of similar frequencies (Clark *et al*., 2009). In the long term, shipping noise may also affect coral reef communities and fish (Andre et al., 2011; Merchant et al., 2012).

There is still a lack of information on how exposure to anthropogenic noise affects marine mammals, fish and marine ecosystems in general. The International Maritime Organization (IMO) has made recommendations ranging from technical suggestions, such as silent propeller designs, to operational changes, such as the implementation of regulatory vessel speeds, transit hours and limited whale watching (Ameer and Linden, 2008).

Anderson and Gruber (1971) carried out underwater ambient noise measurements at 30 kHz, 90 kHz and 150 kHz at different ports in the North American continent, including a brief assessment at ports located on both sides of the Panama Canal: Port of Cristobal at the Atlantic entrance and Port of Balboa at the Pacific entrance. That study described high variability in levels of noise that were characteristic of shallow waters, and attributed this to biological noise. Apart from this, there is no published study regarding shipping noise in the region of the Panama Canal, where the traffic is set to increase with the construction of the third set of locks (Panama Canal, 2012), which will allow passage of bigger ships.

The objective of this chapter is to produce a first characterization of the underwater ambient sound within the entrance on the Pacific side of the Panama Canal. To achieve this, this chapter seeks to address the following questions:

1. What is the distribution of sound energy as a function of the selected frequency bandwidths?
2. How do spectrum density levels across different frequency bandwidths vary diurnally, seasonally and spatially? What are the possible biological, environmental or anthropogenic sources of this variation?
3. What sources of sound explain variation in received sound levels at each centre frequency?

It is my aim that the results of this study may be helpful in the future to mitigate the impacts of all types of anthropogenic noise in this region caused by shipping activities.

3.2 METHODS

The general data collection, data processing and data analysis methodology used is described in Chapter 2: General Methodology. Only data from the stationary bottom-based hydrophone were used. Figure 2.3 show the sampling sites where the stationary hydrophone was used to collect data.

3.2.1 Acoustic data processing

Audio data obtained from the bottom-based hydrophone (see §2.2.1.2) were analyzed using Pamguard Beta Core software v.1.10.04 (www.pamguard.org) (see §2.3.1. for details). 1/3 octave bands from 20 Hz up to 20 kHz were extracted from the recordings. To achieve this, it was necessary to adjust the calibration settings of the noise band monitor in Pamguard prior to data acquisition. Pamguard automatically enters the sample rate of the audio files (50kHz), but other calibration details needed to be manually entered: peak-peak voltage range = 0.20 V, bandwidth = 10 Hz to 25 kHz, preamplifier gain = 19.8 dB and hydrophone sensitivity = -185.9 dB re 1V/µPa. Once the calibration was set, each folder was given to Pamguard to run the audio files automatically. The output was automatically saved in a Microsoft Access database. The output included the specified statistics (mean, median, min, max, lower 95% confidence limit and upper 95% confidence limit) of the absolute received levels of the 38 1/3 octave bands from each unit of recording (150 seconds in each audio file).

For analysis, mean received levels (RL) of nine out of the 38 1/3 octave bands were selected to illustrate the variations in sound pressure levels across frequency, diurnal cycles, and seasons and at particular sites and months of the year. The centre frequencies of the 1/3 octave bands chosen were 20Hz, 160Hz, 400Hz, 1kHz, 1.6kHz, 5kHz, 10kHz,16kHz and 20kHz The means of these 1/3 octave band RL were then converted to spectrum density levels using the formula:

$$\mathbf{SDL = RL_{1/3Octave} - 10\,Log_{10}(Bandwidth).}$$

The criterion for comparison of biological sounds (i.e., selecting sounds of similar fish species found in this region) is explained in Chapter 2 (§2.3.1.). Furthermore, sounds of different types of engines (i.e., different types of vessels) were compared to those identified on site when listening with the boat hydrophone that was used in this study (§2.3.1.).

3.2.1.1. Analysis of sources of ambient sound

Audio files that provided clear signals of different sources of sound were selected to be subsampled to produce a spectrum density plot, which illustrates the contribution of sources of sound present across the frequency bands investigated in this study. Six random audio files dominated by fish noise, snapping shrimp, physical sources (light/medium rain, medium breeze, steady water movement), small boat noise, and trawler noise (each in turn), were analysed in a spectrogram. Then, a 10 second cut of the spectrum of this audio file was selected when the sound was heard and seen clearly. The selection was saved as another wav file. These six new 10-sec audio files were ran through Pamguard to analyse the 1/3 Octave bands power contribution at 1 second intervals. The output of Pamguard analysis was entered to an access file which produced 63 rows of data per octave band per source. Then, per source, the power contribution was averaged over each 1/3 octave band. Each of these means per band corresponding to each source produced a plot of average power spectra per source.

3.2.2 Environmental Data

The environmental data that were collected at each site are described in Chapter 2 (§2.2.2.1). There were data available for each of the days that the hydrophone was recording. The instruments that registered wind speed and precipitation were located on land (8.966667°N, 79.56667°W, Figure 2.4) at 6-40 km from sampling points.

3.2.3 Statistical analysis

The statistical analysis followed the methods described in Chapter 2 (§2.4)

Generalized Additive Models (GAM) (described in §2.4) were used to relate received levels of background sound at each 1/3 octave band (response variable) to explanatory spatial variables (distance to the centre of the anchorage, distance to the coastline, distance to the entrance buoys and depth; these variables offer 1-14 observations because they are the distance measurements to the 14 different sites and therefore resulted in 14 different measurements per landmark), temporal variables (time of day, month, season) and environmental variables (wind speed and rainfall; measured daily corresponding to each recorded deployment day). Models were fitted to investigate the effects of distance from the shipping anchorage, distance to the entrance buoys, and to the coastline (correlated with depth) on the sound levels at the different 1/3 octave bands. Season was entered as a factor and all other explanatory temporal and spatial variables were included in the model as continuous variables.

3.3 RESULTS

Appendix Tables A.2-A.18 include summary statistics for all variables in relation to deployments of the hydrophone. In total, 408 hours of recordings were collected with the bottom-based hydrophone system from 15 deployments at 14 sites (Fig.2.3). The number of days and hours recorded varied in each deployment.

3.3.1 Sound pressure level variation

There was significant variation in sound pressure level (SPL) across the frequency bands (Fig. 3.1; Table 3.1, ANOVA, df = 8, $p < 0.001$). Results (reported as the mean of received levels (RL) with their standard deviations) showed the highest SPL in the 160Hz band. Sound pressure levels increased from an average of approximately 82 ± 4 dB re 1µPa at 20 Hz to 86 ± 5 dB re 1µPa at 160 Hz, which was the highest mean recorded. The mean RL declined to 77± 9 dB re 1µPa at 400 Hz, 71± 9 dB re 1µPa at 1000 Hz and 70 ± 8 dB re 1µPa at 1600 Hz and then increased to 75 ± 8 dB re 1µPa at 5000 Hz. There was a steady decline in RL as frequency increased from 5000 Hz to 72± 5 dB re 1µPa at 20000 Hz.

Figure 3.1 shows that there is variation in mean RL among the different selected 1/3 octave bands; however, there was little variation within each band. The standard deviations given in Table 3.1 show that RL values were distributed close to the mean for most 1/3 octave bands, but that there was greater variation for centre frequencies 400Hz, 1000Hz, 1600Hz, 5000Hz and 10,000Hz.

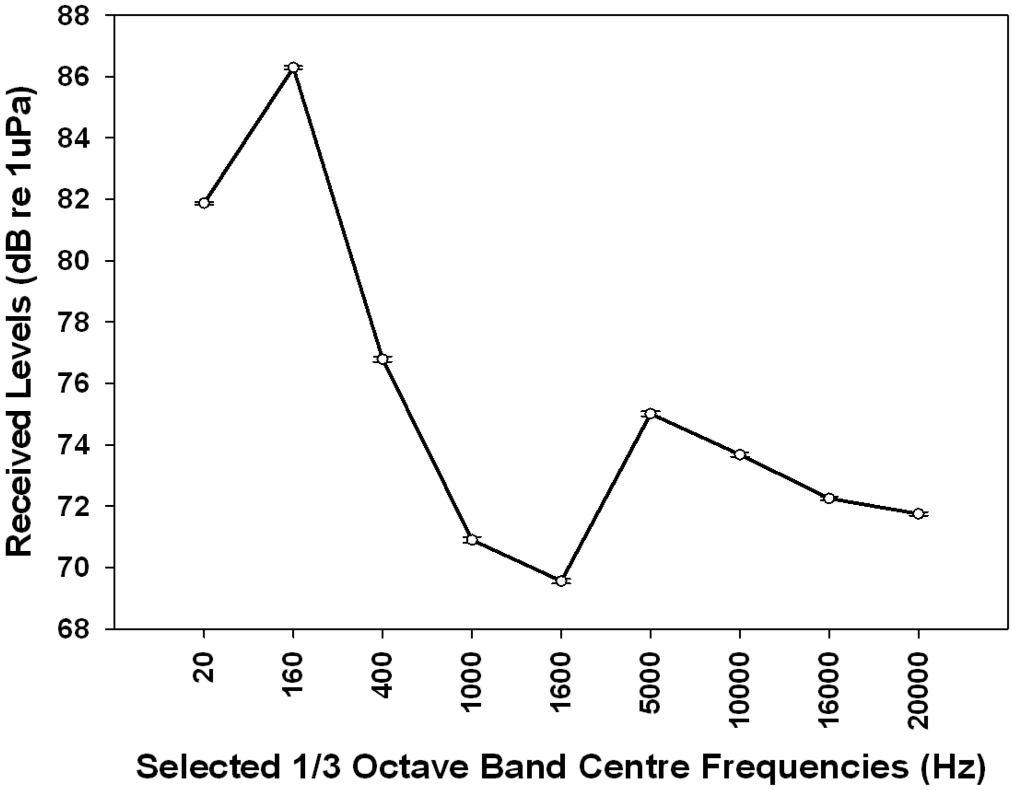


Fig. 3.1. Mean received sound levels (RL) recorded with the bottom-based hydrophone (DSG) across nine 1/3 octave bands. The graph shows the total mean RL at each centre frequency extracted from all the recordings collected from 15 deployments in the course of 12 months and in a 24 hour cycle.

	RL @ 20 Hz	RL @ 160 Hz	RL @ 400 Hz	RL @ 1000 Hz	RL @ 1600 Hz	RL @ 5000 Hz	RL @ 10,000 Hz	RL @ 16,000 Hz	RL @ 20, 000Hz
	dB re 1uPa	dB re 1uPa	dB re 1uPa	dB re 1uPa	dB re 1uPa	dB re 1uPa	dB re 1uPa	dB re 1uPa	dB re 1uPa
MEAN	81.87	86.29	76.79	70.90	69.56	75.01	73.68	72.25	71.75
MEDIAN	81	85	76	69	68	74	73	72	72
MIN	65	71	56	53	54	34	35	38	38
MAX	125	130	125	141	122	124	107	107	106
SD	3.81	4.84	8.94	9.23	7.85	7.91	6.48	5.70	5.31
SE	0.04	0.05	0.09	0.10	0.08	0.08	0.07	0.06	0.06
1st-3rd Quartiles	*80.25-82.23*	*83.57-87.13*	*69.59-82.07*	*64.11-76.70*	*63.87-74.84*	*68.36-82.35*	*68.39-79.34*	*67.59-77.03*	*67.38-76.20*

Table 3.1. Summary statistics for received levels of each of the centre frequencies (9311 observations per centre frequency), showing the mean, median, minimum and maximum

received level, and the standard deviation (SD), standard error (SE) and 95% confidence intervals.

3.3.1.1 Background noise models

The variation in RL for each of the 1/3 octave bands was modelled with Generalized Additive Models to explore which environmental, temporal or spatial variables explain most variation in the data. Results are shown in Table 3.2, where each row describes the variables retained in the model for each frequency bandwidth. Precipitation was retained by the best model in all of the bandwidths, and wind speed in all except those centered on 20 Hz and 160 Hz. Month was retained in all except center frequency 400 Hz. Hour was retained in all except center frequencies 10,000 Hz and above, and the covariate retained within the spatial category varied depended on the bandwidth. The models for bandwidths at higher frequencies explained more of the deviance (variation in the data) than those at lower frequencies.

Bandwidth	Deviance Explained	Variables			
		Temporal	*Time of Day*	*Spatial*	*Environmental*
17.8-22.4 Hz (C.F. 20Hz)	6%	Month	Hour	Distance to buoy	Precipitation
141-178 Hz (C.F. 160Hz)	9%	Month	Hour	Distance to buoy	Precipitation
355-447 Hz (C.F. 400Hz)	25%	Season	Hour	Distance to coast + anch	Precipitation, Wind Speed
891-1122 Hz (C.F. 1000 Hz)	21%	Month	Hour	Distance to coast	Precipitation, Wind Speed
1413-1778 Hz (C.F. 1600 Hz)	30%	Month	Hour	Distance to coast	Precipitation, Wind Speed
4467-5623 Hz (C.F. 5000 Hz)	67%	Month	Hour	Depth, Dist to Anchorage	Precipitation, Wind Speed
8913 - 11,220 Hz (C.F. 10 000Hz)	58%	Month	-	Distance to Anchorage	Precipitation, Wind Speed
14,130 - 17,780 Hz (C.F. 16 000Hz)	45%	Month	-	Distance to Coast	Precipitation
17,780 - 22, 390 Hz (C.F. 20 000Hz)	42%	Month	-	Distance to coast	Precipitation

Table 3.2 Variables retained in the best fitted GAMs for each 1/3 octave bandwidth (C.F. = centre frequency).

The plots shown in Figure 3.2. illustrate the variables that best explained the variation in received levels at each center frequency. Note that this is not a comparison among frequency bands but an analysis of how these predictors explain variability within each frequency band. Each model was fitted by limiting the number of knots to five (k=5) to restrict the amount of “wiggliness” in the plot. This was done to ensure that a clear fitted smooth relationship emerged, rather than one that was dominated by excessive variation in the response variable that did not have a reasonable explanation.

Center Frequency 20 Hz

Of the variables retained in the best model (Figure 3.2a), month and distance to buoy seem to explain the most variability in the received levels. Strong monthly variation in RL was evident. Received levels generally decreased with increasing distance from the buoy.

Center Frequency 160 Hz

Similarly to 20 Hz, RL varied through the year (by month) and, after an initial increase, decreased with increasing distance to the buoy (Fig 3.2b). However, there was a slight dip in RL at around 9-13 km from the buoy.

Center Frequency 400 Hz

The best fitting model retained the variables hour, distance to anchorage, distance to coast, wind speed and precipitation. The removal of any of these variables resulted in a poorer fit. However, Fig 3.2c shows that hour, wind speed and precipitation did not explain as much variability as did distance to anchorage and distance to coast. The former shows a generally increasing relationship between RL and distance to the anchorage (with a dip at around 10-13 km), while the latter shows a steady increase but then decreases after a distance from the coast of about 13km.

Center Frequency 1000 Hz

Received level showed the strongest relationships with month and distance to coast but all retained covariates appeared to explain quite a lot of variability in the data (Fig 3.2d). RL generally increased with distance to the coast, especially at distances greater than 10 km. RL was lower at precipitation levels between about 30-70 mm and lower at wind speeds between approximately 10-20 km/hr.

Center Frequency 1600 Hz

The variables retained in the best model for this frequency band had a similar influence on received level to 1000 Hz except for wind speed (Fig 3.2e). RL generally decreased as wind speed increased, except for the same dip at around 10-20 km/hr as for 1000 Hz. The implications of this with respect to shipping noise are discussed below.

Center Frequency 5000 Hz

The strongest relationships between received level and the candidate covariates at this frequency band were shown for distance to anchorage (higher RL at 4-8 km and >12 km and lower between 8-12 km) and depth (decreasing RL with increasing depth) (Fig 3.2f).

Center Frequency 10000 Hz

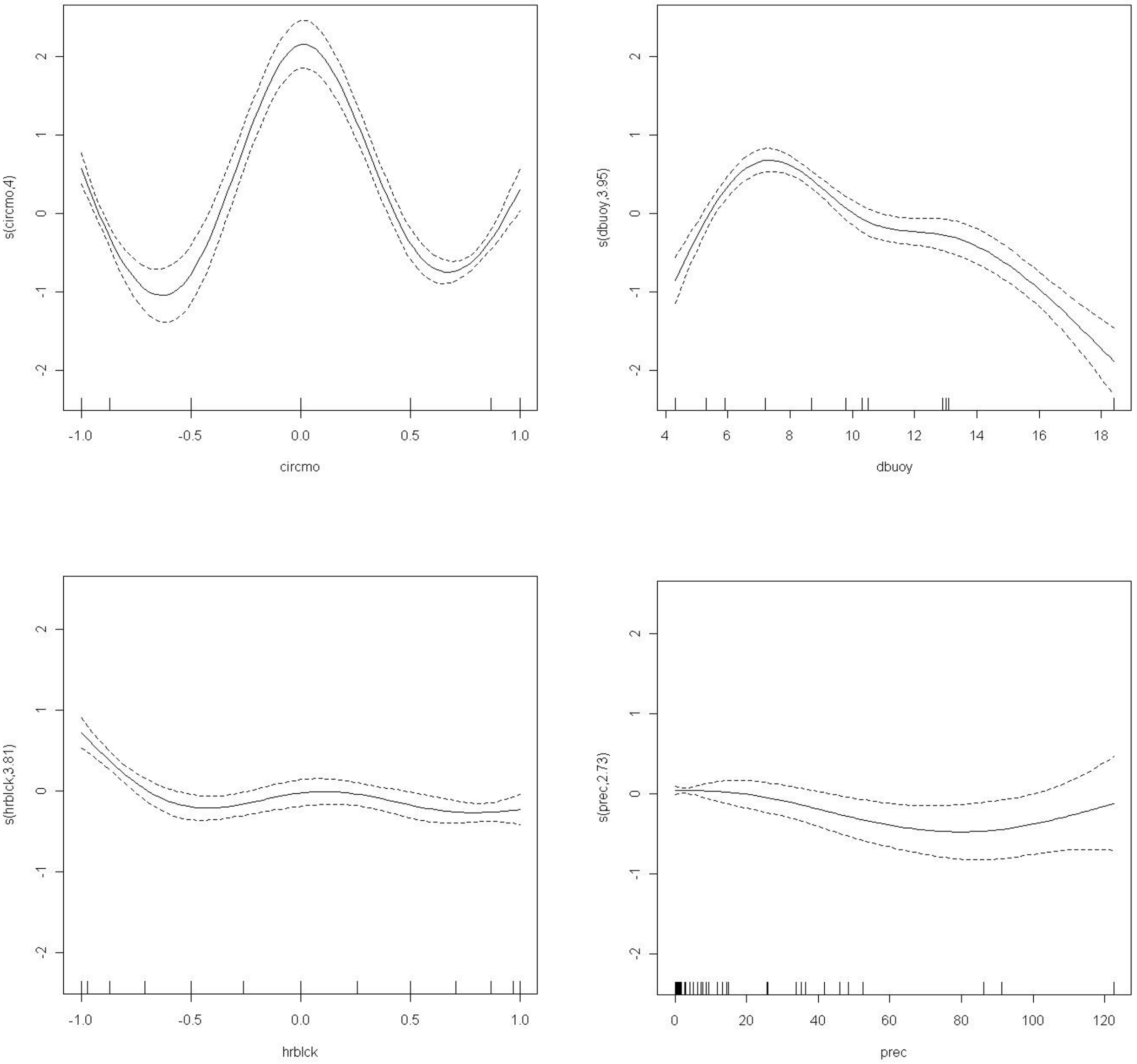
Of the covariates retained by the best model for this frequency band, month and distance to anchorage explained the most variability in the received levels (Fig 3.2g). The pattern in the relationship between RL and distance to the anchorage was similar to that for 5000 Hz.

Center Frequency 16000 Hz and 20000 Hz

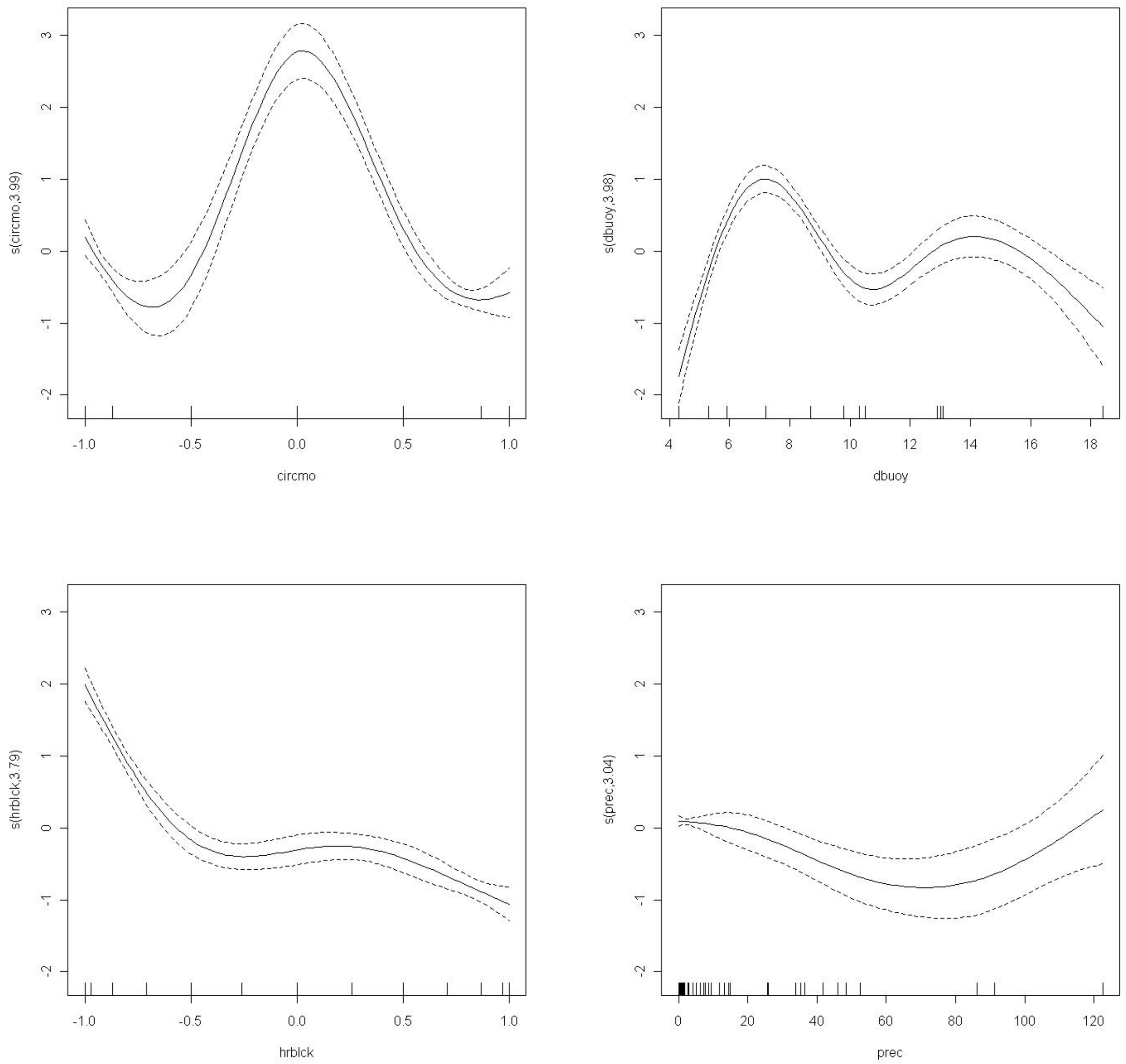
Independently, the best models for these two center frequencies showed remarkably similar patterns in the relationships between received level and the covariates (Fig 3.2h, i). Month and distance to coast explained the most variability in the data. These results show that at these higher frequencies, RL decreased as wind speed increased, an unexpected result that casts doubt on the usefulness of these remote measurements of wind speed to explain variability in RL. Models were refitted without this covariate and results showed this change had little effect on the fitted relationships with the other covariates (Table 3.2, figs. 3.2h,i).

Fig. 3.2 (a-i) GAM plots of variables retained in the best model of each of the center frequency fitted to explain variation between received levels and each of the variables as described in table 3.2. The middle line of the smooth shows the relationship between the response (RL) and the predictor variable. The dotted line represents the 95% confidence interval. Tick marks above the x-axis indicate the distribution of observations.

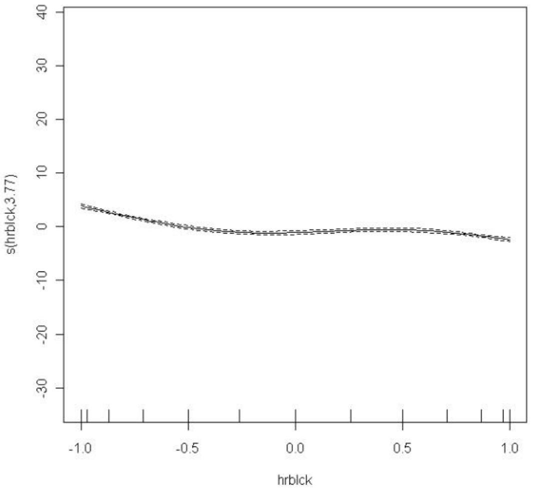
a) **GAM for f20Hz: Month (sin(month)), distance to buoy (km), hour (sin(hour)) and precipitation (mm).**

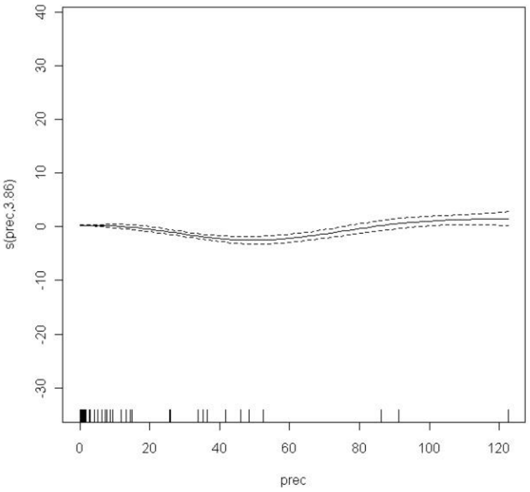


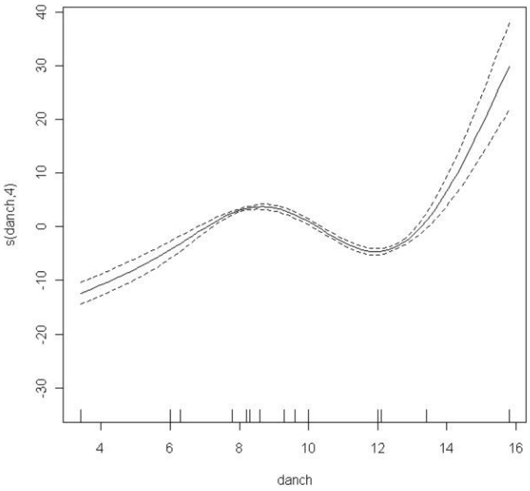
b) GAM for 160 Hz: Month (sin(month)), hour(sin(hour)), precipitation(mm), distance to buoy(km)

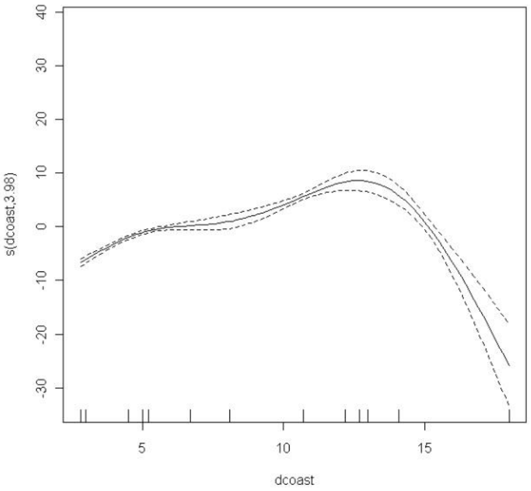


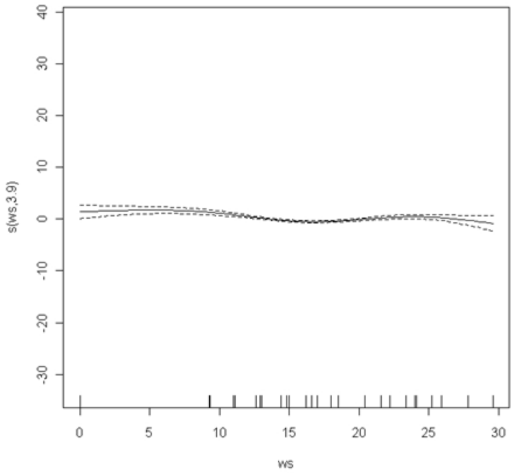
c) GAM for 400 Hz: Hour (sin(hour)), distance to anchorage(km), distance to coast (km), wind speed(km/hr), precipitation(mm).



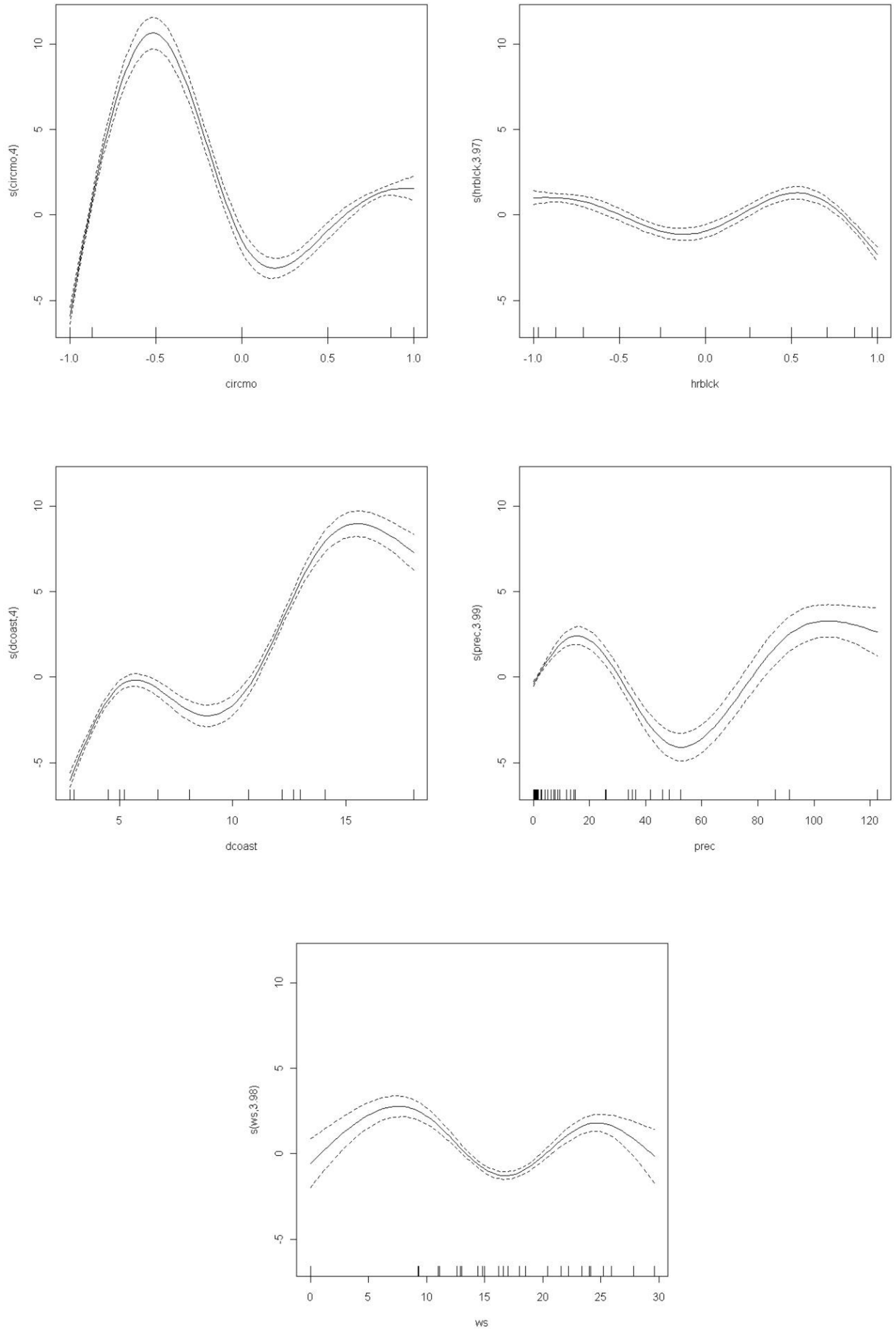




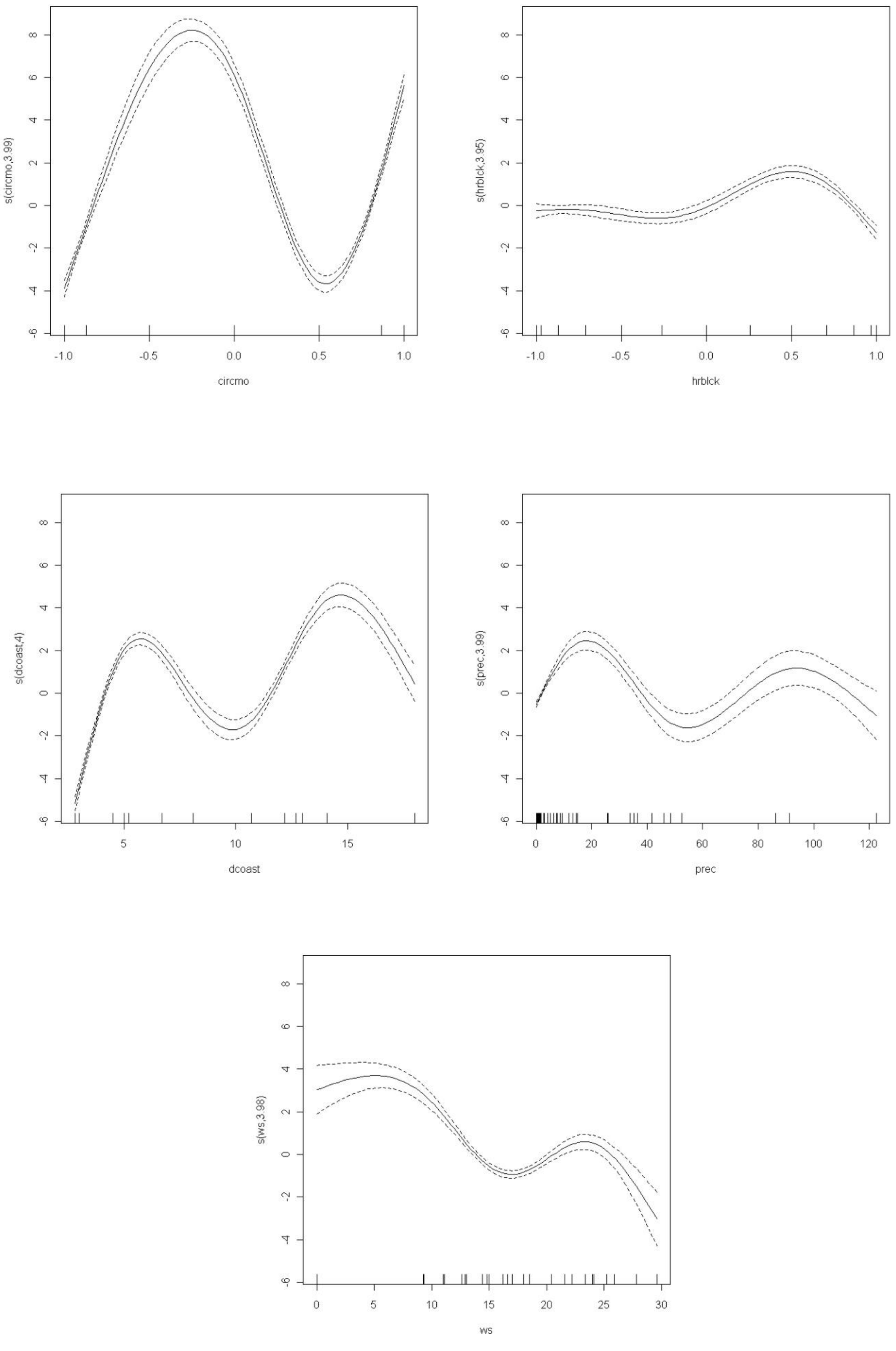




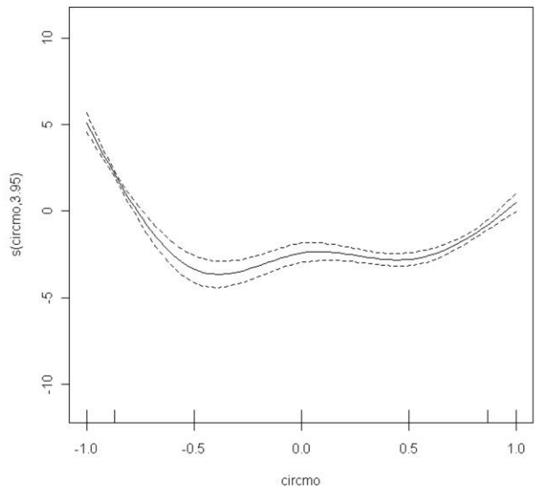
d)GAM 1000 Hz: Month(sin(month)), hour(sin(hour)), distance to coast(km), precipitation(mm), wind speed(km/hr).

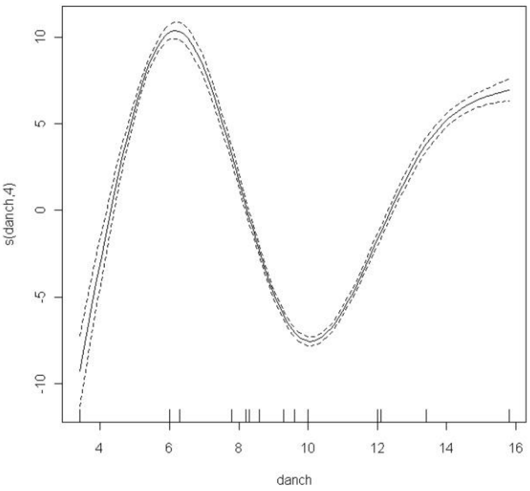


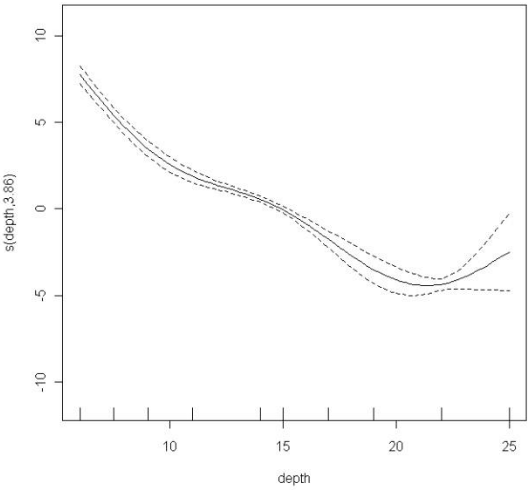
e)GAM 1600 Hz: Month(sin(month)), hour(sin(hour)), distance to coast(km), precipitation(mm), wind speed(km/hr).

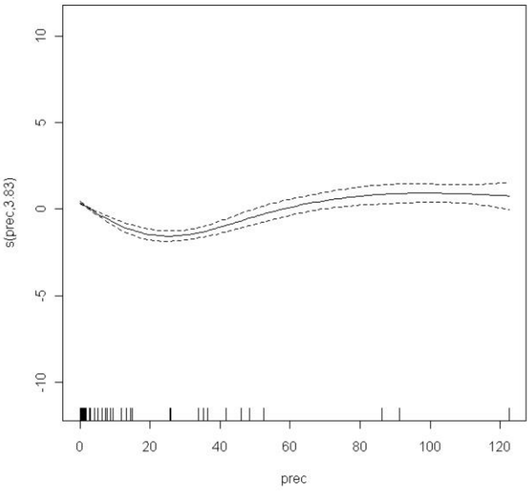


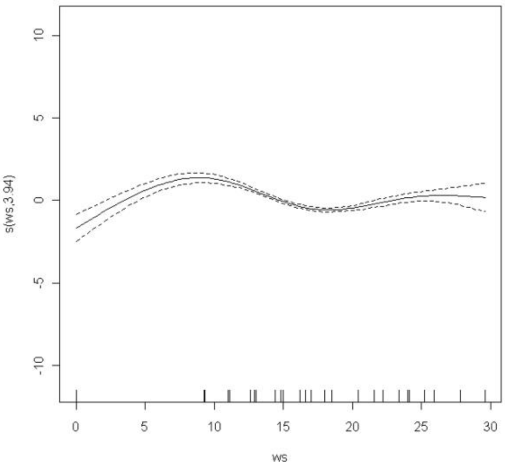
f) GAM for 5000 Hz: Month(sin(month)), distance to anchorage(km), depth(mts), precipitation(mm), wind speed(km/hr).



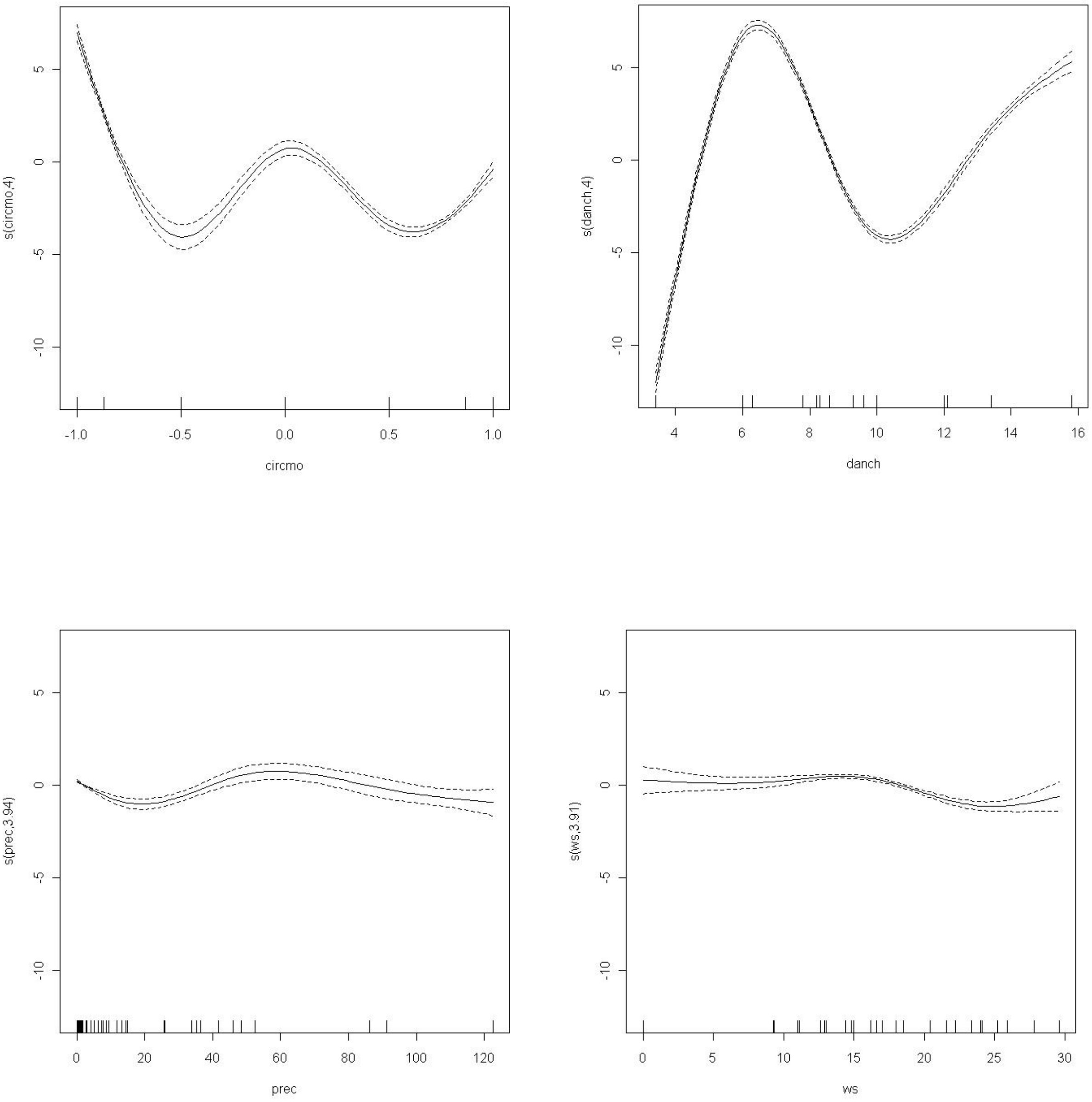




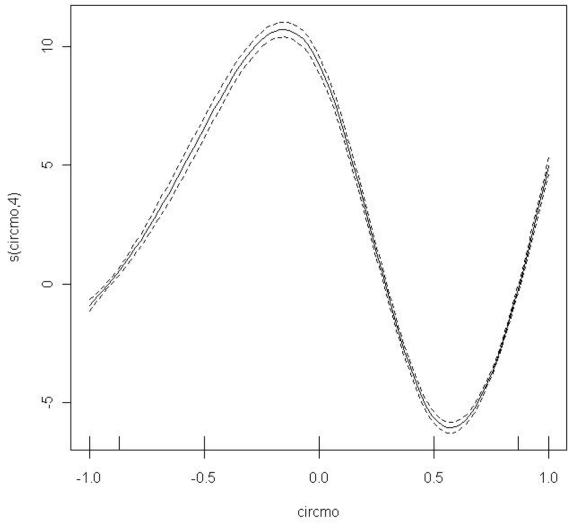


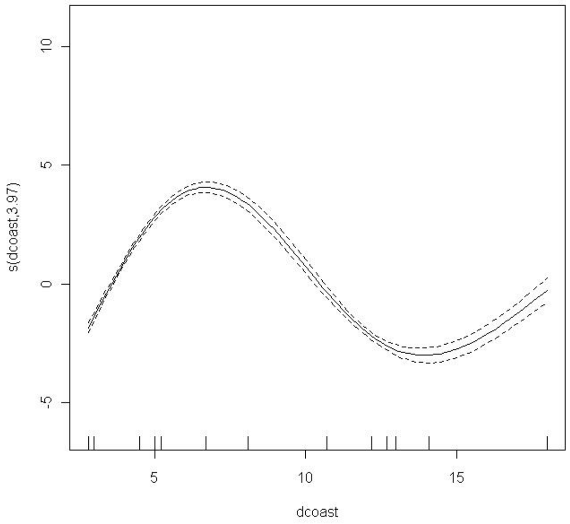


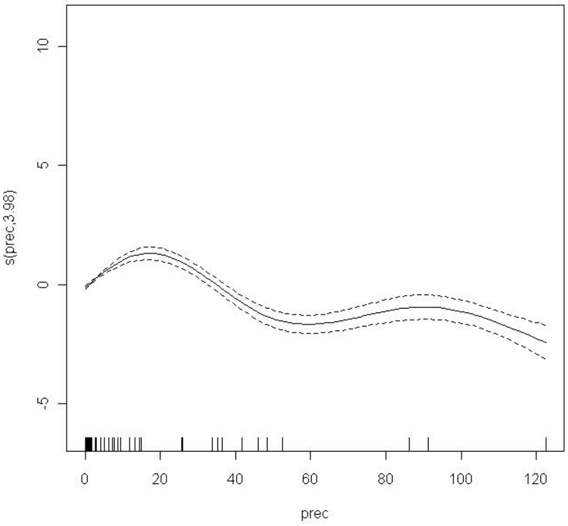
g) GAM for 10,000Hz: Month(sin(month)), distance to anchorage(m), precipitation(mm), wind speed(km/h).



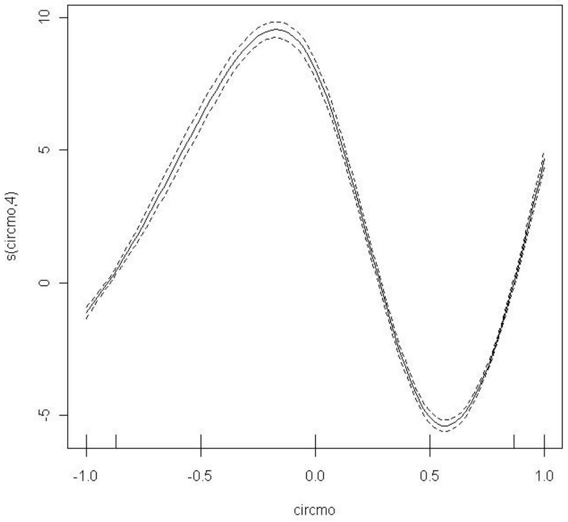
h) GAM for 16,000Hz: Month(sin(month)), distance to coast(m), and precipitation(mm.

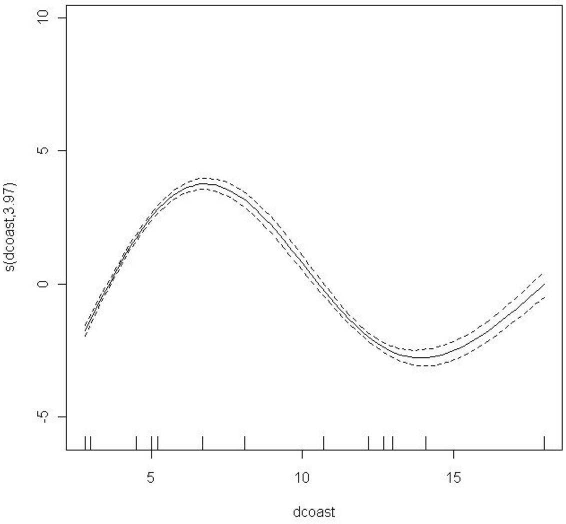


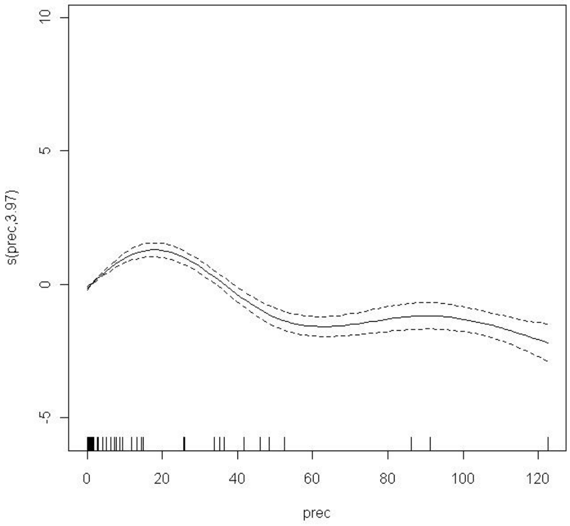




i)GAM for 20,000Hz: Month(sin(month)), distance to coast(m) and precipitation(mm.







3.3.2. Spatial variation in sound pressure levels at different frequencies

The sites where measurements were made were at different distances from the anchorage area, where we would expect the greatest concentration of ship movements, and at different distances from the coastline (see Chapter 2, §2.4.1.1.2.). Models showed that there were significant effects on RL of distance to the entrance buoys at lower frequencies (20Hz and 160Hz), effects of distance to the coast in the centre frequencies 1000Hz, 1600Hz, 16,000Hz and 20,000Hz, and effects of distance to the anchorage in the centre frequencies 400Hz, 5000Hz and 10,000Hz. There was no significant effect of depth except at the 5,000Hz centre frequency (Table 3.2).

3.3.3 Spectral Density Analysis

Figure 3.3 shows a spectral density plot describing the distribution of sound pressure as a function of frequency bandwidth. As expected, sound density decreases with increasing frequency, except for bandwidth 4,467-5,623Hz where there is a slight increase of 2 dB re 1uPa^2/Hz. Small boat noise is a common source of sound at this bandwidth. Figure 3.4 shows a 1/3 octave band level plot describing the distribution of sound pressure of each source of sound that was fairly easy to recognize when dominating the spectrum (§3.2.1.1). Although frequencies overlap for all sources, the plot shows the dominant level for a range of frequency for each source. For example, above 5 kHz sounds can be a contribution of either small boat noise or snapping shrimp (above physical sources of sound), between 400 Hz and 1.6 kHz, the plot shows fish noise contributes sound above all other sources, and between 20 Hz and 400 Hz intermittent trawler noise seems to show higher levels above other sources.

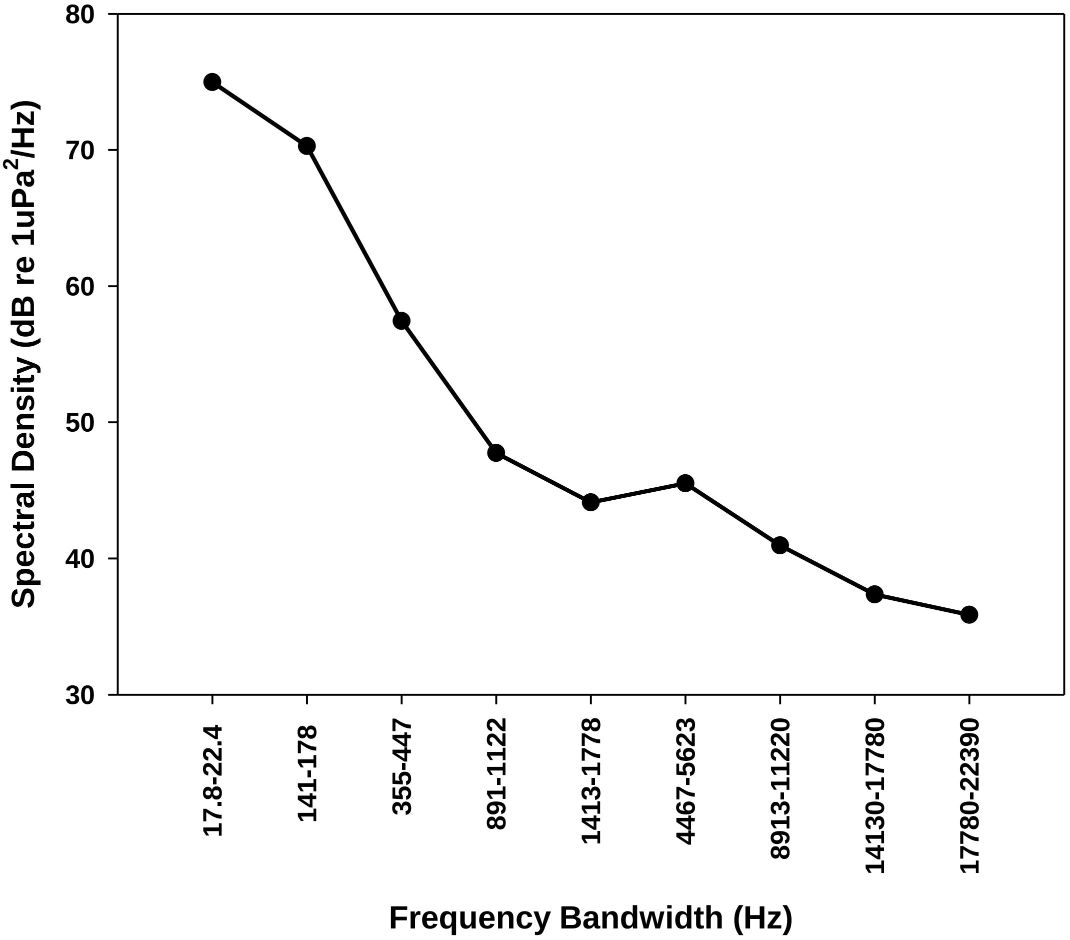


Figure 3.3. Spectral density plot showing sound pressure density versus frequency.

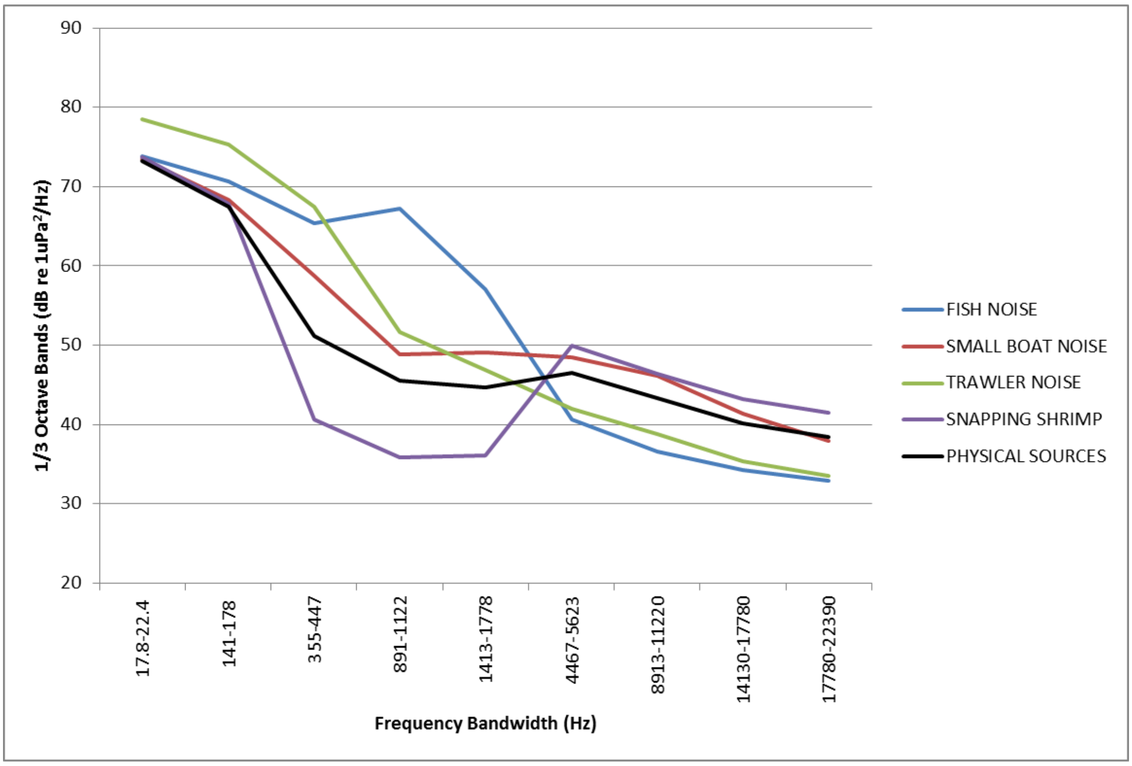


Figure 3.4. 1/3 octave band level plot of sources of sound dominant in the study. The plot shows sources of sound that presented higher levels than other sources at certain frequency ranges, however overlapping in most frequency ranges (see §3.3.3.).

3.3.4. Diurnal Variation

To investigate diurnal variation, spectrum density levels were compared between day and night. For the purpose of this study, day is defined as between 6am and 6pm, and night is defined as between 6pm and 6am. Figure 3.5 shows that SPL was higher at night-time compared to daytime at frequencies bandwidths >141-178 Hz (centre frequency 160Hz), at 14,130-17,780 Hz (centre frequency 16kHz) there was no difference and then night-time SPL was again higher than daytime SPL at 17,780-22,390 Hz (centre frequency 20kHz).

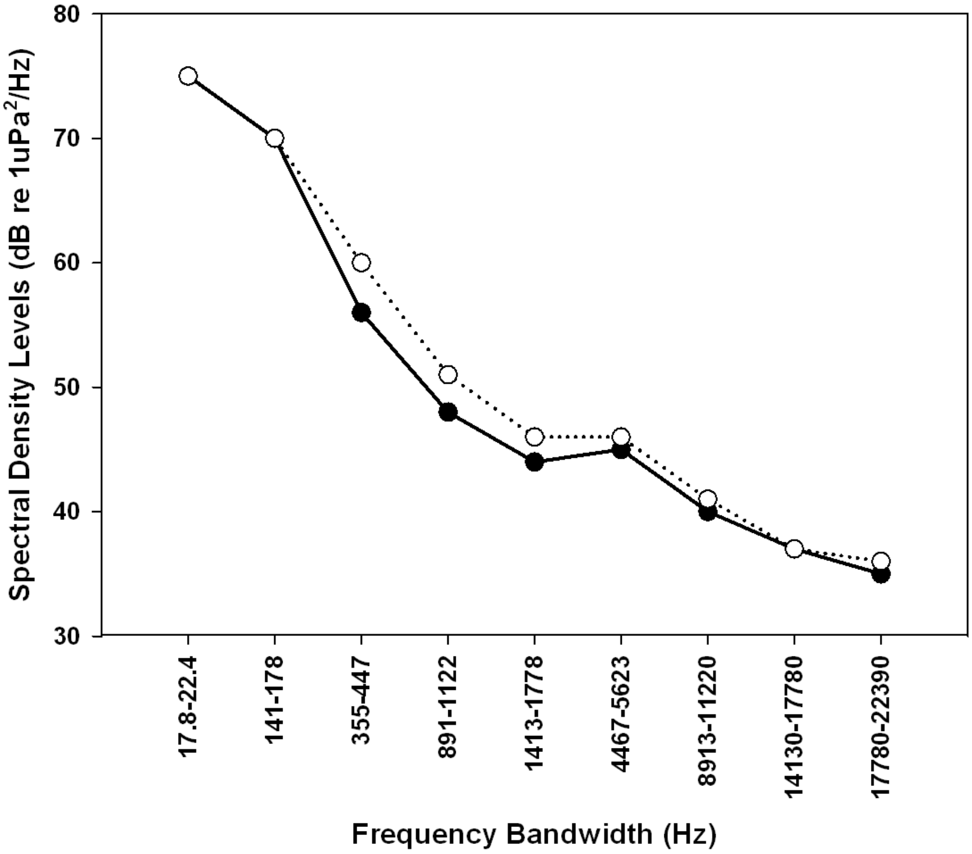


Fig. 3.5. Diurnal difference in 1/3 octave band levels from the 14 recordings using the bottom-based hydrophone. The dotted line with white circles shows night-time levels and the solid line with black circles shows daytime levels.

However, analysis of variance showed that there was no significant difference between daytime and night-time levels among frequency bandwidths (Table 3.3, *p* =0.8).

Bandwidth	Day	Night	Difference	SD	SE
17.8-22.4	75	75	0	0.2	0.1
141-178	70	70	0	0.1	0.1
355-447	56	60	4	2.6	1.8
891-1122	48	51	3	2.2	1.5
1413-1778	44	46	2	1.6	1.1
4467-5623	45	46	1	0.8	0.6
8913-11220	40	41	1	0.5	0.4
14130-17780	37	37	0	0.3	0.2
17780-22390	35	36	1	0.4	0.3
Mean	50	51			
Sum	451	463			
Variance	203	197			
Source of Variation	***Sum Squares***	***df***	***P-value***	***F crit***	
Between day&night	7.7	1.0	0.8	4.5	
Within day&night	3196	16			

Table 3.3. Summary statistics for diurnal differences in spectrum density levels. Analysis of Variance between day and night shows no statistically significant (α=0.05) differences between day and night at different frequency bandwidths.

3.3.5. Seasonal Variation

There was no significant seasonal difference in SDL between the Wet and Dry seasons among frequency bandwidths (Figure 3.6; Table 3.4, *p*=0.5).

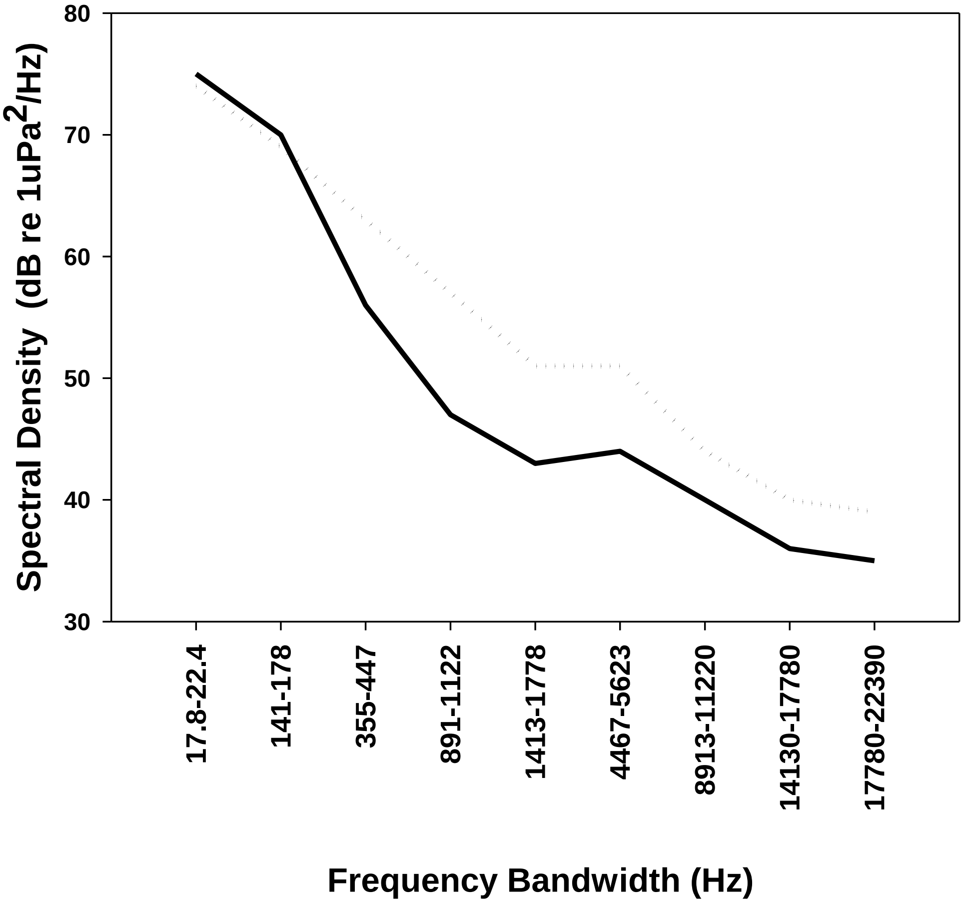


Figure 3.6. Variation in 1/3 octave band levels at different frequency bandwidths between the Wet season (solid line) and the Dry season (dotted line).

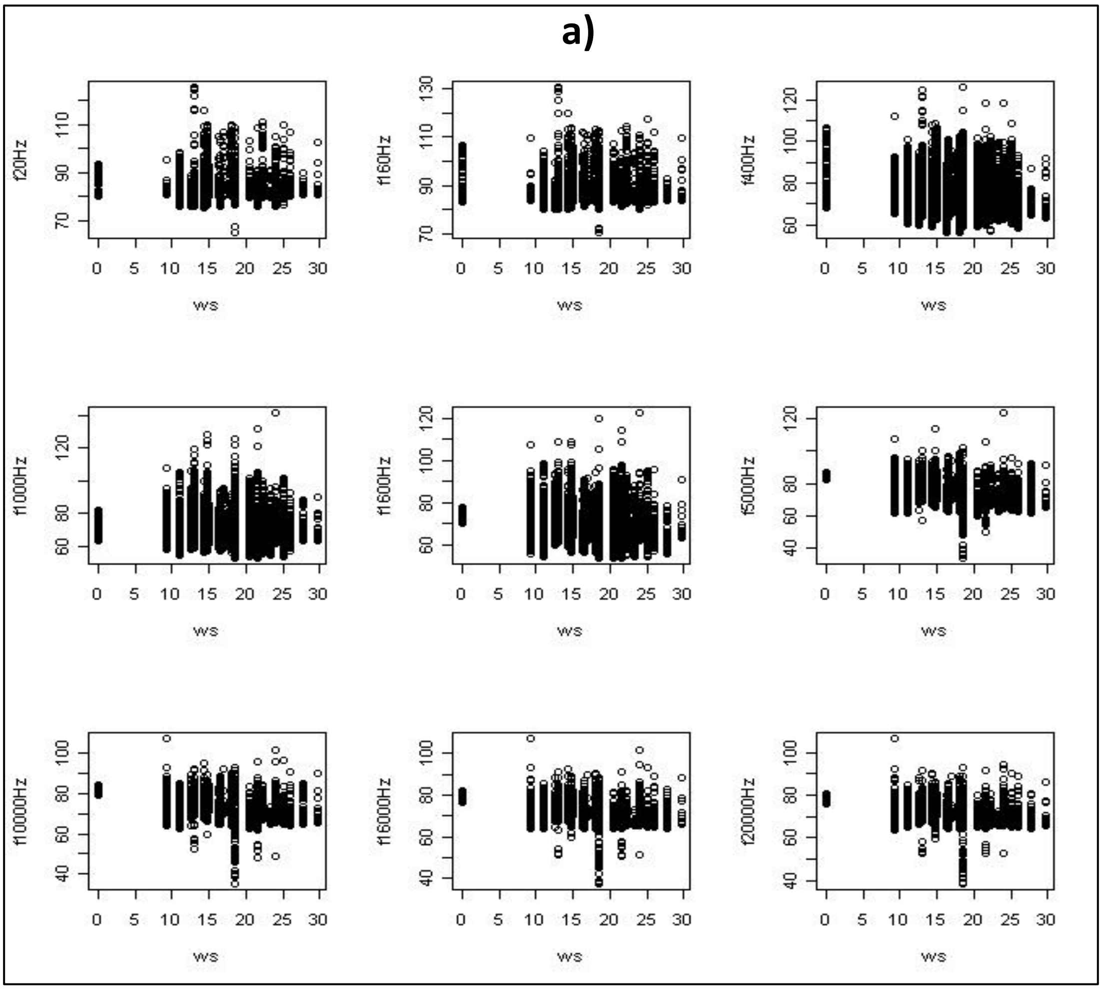
Bandwidth	**Wet**	**Dry**	**Difference**	**SD**	**SE**
17.8-22.4	75	74	1	0.8	0.6
141-178	70	69	1	0.8	0.6
355-447	56	63	7	4.7	3.3
891-1122	47	57	10	7.1	5.1
1413-1778	43	51	9	6.0	4.3
4467-5623	44	51	7	4.6	3.3
8913-11220	40	44	4	3.0	2.1
14130-17780	36	40	4	2.9	2.1
17780-22390	35	39	4	2.9	2.1
Mean	50	54			
Sum	447	489			
Variance	213	157			
Source of Variation	***Sum Squares***	***df***	***P-value***	***F crit***	
Wet&Dry	97.9	1.0	0.5	4.5	
Within Wet&Dry	2961	16			

Table 3.4 Summary statistics for seasonal differences in spectrum density levels. Analysis of Variance between wet season and dry season shows no statistically significant (α=0.05) differences between seasons at different frequency bandwidths.

3.3.6. Hydro-meteorological Data

Throughout the sampling period there was a monthly average wind speed of 17 (SE=0.8) km.h^{-1}, and a monthly average precipitation of 9 (SE=2) mm. Appendix Table A.1 shows daily averages of both precipitation and wind speed provided by the weather station located on land (see Chapter 2). Sea surface temperature was obtained *in situ* when hydrophones were deployed and retrieved (Chapter 2). Sea surface temperature averaged 27 (SE=0.7) ºC, with a minimum of 18ºC during the coastal upwelling months of December through February.

Received levels were not correlated with wind speed or precipitation at any frequency bandwidth throughout the sampling period (Fig. 3.7a-b). The fact that the weather station that supplied the daily averages was far from the deployment sites may have had an influence on this lack of correlation (see Chapter 2).



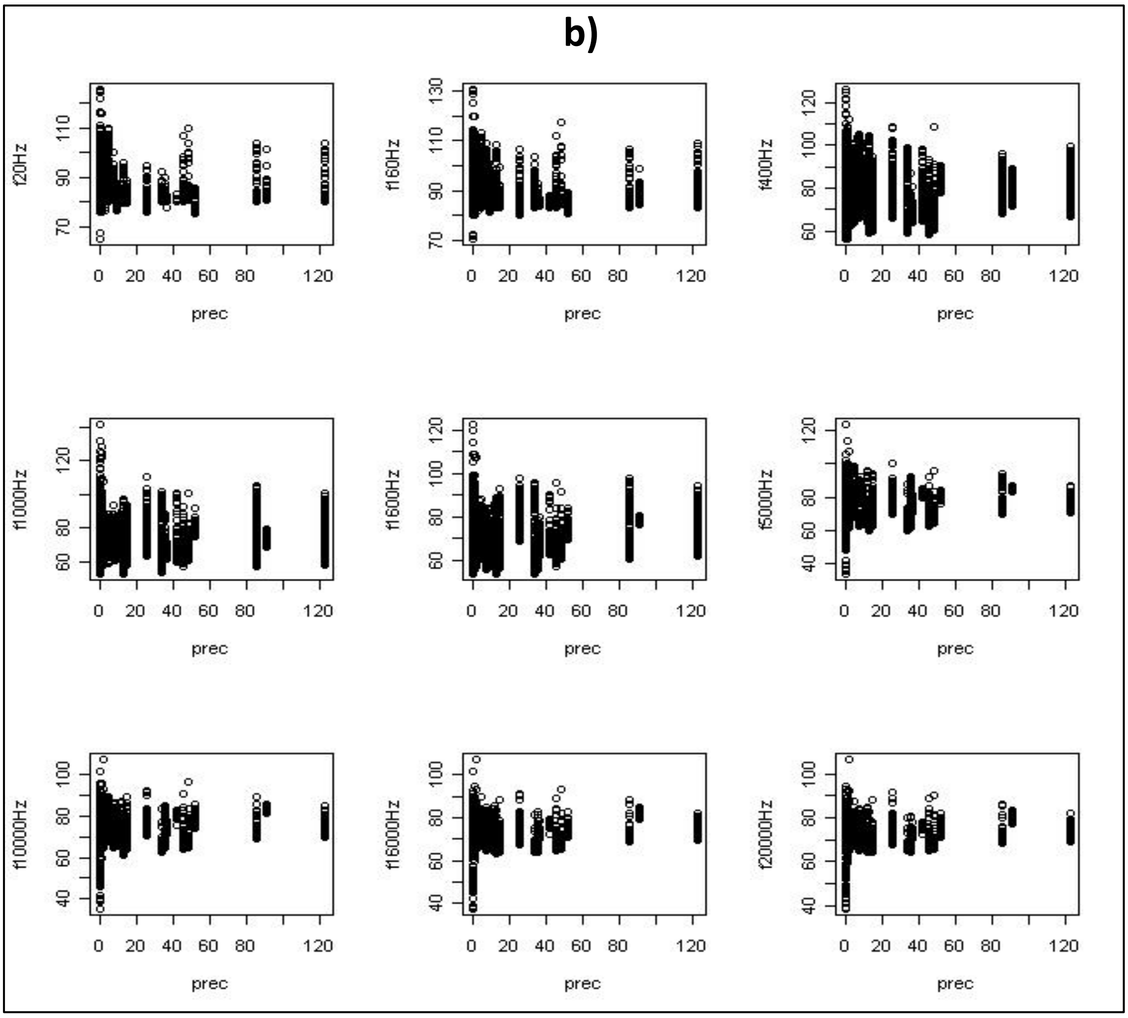


Figure 3.7. (a-b) Correlation plots between received levels (RL) at each centre frequency of the 1/3 octave bands and a) Wind Speed, and b) Precipitation. The vertical axis of each plot is RL (dB re 1 μPa) at each of the shown centre frequency against wind speed (km/hr) and precipitation (mm).

In Fig 3.8, the mean wind speed, precipitation and Spectrum Density Level for each month were calculated from the specific days in a particular month when recording was made. Data were not available at a resolution finer than a day. The highest wind speeds (>22km/h) in September match the second highest spectrum density levels in bandwidths 17.8-22.4 Hz and 141-178 Hz. The highest levels of precipitation (>15mm) in June are matched to the highest spectrum density levels in these same bandwidths.

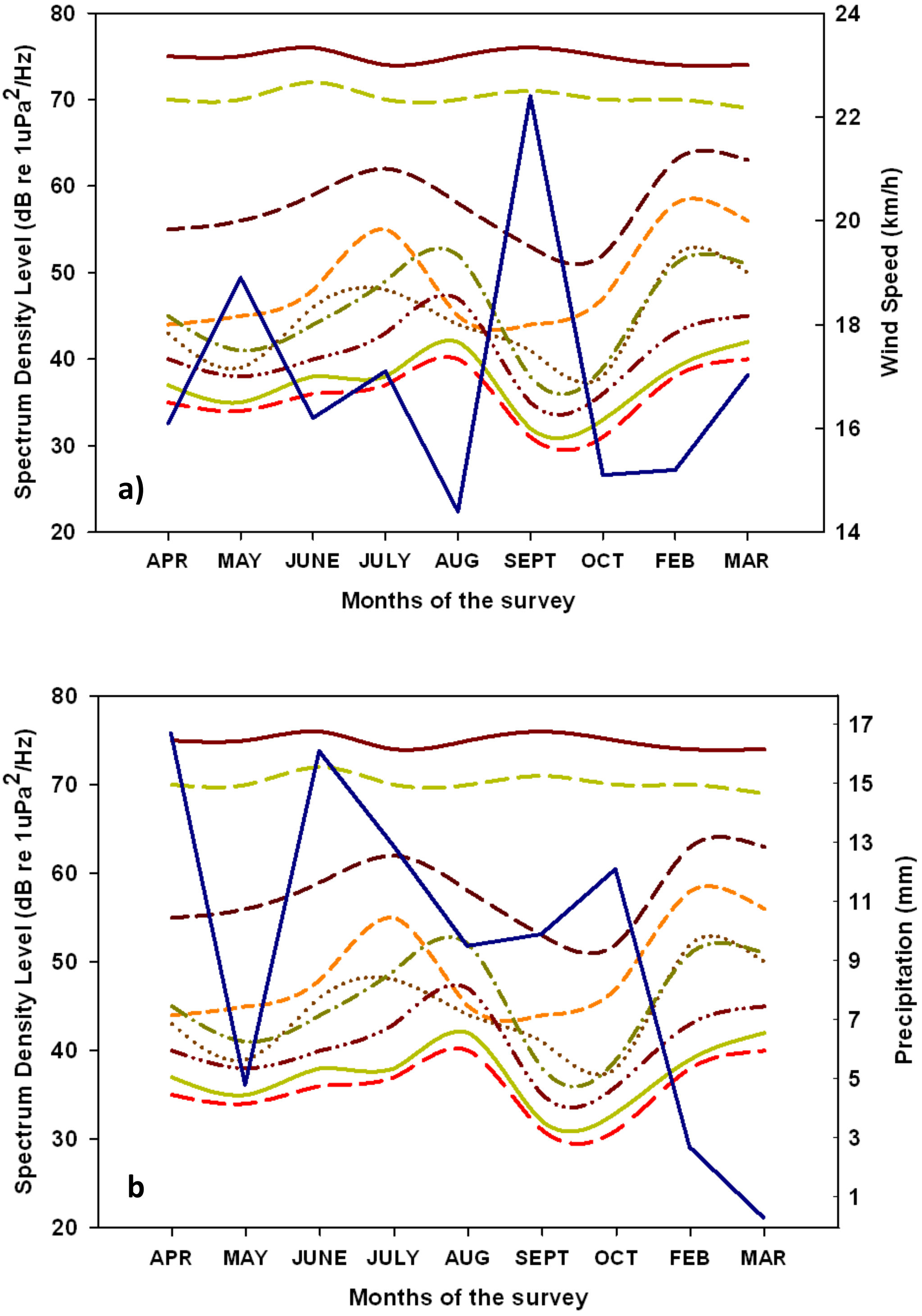


Fig. 3.8 **Mean of a) Wind Speed (km/h) and b) Precipitation (mm) shown in dark blue colour together with spectrum density level mean for the nine bandwidths analysed (see panel) grouped per month of deployments.**

3.3.7 Shipping activity

During the sampling period (April 2010 - March 2011), 14,457 ocean-going (commercial) vessels were reported as transiting the Canal (Panama Canal Authority, 2012b). In addition to this, the area of study included an unrecorded mixture of different types of local vessels including fishing vessels, tugs, and trawlers transiting the area. Data from the Authority of the Panama Canal (Panama Canal Authority, 2012b) show there is no significant variability among months in large vessel transit (Table 3.5, P>0.05).

Month	**Number of Transits**			
April	1,046.00			
May	1,069.00			
June	971.00			
July	1,032.00			
August	1,021.00			
September	995.00			
October	1,102.00			
November	1,063.00			
December	1,080.00			
January	1,158.00			
February	1,109.00			
March	1,212.00			
Mean	1,072.00			
SD	67.00			
SE	19.00			
ANOVA				
Source of Variation	***SS***	***df***	***P-value***	***F crit***
Between Groups	1.23571E+13	11	1	2.717331
Within Groups	3.75712E+15	12		

Table 3.5 Number of transits of large vessels per month, and monthly mean, during the period when the study took place (April 2010 - March 2011). Data were not available for shorter time periods.

3.3.8 Biological noise

Biological noise present in the acoustic data was characterized to the extent possible by manually observing the spectrograms whilst simultaneously listening to the playback of the sound recordings. Snapping shrimp sound was present throughout all the audio files and results documenting the occurrence of fish sound and dolphin whistles are described in Chapter 4. Figure 3.9 illustrates the characteristic high frequency snapping shrimp "clicks" occupying most of the spectrogram and shows the presence of fish chorus at lower frequencies. Figure 3.4 shows the contribution of fish chorus between 400 Hz and 1.6 kHz and that of snapping shrimp between 5 kHz and 20 kHz (in this study).

3.4 DISCUSSION

This is the first study to measure underwater ambient sound over 12 months in the region of the entrance to the Panama Canal. More than 400 hours of acoustic data were recorded.

3.4.1 Overall description of ambient sound in the area

The results of this study show that the sound spectrum in this region has some general characteristics that appear to be robust to the effects of location of recording relative to the distance from the coast and from the main shipping lanes, and also to seasonal and diurnal effects and the effects of weather. Overall this environment shows sound pressure levels (SPL) similar to those seen in the Wenz curves (Fig. 1.4). The presence of large numbers of ships provides an opportunity to examine the levels of ambient noise that might be reached elsewhere if shipping traffic continues to increase in those other sites.

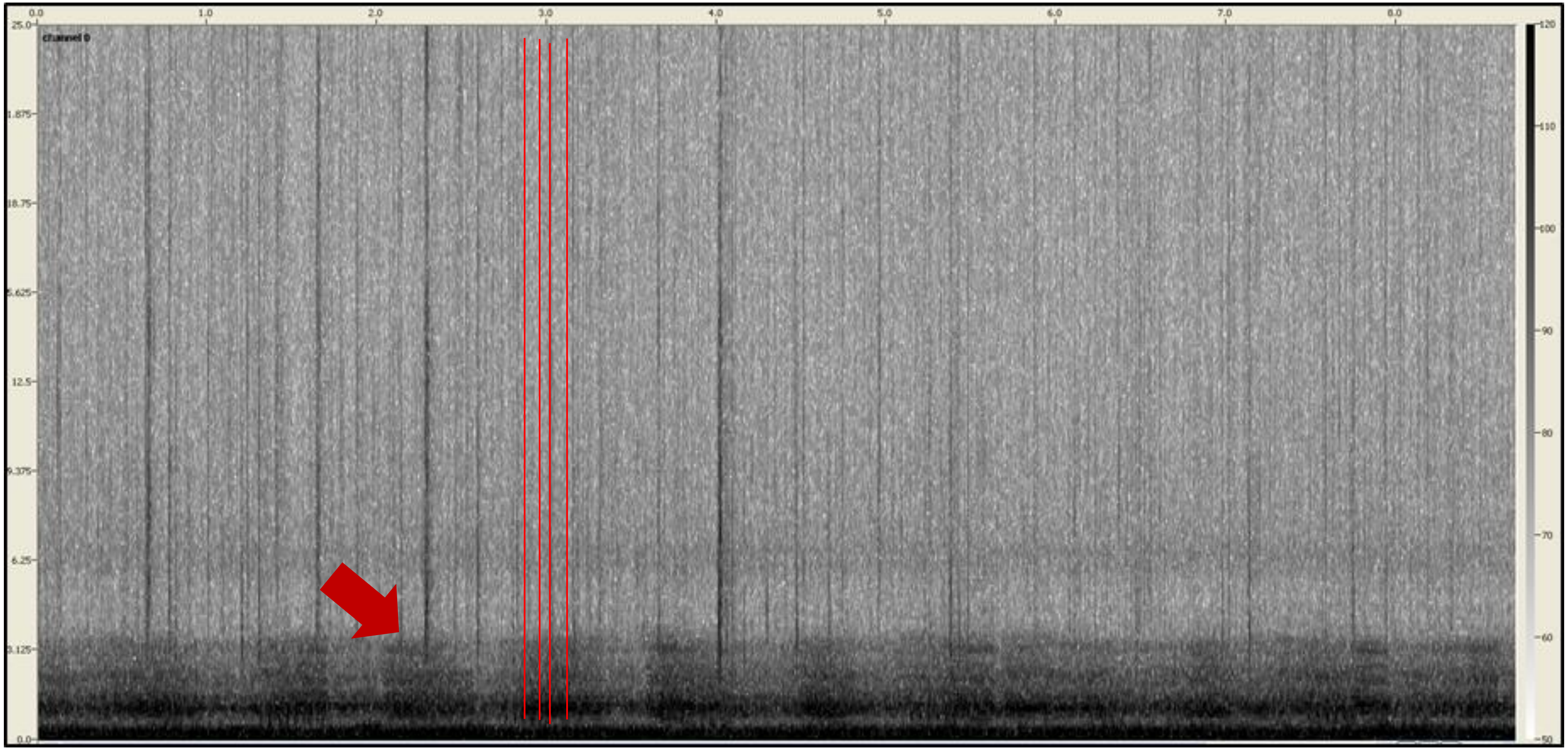


Fig. 3.9. A 10 second cut of a spectrogram (upper x-axis) showing high frequency clicks of snapping shrimp (parallel red lines) and medium to lower frequency (<6000Hz) detection of fish chorus (red arrow). Frequency is shown in the left hand y-axis, and amplitude levels are on the right hand y-axis.

Several authors have used Wenz (1962) curves to document overall increases in ambient noise within sound profiles under similar conditions to those examined in this study (Knudsen et al., 1948; Urick, 1984; Andrew et al., 2011). Increases of 10 dB appear to have occurred over the range of 20 Hz to 80 Hz bands (McDonald *et al.*, 2006; Andrew *et al.*, 2011). Overall, these studies were in deeper waters than this study but were well used by commercial shipping. They show that there has been an increase of 5dB to 15dB in ambient noise in different environments in the 5 Hz to 500 Hz frequencies due to an increase in commercial shipping; both in terms of numbers and types of vessels (Ross, 2005; McDonald *et al.*, 2006; Andrew *et al.*, 2011; Chapman and Price, 2011; Roth *et al.*, 2012).

The red thick line in Fig. 3.10 shows the results of this study overlaid on Wenz curves. There is a similarity in SPL at some frequencies described for heavy traffic noise shallow water (Wenz's shaded yellow area, <500Hz) but with an additional increase of 5-10 dB at higher frequencies, above 1000 Hz. However, the results are within the limits of prevailing noise defined by Wenz. The change in SPL apparent in Fig. 3.10 at these higher frequencies (specifically 4,467-5,623Hz) is likely attributable to small boats that mainly contribute sound between 5,000 Hz and 10,000Hz, and snapping shrimp (5, 000 Hz to > 20,000Hz) (§3.3.3.). The contribution of sound attributed to small vessels in this area was found to be intermittent as opposed to the continuous sound from distant shipping.

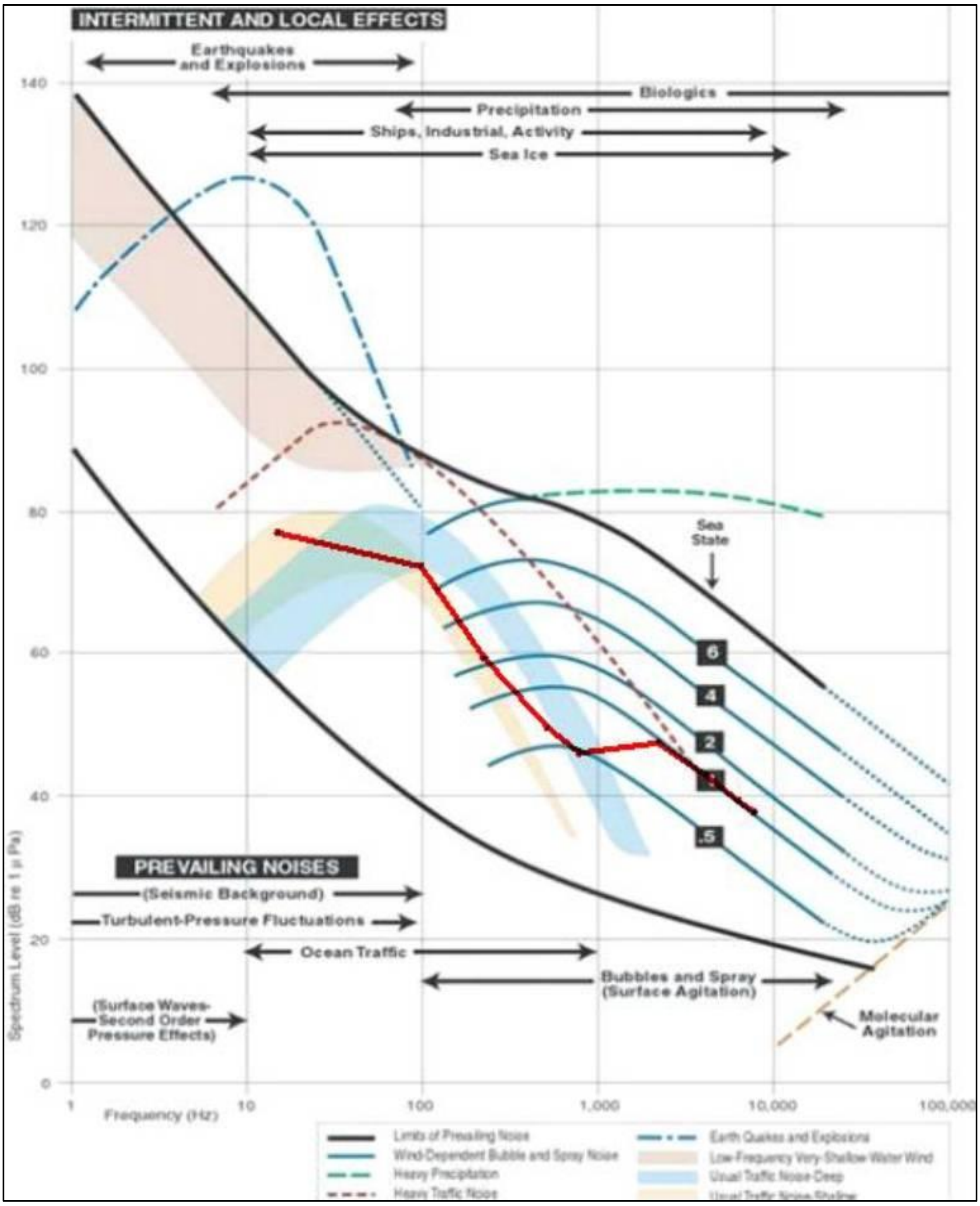


Figure 3.10. Ambient noise spectra obtained from this study and plotted in logarithmic form (thick red line) overlaid over Wenz curves spectrum levels (Fig. 1.4) for comparison.

Other authors have reported higher background sound pressure levels to those observed in the present study. Hatch *et al.* (2008) reported the highest means of RL for the frequency range between 10 Hz to 400 Hz at a received level of 120.6 (SE=0.4) dB re 1 µPa, which was significantly higher than this study (mean = 81 (SE=0.06) dB re 1 µPa) for that same frequency range (Table 3.1).

Similar to the analyses in other locations, and especially those of Wenz (1962), the sound spectrum decreased toward higher frequencies showing that most of the power was focussed in the low to mid frequency bands (Fig. 3.3). There was some evidence for a further increase in power at 5,000 Hz. The received source sound levels increased at night and the most pronounced variation between day and night was found in the frequency bands centred at 400Hz and 1,000Hz. Higher sound pressure levels have been recorded at night than during the day at Port Balboa, within the study area (Anderson and Gruber, 1979). As in the present study, local spectrum density levels in the region of the Panama Canal were 20dB higher than reported for similar shallow areas at high frequencies (Cato, 1976).

The sound spectrum of this region is similar to those reported in the literature but with higher than expected levels for the bandwidth centred on 5,000 Hz, the frequency representative of small fishing boats.

3.4.2 Effects of weather

Sound due to wind can be a major contributor to the sound spectrum at a wide range of frequencies (100Hz-30kHz, see §1.2.2.1) but shipping can also contribute to energy in the lower end of these frequencies (<1kHz) (Knudsen et al., 1948; Wenz, 1962; Cato, 1976; Urick, 1984; McDonald et al., 2006; Hatch et al., 2008b; Nystuen et al., 2010; Chapman and Price, 2011; Reeder et al., 2011). Wind speed noise measured in shallow waters (<200m) has been found in the lower end of the spectrum (<100Hz) by Wenz (1962), Zakarauskas *et al*. (1990) and Cato (1976) (Fig. 3.4). These studies refer to variations due to differences in local wind and depth or distance to coastal regions. There was an increase in SPL at the lower frequency bands (centred on 20 and 160Hz) in September when wind speed was highest, as shown in Figure 3.8. Precipitation was also associated with an increase in SPL in the frequency bands centred on 20Hz, 160Hz and 1600 Hz during the wet season (April-November) (Fig. 3.8)

La Niña conditions prevailed at the time of this study (NOAA/National Weather Service) , which means that the wet season extended until February 2011 resulting in sea water temperatures below normal and rainfall levels above normal (Table A.1). Heavy rain can result in an increase in SPL at frequencies between 1 and 25 kHz (Nystuen *et al.*, 2010). Rainfall is a high intensity sound and it is clearly identifiable in the audio files but was neither sufficiently heavy nor persistent to have a significant overall effect upon the soundscape.

3.4.3 Effects of shipping

The area where hydrophones were deployed is used by all types of vessels to enter or exit the Panama Canal. Noise generated by traffic is a combined result of number, type and distribution of ships and transmission loss (Wenz, 1962). General shipping noise from large vessels has been found at low frequencies (2-200 Hz, Urick, 1984, Richardson *et al*., 1995). Given the large number of vessel movements and the apparent small effects of variation in the sound spectrum caused by weather, the most parsimonious explanation for the general form of the sound spectrum recorded in the present study is that, at least at lower frequencies (<500 Hz), the spectrum is dominated by distant ship noise, whereas noise at higher frequencies (>1250 Hz) is mostly caused by nearby small vessels, tugs and trawlers.

Sound pressure level tends to decline with increasing frequency (Knudsen *et al.*, 1948; Wenz, 1962; Anderson and Gruber, 1971; Urick, 1984; Andrew *et al.*, 2011). Fishing boats, tugs and trawlers operating within this region use a combination of inboard and outboard high-speed diesel engines which have a relatively high frequency component in their sound spectrum (Richardson *et al*., 1995a). The anthropogenic activity of boats constantly arriving and leaving different areas where and when the hydrophones were placed, as well as tug boats approaching large commercial vessels to transit through the Panama Canal, might explain the contribution of this source of intermittent noise at the higher frequencies. During the bottom-based hydrophone deployments, some of the time a hand-held hydrophone immersed in the water was used to record the sounds received in real time allowing the sounds of different types of vessels in the area to be characterised. In shallow areas, local shipping may define the ambient noise, in comparison to distant shipping defining sound in deeper waters (Zakarauskas *et al.*, 1990;

Ainslie and de Jong, 2011; Ainslie *et al.*, 2011b). Results showed no significant diurnal variation in the lower frequency range (<400Hz), supporting the conclusion that commercial shipping noise was the source of this sound because the Panama Canal operates throughout the 24 hour cycle.

3.4.4. Effects of biological sound sources

Dolphin clicks and whistles have been identified from the data collected and are considered further in Chapters 4, 5 and 6. These sounds were mainly at frequencies > 1 kHz. Humpback whale sounds were also identified during their breeding season (between August and November/Wet Season) suggesting this source also contributed to SPL at lower frequencies (<500Hz), as has been described for Hawaiian waters by Au et al. (2000). Both dolphins (Jackson *et al*., 2004b) and humpback whales (Acevedo et al., 2007; Rasmussen, 2007; Rasmussen et al., 2007; Rankin et al., 2008; Whitehead, personal communication, 2009) have been widely reported to be present in this area and were observed and recorded during the present study.

Fish sound contributes to diurnal and seasonal variation in ocean noise (Fish and Cummings, 1972; Mann and Grothues, 2009; Ainslie et al., 2011a; Ainslie et al., 2011b). Fish and Cummings (1972) recorded underwater sound at different periods of time and found an increase of 50dB at a frequency of 1,000Hz during the corvina (*Cynoscion albus*) breeding season compared to non-breeding seasons. This species of corvina is one of the most common fish found in these waters (Robertson and Allen 2008). Luczkovich and Sprague (2011) also found increases in sound pressure levels in the bandwidth 100-1,500Hz related to the breeding seasons of different type of fish at different times of the year. Sounds generated by fish bladders from Family Sciaenidae (which includes croakers and drumfish) and from Family Ariidae (marine catfishes) are found in these waters (Robertson and Allen, 2008), and were identified throughout selected audio files as described above (§3.2.1.1.) and in Chapter 4. These fish also show diurnal (and seasonal) variability, increasing the intensity of their choruses at sunset and decreasing them from midnight onwards (Knudsen *et al.*, 1948; Ainslie *et al.*, 2011b).

The most common source of sound at higher frequencies is likely to be that of the tropical snapping shrimp (genus *Alpheus*) which produces a peak-to-peak source level from 183 to 189 dB re 1µPa between 2 and 5 kHz and up to 200kHz (Au and Banks, 1998; Chitre *et al.*, 2006). Many species of this genus of snapping shrimp are found in the waters around the entrance of the Panama Canal (Anker *et al.*, 2007). A typical example is the species *Alpheus naos* n. sp. (first identified in this particular area and named after Isla Naos, less than 3km from one of the recording sites). Sounds of snapping shrimp were present throughout all of the audio files examined (§3.2.1.1., Fig. 3.4, and Chapter 4) and probably contributed considerably to the power in the higher frequency bands (>5,000Hz).

Biological sound is of higher intensity at night than during the day but also varies with frequency. The higher intensity sound at night was at 400 Hz and at 1 kHz, which are similar to those at which fish sound (Fish and Cummings, 1972) and snapping shrimp (Everest *et al.*, 1948; Au and Banks, 1998; Radford *et al.*, 2008) make sound, respectively. Biological sound is likely to be a common source of diurnal and seasonal variation in SPL in this study.

3.4.5. Seasonal change

The highest sound pressure level in both the wet season (April through November) and the dry season (December through March) was in the 17.8-22.4 Hz and 141-178 Hz frequency bands and here the wet season showed slighter higher levels than the dry season. Environmental data showed an increased average precipitation and wind speed in the wet season. Franz (1959) was the first to investigate the noise from a spray of water droplets and proposed a model using droplet size to calculate the spectrum. Wenz (1962) used these observations and reported precipitation noise between 100Hz-10 kHz, highlighting that rain may be easily distinguished even at 100 Hz with little ambient noise. Medwin (1992) reported the effect of small drops to radiate at frequencies of 15kHz and large drops in ranges from 1.8 to 8.5 kHz. Finally, Nystuen (1986) reported the spectral shape of rain noise with high sensitivity of sound level at 15 kHz.

Noise due to rain is an important sound contributor and the frequency spectrum and SPL depend on the size of the droplets (how heavily it rains) (Franz, 1959; Nystuen, 1986).

The sound of rain is easily distinguished from other sound sources and although found statistically non-significant between seasons, manual analysis of the spectrogram allowed me to hear the differences between mild rain and heavy rain. In addition, Fig. 3.8 showed the highest precipitation mean (>15mm) coincides with the highest peaks in SPL at 75 dB re $1uPa^2/Hz$ at 17.8-22.4Hz and 70 dB re $1uPa^2/Hz$ at 141-178 Hz, which is similar to what Wenz reported in Fig. 1.4.

The elevated SPL in the frequency band centred at 160 Hz during the wet season also coincides with humpback whale migration to this area at this time of the year (July to November). A combination of seasonal sources reported in other studies caused increases in low frequencies at a particular time of the year, mainly identified as ship tonal and wind speed, as well as whale sounds when in migratory season (Curtis et al., 1999; Au et al. 2000; McDonald et al., 2006; Andrew et al., 2011). Other studies have shown greater seasonal variation relating to water temperature (Zakarauskas et al., 1990; Hatch et al., 2008b; Roth et al., 2012), which is not the case in this study. Results suggest that weather factors may have influenced the overall seasonal variation in sound pressure level, in addition to the biological factors described above in section 3.4.4.

3.4.6. Spatial distribution

The models showed that there was an effect of distance to the anchorage area, distance to the entrance buoys and distance to the coastline as predictors explaining variation of sound pressure levels in at least one of the frequencies modelled (Table 3.2). No information was available on the distance of vessels from the shore. Distance to the buoy was a significant predictor at bandwidths centred on 20 Hz and 160 Hz, possibly explained by the fact that large vessels entering or exiting the Panama Canal transit next to these buoys producing sounds at these frequencies. Distance to the anchorage explained variability in SPL for frequencies at 5,000 Hz and 10,000Hz which may be explained by small fishing boats and tug boats operating from the Panama Canal that circle the anchorage area. Distance to the coast seems to be a generalized explanatory variable because it was retained in the models of several bandwidths, centred on frequencies at 400 Hz, 1,000 Hz, 1,600 Hz, 16,000 Hz and 20,000 Hz. Many biological sound sources may overlap in these frequencies: fish chorus, snapping shrimp and dolphin whistles. Wilson *et al.* (1985) showed significant changes in sound levels at different distances from shore finding a positive relationship in the frequency range 50-700Hz. The distances to shore for the bottom-based hydrophone were similar to those analysed by Wilson *et al.* (1985) and also showed a similar positive effect of distance from shore in the frequency range 2-400Hz.

3.5. CONCLUSIONS

The data collected in this study suggest that small boat noise and biological sound (fish chorus and snapping shrimp) are the major contributors to ambient sound in the waters around the Pacific entrance to the Panama Canal (§3.2.1.1, Fig. 3.4). The sources appear to be characterised by distant shipping noise at frequencies around 20 Hz and 160 Hz; by fish sound at mid-frequencies between 400 Hz and 1,600 Hz; by snapping shrimp at higher frequencies between 5,000 Hz and 20,000 Hz and transient small fishing boats at higher frequencies between 5,000 Hz and 10,000Hz (but mostly centred at 5,000 Hz).

Overall, the area studied showed slightly elevated sound pressure levels of background sound when compared to other studies in shallow waters (Anderson and Gruber, 1971; Zakarauskas *et al.*, 1990; Hatch *et al.*, 2008a; Andrew *et al.*, 2011). Based on the generalized additive modelling, the variability in sound pressure levels is best explained by biological sources, seasonality, diurnal variation and (in part) spatial distribution.

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CHAPTER 4

Characterization of dolphin whistles in the vicinity of the Panama Canal

ABSTRACT

Sound is a critical sense in cetaceans and it is important to investigate how changes in the environment can affect the acoustic characteristics of the ocean. The vocalizations of dolphins have not previously been documented for the Pacific side of the Panama Canal; this study presents the first quantitative description of whistle characteristics using whistle detections collected with passive acoustic monitoring from April 2010 until March 2011. A total of 9,789 audio files (453 hours) were recorded of which 4,233 were manually analysed to obtain a total of 4,567 whistles present in 427 files. Previously documented whistle contour characteristics in other studies were recognised in these whistles. The whistles ranged in mean frequency from 5.18 kHz (SD=2.49) to 23.53 kHz (SD=1.71), and ranged in mean duration from 68.66 ms (SD = 18.09) to 412.44 ms (SD=318.45). A significant relationship between dolphin whistles and fish sound was found, in which there was a 40% greater probability of them occurring together than by chance. Observations suggest an effect of diurnal variation, with dolphin whistles and fish noise co-occurring more at night-time than during the daytime.

4.1 INTRODUCTION

The characterization of dolphin sounds has been well documented for a number of different species in a wide range of locations, including spinner (*Stenella longirostris*) and pantropical spotted dolphins (*Stenella attenuata*) (Bazua-Duran and Au, 2002; Lammers et al., 2003; Camargo et al., 2006), rough-toothed dolphins (*Steno bredanensis*) , dusky dolphins (*Lagenorhynchus obscurus*) (Vaughn-Hirshorn et al., 2012) common dolphins (*Delphinus delphis*) (Petrella *et al*., 2012), Pacific Fraser's dolphins (*Lagenodelphis hosei*) (Oswald *et al*., 2007), Irrawady dolphins (*Orcaella brevirostris*) (Van Parijs *et al.*, 2000), and common bottlenose dolphins (*Tursiops truncatus*) (Wang *et al.*, 1995; Dos Santos *et al.*, 2005; Azevedo *et al.*, 2007b; Hernandez *et al.*, 2010).

Dolphin sounds have provided information on their distribution (Oswald *et al.*, 2003; Camargo *et al.*, 2006; Oswald *et al.*, 2008; Hawkins, 2010), behaviour (Van Parijs *et al.*, 2000; Camargo *et al.*, 2006; Hawkins and Gartside, 2010; Hernandez *et al.*, 2010), and social group structure (Janik and Slater, 1998).

Most dolphin species produce three main types of sounds: whistles, clicks and burst pulses (Richardson *et al.*, 1995d; Au and Hastings, 2008; Janik, 2009). Whistles are defined as narrow band, tonal frequency modulated signals with fundamental frequencies between 1 kHz and 28.5 kHz, lasting from 100 ms up to 4 seconds (Richardson *et al.*, 1995d; Au and Hastings, 2008; Janik, 2009). Dolphins, such as the common bottlenose dolphin *Tursiops truncatus* are considered "mid-frequency cetaceans" because their estimated auditory bandwidth is from 150 Hz to 160 kHz (Southall *et al*., 2007). However, the frequency ranges and duration of whistles recorded vary depending on the environment and whether studies were conducted in the wild or in captivity (Bazua-Duran, 2004; Quintana-Rizzo and Mann, 2006; Janik, 2009; van der Woude, 2009; Hernandez *et al*., 2010). The maximum source level reported for dolphins in the wild is approximately 169 dB re 1µPa at 1m (Richardson *et al*., 1995d; Au and Hastings, 2008; Janik, 2009). Whistles are commonly represented in spectrograms showing frequency plotted against time. Another component of a whistle is the harmonic range, which extends considerably beyond the ultrasonic frequency range (Lammers *et al.*, 2003; Au and Hastings, 2008b).

Studies to characterize dolphin whistles have been carried out under controlled conditions with dolphins in captivity (Tyack, 1986; Janik and Slater, 1998; Miksis *et al.*, 2002) and in the wild (Janik, 2000b; Van Parijs *et al.*, 2000; Boisseau, 2005; Dos Santos *et al.*, 2005; Azevedo *et al.*, 2007a; Hernandez *et al.*, 2010; Petrella *et al.*, 2012). Studying dolphins in the wild is more challenging because of the effects of ambient noise, variable weather conditions, and difficulties in identifying the animals making the sounds. Studies have shown that whistles produced by captive dolphins can be considered similar to those produced by animals in the wild (Watwood *et al*., 2005; Sayigh *et al*., 2007).

Dolphins prey on a variety of animals from invertebrates to fish depending on the habitat (Reeves *et al.*, 2002). However, research has demonstrated that soniferous fish (e.g. Scianids) are the preferred prey because they are easier to locate (Hanson and Defran, 1993; Wilson *et al.*, 1997; Barros and Wells, 1998; Hastie *et al.*, 2004; Gannon *et al.*, 2005; Berens McCabe *et al.*, 2010). Fish produce sound in two ways: by stridulation (i.e., croakers and drums) and by manipulation of the muscles around the swim bladder (i.e., catfishes) (Au and Hastings, 2008; Mann, 2012). Fish produce sound as individual animals but it is the sound produced by the “fish chorus” that characterizes the biological background sound in the ocean (Knudsen *et al.*, 1948; Cato, 1976) and they show unique patterns for identification in spectrogram analysis (Sprague *et al.*, 2000). These choruses tend to occur mostly at night and just before dawn (Ainslie and de Jong, 2011), which is also reported as the most usual foraging schedule for dolphins (Hanson and Defran, 1993; Allen *et al.*, 2001); however, only a few studies have addressed diurnal whistle variation (Acevedo-Gutierrez and Stienessen, 2004; Oswald *et al.*, 2008). Dolphins also increase their whistle rate and whistle frequency during feeding events, therefore attracting more dolphins to the area (Acevedo-Gutierrez and Stienessen, 2004; Nowacek, 2005; Oswald *et al.*, 2008). Nowacek (2005) suggested that single animals tend to produce whistles at a higher rate than animals in a group. Dolphin feeding habits consist of a variety of techniques, such as trapping schools of fish against a sandy area (Leatherwood, 1975; Duffy-Echevarria et al., 2008); herding fish in a circle (Rossbach, 1999), mud-ring feeding (Torres and Read, 2009), cooperative fishing with fishermen (Pryor *et al.*, 1990); throwing fish in the air and catching them (Gazda *et al.*, 2005), among other techniques; but they have also been seen following fishing boats, such as trawlers (Leatherwood, 1975; Reeves *et al.*, 2002).

As shown in Chapter 3, the background noise level is high in the study area on the Pacific side of the Panama Canal. This is partly because it is a tropical habitat rich in marine life such as coral reef fish and snapping shrimp, but mainly because it is one of the busiest areas in the world for maritime traffic, both large vessels and small boats. Low frequency noise from large vessels has been found to have little effect on the whistle repertoire of dolphins compared to the effects of mid to high frequency noise caused by small vessel (outboard) engines (Buckstaff, 2004; Jensen *et al.*, 2009; Jensen *et al.*, 2012). These latter forms of background noise can cause an increase in whistle rate and whistle frequency (Jones and Sayigh, 2002; Nowacek *et al.*, 2007).

Masking of sounds is a result of noise interfering with the sounds that dolphins produce to communicate among each other and also to find prey (Richardson *et al.*, 1995d). The effect of masking on baleen whales (Richardson *et al.*, 1995d; Erbe and Farmer, 2000; Croll *et al.*, 2001; Parks *et al.*, 2007; Southall *et al.*, 2007) has been studied more so than in toothed whales (Au and Moore, 1990; Branstetter and Finneran, 2008; Mallawaarachchi and Ong, 2008; Trickey *et al.*, 2010; Kastelein *et al.*, 2011). In these studies it is argued that, although there is some masking caused by the background noise in the environment, it is not significant enough to cause changes in distribution. For example, Croll *et al.* (2001) suggest that the occurrence of whales in their study was more related to prey abundance. Vocal behaviour in dolphins can also be masked to a certain level due to biological sources of ambient sound, such as snapping shrimp and fish chorus (Au and Hastings, 2008). However, acoustic masking caused by anthropogenic noise is becoming an important concern when animals rely on acoustic communication to navigate and to send or receive signals of social content (Clark *et al.*, 2009) interfering also with acoustic behaviour of echolocation (Au *et al.*, 1982). In addition, this noise may also interfere with biological sounds that may represent important cues for prey for marine mammals (Popper, 2011).

Dolphin whistles in Pacific coastal waters of Panama have not previously been characterized. The aim of this study was to make a first characterization of the whistles of the animals found in the region near the entrance to the Panama Canal. This information is important as a first step to study local populations of dolphins in closer detail and, in particular, to provide background information about areas that may need protection from anthropogenic activities.

This chapter has the following objectives:

a) Characterize the parameters of the dolphin whistles detected to create a first catalogue of their qualitative and quantitative characteristics;
b) Compare the whistle characteristics to previous studies under similar conditions;
c) Address the question: can diurnal variation in whistle characteristics be explained by variation in background noise or biological factors?

4.2 METHODOLOGY

The details describing the study site and data collection are given in Chapter 2: General Methodology. Data collected with the CR55 included recordings sampled by mistake at 22 kHz. These recordings have not been taken into account for whistle characterization in this chapter.

4.2.1 Qualitative analysis of whistles

A whistle contour is defined as a narrow band sound displaying its frequency as a function of time on a spectrogram (Au and Hastings, 2008) (Fig 4.1). Qualitative analysis involves a description of the parts of the contour of a fundamental frequency whistle in terms of the frequency modulation whereas quantitative analysis includes the determination of various parameters of the whistle. Some species of dolphins have developed individually distinct whistles, called signature whistles, some of which can be highly stereotyped while others can display variable features (Caldwell *et al*., 1990; Janik *et al*., 2013). These features include variations in the number of repetitive elements and variation in duration and frequency. The methods followed in this study were similar to those used by many researchers who have characterized whistle contours from whistle-producing odontocetes (Wang *et al.*, 1995; Rendell *et al.*, 1999; Bazua-Duran and Au, 2002; Lammers *et al.*, 2003; Oswald *et al.*, 2003; Oswald *et al.*, 2004; Camargo *et al.*, 2006; Azevedo *et al.*, 2007a; Oswald *et al.*, 2007; Hawkins, 2010; Hernandez *et al.*, 2010; Seabra de Lima *et al.*, 2012; Vaughn-Hirshorn *et al.*, 2012).

Whistles were characterized by inspecting whistle contours on spectrograms. There is some lack of consistency in how to name certain contour categories and some researchers have sub-classified the main categories. The six fundamental categories for qualitative analysis, as agreed by the majority of researchers (Bazua-Duran and Au, 2002; Bazua-Duran, 2004; Janik, 2009) and defined by Au and Hastings (2008), are:

1) Constant frequency: a contour with the least amount of frequency change across time;
2) Upsweep: a contour that has a start frequency lower than the end frequency and contains no significant inflection points;
3) Downsweep: a contour that has a start frequency higher than the end frequency and contains no significant inflection points;
4) Concave: a contour in which frequency initially increases with time and then decreases with time;
5) Convex: a contour in which frequency initially decreases with time and then increases with time;
6) Sinusoidal or Multiple: a whistle with multiple repetitions of a concave or a convex shape and appearing as a sinusoidal shape with at least two inflection points.

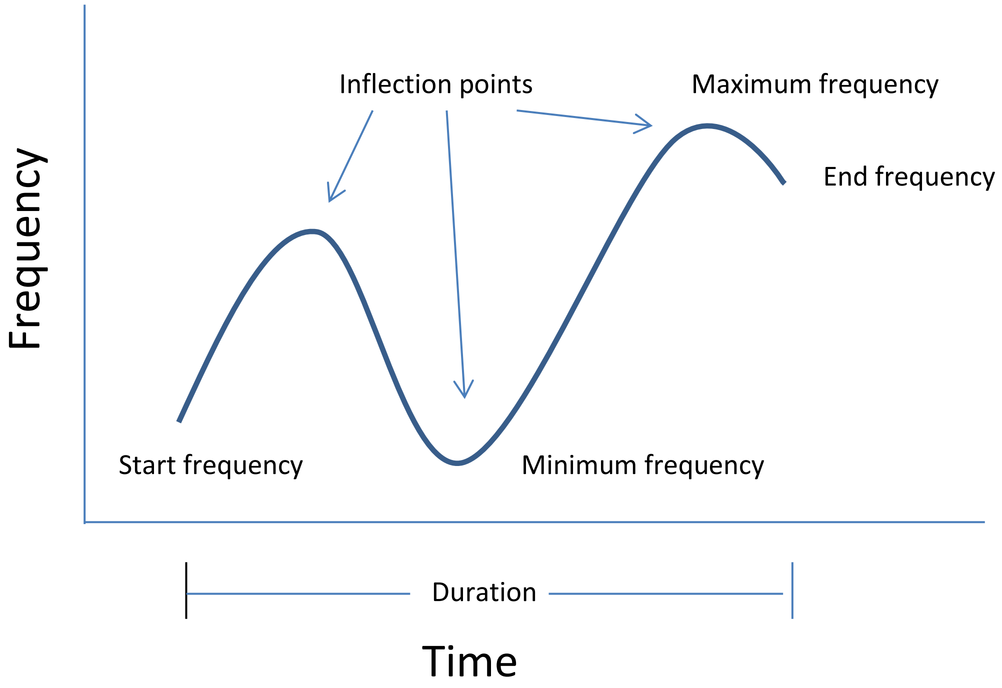

Fig. 4.1 A typical spectrogram representation of a whistle, showing some of the qualitative and quantitative characteristics usually recorded when describing whistle contours.

Some authors have preferred manual analysis of spectrograms to program-based procedures (Dos Santos *et al.*, 2005). The qualitative description used here was the result of a manual visual identification of different types of contours looking at spectrograms produced using Adobe Audition 3.0 (Copyright © 1992-2007 Adobe Systems Incorporated). Spectrograms were analysed using a Blackman-Harris window, which allowed for the widest frequency band viewing and least noise, on a 10 second window frame and a Fast Fourier Transform size of 512 points for good visual resolution.

Qualitative features of the whistle contours were manually extracted from the spectrograms with the clearest resolution and these are presented in the result section. A statistical summary (i.e. how many upsweep whistles, how many concave whistles, etc.) is not provided per category of these contours because of a lack of clear resolution of whistles in the majority of spectrograms. The background noise surrounding the whistles, (mainly caused by high frequency snapping shrimp occupying the spectra, as well as high frequency vessel noise on most occasions, see Chapter 2) made it difficult to extract whistle contour characteristics. Special filter algorithms using automated contour analysis programs are needed when simple manual whistle characterization proves impossible because of the degree of background noise from other sources (Mallawaarachchi and Ong, 2008; Roch *et al*., 2011). . The additional time required for this type of analysis was not available and therefore this will be conducted in a future study.

4.2.2 Quantitative analysis of whistles

The quantitative method involved measuring a number of parameters (e.g. Fig. 4.1) that can be extracted from a whistle, either manually or by the use of a specialized software programs. The parameters commonly reported (Bazua-Duran and Au, 2002; Bazua-Duran, 2004; Azevedo *et al.*, 2007b; Janik, 2009) are:

1. Start frequency of the whistle;
2. End frequency;
3. Minimum frequency;
4. Maximum frequency;
5. Frequency range (difference between maximum and minimum frequency);
6. Number of inflection points;
7. Duration;
8. Presence of harmonics.

In this study, a whistle was considered for quantitative analysis when the frequency detected was between 3 kHz and 25 kHz (this latter is the upper frequency of the recordings). The quantitative parameters of the whistles were extracted using the open source acoustic analysis software Pamguard (Passive Acoustic Monitoring Guardianship, Version 1.10.04 Beta), with a whistle and moan detector (available from www.ifaw.org/). The selection for a whistle and moan detector plug-in was made in the settings and automated detections and qualitative parameters for each audio file were recorded and exported to a blank Access database table (Yack *et al*., 2009). The detector sweeps the spectrogram in search of high intensity sounds and areas exceeding the background noise are selected. Consecutive peaks are then joined resulting in a time-frequency contour. A whistle is considered a whistle event by Pamguard when the number of whistles exceeds some minimum value within a set time period (i.e. 1 sec). A problem to highlight here is that single whistles are often counted as multiple whistles in the presence of rapid and large amplitude changes or marked frequency steps in the signal (Yack *et al.*, 2009).

Pamguard produced the following quantitative parameters for each whistle: start time of the whistle, duration of the whistle, minimum frequency, maximum frequency, and received level. Most of the whistles detected by Pamguard were found to be “false-positives” (i.e., there were false counts of whistles), and manual confirmation was required. This may have been, in part, because of high frequency noise dominating the spectrograms during some of the recordings and being taken by Pamguard as whistles. Therefore, a manual visual inspection of the spectrograms while listening to a percentage of the audio files was performed where Pamguard had made detections, in order to eliminate false positive detections to the extent possible.

In addition, in order to provide a representative dataset for further analysis, a sample of audio files in which Pamguard had not detected any whistles was also investigated manually in the same way to check for false negative detections (missing detections). Details of this process are described in §2.3.1.2.

The identification of whistles through manual analysis of audio files could be accurately accomplished. However, the whistle parameters could not be quantified during manual analysis in the same as they were by Pamguard. For example, the determination of minimum and maximum frequencies cannot be assumed to be the equivalent. Consequently, no quantitative data were used from the manual checking of the audio files in this chapter. However, the data on number of whistles were used in analysis in Chapters 5 and 6.

This process of manual analysis to check for false positive and false negative whistles incurred extra time but, importantly, as well as providing a balanced sample of data for analysis, it also allowed for a closer visual and acoustic analysis of whistles and other sounds occurring at the same time, including whistles and fish sound (see below).

Because other sounds from boats or fish often overlapped with whistles, it was not possible to associate received levels recorded by Pamguard to whistles. Consequently, information on received levels was not taken into account in the analysis.

The methodology described above allowed the following quantitative parameters characterising whistles to be used in this study: duration, minimum and maximum duration, minimum and maximum frequency, and frequency range. Lammers *et al*. (2003) also presented characterization of whistles using only these parameters.

4.2.3 Fish sound detection

During spectrogram analysis of each audio file to identify false-positive and false-negative whistle detections by Pamguard, data were also extracted regarding the occurrence of fish sounds in each of the analysed audio files (see §2.3.1.3). Observations of the time of day that fish sounds were detected were recorded, as well as an assessment of the type of fish sound. This assessment was informed by listening to fish audio files from the Macaulay Library (Macaulay Library (ML) and the pattern of the spectra of the fish chorus was compared to those presented by Sprague *et al.* (2000). A list of all audio files consulted is given in the Reference section (§4.5) at the end of this chapter. Once the type of fish was confirmed with the Macaulay library, I checked with the list of shore fishes of this area to confirm its occurrence in this same area (Robertson and Allen, 2008). Confirmation of fish sounds was also achieved through extensive personal communication in 2010 and 2011 with Dr. D. Mann (Mann, 2012).

The presence of fish sounds in each audio file was recorded in the same way as for dolphin whistles. The probability of fish sounds co-occurring with dolphin whistles was calculated as the number of co-occurrences divided by the total number of audio files. The probability of co-occurrence by chance is the probability of occurrence of dolphin whistles multiplied by the probability of occurrence of fish sound. To test whether the observed probability of co-occurrence was significantly different from that occurring by chance, a bootstrap resampling procedure was conducted. In each bootstrap iteration, audio files were randomly selected with replacement to generate a sample dataset of the same size as the original dataset, from which the probability of co-occurrence by chance was calculated. This was repeated 1000 times and the 95% confidence interval of the resampled probabilities calculated using the percentile method (lower and upper 2.5%-iles of the distribution). If the observed probability of co-occurrence of whistles and fish sound fell outside the confidence interval, it was significantly different from the probability of co-occurrence by chance.

4.3 RESULTS

During recordings with both hydrophones, common bottlenose dolphins (*Tursiops truncatus*) were sighted and identified 13 times (see Table 2.1). There were no visual identifications matching the recordings made in the 24-hr cycle with the stationary hydrophone (i.e., no video was attached to the hydrophone). However, on a few occasions when the equipment was being deployed or retrieved, common bottlenose dolphins were seen nearby (see Table 2.1). No other dolphin species was identified during the study. This suggests a high probability that the dolphin whistles detected were made by this species, and this is assumed here.

Three types of dolphin sounds were detected in this study: whistles, clicks and burst-pulses. In total, 4,567 whistles were detected from 453 hours of recorded audio with both hydrophone types; 3125 whistles were detected from 408 hours of recording with the bottom-based hydrophone, and 1,442 whistles were detected from 45 hours of recording with the boat-based hydrophone. Clicks and burst pulses were not analysed because the presence of snapping shrimp sound (as described above) generated a large percentage of false positive click counts.

4.3.1 Qualitative analysis of whistles

Spectrograms to illustrate the most common whistle contours found within this dataset are shown in Figures 4.2 through 4.8. Some of these spectrograms (annotated as appropriate) also show snapping shrimp dominating the sound and fish chorus in the low to mid frequencies. The three types of dolphin vocalisations are shown in the spectrograms: fundamental (and harmonic) components of whistles, as well as clicks and powerful burst pulses (the latter shown in Fig. 4.8).

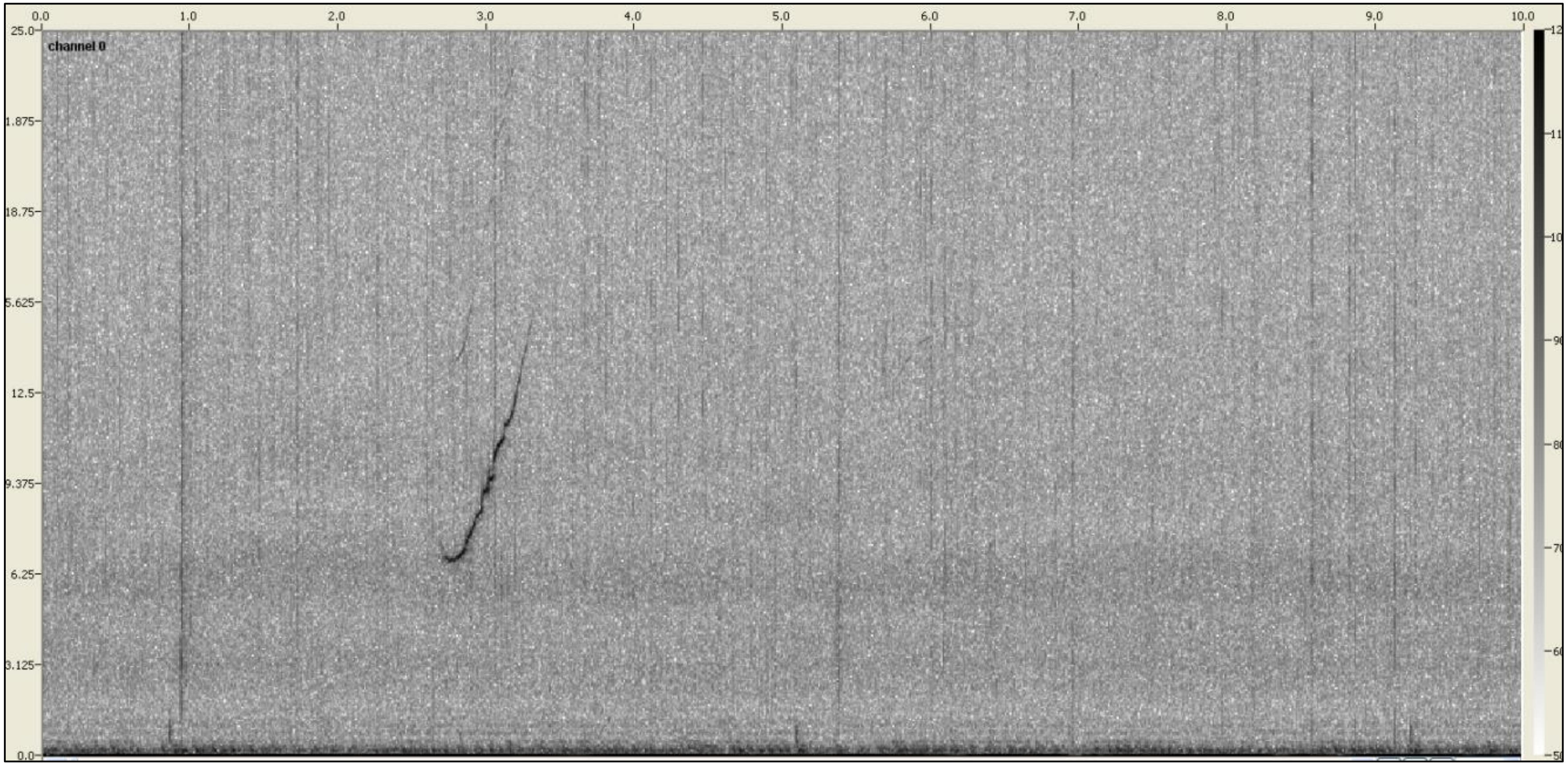

Fig. 4.2 Upsweep whistle contour. Frequency (kHz) is represented in the y-axis to the left and to the right the grey shade variation illustrates the intensity of the sound (dB). The upper x-axis shows duration of the sound in seconds.

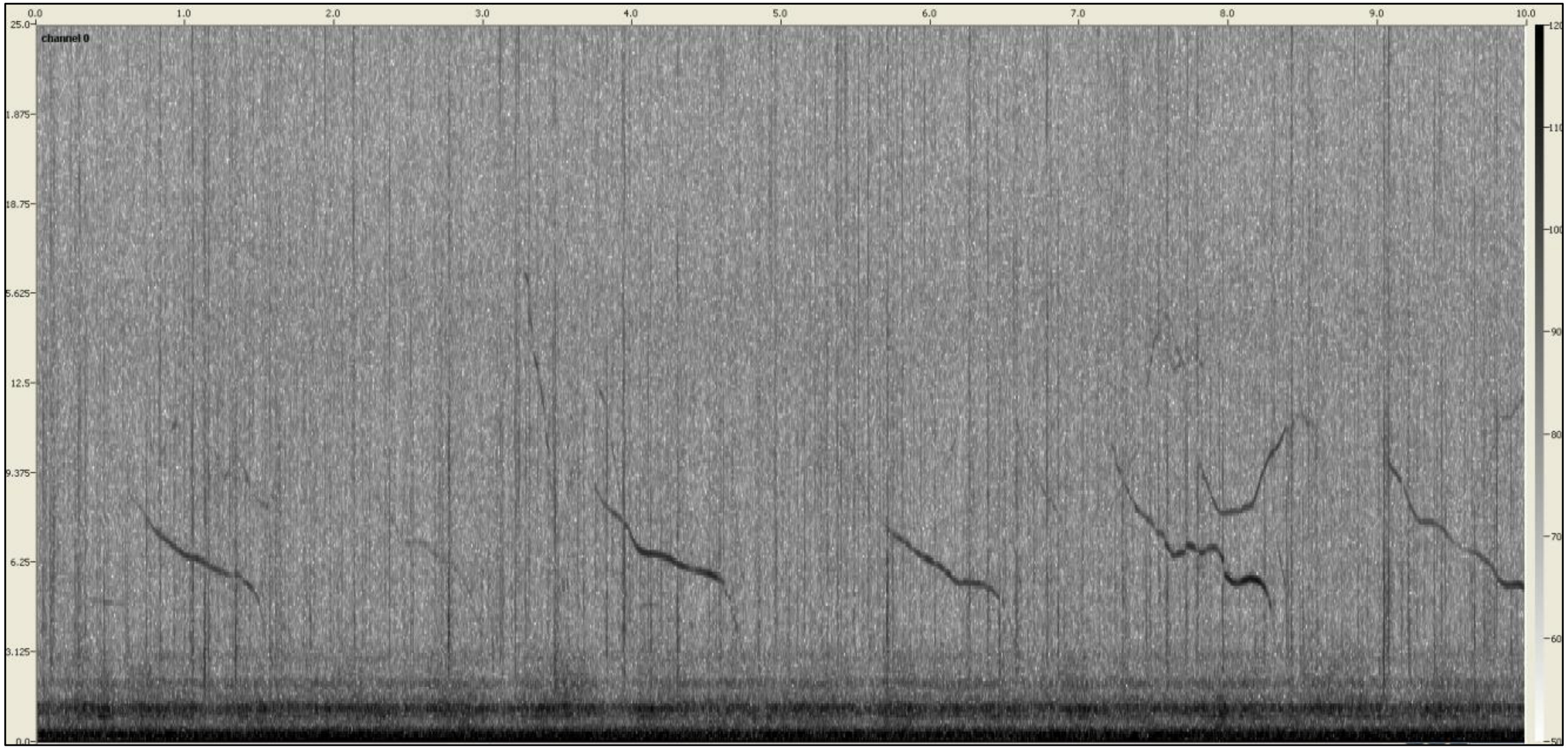

Fig. 4.3 Downsweep whistles; clicks and burst pulses are also present in this image. Also present is a convex whistle at 8 seconds and below it a multiple whistle. Fish chorus is presented (<1 kHz). Details of axes are as for Figure 4.2.

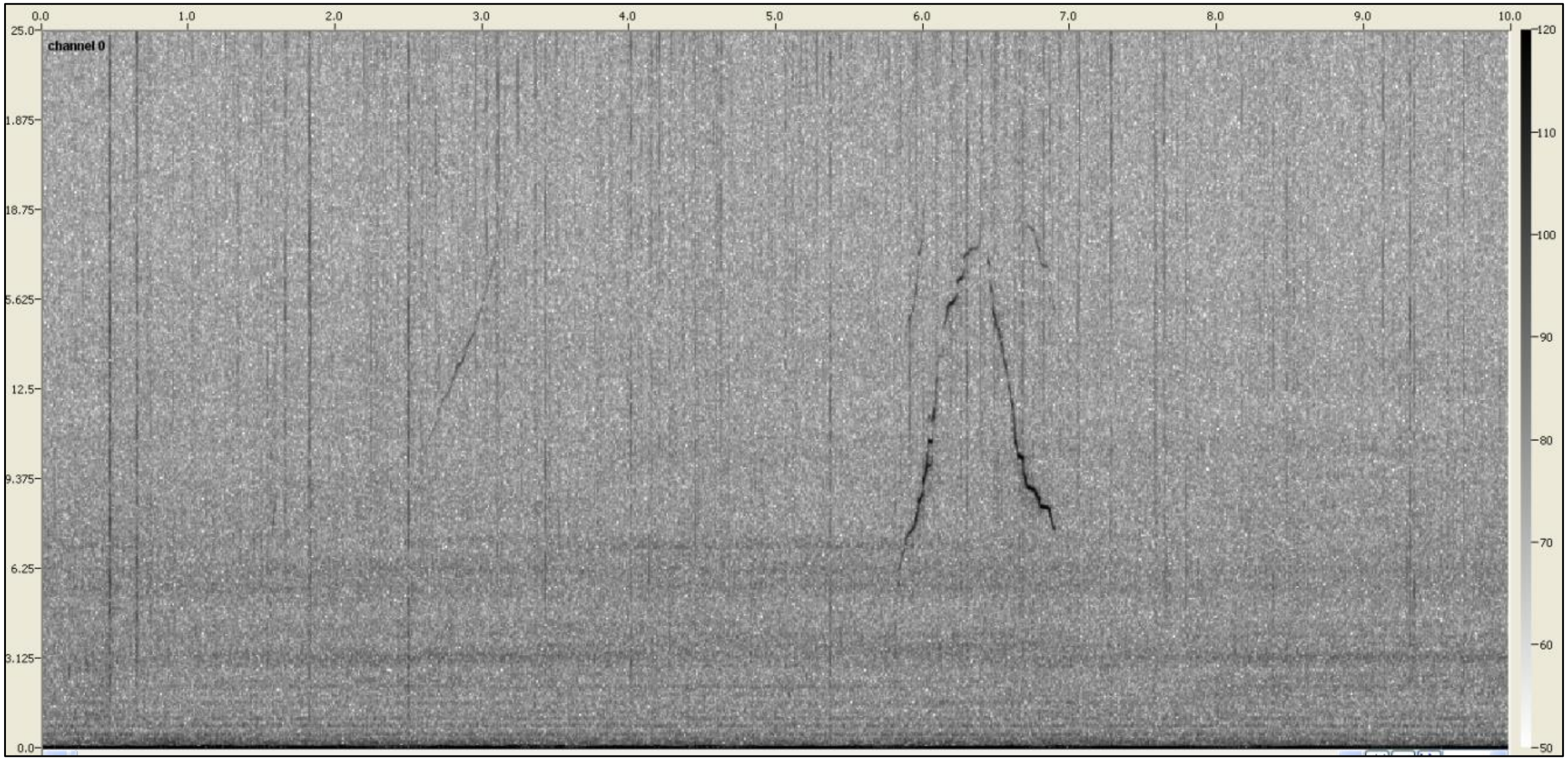

Fig. 4.4 Concave whistle contour. Details of axes are as for Figure 4.2.

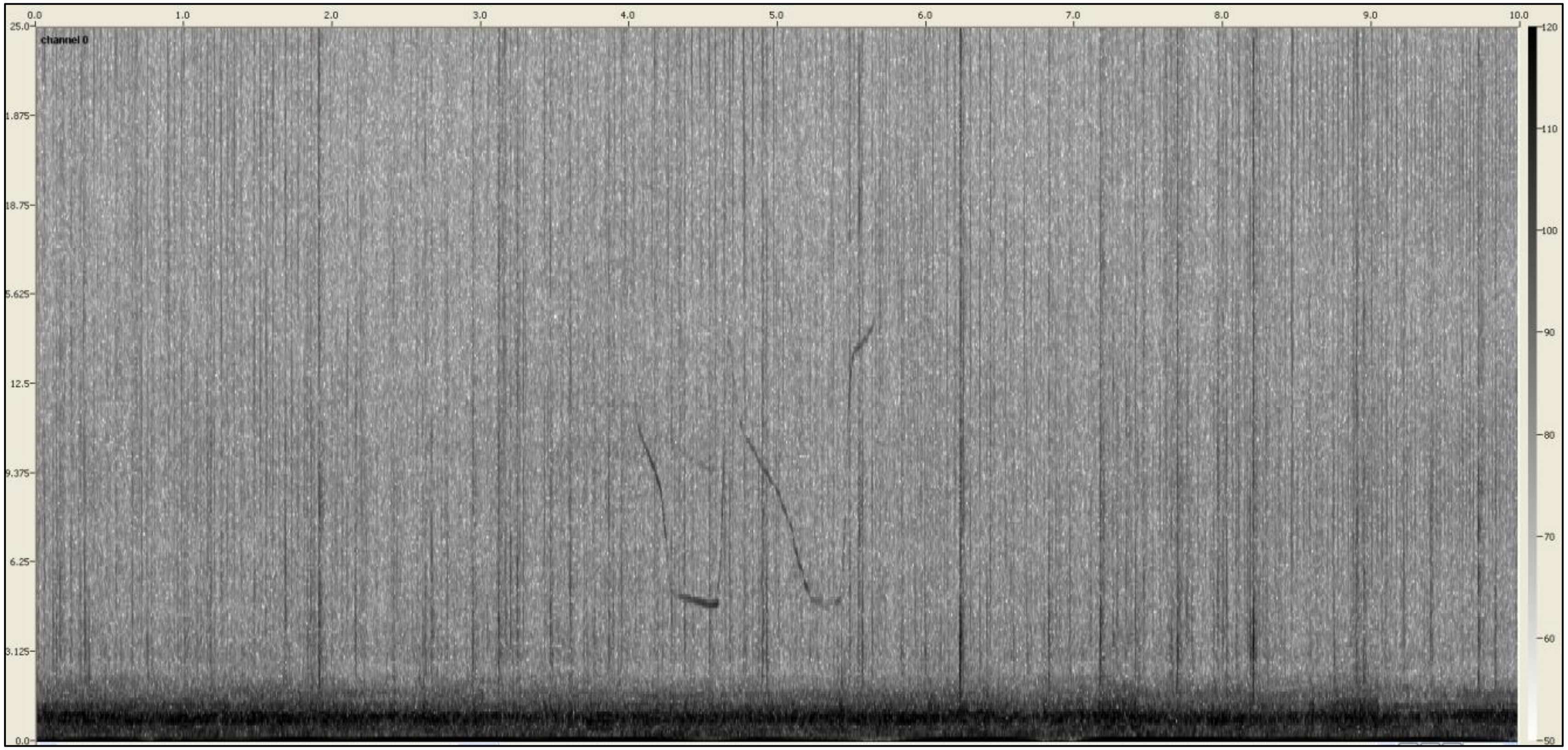

Fig. 4.5 Convex Whistle contour. Loud fish chorus is also shown (Approximately at 2 kHz). Details of axes are as for Figure 4.2.

Fig. 4.6 Multiple or Sinusoidal Contour. This example shows a particular high frequency whistle. On many occasions, dolphin whistles would start at approximately 6 kHz, increase to approximately 18 kHz, and decrease back to 6 kHz and repeat this cycle, the whistle lasting approximately 1.45 sec, following the shape of an "M" as illustrated. During manual analysis of the files, it was observed that very often these whistles occurred in the presence of fish chorus (red arrow) and of small vessel engine noise (red bracket). Details of axes are as for Figure 4.2.

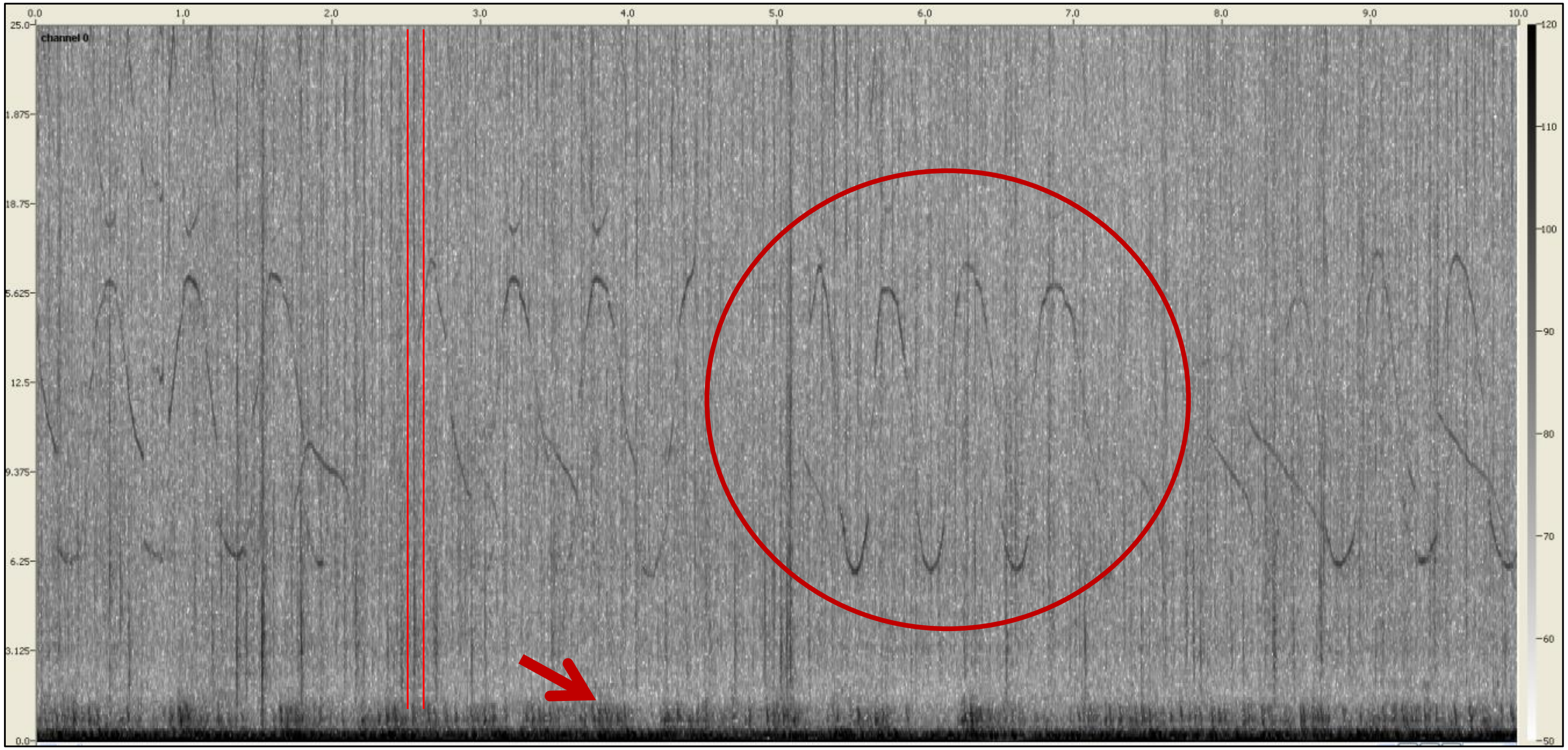

Fig. 4.7 Multiple/Sinusoidal. This example shows continuous sinusoidal whistles, in combination with multiple clicks (very close vertical lines running parallel to vertical very thin line inserted to demonstrate clicks). The red arrow shows another figure of how fish chorus is showed in the spectrogram (different type of fish sound). Details of axes are as for Figure 4.2.

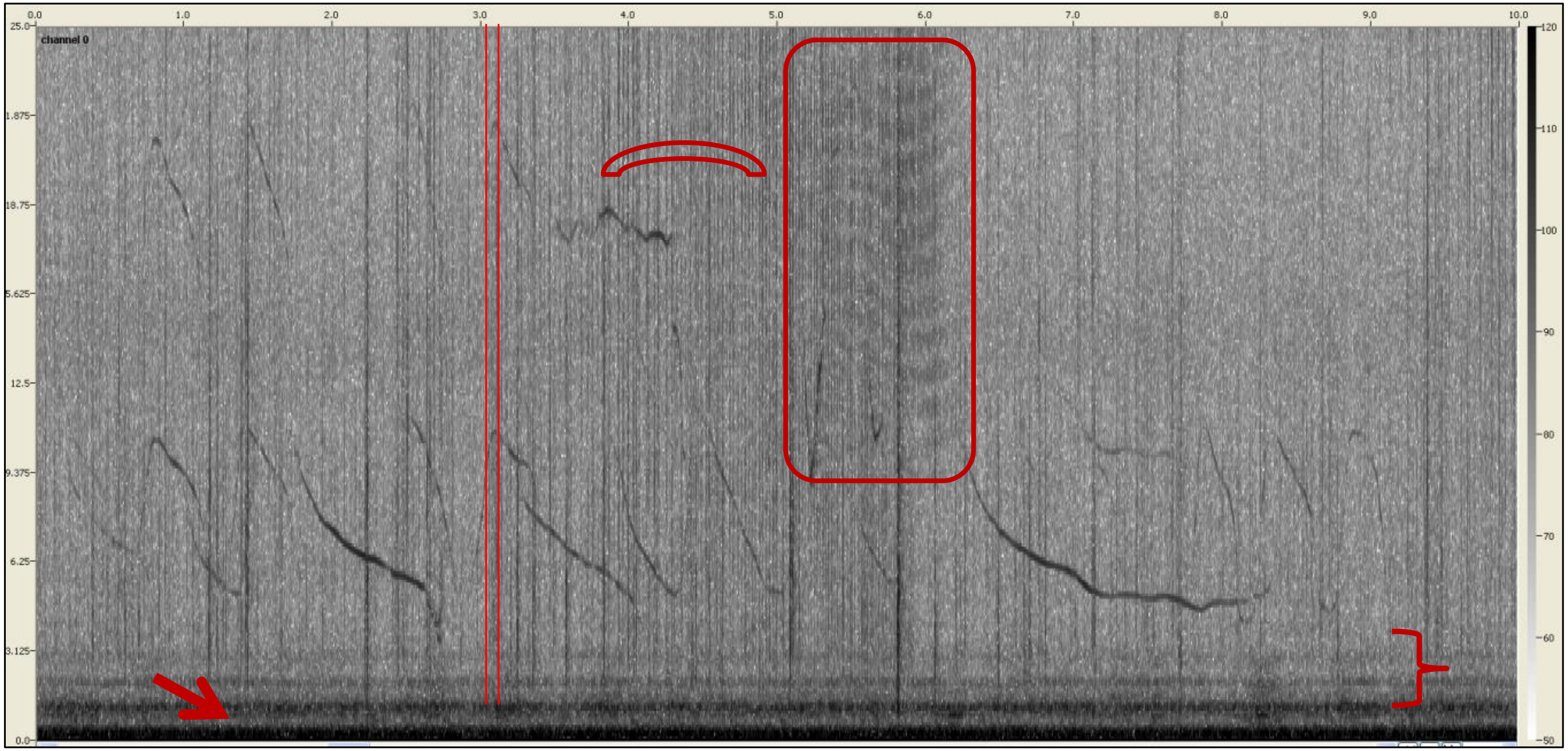

Fig. 4.8 Example of a spectrogram that included clicks (red vertical lines), burst clicks (clicks showing to be packed together, red arc), long whistles, harmonics (red rounded rectangle), as well as fish noise (red arrow) and small vessel noise (red bracket). Details of axes are as for Figure 4.2.

4.3.2. Quantitative analysis of whistles

Table 4.1 shows a summary of the quantitative parameters of whistles recorded from both the bottom based hydrophone (DSG) and the boat based hydrophone (CR55). These are presented separately because data collected with the boat-based hydrophone (CR55) were recorded during point sampling in daylight hours and data collected from the fixed hydrophone (DSG) were recorded during a continuous 24 hour cycle.

For each whistle event that Pamguard detected, that were confirmed not to be false positive detections (see Section 4.2.2) there was information regarding duration, minimum frequency and maximum frequency of the whistles. Table 4.1 summarises these data by month separately for both hydrophones, including the following: mean duration of whistles, the smallest whistle duration in each month, the largest whistle duration in each month, the minimum frequency of a whistle of each month (which could not be <3kHz as that was the high-pass filter for whistles during Pamguard analysis), the maximum frequency of a whistle of that month; and frequency range (the difference between maximum and minimum frequencies). Also given are the mean difference between minimum and maximum frequencies and the mean of monthly frequencies calculated with all entries from Pamguard from each month.

Data were collected with the CR55 in all months of the sampling period except May and July, and data were collected with the DSG in all months except November, December and January.

An analysis of variance was conducted to test where there were significant differences in summary statistics between hydrophones. Table 4.2 shows mean duration of whistles, minimum frequency, maximum frequency and overall frequency for both hydrophones and the difference between them. Results show that there was no significance in difference between duration and minimum frequency between hydrophones but that there were significant differences in maximum frequency and total mean frequency. Based on these results, the parameters have been kept separate for each hydrophone.

Month	Mean Duration DSG (ms)	Smallest Wh Duration (ms)	Largest Wh Duration (ms)	DSG Min Freq (kHz)	DSG Max Freq (kHz)	Frequency Ranges	MEAN (Min & Max) Freq. DSG (kHz)	TOTAL MEAN OF MONTHLY DSG SAMPLE (kHz)
Apr-10	109.21	56.32	860.16	3.00	24.60	21.60	13.80	10.38
May-10	92.28	61.44	491.52	3.22	24.70	21.48	13.96	11.41
Jun-10	75.92	58.71	148.48	6.64	23.30	16.66	14.97	15.30
Jul-10	75.11	66.56	122.88	3.71	24.90	21.19	14.31	14.72
Ago-10	87.27	76.80	250.88	4.98	24.53	19.55	14.76	13.70
Sep-10	118.82	71.68	962.56	3.00	23.92	20.92	13.46	11.22
Oct-10	114.16	57.80	501.76	4.20	24.12	19.92	14.16	11.48
Nov-10								
Dec-10								
Jan-11								
Feb-11	163.07	112.64	266.24	7.71	22.07	14.36	14.89	12.42
Mar-11	71.41	55.10	107.52	10.15	19.62	9.47	14.89	14.31
TOTAL MEAN	*100.80*	*68.56*	*412.44*	*5.18*	*23.53*	*18.35*	*14.35*	*12.77*
S.D.	*29.26*	*18.09*	*318.45*	*2.49*	*1.71*	*4.13*	*0.55*	*1.77*
S.E.	*9.75*	*6.03*	*106.15*	*0.83*	*0.57*	*1.37*	*0.18*	*0.59*
Conf. Interval	*78.31-123.29*	*54.65-82.47*	*167.66-657.22*	*3.26-7.09*	*22.21-24.82*	*15.17-21.52*	*13.93-14.77*	*11.40-14.13*
C.V.	*29.03%*	*26.40%*	*77.20%*	*48.14%*	*7.26%*	*22.50%*	*3.83%*	*13.89%*

Month	Mean Duration CR55 (ms)	Smallest Duration (ms)	Largest Duration (ms)	CR55 Min Freq (kHz)	CR55 Max Freq (kHz)	Frequency Ranges	MEAN (Min & Max)Freq. CR55 (kHz)	TOTAL MEAN OF MONTHLY CR55 SAMPLE (kHz)
Apr-10								
May-10								
Jun-10	69.81			5.16	18.43	13.27	11.80	18.21
Jul-10								
Ago-10	64.00			13.90	15.25	1.35	14.58	15.11
Sep-10	185.00	128.00	477.00	4.50	10.98	6.46	7.75	9.77
Oct-10								
Nov-10	203.63	115.27	407.27	7.70	10.98	3.28	9.34	9.60
Dec-10	194.00	151.27	221.10	7.96	11.00	3.04	9.48	10.31
Jan-11	74.18	69.81	87.27	10.42	22.00	11.58	16.21	15.33
Feb-11	88.43	73.51	128.00	3.01	21.96	18.95	12.48	10.94
Mar-11	147.82	64.00	1006.55	3.01	21.96	18.95	12.49	10.14
TOTAL MEAN	*128.36*	*100.31*	*387.87*	*6.96*	*16.57*	*9.61*	*11.76*	*12.43*
S.D.	*60.55*	*36.21*	*339.64*	*3.82*	*5.16*	*7.10*	*2.83*	*3.30*
S.E.	*21.40*	*14.78*	*138.65*	*1.35*	*1.82*	*2.51*	*0.99*	*1.16*
Conf. Interval	*77.74-178.97*	*62.31-138.30*	*31.43-744.30*	*3.76-10.15*	*12.25-20.88*	*3.67-15.54*	*9.40-14.12*	*9.67-15.18*
C.V.	*47.16%*	*36.09*	*87.56*	*55.00%*	*31.13%*	*73.90%*	*24.02%*	*26.50%*

Table 4.1. Quantitative parameters of whistles recorded with DSG (top table) and CR55 (bottom table) per month. Both tables show mean, standard deviation, standard error and coefficient of variance of each of the parameters for each of the hydrophones.

While doing analysis the shortest whistle found in the raw dataset was 56.32 ms and some spectrograms showed whistle durations greater than 1000 ms. (Figs. 4.6 and 4.8, Table 4.1).

Between both Hydrophones DSG & CR55	Mean Duration	Mean Min Frequency	Mean Max Frequency	Total Mean Frequency
Mean (ms, kHz, kHz, kHz)	**114.58**	**6.06**	**20.12**	**13.05**
Standard Deviation	**44.90**	**3.15**	**3.31**	**1.68**
Standard Error	**15.58**	**1.09**	**1.15**	**0.60**
SS total	**35726.69**	**165.31**	**389.97**	**86.79**
df	**16.00**	**16.00**	**16.00**	**16.00**
P-value	**0.24**	**0.26**	**0.001**	**0.02**
F crit	**4.54**	**4.54**	**4.54**	**4.54**

Table 4.2 Statistical analysis of combining both DSG and CR55 whistle parameters. Summary statistics were calculated from the mean of every parameter between hydrophones. Analysis of Variance shows the significance level for each parameter.

Whistle Detections	*Mean Frequency (kHz)*	*SD*	*SE*	*Range*
DAY	9.6	5.37	1.38	15.03
NIGHT	11.28	4.89	1.26	16.3
Source of Variation (Count=15)	***Sum Squares***	***df***	***P-value***	***F crit***
Between Day&Night	27.3614931	1	0.31812	4.19597
Within Day&Night	741.540849	28		

Table 4.3 Summary statistics for diurnal differences in whistle frequency means per day and per night of each deployment (DSG). Analysis of Variance between day and night shows no statistically significant (α=0.05) differences in mean frequency between day and night.

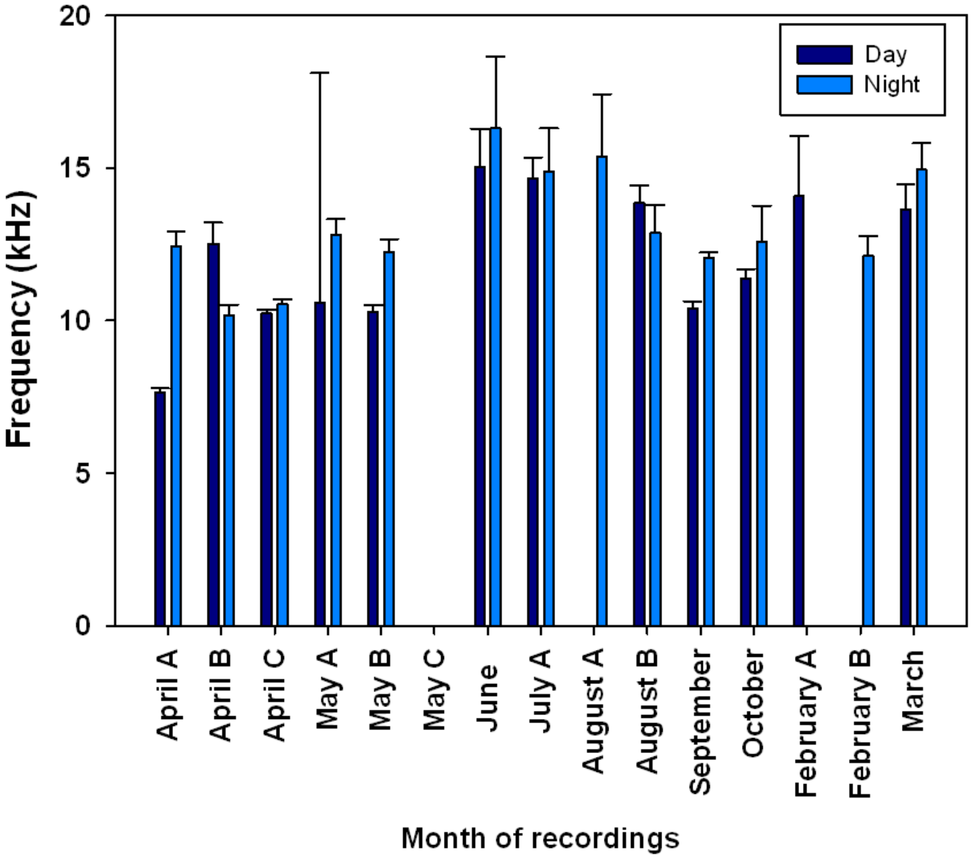

Fig. 4.9 Mean frequency per recording during day and night with standard error bars. May A shows a large SE because only two files at daytime had whistle detections. No whistles were detected for May C. August A and February B had no whistle detections at night, and February A had any detection during the day.

Whistles were of higher frequency at night (Mean= 11.28 kHz, SD=4.89) than during the day (Mean= 9.62 kHz, SD=5.37) (Fig. 4.9). However, in an analysis of variance of data comprising a single (mean) whistle frequency for day and another for night for each deployment (date) there was no significant difference in frequency between day and night ($p>0.05$, Table 4.3). Any non-independence of the data caused by serial correlation of whistles would have caused the SE of overall mean frequency for day and for night to be underestimated and therefore the chance of a significant difference would have been increased. Since the result was non-significant, failure to take account of any such non-independence does not affect the conclusions. The graph shows absence of data in some deployments where no whistle was detected either at daytime or at night-time or both (May C, August A, February A, February B).

Statistical summaries for data recorded with the boat-based hydrophone (CR55) are presented per month in Table 4.1. Summaries per location are given in Table A.21 in the Appendix because of the large number of locations, however, Table 4.4 shows the summary statistics per location (N=27). The overall mean of frequency with the CR55 per site was 9.60, SD = 4.66. As described above, recordings made with the boat-based hydrophone (CR55) covered more sampling points, but only during daylight hours. Mean whistle duration from all recordings was 102.16ms (SD=42.22) with a smallest duration within the means of 28.16 ms found in one of the samples, and a maximum duration of 1006.55 ms. The mean minimum frequency was 7.16 kHz (SD5.57) and the mean maximum frequency was 13.45 kHz (SD = 6.12). Analysis of Variance between locations shows highly statistically significant results (α=0.05, *p* < 0.001, Table 4.4).

CR55 per location (N=27)	Duration (ms)	Min Freq (kHz)	Max Freq (kHz)	Freq Mean per location	Range
Mean	***102.16***	***7.16***	***13.45***	***9.60***	***6.28***
Stand. Dev.	***42.22***	***5.57***	***6.12***	***4.66***	***6.34***
Stand. Error	***7.98***	***1.05***	***1.15***	***0.88***	***1.19***
Variance	***1783.30***	***31.11***	***37.53***	***21.73***	***40.30***
p-value	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***

Table 4.4 Summary statistics for whistle parameters per location recorded with the boat-based hydrophone (CR55). The complete database is in Appendix section (Table A.20).

4.3.3 Audio and Spectrogram analysis

Low frequency noise from large ships occurred continuously through all recordings. Noise recorded from small engines from artisanal fishing boats was infrequent but very noticeable when present because of its distinctive signal dominating the spectrogram at frequencies greater than 1,600Hz and masking almost any other noise (Chapter 3, Fig.

3.4). The two most distinctive forms of biological noise were from snapping shrimp (greater than 5 kHz and as high as the limit of these spectrograms, 25 kHz), which was also continuously present in all recordings, occupying dolphin-click like frequency bands; and that of fish sound or fish choruses, at frequencies between 400 Hz and approximately 1,600 Hz. Figure 4.10 shows part of a spectrogram illustrating the presence of fish chorus sound lower than 500Hz and up to 1 kHz, and the sound of an approaching vessel between 3 kHz and 9 kHz.

The occurrence of dolphin whistles when fish sounds were present became evident through manual analysis of the spectrograms and in this chapter spectrograms are presented to illustrate this event and also when these occurred in the presence of small boat noise. Table 4.5 tabulates the total number of audio files manually analysed (4,233) and how many of these resulted in fish sound detection, whistle detection and both in the same file. Fish choruses were mostly present in the early hours around sunrise, at dusk and during the night, whereas whistles were detected almost at the same rate at both times of the day, however both occurred together more at night-time. The empirical and theoretical probabilities of both events (whistles and fish sound) occurring at the same time and the 95% confidence interval of the theoretical probability of co-occurrence from the bootstrap procedure calculated in R, are shown in Table 4.5. The observed probability of whistles and fish sound occurring together was close to 40% greater than expected and this has a probability of less than 0.05 of occurring by chance.

	Total Observations (Number of audio files)	Observed Files with Whistle Detections	Observed Files with Fish Sound Detections	Co-occurrence of Whistle and Fish Sound (Obs. fs & wh)
Total Number	***4233***	***427***	***1625***	***228***
Daytime	2347	239	571	85
Nightime	1886	188	1054	143

Empirical probability of fish sound detection - Pe(fs)	**(obs.fs/Total)**	0.384
Empirical probability of whistle detection - Pe(wh)	**(obs.wh/Total)**	0.100
Theoretical Probability of *both* occurring together - Pt	**(Pe(fs) * Pe(wh))**	0.039
Empirical Probability of *both* occurring together - Pe	**(obs. fs & wh/total)**	0.054
Percentage of the observed probability	**[Pe(fs&wh)-Pt(fs&wh)/Pt(fs&wh)]**	39%
95% Confidence Interval (Empirical probability falls outside C.I. = Significant)		0.034-0.043

Table 4.5. Observed occurrences of whistle detections and fish sound detection. Daytime occurrence refers to the period between 6:00 to 18:00 and night-time between 18:00 to 6:00. Diurnal co-occurrence of fish sounds and whistle detections are also presented. Empirical and theoretical probabilities of co-occurrence are shown, and the 95% confidence interval of the theoretical probability of co-occurrence from the bootstrap resampling procedure.

There was no visual confirmation of feeding events, but the combined detection of clicks, click bursts and whistle activity heard and visualised in spectrograms when fish chorus frequencies and sounds were present (and sometimes boats) suggest that feeding events were taking place.

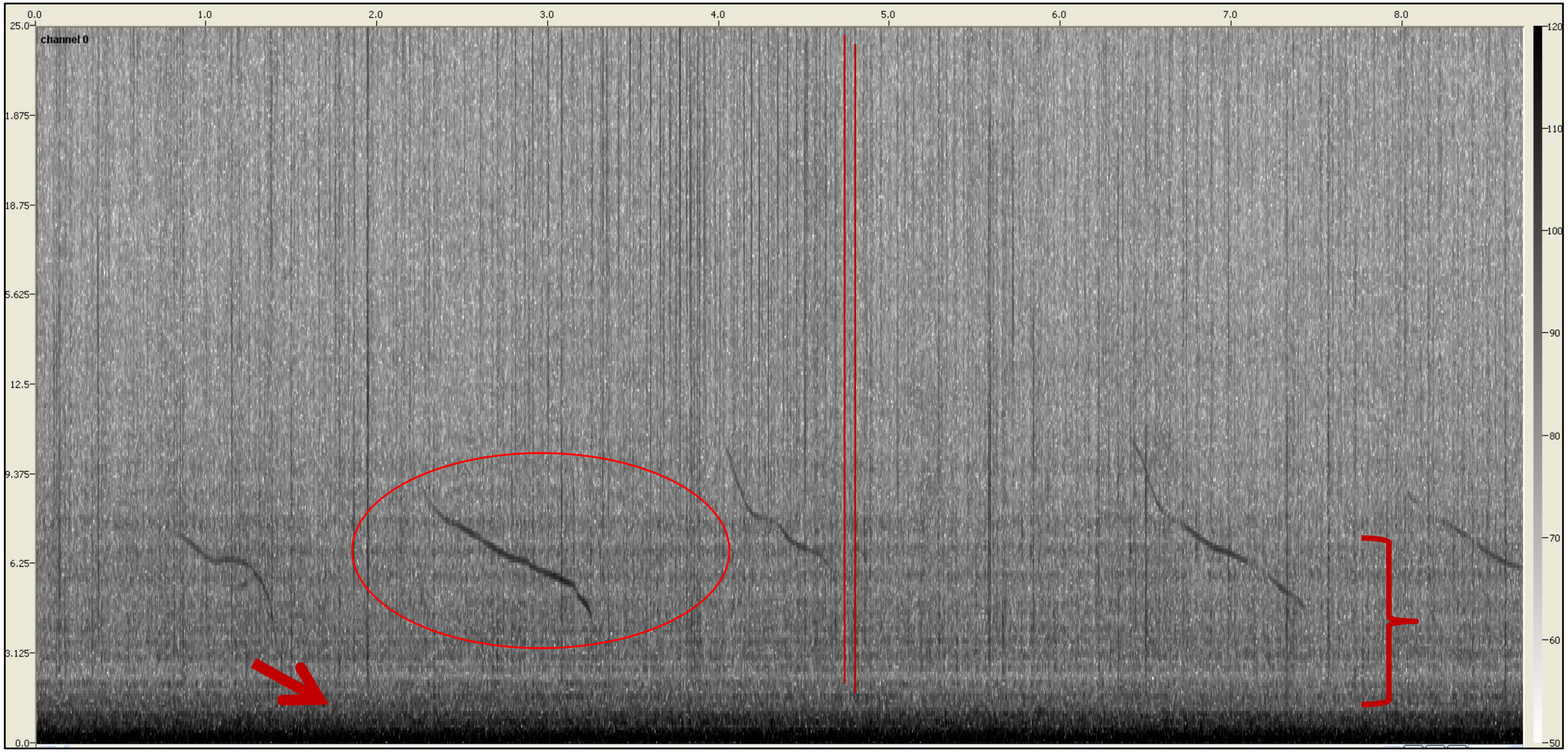

Fig. 4.10 A 10 second window of a spectrogram showing fish chorus (red arrows), approximately 500 Hz – 1kHz; noise from an approaching small fishing boat engine (red right brace), in frequency range 3kHz to 9kHz). A few whistles (circle) can be seen in this example whereas clicks are distinguished by the very thin and very close together vertical lines (red lines), and with frequencies that seem to rise above 25 kHz (which is the ceiling of the spectrogram).

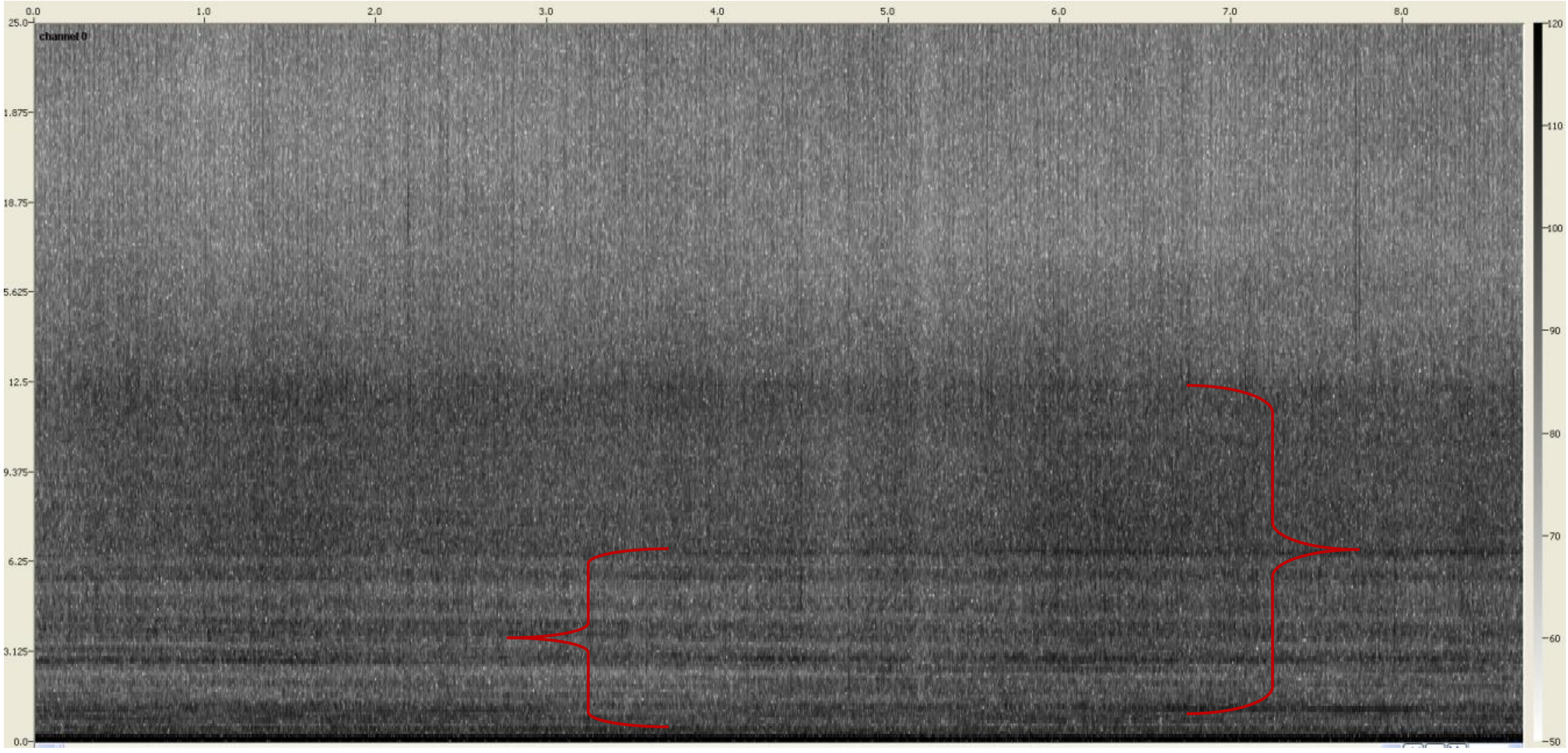

Fig. 4.11 Spectrogram showing two types of vessels: a trawler type (up to 9 kHz, red brace facing right) and small boat up to 12 kHz (red brace facing left).

4.4. DISCUSSION

4.4.1 Comparison of dolphin whistles with previous studies

This is the first description of the whistle repertoire of dolphins (assumed to be bottlenose dolphins) in the region of the Pacific entrance to the Panama Canal. The whistles detected in this study represented all the common contours reported by most authors (Bazua-Duran, 2004; Azevedo et al., 2007a; Janik, 2009). Nevertheless, most of the shapes belong to combined types of descending-ascending-descending and multiple or sinusoidal shapes (i.e. Fig.4.5 and Fig.4.7). Further study is necessary to provide a more complete analysis of dolphin whistles in this area, such as number of inflection points, harmonics, and percentages of different contours. These were not included in this study (see §4.2.1) but completing a profile of the acoustic characteristics of dolphins is an important tool to examine the social structure and distribution of populations because call variation can occur between groups, between individuals and/or between populations (Rendell *et al*., 1999) and it is through acoustic communication that dolphins maintain group cohesion (Acevedo-Gutierrez, 2009). Dolphins in this region of the Panama Canal produced whistles characterized by different contours (not quantified), and a wide range of whistle duration and frequencies (Table 4.1). Similar variation has been found when whistles have been compared from locations that are far apart from each other, and therefore show geographic variation (May-Collado and Wartzok, 2008; Oswald *et al*., 2008).

Author	Location	Mean Duration (ms)	Coefficient of Variation	Duration - SD	Min Freq (khz)	Max Freq (kHz)	Frequency Range
Wang *et al*., 1995	Galveston, Gulf Mex (GM)	750	*61.80*	*0.46*	5.98	11.95	5.97
Wang *et al*., 1995	Corpus Christi, GM	690	*60.50*	*0.41*	5.88	11.43	5.55
Wang *et al*., 1995	South Padre Island, GM	600	*43.66*	*0.26*	5.37	10.33	4.96
Wang et al., 1995	Gulf of California	660	*53.10*	*0.35*	6.91	13.68	6.77
Azevedo *et al*., 2007	Patos Lagoon, Brazil	550	*71.20*	*0.39*	5.96	12.21	6.25
Hernandez *et al*., 2010	Mississippi Sound, GM	630	*10.00*	*0.63*	5.94	12.00	6.06
Quintana-Rizzo et al., 2006	Shallow water, Sarasota Bay	N/A	*N/A*	*N/A*	7.50	13.00	5.50
Quintana-Rizzo et al., 2006	Channels, Sarasota Bay	N/A	*N/A*	*N/A*	12.00	20.00	8.00
May-Collado and Wartzok, 2008	East-Caribbean, Panama	1130	*27.43*	*3.10*	5.61	15.80	10.19
Acevedo-Gutierrez & Stienessen, 2004	Isla del Coco, Costa Rica	380	*7.60*	*0.29*	7.51	12.41	4.90
Acevedo-Gutierrez & Stienessen, 2004	Isla del Coco, Costa Rica	660	*6.20*	*0.41*	8.51	13.96	5.46
Jensen *et al.,* 2012	Koombana Bay, Australia	N/A	*N/A*	*N/A*	5.20	9.80	4.60
Oswald et al., 2003	Eastern Tropical Pacific	1140	*6.14*	*0.70*	7.40	17.20	9.80
Morisaka et al., 2005	Indo-Pacific	400	*8.25*	*0.33*	5.74	11.31	5.57
This study (DSG)	Pacific, Panama Canal region	*101*	*29.03*	*9.75*	*5.18*	*23.53*	*18.35*

Table 4.6. Frequency parameters reported by other authors for *Tursiops* sp. at different locations, including reported measures of uncertainty.

Whistle duration seems to be one of the characteristics that vary the most among dolphins. Table 4.6 shows published values for mean whistle duration for *Tursiops* sp, the genus assumed here. The mean duration of the whistles in this study is the lowest of all compared in this table (101 ms). Oswald *et al.* (2003) reported mean whistle duration in the Eastern Tropical Pacific of 1140 ms, much greater than the mean reported here, and the closest mean duration to this study is that reported by Acevedo-Gutierrez & Stienessen (2004) of 380 ms (Table 4.6). Throughout the analysis of data, specific events showed whistles to vary from very short duration whistles (28.52 ms) to a few whistles of much longer duration (1006 ms). However results showed the mean were very short whistles and this may support the fact that background noise forces the program to identify short whistles that were being interfered with by other sources of sound and would be interpreted as shorter in length.

Regarding frequencies, the overall minimum mean frequency recorded in this study (5.18 kHz, Table 4.1) was similar to that given by most of the studies shown in table 4.6. Quintana-Rizzo *et al*. (2006) showed the highest frequency for the mean maximum frequency (20 kHz) of bottlenose dolphins in the Atlantic (Table 4.6) which is similar to the mean maximum frequency found in this study (23.53 kHz).

4.4.2 Diurnal variation and co-occurrence of fish sound and whistle detections

Only a few other studies have made an analysis of whistle variation across diurnal cycles (Acevedo-Gutierrez and Stienessen, 2004; Oswald *et al*., 2008). In this study, a high rate of sound-producing fish presence was found between 18:00 and 06:00, which occurred in parallel to whistle detections (Table 4.5). Common bottlenose dolphins feed on a variety of soniferous fish, such as sciaenids, scombrids and mugilids (Barros and Wells, 1998; Gannon et al., 2005; Berens McCabe et al., 2010). All these species of fish are documented to be in these waters (Allen and Robertson, 1994; Robertson and Allen, 2008). One of the main landings of fish in the area includes different species of Corvina (*Cynoscion spp.*), which belong to the family Scianidae (http://www.oas.org/dsd/publications/Unit/oea30s/ch050.htm). These species of fish are considered noise-producing fish and it has been demonstrated that dolphins prefer this type of prey (Barros and Wells, 1998; Berens McCabe et al., 2010). Although no results are presented here confirming feeding events visually, manual examination of spectrograms suggested that these took place when fish chorus sounds were present at the same time as dolphin feeding vocalizations (Nowacek, 2005) such as buzzes and clicks. Examples of possible night-time feeding events are shown in spectrograms when detecting high-frequency whistle activity in the presence of very loud and mid frequency fish chorus (Figs 4.5-4.8). However, more analysis is required to investigate the relationship between feeding and whistles that these spectrograms are preliminarily suggesting. It has been reported (Hanson and Defran, 1993) that Pacific coast bottlenose dolphins have diel activity cycles, feeding more during early morning hours and late afternoon.

Through visual and audio analysis of 4,233 audio files, it was found that 53% of whistle detections occurred together with fish sound detection (228 out of 427). The observed probability of them occurring together was 40% greater than occurring by chance alone and this result is highly significant because the empirical probability falls well outside the confidence interval of the probability of co-occurrence by chance (Table 4.3). This relationship was found more often at night-time than during daytime, which is consistent with soniferous fish emitting sounds mostly from dusk to dawn.

4.4.3 The effects of background noise on whistles

Preliminary spectrogram analysis suggested that whistle rate and frequency may increase in the presence of background noise. However, a different methodology and closer statistical analysis is required to find the relationship between boat noise and whistle parameter variation. As described above, a different filter is needed to isolate boat noise and whistles to extract clear signals and received levels of both sources (Mallawaarachchi and Ong, 2008; Roch *et al*., 2011).

It has been suggested that when cetaceans are exposed to anthropogenic activities they are forced to overcome background noise by altering their communication sounds (Croll *et al*., 2001). The literature documenting the effects of outboard engines and speedboats, such as those used for dolphin and whale watching, on cetacean communication is extensive (Janik, 1996; Croll *et al*., 2001; Acevedo-Gutierrez and Stienessen, 2004; Buckstaff, 2004; Lemon *et al*., 2006; Branstetter and Finneran, 2008; Clark *et al*., 2009; Jensen *et al*., 2009; Trickey *et al*., 2010). In these studies, it has been shown that the closeness of these boats provoke not only surfacing behaviour changes in the breathing patterns of dolphins, but also that the noise generated by the constant changing of gear, characteristic in outboard engines, contributes to acoustic behaviour changes as well. For example, Buckstaff (2004) found that dolphins increase their whistle rate at the onset of approaching vessels, Lemon *et al.* (2006) found that when a boat approaches, dolphins change their travelling behaviour to that of milling until the vessels are out of their area, and Jensen *et al.* (2009) found that small boats with outboard engines moving at speeds of more than 5 knots and constantly changing gear, produce noise sufficiently loud to reduce dolphin acoustic communication ranges. In this study, a common observation was that when dolphins were sighted near a sampling site, they tended to avoid the boat and they could only be followed visually at a distance (although they were heard with the hydrophone). Surfacing time was not constant and there was no definite direction of travelling. However, fishermen often reported presence of dolphins around their boats when they conduct fishing activities with the engine in neutral to very low speeds.

4.4.4 Factors affecting whistle detection and analysis during the study

The results show a difference between the frequency ranges recorded from the bottom-based hydrophone and the boat-based hydrophone. This may be attributed to the fact that the former recorded at a sample rate of 50 kHz, whereas the latter had the option to record at the sample rate of 48 kHz, 44 kHz and some were mistakenly calibrated at 22 kHz, which would not have allowed higher frequency whistles to be detected to their maximum range and were not counted for characterization analysis. Therefore, the recommendation for the future is to keep the recordings at 48 kHz throughout all the recordings.

Another technical issue relates to the filters through which dolphin detections must be studied. It has been reported that bottlenose dolphins can produce low frequency sounds below 1 kHz described as tonal low-frequency vocalizations apparently related to interactions with humans (van der Woude, 2009), bray calls as a strategy to feed on salmonids (Janik, 2000a) or as continuous narrow-band harmonic sounds (Schultz *et al.*, 1995). For this study, a high pass filter of 3 kHz was applied during sound processing after testing that Pamguard was returning most false-negatives below this frequency, so that lower frequencies were not analysed.

The study area is characterized by high levels of background noise (Chapter 3); and the results from this study suggest that dolphins vocalized regardless of the levels of anthropogenic disturbance; however, a more extensive analysis is needed to investigate the relationship between dolphin whistles and boat noise. Such an analysis should take into account the potential bias that whistles may be less likely to be detected in high boat noise. Nevertheless, this study presents new data that provide an important baseline to start an assessment of the effects of anthropogenic noise in the area close to the Pacific entrance to the Panama Canal.

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CHAPTER 5

Modelling temporal variation in occurrence of dolphins in the Bay of Panama

ABSTRACT

Dolphins occur in the local region of the Pacific Ocean adjacent to the entrance of the Panama Canal. No formal assessment has been made of their temporal distribution in this heavy shipping area and how their occurrence relates to seasonal or diurnal variation and to ambient noise. Passive acoustics was used from March 2010 to April 2011 to record ambient sound that included whistles to indicate the occurrence of dolphins. The temporal occurrence of dolphins was studied in relation to anthropogenic activities, such as shipping noise and fishing activities, as well as physical and biological features of the environment. Generalised Linear Modelling found that month was an important factor. Fish noise was retained as a covariate in all of the models suggesting that prey is an important factor influencing dolphin occurrence. The 1/3 octave bands that explained most variability in the data were centred at frequencies 160 Hz and 20,000 Hz in the models of whistle counts, and 20,000 Hz in the presence-absence models. Sound at 20,000 Hz could have come from snapping shrimp or small boats (Chapter 3). Data collected over a longer period of time are needed to make a more accurate assessment of changes in distribution over years.

5.1 INTRODUCTION

Cetacean distribution can be influenced by various natural features of the environment including physical habitat (e.g. water temperature, salinity), food availability, suitable breeding habitat and avoidance of predators that may vary at different times of the year and times of the day. Anthropogenic activities and associated noise can also change over months and/or seasons (Forcada, 2009). Generally speaking, our knowledge of relationships between species occurrence and temporal factors is limited. Statistical modelling can help us to understand the ecological basis for these relationships and therefore provide valuable information to help the development of conservation and management plans (Austin, 2002; Garaffo *et al.*, 2007).

Most studies where temporal variation in marine mammal distribution has been modelled also investigate the influence of physical and biological oceanographic variation, such as sea surface temperature (Gaskin, 1968), indices of primary productivity, salinity, precipitation (Croll *et al.*, 2005) and prey distribution information when available (Gaskin, 1968; Wilson *et al.*, 1997; Griffin and Griffin, 2004; Croll *et al.*, 2005). There is an extensive literature about how these factors may influence the seasonality of many species of whales including blue, fin, beaked, minke whales, (McDonald and Fox, 1999; Hamazaki, 2002; Hastie *et al.*, 2003a), local seasonality of humpback whale populations (Morete *et al.*, 2007) and humpback whale migration to tropical wintering grounds (Rasmussen *et al.*, 2004; Acevedo *et al.*, 2007; Rasmussen, 2007; Rasmussen *et al.*, 2007), harbour porpoises (Weir *et al.*, 2007; Embling *et al.*, 2010), finless porpoises (Akamatsu *et al.*, 2008), and spinner, spotted and striped dolphins (Reilly, 1990; Fertl, 1994; Wilson *et al.*, 1997; Griffin and Griffin, 2004; Laran and Drouot-Dulau, 2007). There are many more studies investigating spatial distribution than temporal and seasonal distribution, especially for bottlenose dolphins in tropical environments (see Chapter 6).

There is also an extensive literature investigating how background noise, in particular vessel noise, may affect the distribution of delphinids in different areas. Au and Hastings (1982) provide a review of this topic. Nevertheless, there are few studies describing the effect of vessel noise on the occurrence of dolphins that also examine temporal factors. (Lusseau, 2005) assessed the relationship between residency pattern of bottlenose dolphins and the occurrence of boat noise caused by tourism trips. He found there was seasonal variation in the occurrence of dolphins but concluded it was not related to water temperature, and could not conclude it was related to prey availability. Instead, the dolphins chose to leave the area when it was the peak of dolphin watch tourism activity. Klinck *et al.* (2012) looked at the effects of seismic airguns in the North Atlantic, but only recorded shipping noise as present or absent, and only for two of the 1/3 octave bands. However, the study found that anthropogenic activity caused seasonal variations in ambient noise, as did surface wind. Usually, studies investigating seasonal variation in species distribution explore whether this is related to environmental variables. In this study, I investigate whether temporal variation in dolphin occurrence is related to background noise.

The Gulf of Panama is characterized by an upwelling event that occurs every year bringing very productive waters to the surface usually between January and March (D'Croz and Robertson, 1997; D’Croz and O’Dea, 2007) (Chapter 2.1). This seasonality may be expected to influence the occurrence of dolphins in the area because their prey is more abundant at certain times of the year. Therefore, intra-annual seasonal variability may be directly related to availability of food, which can be an important feature in models of the occurrence of dolphins in a particular area at any time of the year (Griffin and Griffin, 2004). The distribution of fish species in different seasons has been documented in many parts of the world but, unfortunately, data are scarce in this region. Nevertheless, artisanal fishermen almost always have a good understanding of fish reproduction patterns and occurrence in coastal areas. Fish abundance may also be an important factor influencing the occurrence of dolphins at particular times of the day.

The aim of this study is to consider whether the occurrence of dolphins in the area is influenced by temporal variation at various scales and if background noise affects any of these relationships. There are no baseline data on the local populations so investigating inter-annual variation or a comparison with previous years is not possible. Temporal variation is thus assessed diurnally, monthly and seasonally.

5.2 METHODS

The data collection, data processing and data analysis methodology used is described in Chapter 2: General Methodology. Data from both the stationary hydrophone and the boat hydrophone were combined to assess temporal variation using Generalised Linear Models (GLM).

Prior to modelling, a Pearson’s Rank Correlation test was carried out for each pair of variables, including the relationship between each response variable (whistle count and presence/absence of whistles) and each explanatory variable. These analyses were performed using R. 2.13.1 (R Development Core Team, 2011). If there was a strong correlation between explanatory variables (R>±0.5), only one of the variables of that pair was included in the first full model containing non-correlated variables. There were some exceptions to this rule if the variable was considered to be sufficiently biologically important to be included in the initial full model for the step-wise model selection procedure (described in Chapter 2). In addition, a Generalized Variance Inflation Factor (GVIF) was calculated to assess any collinearity between model covariates. VIF values were obtained for each variable in each model performed using R.2.13.1 (R Development Core Team, 2011); variables with values exceeding 5 were considered to be strongly influenced by collinearity and were therefore excluded from subsequent models.

Two response variables were considered: the count of whistles and the presence-absence of whistles, (entered as “1” or “0”, respectively). Each file from the bottom-based hydrophone (DSG) was 2.5 minutes in duration and for logistical reasons each file from the boat-based hydrophone (CR55) was divided into files of 2 minutes. Therefore, counts from the DSG fileswere multiplied by 0.8 to make them equivalent to the length of the 2 minute CR55 files (§ 2.4.1).

The count data were strongly over-dispersed (variance much greater than the mean) (Table 5.1, Figure 5.1). Therefore, models with a quasi-Poisson error structure were used with a log link function. The presence-absence data were also over-dispersed (Table 5.1) so models with a quasi-binomial error structure were used with a logit link function for these data. The explanatory variables considered for these temporal models were drawn from those described in Table 2.2 (Chapter 2). For the models developed in this chapter the variables used were: precipitation and wind speed as variables potentially affecting sound detection; time of day (hour), month and season (factor) as temporal variables; temperature and salinity as environmental variables, and fish noise (factor) and received levels of 1/3 Octave Bands. Fish noise measurements were recorded by manual analysis of spectrograms and confirmed by comparison with recordings of known sounds of various species of soniferous fish. Every time a fish sound was positively recognized it was annotated as present or absent (1 or 0) in the file (See Methods section 2.3.1.3 for details).

The Dredge function (R package MuMIn) (§2.4.2.4.) was run to find the best fitting models among all possible combinations of the explanatory variables. Models for which the estimated VIF for any variable was greater than 5 were disregarded to avoid collinearity in explanatory variables.

In addition to these methods, anecdotal data were collected by carrying out a survey of a local group of fishermen (§2.2.2.1). The survey contained illustrations for the fishermen to select the type of cetacean they have seen when out at sea fishing. It also contained questions related specifically to their fishing activity: which months, time spent out at sea, the type of fishery, amount of animals seen and where they usually go fishing. Results of these surveys are shown in Table 2.1 (Chapter 2).

5.3 RESULTS

5.3.1 DATA COLLECTED

A total of 453 hours of audio data from both hydrophones combined were analysed (see §2.3.1.2). Out of 9,789 audio files (observations) that were collected with the DSG, Pamguard detected whistles in 2,925 files. To eliminate false positive detections, these 2,925 files were manually re-analysed and a random sample of 1,212 files (40%) was retained for statistical analysis. Of the 6,864 files in which Pamguard did not detect whistles, 2696 files (40%) were manually analysed to look for false negative detections that Pamguard may have missed (§ 2.3.1.2.). In the same manner, 40% of total number of audio files recorded with the CR55 was analysed (325 audio files from a total of 812 audio files). This gave a total sample of 4,233 audio files (40% of the total number of audio files) selected for analysis. From this sample, a total of 4,567 dolphin whistles were detected in 427 audio files from 101 sample locations over a period of 12 months.

In the presence-absence data, there were 427 presences and 3,806 absences.

Data collected with the stationary hydrophone provided a 24 hour cycle window of detections over consecutive days, while data collected with the boat hydrophone provided daily data during daylight hours. Table 5.1 shows summary statistics for the response variables based on an audio file as a sampling unit. As described above, because of the difference between hydrophones in audio file duration, whistle counts from the DSG hydrophone were multiplied by 0.8 so that mean counts could be calculated from the dataset for both hydrophones combined (§2.4.1., §5.2.). Summary statistics per deployment for both the response and the explanatory variables are shown in the

Appendix (Tables A.2. through A.18). In general, dolphin whistle detections were present during most months of the year (see Table 4.1).

Audio Files Analysed N=4233	**Count Data: Whistles**	**Binomial Data: Presence/Absence**
Total counts	4567	427
mean	1.07	0.10
variance	129.11	0.091
standard deviation	11.36	0.301
standard error	0.1740	0.0046
95% Confidence Interval	0.73-1.42	0.09-0.10

Table 5.1 Summary statistics of the response variables based on an audio file as a sampling unit. The table includes audio files of both hydrophones combined.

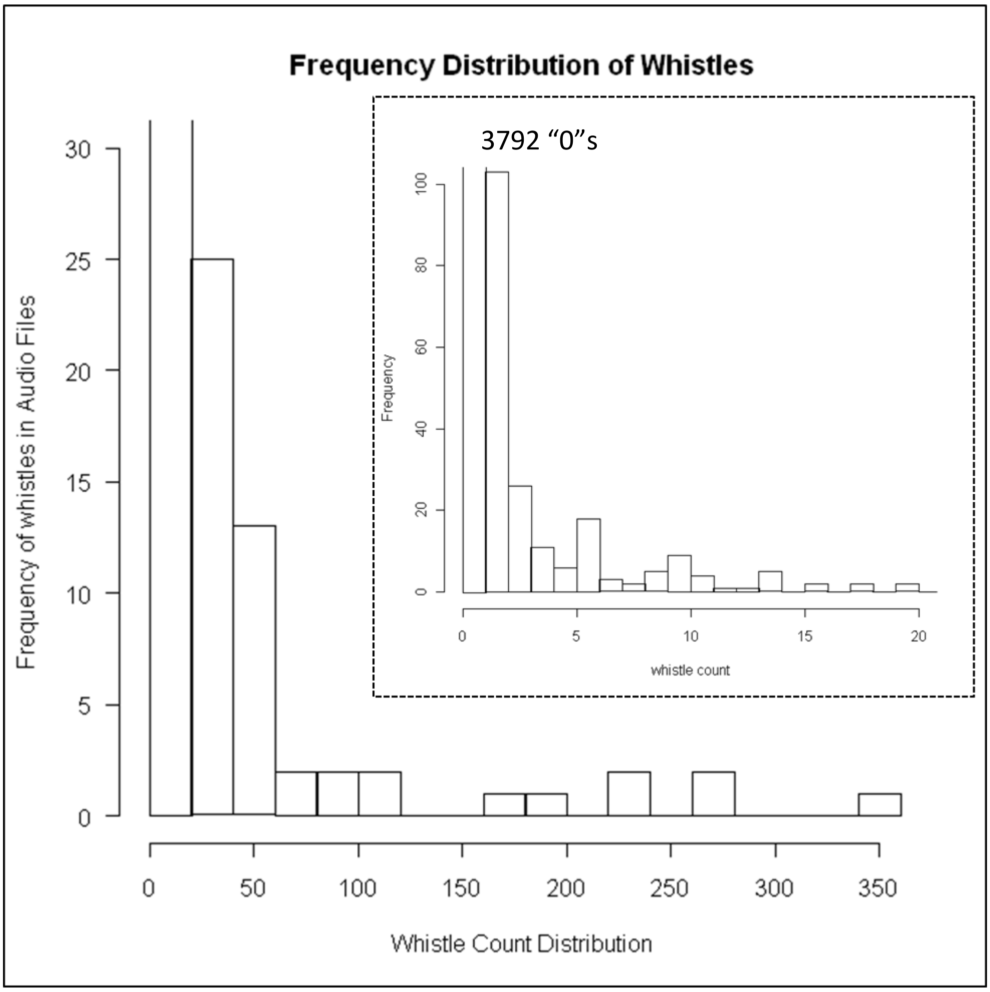

Fig. 5.1 Frequency distribution of whistles counted in the study. In the main histogram, the first bar has a frequency of 4,184 audio files with 0-20 whistles per audio file, including 3,792 zeroes. The y-axis has been limited to 30 to allow frequencies greater than 20 to be clearly visible. The insert histogram shows the detail for audio files with 0,1,2 …20 whistles. The y-axis has again been limited to allow frequencies greater than 0 to be visible. As in the main histogram, the first bar has a frequency of 3,792 files with 0 whistles.

5.3.2 MODELS OF WHISTLE COUNTS AND PRESENCE/ABSENCE

Table 5.2 shows the best fitting models to investigate the extent to which variation in whistle count could be explained by temporal, physical, environmental and biological variables (see section 5.2). Explanatory variables are described in section 5.2 and, in more detail, in sections 2.2 and 2.3. The variables retained in the best model were fish noise, month and the 1/3 octave bands centred on frequencies 160 Hz and 20,000 Hz. The best model for whistle counts explained 15% of the deviance in the data. Table 5.3

shows the coefficients of the variables retained in the best fitting model and their significance. Fish noise and 160 Hz were significant.

Quasi-Poisson GLM	*Response Variable*	*Fish Noise*	*Month*	*f160hz*	*f20000hz*	*QAIC*
1	Whistles	X	X	X	X	263.87
	VIF	1.59	1.11	4.4	4.21	
2	Whistles	X		X		306.67
	VIF	1.5		1.50		
3	Whistles		X	X		326.64
	VIF		1.13	1.13		

Table 5.2 Variables retained in the best fitting Generalized Linear Models with quasi-Poisson error distribution for whistle counts. The lowest QAIC value shows the best model fit. The variables retained in each model are marked with an "X". VIF values are shown for each model to confirm that variables causing collinearity were excluded from the models.

Variable	Coefficient	Stand. Error	t-value	Prob (>|t|)
Intercept	-4.73	2.08	-2.27	<0.01
Fish Noise	1.44	0.415	3.48	<0.001
Month	0.316	0.251	1.25	0.20
160Hz	0.047	0.016	3.00	<0.001
20,000Hz	0.047	0.0096	-0.837	0.40

Table 5.3. Coefficients and standard errors of each variable in the best fitting model with quasi-Poisson error structure and log link function for whistle counts.

As discussed above in Chapter 2 (§2.4.1.1), whistles tend to occur clumped together violating the assumptions of randomness and independence. To address this, autocorrelation function (ACF) plots were produced to assess the serial correlation in counts in audio file from the boat-based (CR55) and bottom-based hydrophone (DSG). The DSG data were not serially correlated (Fig.5.2a) but the CR55 data were (Fig. 5.2b).

If the fitted models fail to account for this serial correlation so that the model residuals are serially correlated, the significance of the coefficients of the covariates retained in the model will be over-estimated.

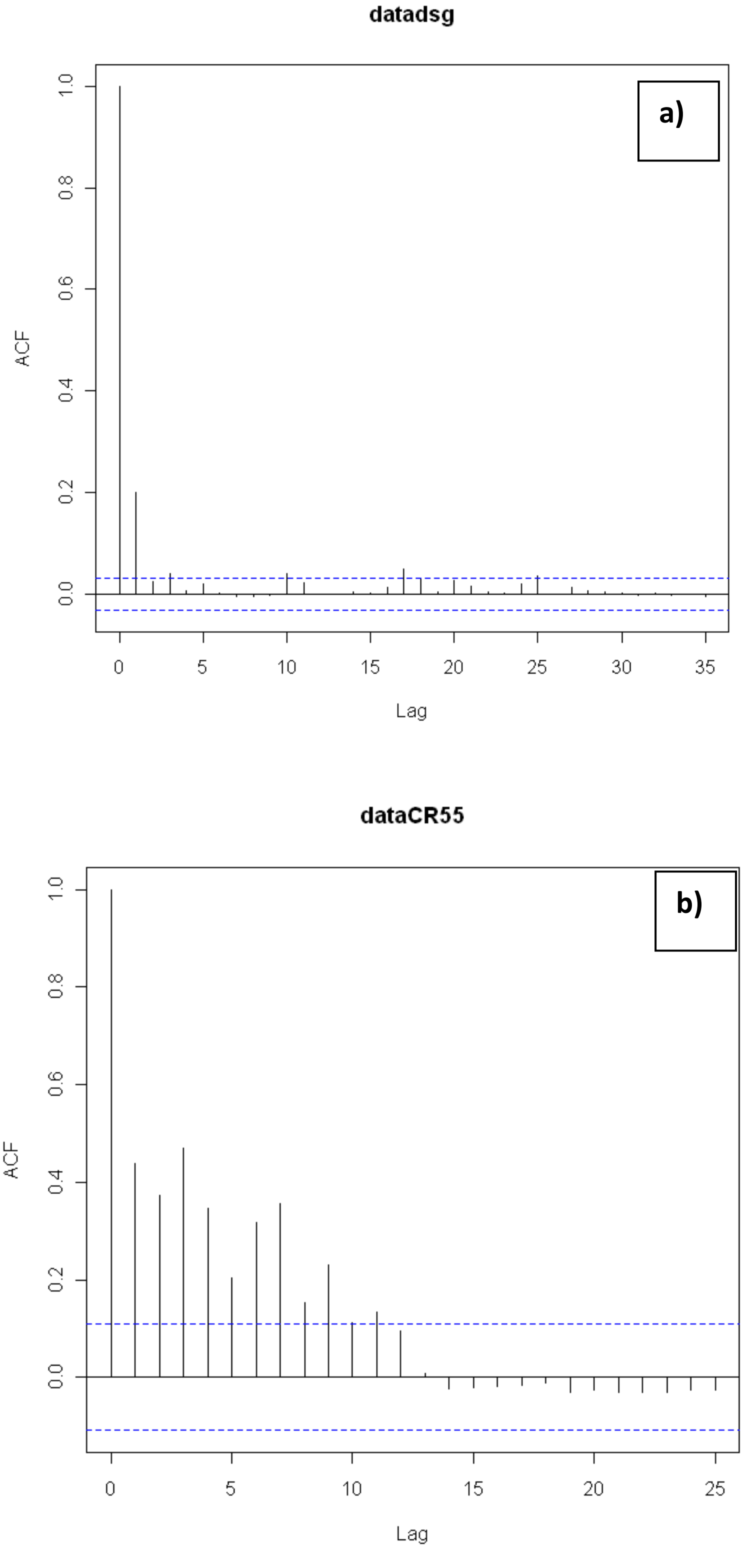

Fig. 5.2 Autocorrelation function (ACF) plots showing the autocorrelation coefficient for the DSG data (5.2a) and CR55 data (5.2b). Zero lag represents the data correlated with themselves, i.e. correlation = 1.0. Autocorrelation is apparent when correlation coefficient falls outside the horizontal blue dotted lines. There is a small correlation at a lag of 1 file (10 minutes) for the DSG data and a higher correlation up to lag of 7 files (approximately 15 minutes) for the CR55 data.

Quasi-Binomial GLM	***Response Variable***	***Fish Noise***	***Month***	***f5000hz***	***f400hz***	***f20000hz***	***QAIC***
1	Pres/Abs	X	X	X		X	2635
	VIF	1.09	1.03	1.29		1.41	
2	Pres/Abs	X	X	X		X	2661
	VIF	1.09	1.03			1.12	
3	Pres/Abs	X	X		X	X	2668
	VIF	1.09	1.07		1.62	1.64	

Table 5.4 Variables retained in the best fitting Generalized Linear Models using quasi-Binomial error distribution for Presence/Absence data. The lowest QAIC value shows the best model fit. The variables selected for each model are marked with an "X". VIF values are shown for each model to confirm that variables causing collinearity were excluded from the models.

For the quasi-binomial GLMs of the presence-absence data, the variables retained in the best fitting models that showed the most consistency were Fish Noise, Month and the 1/3 octave bands centred at frequencies 5,000 Hz and 20,000 Hz (Table 5.4). These variables were similar to those retained in the best model for whistle count; with the difference that 160 Hz replaced 5000 Hz. The other variable retained in the top three models was the 1/3 octave band centred at frequency 400 Hz. The best quasi-binomial model explained only 3% of the deviance in the data.

Table 5.5 shows the coefficients of the variables retained in the best fitting presence/absence model and their significance. Fish noise and month were highly significant (p<0.001).

Variables	Coefficient	Standard Error	t-value	Prob (>|t|)
Intercept	-1.30	0.54	-2.42	0.015
Fish Noise	0.7060	0.1090	6.46	<0.001
Month	0.2780	0.0710	3.90	<0.001
5,000 Hz	-0.0093	0.0053	-1.74	0.080
20,000 Hz	-0.0076	0.0031	-2.50	0.014

Table 5.5 Coefficients and standard errors of the variables of the best fitted model with quasi-binomial error structure and logit link function for presence/absence data.

5.3.3. MODEL DIAGNOSTICS

5.3.3.1 Quasi-Poisson GLMs for whistle counts

Diagnostic plots for whistle counts are shown in Figures 5.2, 5.3 and 5.4.

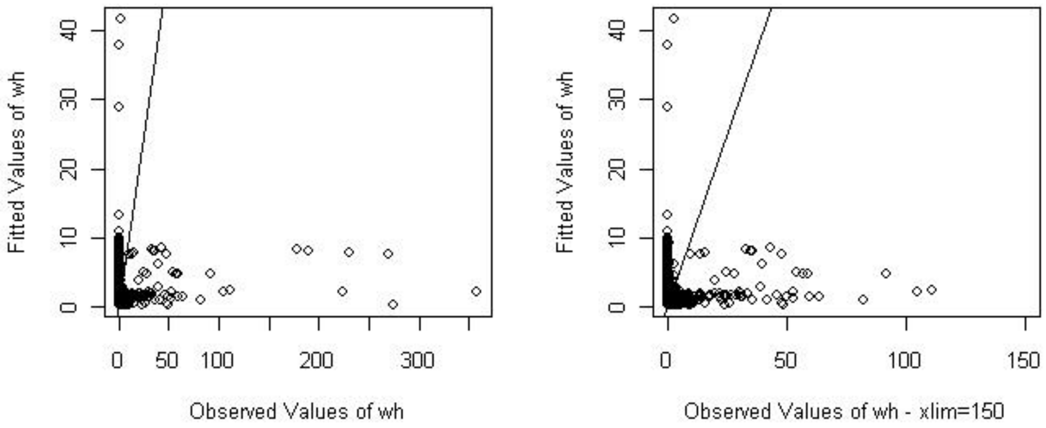

Fig. 5.2. Diagnostic plots for the best quasi-Poisson model of whistle counts showing fitted values vs observed values. The plot on the right shows a truncated scale in the x-axis for a clearer view of the fitted values of the plot on the left.

The plots of fitted values vs observed values in Figure 5.2 show that the model is overestimating for small counts of whistles (fitted values above the line) and underestimating for larger counts (fitted values below the line). In Figure 5.3, the scaled residuals are clumped with respect to the fitted values but do not show an overall increase in variability as the fitted values increase.

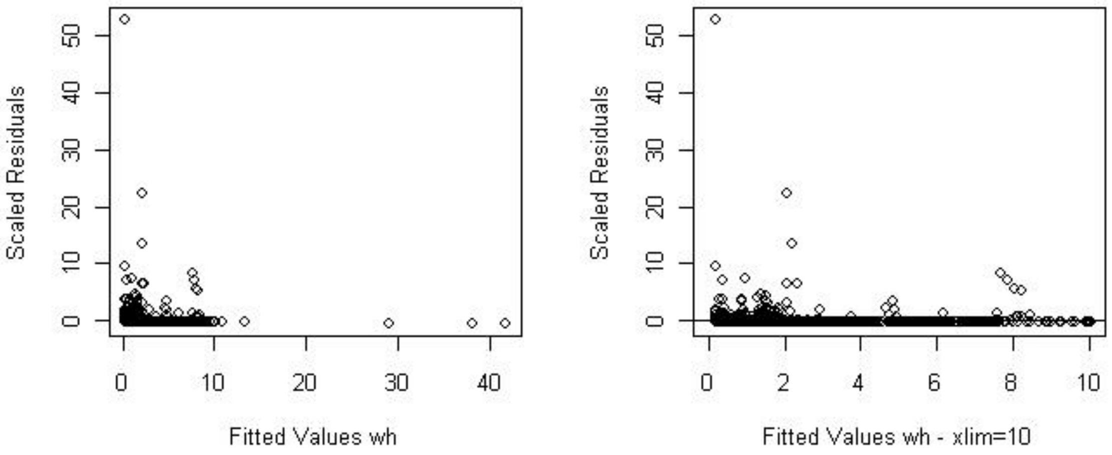

Fig. 5.3 Diagnostic plots for the best quasi-Poisson model of whistle counts, showing residuals vs fitted values. The plot on the right shows a truncated scale in the x-axis for a clearer view of the residuals of the plot on the left.

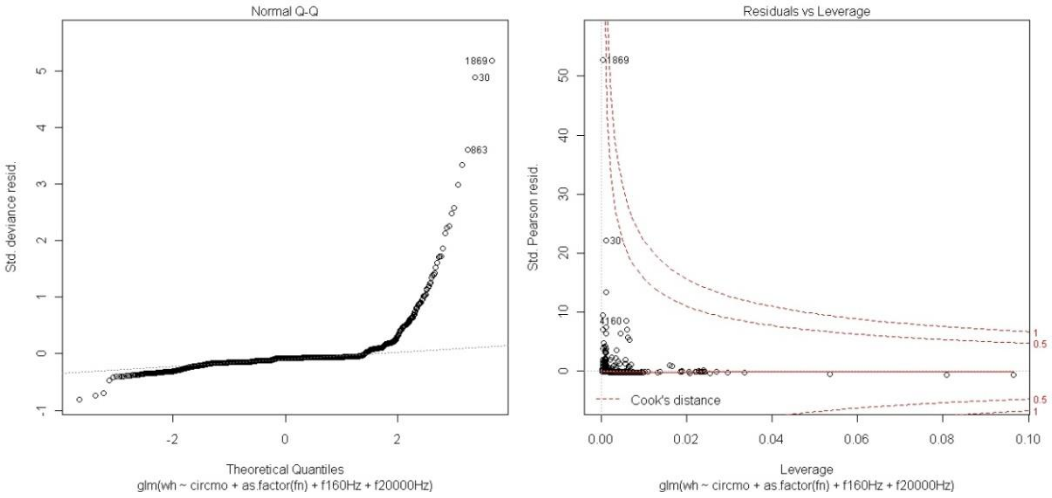

Fig. 5.4. Quantile-Quantile (Q-Q) plot (left) and Residuals vs Leverage plot (right) for the best model for whistle counts. Three outliers can be identified. Large values for Cook's distance mean unusual observations, but these data points are within normal values (<1).

These residuals are assessed for normality in the Quantile-Quantile plot (Fig. 5.4, left plot). In a well-fitting model the points are located on or near the line across the whole range of the data. Here, the model fits well at first but then the residuals show a sharp departure from the line indicating skewness; a consequence of overdispersion.

In these diagnostic plots three outliers are visible. These represent three of the highest whistle counts in the dataset and signify unusually high counts of whistles. Figure 5.4 (right plot) shows that these data points are not overly influential because the Cook's distance values are not greater than 1 (Faraway, 2006), and therefore do not represent high leverage.

Overall, these diagnostic plots show the models of counts of whistles do not fit well primarily because of the very high over-dispersion in the data; the data are highly variable and the available covariates fail to explain much of that variability. Nevertheless, QAIC, as a measure of relative model fit amongst models with different combinations of covariates, does determine which covariates best explain the small amount of variability that can be explained. Thus, although strong caution should be taken to avoid over-interpretation of the results, some limited inference can be made about which of the candidate explanatory variables have most influence on the counts of whistles.

5.3.3.2. Quasi-Binomial GLMs for presence/ absence data

The diagnostic plots in Figure 5.5 show the best model fit possible with the quasi-binomial models of presence-absence of whistles. Fig. 5.6 shows a substantial departure of the residuals from normality for part of the range of the data (left plot) but that the Cook's distance values are not significantly high (<1).

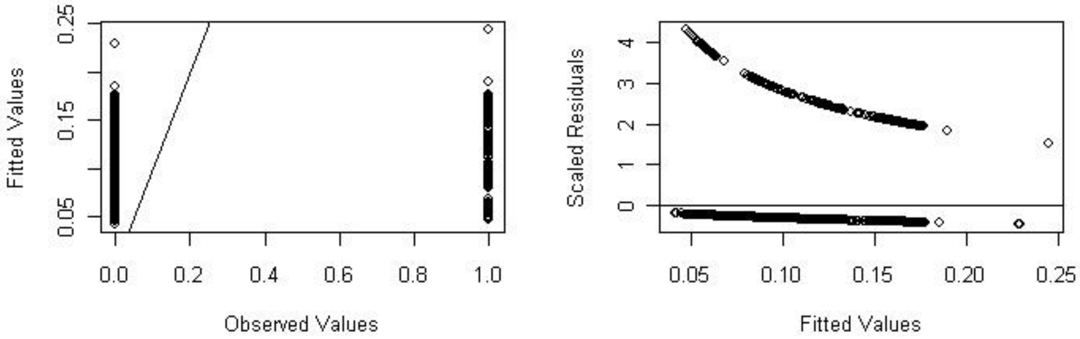

Fig. 5.5. Diagnostic plots for the best fitting quasi-binomial model of presence-absence of whistles. The plot on the left represents fitted values vs observed values. The plot on the right shows the scaled residuals against the fitted values.

These diagnostic plots show that the models of presence-absence data do not fit well, and do not fit as well as the models of counts. However, there is some consistency with the models for whistle counts in the variables retained in the best fitting models. However, the results of these models should be interpreted more cautiously than the results of the models of whistle counts.

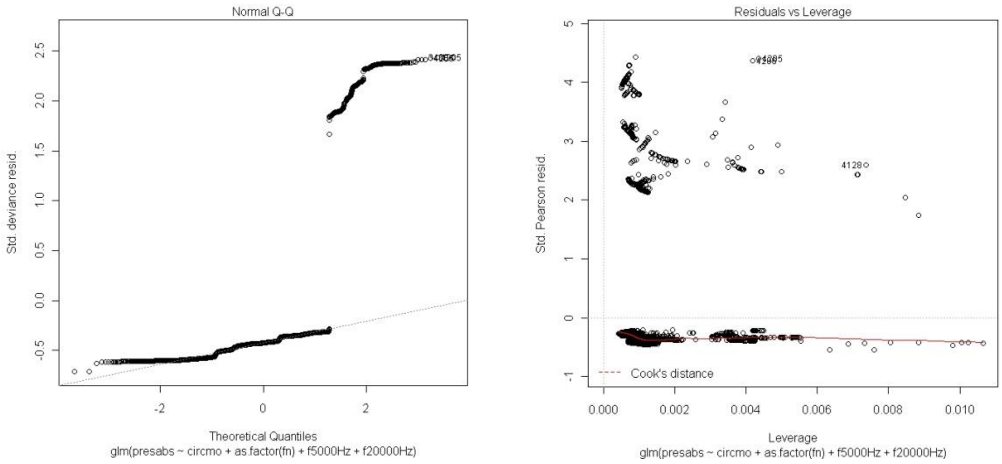

Fig. 5.6. Quantile-Quantile (Q-Q) plot (left) and Residuals vs Leverage plot for the best fitting model of Presence-Absence data.

Overall, the explanatory variables retained by the best fitting quasi-Poisson models of count data were somewhat similar to those retained in the best quasi-binomial models of presence-absence data. That is, fish noise, month and some of the same 1/3 octave band frequencies were retained in the best of both types of model. According to the diagnostic plots, none of the models fitted very well. However, the quasi-Poisson models of count data fitted better than the quasi-binomial models of presence-absence data.

5.4 DISCUSSION

Although none of the models fitted the data very well, they did show some consistency in the variables that were retained in the best models and demonstrated that the relative abundance of dolphins, as measured by the whistle counts or the presence-absence of whistles, did vary temporally, as well as being influenced by some other factors including fish noise.

5.4.1. Seasonal variation in dolphin occurrence

Month was a significant factor in both types of model (Tables 5.2 and 5.4).

In the west Florida continental shelf, change in water temperature is the main cause of intra-annual variation in bottlenose dolphin densities (Griffin and Griffin, 2004). . This area of the Gulf of Panama and, in particular, the Bay of Panama where most of the sampling took place, is influenced annually by the upwelling effect from January to March (Gonzalez and D'Croz, 2007). This brings cooler waters to the surface, which means higher productivity in the upper layers of water in this area during this time of the year (D'Croz and O'Dea, 2007). A seasonal increase in food availability due to this higher productivity would lead to the expectation that the occurrence of dolphins would be greater during the first months of the year (D'Croz and O'Dea, 2007). In this area, there are no data available on how fish abundance varies seasonally and therefore a direct comparison cannot be made between seasonal presence of fish and dolphin relative abundance. However, it is known that certain sound producing fish are seasonal in tropical coastal areas (Mann and Grothues, 2009). Studies have reported seasonal changes in dolphin distribution related to the greater presence of fish in certain seasons than in others (Kimura et al., 2012).

There were no diurnal data collected during December and January because of bad weather, and deployments in February were of short duration and this may have limited the overall seasonal or monthly pattern of dolphin relative abundance shown by the data.

5.4.2. Influence of fish noise on dolphin occurrence

Fish noise was the variable that was retained in all the best fitting models (for both types of response variable). The relationship was positive indicating that there were more dolphin whistles detected when there was also detection of fish noise (Chapter 4). It has been reported that dolphins, and especially bottlenose dolphins living in coastal areas, prey preferably on sound producing fish (Barros and Wells, 1998; Gannon and Waples, 2004; Gannon et al., 2005; Berens McCabe et al., 2010). Gannon and Waples (2004) analysed the stomach content of coastal bottlenose dolphins and found the diet to comprise 66% fish of the Family Scianidae, which includes a large variety of soniferous fish (i.e. croakers, weakfish, corvinas)(Knudsen *et al*., 1948). Berens McCabe *et al*. (2010) also found 51.9% of fish belonging to the same family. Fish from this family are some of the most abundant in this area of the Bay of Panama, especially corvinas (D'Croz and Robertson, 1997).

Gannon *et al.* (2005) tested the hypothesis that dolphins tend to use passive listening to detect prey (i.e. soniferous fish) because using their echolocation system has a high energetic or ecological cost. However, this does not mean they cease to use echolocation; they may use both if needed. In this study, it was evident that an increased amount of whistles was most likely to be found in the presence of fish chorus (Chapter 4). When feeding, dolphins have been found to increase the rate of whistles (i.e. number of whistles produced per minute) (Acevedo-Gutierrez and Stienessen, 2004). Therefore, it is suggested that during periods of increased dolphin whistles and clicks, dolphins were feeding on this type of fish, and emitting whistles to attract other dolphins.

Knowledge of how dolphins are attracted to fish at different times of the day is poor but time of day has been found to influence cetacean distribution (Akamatsu *et al*., 2008). Although in this study the models did not highlight the influence of time of day, fish noise was mostly found at night and during the early hours of the morning (Chapter 4). It has been documented that most species of soniferous fish are most active at night (Ainslie and de Jong, 2011; Ainslie et al., 2011a). On the other hand, it has also been shown that dolphins forage usually at dawn and less so in daylight hours Allen et al., 2001). Radford *et al*. (2008) and Ainslie and de Jong (2011) have also reported peaks of fish choruses from dusk to the early hours of the morning.

5.4.3. Influence of other noise on dolphin occurrence

The 1/3 octave bands retained by the best models of both types were centred on frequencies 160 Hz, 400 Hz, 5,000 Hz and 20,000 Hz. The retention of these 1/3 octave bands as important explanatory variables could be indicative of ambient noise related to a biological variable (fish noise and snapping shrimp), or an anthropogenic presence (small boat engine noise). This is discussed further in Chapter 3.

Sound found in the 400Hz to 1,000 Hz frequencies is an indicator of fish choruses (Knudsen et al., 1948; Wenz, 1962; Urick, 1984; Au and Hastings, 2008; Luczkovich and

M.W., 2011) so the influence of the 400 Hz 1/3 octave band on dolphin occurrence is likely related to fish noise (Chapter 3). Likewise, the influence of the 5,000 Hz band is likely related to small fishing vessels and/or snapping shrimp (5,000 Hz - 7,000 Hz, Chapter 3).

Sound occurring in the frequency band centred on 20,000Hz is usually related to rain noise (Richardson *et al*., 1995a; Au and Hastings, 2008), snapping shrimp, with some high frequency energy from engine noise of medium to small vessels. It is difficult to determine which sources may have led to the retention of the 20 kHz band in predicting dolphin whistles. In this study, precipitation was not retained as an explanatory variable in any of the models, but it cannot be discounted as its absence was probably due to the weather station being located so far from the sampling sites. It is possible that dolphins were more likely to occur in the kinds of habitats where snapping shrimp also occur. It is also possible that dolphins were attracted to the engine noise of small fishing boats and trawlers.

For the data set I audited to listen for sources of sound, most whistles were heard in the presence of engine noise of small fishing boats and of trawlers (see Chapter 3). It is known that dolphins follow trawlers attracted to nets in the water that leave a trail of by-caught fish as they pass (Leatherwood, 1975) and vessel activities can cause short-term avoidance responses in dolphins (Au and Perryman, 1982a; Janik, 1996; Bejder et al., 2006), which may lead to long-term changes in their behaviour and distribution. Activities such as that of dolphin/whale watching can be a major disturbance to local populations of dolphins and whales (Erbe, 2002; Constantine et al., 2004; May-Collado et al., 2007); this is discussed in detail in Chapter 7. Whether small fishing vessels represent a threat, because the risk of collision or increased energy expenditure of changing direction to avoid a boat is greater than the rewards of enhanced feeding opportunities, is unknown and it may be that they benefit because increased energy gain from additional feeding outweighs the negative aspects or threats.

5.4.4 Conclusion

Overall, this study suggests that temporal variability in dolphin occurrence is at least partly related to biological factors (Radford et al., 2008). The temporal distribution of dolphins appears to be influenced by fish noise and the frequency of noise that is representative of fishing boats and other sources. Dolphin presence seems, therefore, to be related to prey distribution. When dolphin occurrence was related to fish presence this occurred mostly at night or at dusk (sees Chapter 4).

This study does not allow dolphin distribution to be predicted based on these temporal variables, but it does help explain the relationship between dolphin occurrence and temporal variation defined by other factors such as fish noise and background noise. This region is characterised by seasonal climatic events, such as upwelling, El Niño, La Niña and, therefore, a study covering multiple years would be needed to establish a better idea of how these seasonal changes may influence the occurrence of dolphins in this area especially in the context of future years when the Panama Canal Expansion program will increase vessel traffic. Long term passive acoustic monitoring is suggested to investigate if these changes in vessel traffic may cause short-term temporal changes in dolphin occurrence in this area.

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CHAPTER 6

Modelling Spatial Variation in the occurrence of dolphins in the bay of Panama

ABSTRACT

Dolphins occur in the local region of the Pacific Ocean adjacent to the entrance of the Panama Canal. No formal assessment has been made of their distribution in this heavy shipping area and how their occurrence is related to environmental features and ambient noise. Passive acoustics was used from March 2010 to April 2011 to record ambient sound that included whistle detection indicating the occurrence of dolphins. The spatial occurrence of dolphins was studied in relation to anthropogenic activities, such as shipping noise and fishing activities, as well as physical and biological features of the environment. Generalised Linear Modelling found that fish noise was an important factor, as well as distance to the coast and also background noise in the 1/3 octave band centred on frequency 20,000 Hz, the frequency most associated with snapping shrimp and small fishing boats during spectrogram analysis (Figure 3.4). Dolphin whistle detections were made at each site studied inferring that dolphins were distributed over the majority of the study area. Data collected in several areas over the same period of time would allow for a better understanding of the relationship between dolphin occurrence and spatial factors.

6.1 INTRODUCTION

Understanding the spatial distribution of a species is essential for good conservation of that species and management of human activities that may be a threat (Guisan and Zimmermann, 2000; Pearce and Ferrier, 2000a; Kaschner *et al.*, 2006; Redfern *et al.*, 2006; Gomez de Segura *et al.*, 2007; Panigada *et al.*, 2008). Accurate assessment of conservation status requires information on the relationship between the species and its habitat (Jaquet and Whitehead, 1996; Austin, 2002; Hamazaki, 2002; Guisan and Thuiller, 2005; Embling, 2007; Garaffo *et al.*, 2007). In the area adjacent to the Panama Canal in the Bay of Panama there is a lot of anecdotal information supplied by yacht owners fishing for recreation, from artisanal fishermen, and from scientists conducting non-cetacean related research in the areas where this study took place. But there is no published literature on the distribution or abundance of dolphins in this area. The most relevant publication regarding dolphins in this region is that of Ferguson *et al.* (2006) describing delphinid distribution in the wider Eastern Tropical Pacific.

The distribution of dolphins has been related to a variety of factors, among them sea surface temperature (Gaskin, 1968; Selzer and Payne, 1988; Hastie *et al.*, 2005; Ferguson *et al.*, 2006), depth (Gordon *et al.*, 1997; Hastie *et al.*, 2005), distance to shore (Ferguson *et al.*, 2006), salinity (Selzer and Payne, 1988), chlorophyll concentration (Panigada *et al.*, 2008) and season (Ferguson *et al.*, 2006). All of these are likely to be related to prey distribution (Selzer and Payne, 1988; Panigada *et al.*, 2005). Prey availability is difficult to measure (Gomez de Segura *et al.*, 2007), and some studies have used stomach contents to relate fish abundance to dolphin presence (Barros and Wells, 1998; Berens McCabe *et al.*, 2010). Dolphin distribution has been linked to foraging mostly based on behavioural observations (Hastie *et al.*, 2004). The distribution of cetaceans in coastal areas has been linked to prey availability through a variety of proxy environmental factors. Selzer and Payne (1988) found that the distribution of white-sided and common dolphins was related to sea surface temperature and bottom topography but ultimately that they were related to prey distributions. Similarly, Harzen (1998) concluded that the reason the distribution of bottlenose dolphin in a shallow estuary in Portugal was related to tidal cycle was better explained by the diurnal cycle of dolphin prey. Some studies have found that dolphins prefer deeper areas for foraging (Wilson *et al.*, 1997), whereas others have found dolphins to prefer shallower channels (Allen *et al.*, 2001). Embling *et al*. (2010) found that the relative abundance of harbour porpoises in the Hebrides, west of Scotland was related to tidal current.

Distribution can also be affected by anthropogenic disturbance, but this effect is difficult to measure. A decrease in the number of local resident dolphins after being exposed to intense disturbance caused by tourist boats has been reported (Lusseau, 2005; Williams *et al.*, 2006; May-Collado *et al.*, 2007). Nevertheless, it has been hard to document where these animals move to. The conclusion that dolphins (and whales) will just migrate to another habitat is a comfortable concept that lacks the consideration that all areas may contain threats to marine life (Wilson *et al.*, 1997).

The dolphins in the Bay of Panama have not been studied before and it is not known how many species are present, or whether the most frequently seen species (bottlenose dolphin) represents a local population, a periodic resident population, a year-round population or a combination of migratory and repeated local residency (Wells and Scott, 2009). Even if a local population has been established for a long time, this can change and take the form of short term or intermittent occurrence if disturbance occurs (Wells and Scott, 2009).

This is the first study to investigate the spatial distribution of dolphins in the region adjacent to the entrance of the Panama Canal using passive acoustics. The goal was to provide the first information on the spatial distribution of dolphins in this area, with the aim that it will contribute to understanding the relationship between dolphin occurrence and environmental features.

6.2 METHODS

The data collection, data processing and data analysis methodology used is described in Chapter 2: General Methodology. Data from both the stationary hydrophone and the boat hydrophone were combined to assess spatial variation using Generalised Linear Models (GLMs).

Further steps taken for the specifics of modelling the GLMs are similar to those explained in §5.2, in regards to correlation tests of the variables, the error structure of the models and model selection procedures.

The response variables used were whistle count and presence/absence of whistles. Non-spatial predictor variables used were two categorical variables: month, (included to investigate at least one temporal variable but dropped when not retained after the first model) and, fish noise (see section 2.3.1.3 for methodological details); and continuous variables: depth, precipitation, wind-speed, and the previously described 1/3 octave band centre frequencies. The spatial explanatory variables considered were: latitude, longitude, distance to coastline, distance to buoys, and distance to anchorage. Distance to coastline was measured as the distance to the closest point on the coast, distance to buoys was measured as the distance to the buoys marking the last approach of vessels in the shipping lane towards the first set of locks of the Panama Canal, and distance to anchorage was distance measured to the waiting area where ships are anchored (Fig. 1.2 & 2.1). Spatial variables were more correlated than temporal variables (Chapter 5); therefore careful steps were taken not to include highly correlated variables in the same model. A Variance Inflation Factor (VIF) was calculated to assess any collinearity between model covariates. VIF values were obtained for each variable in each model performed using R.2.13.1 (Development Core Team, 2011); variables with VIF values exceeding 5 were considered to be strongly influenced by collinearity and were therefore excluded from subsequent models.

In addition to these methods, anecdotal data were collected by carrying out a survey of a local group of fishermen (§2.2.2.4). The survey contained illustrations for the fishermen to select the types of cetacean they have seen when out at sea fishing. It also contained questions related specifically to their fishing activity: which months, time spent out at sea, the type of fishery, numbers of animals seen and where they usually go fishing. Results of these surveys are shown in Table 2.2 (Chapter 2).

6.3 RESULTS

A total of 453 hours of audio data from both hydrophones combined were analysed (see §2.3.1.2). Out of 9,789 audio files (observations) that were collected with the DSG, Pamguard detected whistles in 2,925 files. To eliminate false positive detections, these 2,925 files were manually re-analysed and a random sample of 1,212 files (40%) was retained for statistical analysis. Of the 6,864 files in which Pamguard did not detect whistles, an sample of, 2696 files (40%) were manually analysed to look for false negative detections that Pamguard may have missed (§ 2.3.1.2.). In the same manner, 40% of total number of audio files recorded with the CR55 was analysed (325 audio files from a total of 812 audio files). This gave a total sample of 4,233 audio files (40% of the total number of audio files) selected for analysis. From this sample, a total of 4,567 dolphin whistles were detected in 427 audio files from 101 sample locations over a period of 12 months. Table 5.1 (see Chapter 5) shows summary statistics for the response variables.

Data collected with the stationary hydrophone provided a 24 hour cycle window of detections over consecutive days, and data collected with the boat hydrophone provided data during daylight hours. Summary statistics per deployment for both the response and the predictor variables are shown in Appendix (Tables A.2. through A.18). These summary statistics show that dolphin whistles were detected at every point except one sampled with the Stationary Hydrophone (14/15) and they were present in 29 of the 60 recordings with the boat hydrophone. Figure 6.1 shows that dolphin detections were thus found in 43 different locations out of 75 analysed which represents 58% of the studied sites. The 27 recordings made in the Archipelago of Las Perlas (large red ellipse on the map) were not analysed because they were completely contaminated with snapping shrimp noise (Chapter 2). This map indicates that the detections were quite evenly distributed in the main area studied, except in Otoque Islands (small red ellipse).

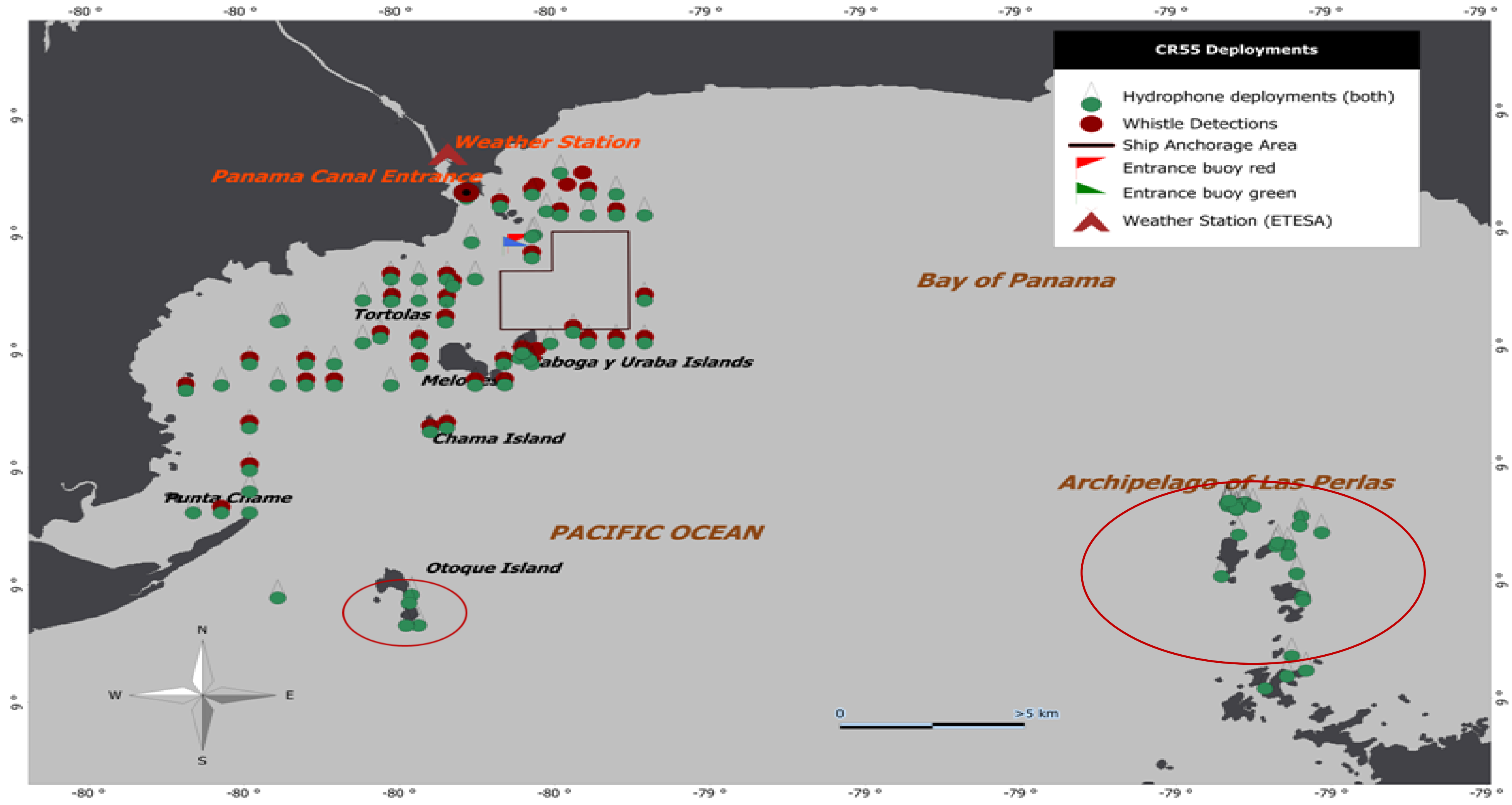

Fig. 6.1. Map showing 43 locations (red dots) where dolphins were detected acoustically, out of 75 analysed (dark green buoys). This represents 58% of the sites studied (See Figs. 2.2 and 2.3 for comparison). The square represents the anchorage area for the Panama Canal, an area prohibited for sampling. The circles in Archipelago of Las Perlas and Otoque Island mark recordings collected outside the main sampling area to test for greater distance. The depth in all these areas ranges from 10-25 meters (high tide).

The distribution of the response variables was investigated prior to modelling and the results are presented in Chapter 5 (§5.3.2).

6.3.2. MODELS OF WHISTLE COUNTS AND PRESENCE/ABSENCE

Table 6.1 shows the best fitting models for whistle counts in order of QAIC. The variables retained in the best fitting model were fish noise, distance to coast and the 1/3 octave band centred at frequency 20,000 Hz. The latter variable was retained in the other two models with less support for the data and in addition: distance to buoy. The best model for whistle counts explained 13% of the deviance.

Quasi-Poisson GLM	***Response***	***Fish Noise***	***dcoast***	***dbuoy***	***f20000hz***	***QAIC***
1	Whistles	X	X		X	304.76
	VIF	1.62	1.08		1.66	
2	Whistles			X	X	320.51
	VIF			1.86	1.91	
3	Whistles		X		X	325.91
	VIF		1.04		1.04	

Table 6.1 Variables retained in the best fitting models using whistle counts. The lowest QAIC value shows the best model fit. The variables selected for each model are marked with an "X". VIF values are shown for each model to confirm that variables showing collinearity were excluded from the models.

Table 6.2 shows the coefficients of the variables retained in the best fitting models and their significance. All covariates were significant.

Variable	Coefficient	Standard Error	t-value	Prob (>|t|)
Intercept	2.32	0.430	5.31	<0.001
Fish Noise	1.29	0.390	3.30	<0.001
dcoast	-0.082	0.038	-2.12	0.03
20,000Hz	-0.037	0.006	-6.32	<0.001

Table 6.2 Coefficients and standard errors of each variable in the best fitting model with quasi-Poisson error structure and log link function for whistles.

Attempts to model presence-absence of whistles with quasi-binomial GLMs were unsuccessful and results are not presented here. The best fitting model was over-parameterised and retained almost all the candidate variables. Therefore, the quasi-binomial GLMs did not allow any discrimination among the different variables and do not provide any useful information about which variables explain the most variance in the data.

6.3.3. MODEL DIAGNOSTICS

6.3.3.1 Quasi-Poisson GLMs for whistle counts

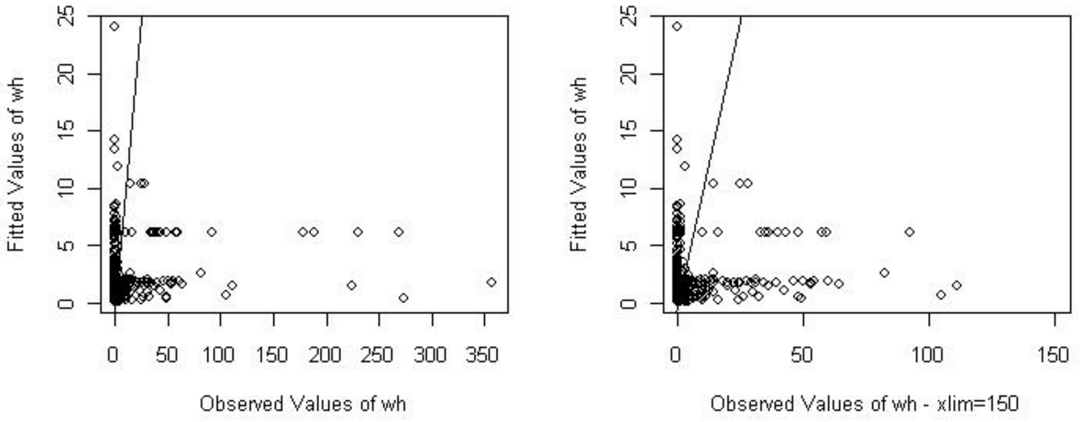

Fig. 6.2 Diagnostic plots for the best fitting quasi-Poisson model of whistles counts showing fitted values vs observed values. The plot on the right shows a truncated scale in the x-axis for a clearer view of the fitted values of the plot on the left.

The plots of fitted values vs observed values in figure 6.2 show that the model is overestimating for small counts of whistles (most fitted values are above the line) and underestimating for larger counts (fitted values are below the line). In Figure 6.3, the scaled residuals are not evenly distributed with respect to the fitted values but there is no evidence of an increase in the size of the residuals as the fitted values increase.

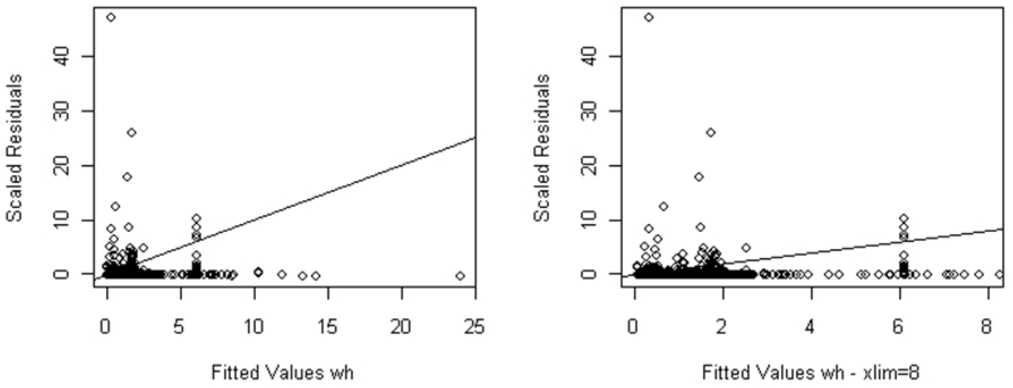

Fig. 6.3 Diagnostic plots for the best quasi-Poisson model of whistle counts , showing residuals vs fitted values. The plot on the right shows a truncated scale in the x-axis for a clearer view of the residuals of the plot on the left.

These residuals are assessed for normality in the Quantile-Quantile plot (Fig. 6.4, left plot). In a well-fitting model the points are located on or near the line across the whole range of the data. As for the best-fitting temporal models (§Fig. 5.4), here the model fits well for most of the range of the data but then points depart sharply from the line indicating skewness; a consequence of overdispersion.

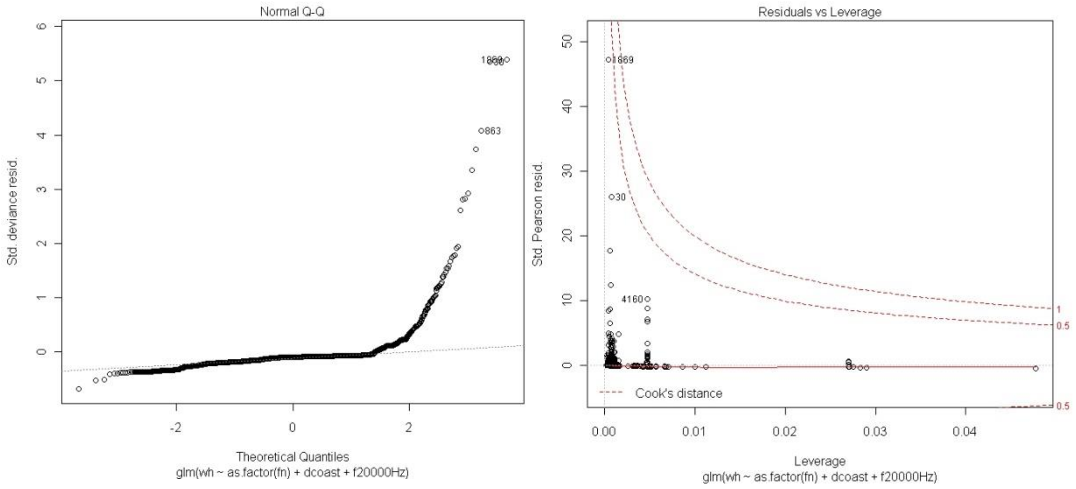

Fig.6.4. Quantile-Quantile (Q-Q) plot (left) and Residuals vs Leverage plot (right) for the best model for whistle counts. Three outliers are identified showing values of Cook's distance (leverage) between 0.5 and 1.0.

In these diagnostic plots three main outliers in the data are visible. These represent the three highest whistle counts in the dataset, which are unusually high counts of whistles. Figure 6.4 (right plot) shows that these data points are not overly influential because the Cook's distance values are below 1 and do not represent high leverage (Faraway, 2006).

Overall, these diagnostic plots show that the models of counts of whistles do not fit well because of the very high over-dispersion in the data. Nevertheless, they are sufficient with regard to showing which of the candidate explanatory variables best explain the variability in the data.

6.4. DISCUSSION

Similar to Chapter 5, the models of whistle counts do not fit well primarily because of the very high over-dispersion in the data; the data are highly variable and the available covariates fail to explain much of that variability. Nevertheless, QAIC, as a measure of relative model fit amongst models with different combination of covariates, does determine which covariates best explain the small amount of variability that can be explained. Thus, some limited inference can be made about which of the candidate explanatory variables have most influence on the counts of whistles. In these spatial models, the variables retained are consistent with the literature and the inferences made by other authors regarding which factors explain the spatial distribution of dolphins, especially *Tursiops truncatus*, the species most commonly sighted in the study area. Nevertheless, these results should be interpreted with caution.

One of the major difficulties in discussing the findings of this work in order to assess the possible effects of background noise is the lack of background information on social structure, abundance and distribution of the dolphins. The models have poor predictive power but the results do allow for some interpretation of the relationships between dolphin occurrence and spatial variables.

6.4.1. Spatial variation in dolphin occurrence

6.4.1.1. Distance to coast and shipping landmarks

Distance to the coast was retained by two of the three best fitting models, including the top model and was the most important spatial variable explaining dolphin occurrence in the model of whistle counts, which explained 13% of the deviance in the data. Distance to the coast was directly correlated with depth (Appendix Table A.15b). Distance to the entrance buoy was also retained by one of the top three best fitting models but was not correlated with depth.

The retention of distance from the coast in the best models is in accordance with what has been reported in the literature. Depth is one of the most important factors in models that explain cetacean distribution in a variety of environments: Arctic waters (Moore, 2000); Mediterranean Sea (Canadas *et al.*, 2002; Panigada *et al.*, 2008); Ligurian Sea (Panigada *et al.*, 2005); Portugal(Harzen, 1998); Eastern Canada (Hooker *et al.*, 2001); Southwest Atlantic Ocean (Moreno *et al.*, 2005); North Atlantic (Hastie *et al.*, 2005); California coast (Tynan *et al.*, 2005); Gulf of Mexico (Davis *et al.*, 2002); and Eastern Tropical Pacific environments (Reilly, 1990). Garaffo *et al.* (2007) found depth and distance to shoreline to be equally important when observing distribution patterns for dusky dolphins, suggesting it could be associated with the distribution of prey.

Another factor that may help to explain distance to the coastline as a retained variable is fishing activity. Fishermen conducting artisanal fisheries are usually close to the shoreline but also to the islands (Chapter 2). As suggested in Chapter 4, dolphin whistles were detected when fishing boats were present at a given time and location suggesting dolphin presence may be related to fish presence (i.e., the fish being targeted by fishermen are of interest to dolphins).

Dolphin detections were evenly distributed in the main area of study (except in Las Perlas Archipelago and Otoque Islands), as shown in Figure 6.4. Although whistles have not been determined to come from a particular species, the species most commonly seen in the study area was the bottlenose dolphin (see §2.2.2.2, table 2.1, 2.2) which has a wide offshore distribution but also seem to prefer coastal areas because they provide shelter and food (Au and Perryman, 1982b; Selzer and Payne, 1988; Ingram and Rogan, 2002; Wells and Scott, 2009).

As shown above, there were three outlier data points (Fig. 6.4) indicating unusual whistle counts at three different locations. To investigate whether or not these high whistle counts occurred under particular spatial characteristics, the location, depth and distance to the coast, buoy and anchorage were inspected. The characteristics of these three highest whistle counts (199, 282 and 1,171 whistles) were no different to that of other detections.

6.4.1.2. Biological and environmental variables

Although depth has been found to be a strong determinant of cetacean distribution, the literature also shows that this is related to prey availability rather than to depth itself (Selzer and Payne, 1988; Moore, 2000; Davis *et al.*, 2002; Hastie *et al.*, 2004; Panigada *et al.*, 2005; Baumgartner, 2006; Hastie *et al.*, 2006). Thus, it is the depth at which prey can be most easily found and consumed that is likely to be most important. Here, the models for spatial variation in dolphin occurrence retained the biological variable fish noise but not depth.

Dolphins are attracted to specific areas that provide suitable physical characteristics of the sea floor for them to capture fish in efficient ways and using a variety of fishing techniques (Barros and Wells, 1998; Allen *et al.*, 2001; Hastie *et al.*, 2003b). These characteristics may include not only depth ranges, but also open bottom spaces and reef areas. The substrate in this area of the Bay of Panama has been described as basaltic and heterogeneous with bare surfaces and certain open deep space with patches of rocks (Lubchencoa *et al.*, 1984). Thus, these areas do not provide shelter to facilitate prey capture by the way of specialised techniques used elsewhere. Allen *et al*. (2001) concluded that coastal dolphins preferred dredged open channels rather than sea grass beds and coral reefs. This may be attributed to the fact that open sea floor characteristics facilitate prey detection, for example, that of sound producing fish which has been heard in this study (Chapter 4).

6.4.1.3. Acoustic variables

The acoustic variable retained by the three best spatial models was the 1/3 octave band centred at 20,000 Hz, the frequency of noise where small vessel noise and snapping shrimp contributed and overlapped the most in the spectrograms shown in this study (Chapter 3). This 1/3 octave band was also retained in the temporal models (Chapter 5) showing consistency. Lusseau (2005) found that dolphins avoid areas frequented by boat traffic (and during seasons of high boat traffic). In this present study, I also expected to find that dolphins stayed away from boat traffic, for similar reasons. However, they remained in the area and perhaps they are more persistent because the presence of these boats may relate to foraging opportunities (Leatherwood, 1975; Fertl, 1994; Pace *et al.*, Prel. res.)); at least when some of these boats are in the area, such as trawlers and small fish boats. Figure 6.4 shows that dolphins are distributed throughout most of the study area. As Chapter 3 has shown, there is ship noise disturbance covering the whole area of the study because low frequency noise can travel greater distances than high frequency noise (Urick, 1984; Richardson *et al.*, 1995). Indeed, that dolphins are distributed widely in the study area may suggest that they are relating this boat noise with cues that indicate where and how to obtain their prey (Leatherwood, 1975).

6.5. CONCLUSION

Dolphin whistles were detected at most of the points sampled in the study area, either with the bottom-based hydrophone or with the boat-based hydrophone; for the latter, positive visual confirmation was possible. Finding more whistle detections closer to the shipping activity was unexpected. It was expected that dolphins would be found farther out among the islands (Las Perlas and Otoque, fig 6.1). However, dolphins were neither visually sighted nor acoustically detected in these areas. However, these recordings were compromised because of heavy noise contamination from snapping shrimp (Chapter 2).

The spatial distribution of dolphins in this area seems to be mostly unaffected by any of the variables included in the models. However, the models did show that some variability was associated with explained by fish noise, distance to coast and high frequency sound sources at 20,000Hz.

Further work is required to assess finer scale spatial distribution of dolphins in this area, comparing specific seasons or months of the year. This may be achieved by deploying hydrophones at different locations over the same time period in order to explain the spatio-temporal variability of these occurrences in a long-term study. Different locations may provide for different environmental, temporal and bathymetric characteristics that may allow models to explain more variability in dolphin distribution.

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CHAPTER 7

GENERAL DISCUSSION

7.1 SYNTHESIS

The overall aim of this thesis was to investigate the effect of shipping noise on the occurrence of dolphins in Pacific waters adjacent to the Panama Canal in the context of biological, temporal and spatial factors. While using the planned methods to obtain results that would draw conclusions on this subject, new observations became evident in regards to ambient noise in this region and in regards to dolphin acoustic behaviour. For example, during audio and visual analysis of audio files, it became evident that other sources of sound were affecting dolphin behaviour; such as the detection of whistles at the same time of fishing boats and fish chorus. However, because these were not the main objectives of this thesis, lack of time did not allow full investigation of all these new questions. Nevertheless, the results provide important new information about ambient noise in this region and the first information about the relationship between dolphin sounds and fish sounds in this local area thus increasing ecological knowledge. The findings of this study can be summarised as follows:

1. The major contributors to background noise were biological noise from soniferous fish and snapping shrimp and anthropogenic noise from vessels characterised by frequencies produced by artisanal fisheries (small boats). There was no significant diurnal variation in sound pressure levels (SPL) among frequencies; but SPL was greater at night than during the day in 1/3 octave bands centred at frequencies 400Hz, 1,000Hz and 1,600Hz. There was no significant seasonal variation at low frequencies but there was some variation at 400Hz and 5,000Hz (Chapter 3).
2. Whistle occurrence in this region varies in the presence of fish chorus and, it is suggested, also in the presence of fishing boats. More whistles were detected during daylight hours than at night, but whistles were of higher frequency at night than during the day. During manual analysis of each spectrogram, a unique relationship was found; dolphin whistles and fish chorus co-occur, especially at

night. Investigating this was not a main objective at the beginning of the study but resulted in an important scientific contribution from this research (Chapter 4).

3. Dolphin detections varied seasonally with month being a significant factor. Models relating whistle counts to environmental variables revealed diurnal variation, as shown by a strong relationship with daily variation in fish noise. Temporal variation was best explained by biological noise and intermittent small vessel engine noise, as suggested by the importance of noise at frequencies representative of fishing boats (Chapter 5).
4. Dolphins were found to be present in most of the sites sampled. However, distance from the coast was an important factor in models explaining variability in whistle counts throughout the area of study. Fish noise was also a significant factor in these models (Chapter 6).

This chapter brings the two main results of this thesis together and discusses the following aspects: the acoustic ambient noise profile of this region of the Panama Canal; the relationship of acoustic behaviour of dolphins in the presence of biological (fish noise) and anthropogenic noise (small vessels); the spatio-temporal distribution of dolphins suggested by the study; the relevance of this information in possible conservation plans for the dolphins in this region; and finally, some technical recommendations and future research.

7.2 CHARACTERISTICS OF THE PACIFIC REGION OF THE PANAMA CANAL

Variability in ambient noise generally has been described in the literature (Knudsen *et al.*, 1948; Wenz, 1962; Urick, 1984) but the characteristics of background noise in the Pacific region of Panama have not been investigated before and knowledge of this is poor. This prevents a comparison of the findings of this study with the situation in the past when background noise was probably increasing.

Background noise in the ocean is composed of acoustic signals defined by different types of sources based upon their frequencies (Wenz, 1962; Urick, 1984; Richardson *et al.*, 1995c). In this study, I attempted to identify the different and overlapping source components in order to describe the background noise of the area. The classic studies by Knudsen *et al.* (1948) and Wenz (1962) showed that in the absence of shipping noise and marine life sounds, background noise is dependent on wind and sea state. However, the sources described in these two pioneer studies were obtained from observations in deep waters. Urick (1984) took a step further and described sources of ambient noise as a function of frequency range and analysed noise variability in shallow water. Data presented in this study was not sufficient to show that wind was a significant source of background noise because the weather station was located on land at different distances from sampling sites (§2.2.2.1.) However, this study cannot ignore the fact that wind is an important source of sound in shallow waters.

In this study, analysis of background noise showed that although low-frequency noise (<1 kHz) from distant shipping is prevalent with high sound pressure levels in the acoustic spectrogram throughout the recordings, it is small boat traffic noise that contributes most to the shipping noise in the frequency range of 5-10kHz in this shallow water environment (Zakarauskas *et al.*, 1990; McDonald *et al.*, 2006) (see Chapter 3). The spectral density plot in Fig. 3.4 and spectrograms in Figs 4.12 and 4.13 (see Chapter 4) show how small boat noise was recognized when manually analysing the spectrograms. There is little information regarding specific frequencies but it is known that boat noise contains tones at mid to high frequencies (300-7,000Hz) (Richardson et al., 1995a) and this relationship was used to confirm that when sound intermittently covered half the range of the spectrogram, it was noise from small vessels (5-10 kHz, see §3.3.1). Figure 7.1 shows a spectrogram containing noise from a small vessel engine to illustrate how it would appear in a spectrogram covering most of the frequencies at which other sources of sound were attempted to be characterized. Therefore, the main anthropogenic sources of sound in this region were attributed to shipping noise (in the lower frequencies, <1000Hz) and, in addition, to intermittent noise from small vessel engines (5,000-10,000Hz, Fig. 3.4) mostly represented by the fishing boats of the area.

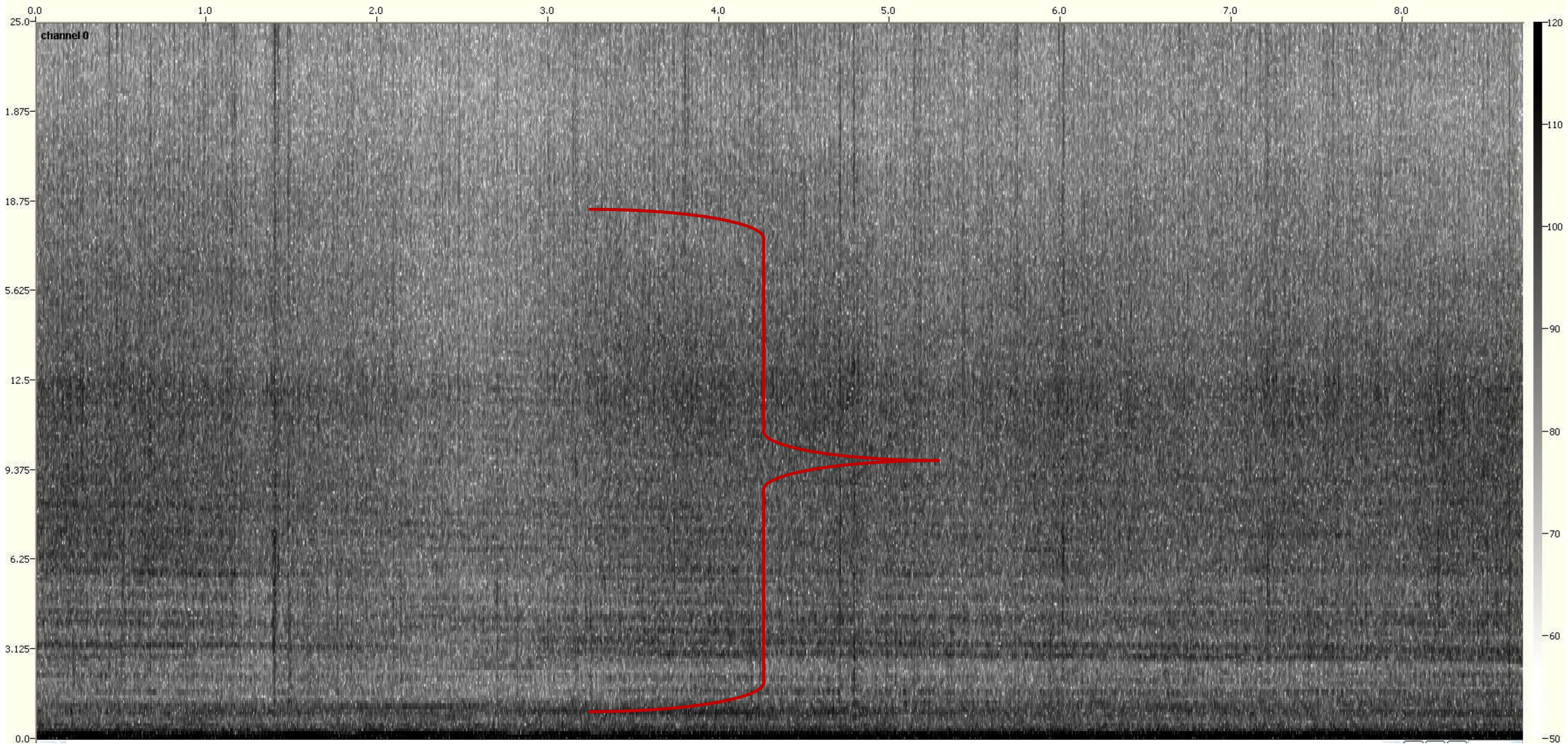

Fig. 7.1. **A 10 second cut spectrogram (upper x-axis) showing the moment when a small vessel engine was passing near the hydrophone showing how a “brushing” type of combined shading spreads over the frequency spectra. Most of this sound is contained in the red bracket. Frequency is shown in the left hand y-axis and amplitude levels are on the right hand y-axis.**

Acoustic analysis of spectrograms (Chapter 4) and temporal variation models (Chapter 5) indicated that biological sound sources present at variable intervals were mainly defined by fish chorus and by dolphin sound (Chapter 4). These were the main biological components of background noise studied in this study.

However, noise from snapping shrimp was heard throughout manual analysis of the audio files. This is consistent with other studies (Johnson *et al.*, 1947; Everest *et al.*, 1948; Knudsen *et al.*, 1948; Anderson and Gruber, 1971; Au and Banks, 1998; Chitre *et al.*, 2006).

Fish sound mostly in the form of fish chorus was the second dominant sound source found in this region (Chapter 3 & 4), as other studies have also shown when characterizing background noise (Cato and McCauley, 2002; Radford *et al.*, 2008; Ainslie and de Jong, 2011; Luczkovich and M.W., 2011; Ainslie *et al.*, 2011b; Mann, 2012). Among all soniferous fish, scianids have been reported to be the loudest fish in coastal environments, producing choruses especially at night (Knudsen *et al.*, 1948; Fish and Cummings, 1972; Mann, 2012).

As described in Chapter 4, fish belonging to the family Scianidae are the most common species found in the region of study. Fish chorus was detected mostly at night-time, between 18:00-6:00 (§4.3.3, Table 4.5). This is consistent with the literature where increased levels of biological noise caused by fish chorus at night have been reported (Fish and Cummings, 1972; Ainslie and de Jong, 2011; Ainslie *et al.*, 2011a).

7.3 Occurrence of dolphin whistles in the presence of different sources of background noise

7.3.1 Co-occurrence of dolphin whistles and fish chorus

While conducting manual analysis of audio files it became evident that when dolphin whistles were detected at night fish chorus was also detected in most of the cases. Although investigation of this was not one of the main aims of this thesis, these observations provided an opportunity to study this phenomenon and co-occurrence of these was further analysed. Chapter 4 shows that the probability of dolphin whistles and fish chorus occurring together was significantly greater, by 40%, than by chance. As described in Chapter 4, soniferous fish have been demonstrated to be the preferred prey for dolphins (Barros and Wells, 1998; Berens McCabe *et al.*, 2010). To determine which fish were making these sounds fish sounds were identified to family level by characterizing their sound in comparison to the documented sounds of a range of species (Chapter 4). The most common fish sound found belonged to the Family Sciaenidae, which represents most of the soniferous fish in these tropical waters.

The hearing sensitivity of fish allows them to detect sound at frequencies below and around 1,000 Hz (Au and Hastings, 2008); that of Sciaenids is reported to be between 100 Hz and 4,000 Hz (Sprague *et al.*, 2000; Cato and McCauley, 2002; Ramcharitar and Popper, 2004). Similar to other animals, fish emit sounds in response to different environmental stimuli for communication (Hildebrand, 2009; Kasumyan, 2009) and the behaviour and biological significance behind these different sounds is a subject of research (Ramcharitar *et al.*, 2011). Fish produce louder sounds at night-time (Fish and Cummings, 1972) and their frequencies may also change during the spawning season, which may differ among species (Luczkovich and M.W., 2011). It has also been shown that certain male sciaenid fish decrease their chorus in the presence of vocalizing bottlenose dolphins to avoid being detected (Luczkovich *et al.*, 2000). Dolphins use echolocation to track their prey once they are found; however, it has been hypothesized that dolphins using passive listening to find location of fish choruses (Gannon and Waples, 2004; Gannon *et al.*, 2005). The biological explanation of the co-occurrence of whistles and fish choruses suggests that after passive listening to the intense fish chorus, dolphins emitted whistles to alert other dolphins. In addition, during analysis of spectrograms, click trains and click bursts were found to follow the co-occurrence of whistles and fish sounds, suggesting that feeding might have been taking place. However, a statistical analysis of the occurrence of these clicks and when they occurred needs to be carried out before this biological inference can be confirmed. In addition, a seasonal comparison of fish chorus sound characteristics should be analysed in order to compare peaks of sound production, in relation to peaks of whistle detection.

7.3.2 Co-occurrence of dolphin whistle and boat noise

It is well documented that bottlenose dolphins and other delphinids follow fishing boats and trawlers for food (Leatherwood, 1975; Pace *et al.*, Prel. res.). Leatherwood (1975) reported that dolphins seemingly were able to distinguish the engines of a transiting trawler and one that had stopped to manoeuvre the nets, which they approached. Other studies have shown similar interactions of whales and dolphins with commercial fishing vessels where depredation occurs very close to the nets and lines deployed (Fertl and Leatherwood, 1997; Hucke-Gaeta *et al.*, 2004).

Noise from small fishing boats occupied the same frequency bands where dolphin whistles were detected; at certain times of the day, occurrence of both fishing activity and dolphins were identified in spectrogram analysis. Surveys of fishermen (§2.2.2.2) corroborated that fishing activity takes place in the early hours of the morning and rarely in the late afternoon and they corroborated the presence of bottlenose dolphins while conducting their activities (§2.2.2.2). Audio files from the boat hydrophone were compared with audio files from the bottom-based hydrophone when these were analysed and similar acoustic scenarios were present in the spectrogram. Dolphin whistles were heard and visualized in the spectrograms in the presence of morning fishing boat noise. This suggests that the sound of fishing boats in the area may be a cue for location of prey. However, this correlation between fishing boat occurrence and whistle detection cannot be used to imply cause and effect between the presence of fishing boats and prey location and this requires further study.

7.4 Spatio-temporal distribution of dolphins

The models presented in Chapters 5 and 6 were constructed with the objective of explaining the relationship between dolphin occurrence and distribution at temporal and spatial scales, not to predict distributions (Austin, 2002). In many cases, predicting species distribution is the main purpose of statistical modelling (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005), and the relationships between species and environment are of secondary importance (Austin, 2002). In this study, the primarily question was to try to understand how dolphins are related to and influenced by their habitat. The results showed that of the candidate variables, fish noise and high frequency sound explained the most variation in dolphin occurrence in the data. The models in this study had poor predictive power, due in part to the substantial over-dispersion in the data and to the lack of deviance explained by the predictive variables. However, the models were sufficient to distinguish which of the different possible variables explained most variability in dolphin occurrence.

One of the more important findings to emerge from this modelling is that the temporal occurrence of dolphins was explained by month, which is probably related to prey availability (as indicated by fish noise) (Chapter 5). Time of day was not retained in the models; nevertheless, the relationship between whistle count and fish noise suggests that whistle count is indirectly related to time of day because dolphins prey on soniferous fish which are detected at night-time as described in Chapter 4 (Hanson and Defran, 1993; Barros and Wells, 1998).

The only spatial factor that was retained in the models was distance to the coast and results suggested an even occurrence of whistles throughout most of the area. A lack of background information makes it difficult to draw more conclusions with respect to the spatial occurrence. It would be useful to know if the dolphins present belong to a local resident population or to a wider ranging population with periodic residency. This information is essential to infer spatial variation between years in future research (Shane *et al.*, 1986; Perrin *et al.*, 2009; Wells and Scott, 2009). It was not possible to evaluate the effect of noise from large vessels (i.e., distant shipping) on dolphin occurrence because none of the models in Chapters 5 and 6 retained low frequency sound as variables to explain variation in dolphin occurrence. Low frequencies are more likely to affect the occurrence of larger whales that communicate in the low-frequency bands (Parks *et al.*, 2007). Displacement of feeding and breeding grounds has been an effect observed in larger whales, whereas smaller cetaceans can shift locations at shorter temporal and smaller spatial scales (Weilgart, 2007).

In general, the results presented in Chapters 5 and 6 show that fish noise, distance to coast and small boat noise are the sources of background noise that explain the temporal and spatial variation in dolphin occurrence. Further modelling of longer-term data would help understand better the differences of a combined spatio-temporal effect of this population.

7.5 Conservation issues

The results presented here about the effects of small vessel noise on dolphin occurrence raise concerns for the area of the Panama Canal for two reasons. First, the fishing activity conducted by small vessels is not well regulated (FAO, 2007). Second, there are plans to promote dolphin and whale watching off the Pacific coast of Panama utilizing these small vessels with an attempt to train fishermen to take tourists. Further regulations for dolphin protection cannot be suggested without published documentation on the state of the "population" of coastal dolphins.

The National Assembly of Panama passed a law in 2005 (Law No. 13 – 5 May 2005) that establishes the Marine Corridor of Panama for the protection and conservation of marine mammals in all waters of jurisdiction according to the Convention on the Law of the Sea, that promotes the investigation of marine mammals and will promote whale/dolphin watching, recreational activities, education, investigation and open water dolphin therapy. It also establishes that this protected corridor will not affect activities of recreational, artisanal, sport or subsistence fisheries in the Gulf of Panama and other territorial waters. The issues mentioned in relation to promoting whale/dolphin watching and not affecting fishing activities are discussed below.

7.5.1. Fishing activity

Although there is evidence that dolphins utilise fishing boats for finding food (Leatherwood, 1975), the high frequency noise emitted by these vessels may be harmful to individual animals and possibly have population consequences (Richardson *et al.*, 1995a; Nowacek *et al.*, 2001; Buckstaff, 2004).

As described above, Law 13 protects marine mammals but without making changes that will affect the fishing activities. However, this study is not suggesting direct effects of fishing activities but that of possible short-term effect of vessel noise on the behaviour of dolphins (Lusseau, 2005).

7.5.2. Whale/Dolphin watching activities.

Recent studies have demonstrated short-term effects of whale/dolphin watching on dolphin behaviour (Nakahara, 1999; Buckstaff, 2004; Foote *et al.*, 2004; Lusseau, 2005; Williams *et al.*, 2006; May-Collado *et al.*, 2007; Parks *et al.*, 2007; Holt *et al.*, 2009; Jensen *et al.*, 2009) and also that behavioural changes can lead to long-term effects on populations (Lusseau and Bejder, 2007).

The Panamanian government has created regulations for whale/dolphin-watching activities; nevertheless, these small boat operators are not regulated by the authorities. It is thus a concern that this activity will continue to impact the animals as long as the activity is conducted in small fishing boat type vessels and as long as it is conducted by non-trained fishermen in an activity that requires full knowledge of the potential harmful effects of small boat noise, as well as conservation and outreach skills.

To try and mitigate any adverse effects of noise on the dolphins it is necessary to look first at the short-behavioural impact at individual level and then at the long-term impact on the ecosystem and habitat (Simmonds *et al.*, 2003). Unfortunately, very little is known regarding the dolphins in Pacific waters of Panama. Particular attention should be paid regarding behavioural effects of boat noise on feeding and social structure of dolphins. This information is essential in order to make any conservation suggestions for protection and mitigation measures that are in accordance with local fisheries and other regulations. Making conservation suggestions to governments is sometimes a very delicate task because some organizations support proper management of natural resources but others promote economic development and exploitation of resources (Thompson *et al.*, 2000). For this reason, the results of research must be robust and reported in detail and with accuracy to ensure the best possible conservation outcomes for cetacean populations.

7.6. Technical Recommendations

As described in detail in chapters 5 and 6, the whistle count data were highly over-dispersed, which was at least partly responsible for poor model fit and limited the inferences that could be made from model results. Reducing over-dispersion in the data would therefore allow more to be learned from their analysis. However, because whistles are produced non-randomly, such data are always likely to be over-dispersed. It is possible that alternative sampling regimes could help, for example by changing the length of the sampling unit. In conjunction with this, more sophisticated analytical techniques that explicitly model the serial correlation in the data, such as mixed effects models or Generalised Estimating Equations, might also help.

In addition, data collection could have been improved in the following ways:

- Data could be collected at different locations at the same time to generate a dataset with an even pattern of temporal and spatial measurements. In this study, weather conditions and the loss of one hydrophone prevented the deployment of the stationary hydrophones in same locations at different months in order to estimate changes in a particular location at different months.

- Register other factors such as tidal cycles. This information can be added to the models to find a temporal relationship of dolphin occurrence at distances from the coastline (Harzen, 1998).

- Obtain wind speed and precipitation data at the time and place samples were collected, rather than a remote location averaged over a period of time. Wind has been reported to be a major contributor to ambient noise (Reeder *et al.*, 2011). One of the possible reasons this was not an important factor for the models presented may have been because of the distance between the sample area and where these parameters where obtained (Chapter 2).

7.7. Future work

It is estimated that noise from shipping traffic noise has increased 8-10 dB from the mid-1960s to now and that it increases at a rough rate of one half decibel per year (Wenz, 1962; Andrew *et al.*, 2002; Ross, 2005; Andrew *et al.*, 2011). Therefore, one useful area of future work would be to conduct a similar analysis of background noise off Panama but covering longer periods of time. The data from such a study could then be used to predict trends in the contribution of different types of noise in what is one of the busiest areas of sea of the world. Similar trend studies have been carried out in other important busy marine shipping areas of the world: off the North American West Coast (Andrew *et al.*, 2011), North Pacific (Curtis *et al.*, 1999), Northeast Pacific Ocean (McDonald *et al.*, 2006; Chapman and Price, 2011), Istanbul Strait (Birpmar *et al.*, 2009), Marine Sanctuary off the coast of Massachusetts (Hatch *et al.*, 2008), Eastern Canadian continental shelf (Zakarauskas *et al.*, 1990), Australia (Cato, 1976), among others. Most importantly, studying the shipping noise contribution over the course of the years will help reveal if shipping activities are increasing noise levels in this region, as some of these referenced studies have shown elsewhere. As explained in Chapter 1, the Panama Canal Expansion project will bring an increase in traffic to the region. Shipping densities do influence traffic noise (Cato, 1976), and vessel size influences mechanical noise (Richardson *et al.*, 1995d). The expansion of the Panama Canal will enable it to receive vessels at least twice the size of those it receives today and will also increase of the number of ships travelling through the new set of locks (http://www.pancanal.com/eng/fn/reports/special-expansion/2012-english.pdf). The data on background noise collected in this study may be considered as pre-study baseline data to allow changes in noise levels to be assessed in the near future when shipping noise in the area increases. A similar survey design such as the one completed but with the appropriate corrections of flaws found in the present study and covering several years is suggested. Manual analysis of spectrograms revealed a statistically significant correlation between fish chorus and whistle detection. This finding raised more questions and it is suggested that for future research this relationship is further investigated to find out if it is related to foraging events. Dolphins emit different types of vocalization to denote different underwater behaviour and accurately relating a dolphin sound to a specific behaviour has been a difficult task in many cases (Herzing, 2000). However, specific vocalization types for *Tursiops truncatus* have been related to feeding/foraging behaviour (Herzing, 1996). Therefore, combining passive listening theory suggested by Gannon *et al.* (2005) (discussed in Chapters 4, 5 and 6) to find their prey (soniferous fish) and comparing the spectral description of dolphin sounds suggested by Herzing (1996) when *Tursiops truncatus* feeds, it is suggested that further spectral analysis of correlated events of fish chorus and whistle occurrence of data from this study may aid in determining whether feeding behaviour occurs during this fish chorus-whistle detection correlation. In addition, temporal variation in this correlation should be studied to investigate if there is a seasonal difference among fish spawning seasons and in relation to fishing boat noise.

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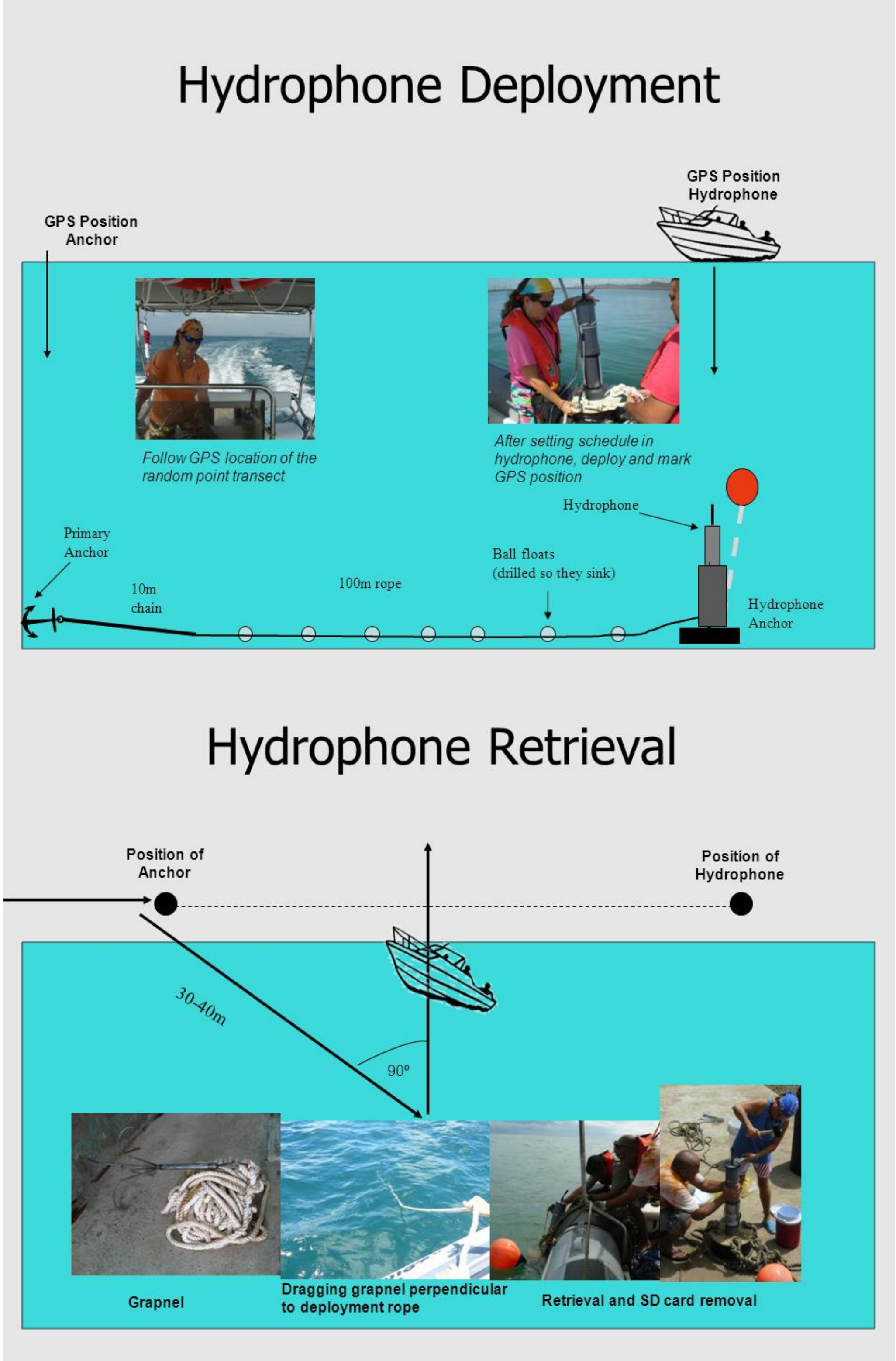
APPENDICES

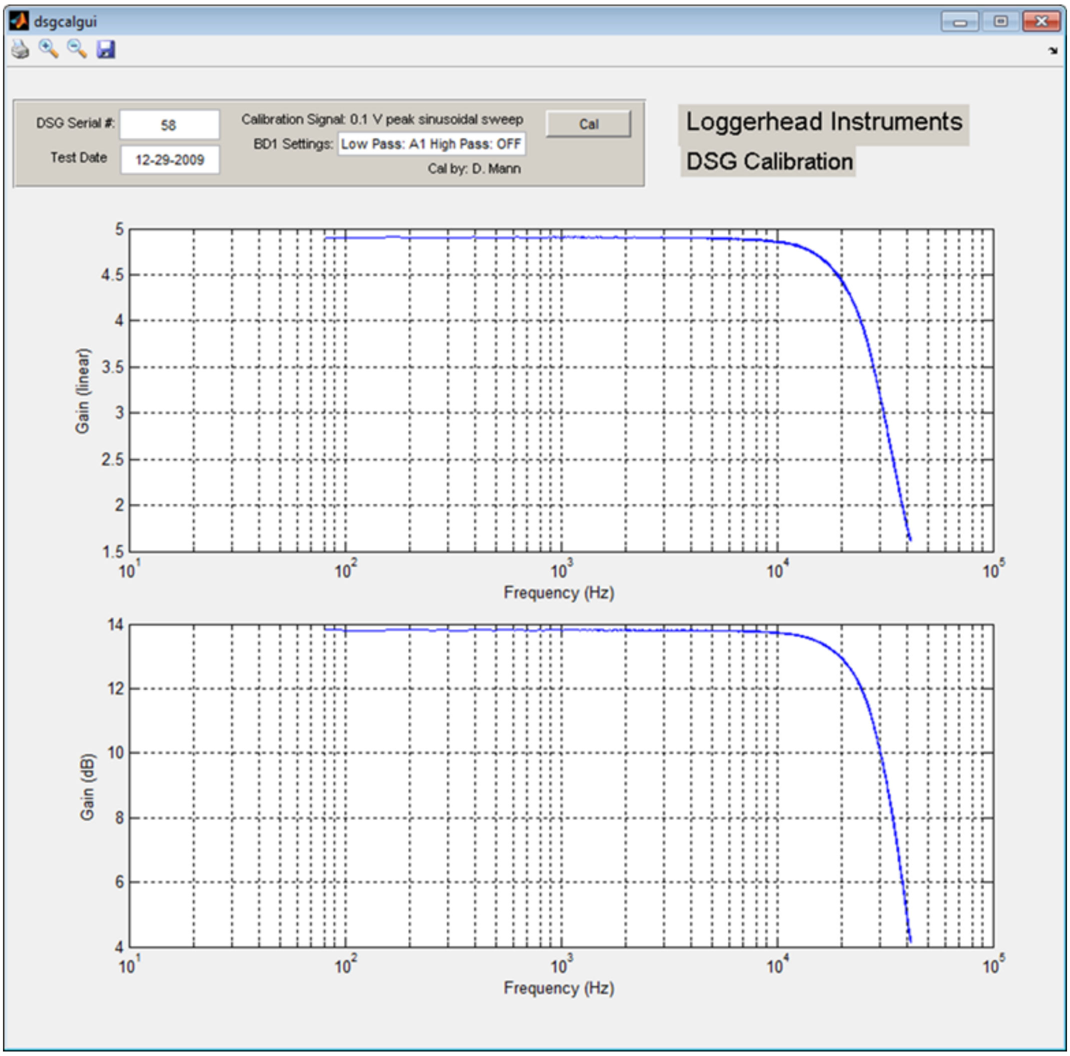
Figure A.1 Diagrams and photos illustrating the Deployment and Retrieval of the bottom-based hydrophone unit.



Hydrophone Deployment

Hydrophone Retrieval

Figure A.2 Calibration plot for bottom-based hydrophone (DSG).



DSG Serial #: 58

Test Date 12-29-2009

Calibration Signal: 0.1 V peak sinusoidal sweep

BD1 Settings: Low Pass: A1 High Pass: OFF

Cal by: D. Mann

Loggerhead Instruments

DSG Calibration

Figure A.3 Photos illustrating the boat-based hydrophone CR55 with Fostex recording unit. Photo also shows the assemblage of cable to minimize unwanted sound caused by friction of cable against the surface of the boat.

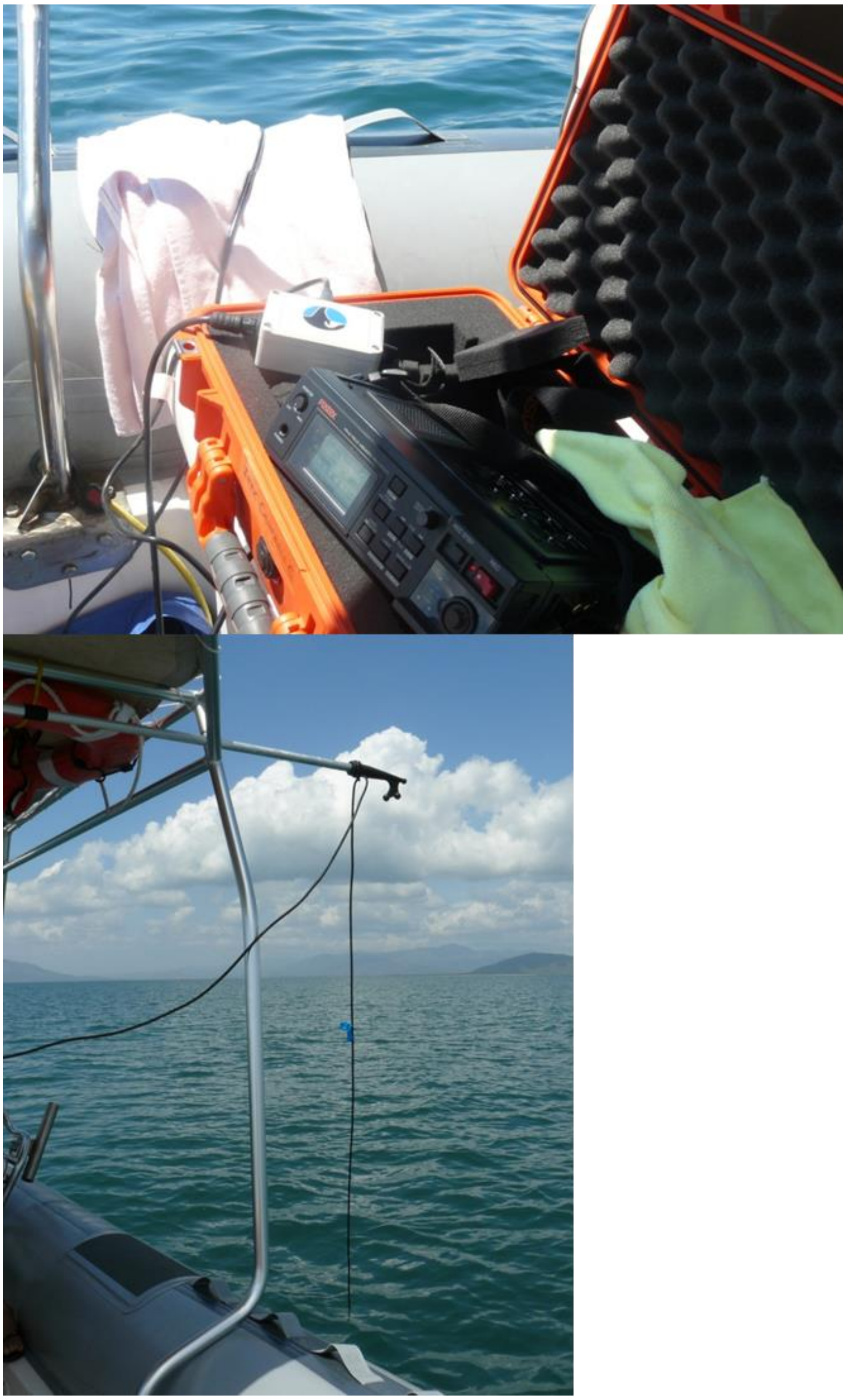
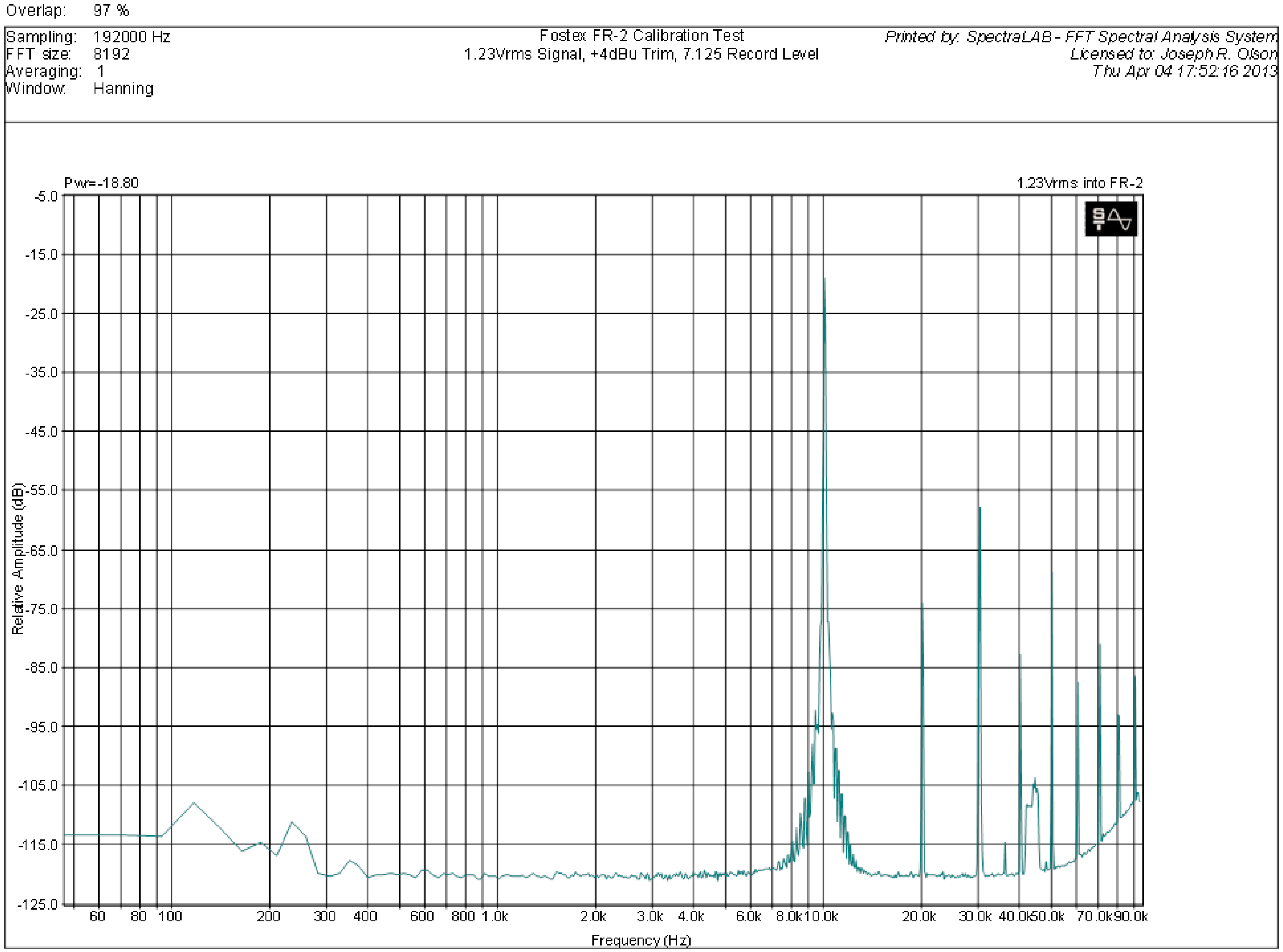


Figure A.4. Calibration plot for boat-based hydrophone CR55.



Overlap: 97 %

Sampling: 192000 Hz
FFT size: 8192
Averaging: 1
Window: Hanning

Fostex FR-2 Calibration Test
1.23Vrms Signal, +4dBu Trim, 7.125 Record Level

Printed by: SpectraLAB - FFT Spectral Analysis System
Licensed to: Joseph R. Olson
Thu Apr 04 17:52:16 2013

Table A.1 Daily means of Precipitation and daily means of Wind Speed per deployment/sample. The days and months shown refer to when the bottom-based hydrophone recorded data *in situ*. The location of weather station is given in Chapter 2.

Precipitation (mm) and Wind Speed (km/h) registered on a daily average basis at Albrook Weather Station. Data shown per deployment dates

Day	Month	Year	Precipitation (mm)	Wind Speed (Km/h)
16	4	2010	36.5	24.1
17	4	2010	2.9	15.0
18	4	2010	0.0	16.6
19	4	2010	0.0	11.1
20	4	2010	0.0	18.5
21	4	2010	0.8	14.4
22	4	2010	0.8	14.4
23	4	2010	0.0	13.0
24	4	2010	0.0	17.0
25	4	2010	86.1	14.8
26	4	2010	0.0	22.2
27	4	2010	0.5	14.8
28	4	2010	122.5	14.8
29	4	2010	0.2	16.6
30	4	2010	0.0	14.8
1	5	2010	0.0	16.6
2	5	2010	0.0	20.4
3	5	2010	14.5	12.6
4	5	2010	5.1	18.0
5	5	2010	0.0	14.4
6	5	2010	0.0	21.6
7	5	2010	0.0	22.2
8	5	2010	0.5	18.5
9	5	2010	0.0	23.4
10	5	2010	0.0	25.2
11	5	2010	0.0	21.6
12	5	2010	0.0	11.0
13	5	2010	13.3	18.5
14	5	2010	33.9	20.4
25	6	2010	1.2	14.4
26	6	2010	0.0	18.5
27	6	2010	91.2	13.0
28	6	2010	4.2	11.1
29	6	2010	0.0	18.5
30	6	2010	0.0	21.6
1	7	2010	52.4	14.4
2	7	2010	9.3	14.8
3	7	2010	0.0	16.6
4	7	2010	0.0	14.4
5	7	2010	2.6	25.2
9	8	2010	41.8	13.0
10	8	2010	0.0	14.8
11	8	2010	1.1	18.5
12	8	2010	8.6	18.5
13	8	2010	6.2	14.8
14	8	2010	0.0	15.0
15	8	2010	1.0	0.0
16	8	2010	25.7	18.0
17	8	2010	4.2	18.5
18	8	2010	7.8	14.8
19	8	2010	7.8	12.9
21	9	2010	1.5	16.2
22	9	2010	0.0	18.0
23	9	2010	46.0	25.9
24	9	2010	48.5	25.2
25	9	2010	0.5	24.0
26	9	2010	1.1	24.0
27	9	2010	0.0	18.5
28	9	2010	1.3	29.6
29	9	2010	0.0	29.6
30	9	2010	0.0	12.9
1	10	2010	0.0	11.1
2	10	2010	0.0	11.1
3	10	2010	82.2	12.0
4	10	2010	2.4	20.3
5	10	2010	0.0	11.1
6	10	2010	0.0	9.3
13	10	2010	7.2	11.1
14	10	2010	35.2	27.8
15	10	2010	14.8	18.0
16	10	2010	10.1	31.5
17	10	2010	1.8	9.3
18	10	2010	1.5	9.3
19	10	2010	1.5	14.8
3	2	2011	0.0	18.5
4	2	2011	0.0	6.0
5	2	2011	0.0	20.4
6	2	2011	0.0	22.2
7	2	2011	0.0	16.7
8	2	2011	0.0	14.8
22	2	2011	0.0	13.0
23	2	2011	0.0	12.6
24	2	2011	26.0	13.0
25	2	2011	1.2	14.8
14	3	2011	0.0	18.5
15	3	2011	0.0	14.4
16	3	2011	1.0	11.1
17	3	2011	0.0	24.1

Table A.2 Summary statistics of all variables in relation to deployments with the stationary hydrophone (DSG). The names correspond to the date when the deployment/recording was retrieved but also the sampling point (location) is noted. Means and standard deviation (in brackets) are provided except for those marked with "*" which are the values collected on the day of deployment.

		DSG Deployments			
Variables		***April 19th***	***April 23rd***	***April 30th***	***May 3rd***
		P01	P192	P191	P190
Month collected		April	April	April	May
Minutes recorded		1072.50	1450.00	2460.00	1047.50
Hours recorded		17.88	24.17	41.00	17.46
Dolphin presence		1	1	1	1
Depth*	meters	6	9	17	15
Latitude*	decimal	8.9263	8.8644	8.8455	8.82813
Longitude*	decimal	79.5332	79.5676	79.5677	79.56857
Temperature*	ºC	28.80	29.2	28.7	29.6
Salinity*	ppm	29.11	28.88	28.88	28.39
Dissolved Oxygen*	mg/L	5.40	5.20	5.00	5.40
Conductivity*	ms/cm	48.43	48.48	47.99	48.10
Barometric pressure*	mmHg	758.60	759.40	755.20	759.30
Precipitation (SD)	mm	9.09(14.9)	0.36(0.39)	28.5(48.3)	0.90(3.52)
min-max		0-36.5	0-0.8	0-123	0-14.5
Wind Speed (SD)	km/h	17.03(4.23)	15.05(2.53)	16.3(2.72)	17.14(2.47)
min-max		11.1-24.1	11.1-18.5	13-22.2	12.6-20.4
Distance to coastline*	km	3.00	3.00	5	6.7
Distance to buoys*	km	4.30	5.90	7.2	8.7
Distance to anchorage*	km	9.60	5.50	8.2	8.6
Received Level @ 20 Hertz (SD)	dB re 1µPa	80.78(0.72)	80.81(1.20)	82.85(5.81)	80.78(2.68)
Received Level @ 160 Hertz (SD)	dB re 1µPa	84.57(1.32)	84.23(2.09)	87.20(6.25)	86.57(4.85)
Received Level @ 400 Hertz (SD)	dB re 1µPa	69.56(3.90)	74.81(4.56)	79.38(8.24)	79.66(10.00)
Received Level @ 1000 Hertz (SD)	dB re 1µPa	66.09(3.61)	61.63(3.64)	73.75(11.48)	69.42(9.08)
Received Level @ 1600 Hertz (SD)	dB re 1µPa	68.37(4.44)	65.66(3.71)	71.79(8.74)	67.09(6.92)
Received Level @ 5000 Hertz (SD)	dB re 1µPa	75.28(4.50)	79.58(1.90)	73.10(4.30)	70.77(3.17)
Received Level @ 10000 Hertz (SD)	dB re 1µPa	72.98(1.34)	76.94(1.51)	72.43(2.72)	71.16(2.26)
Received Level @ 16000 Hertz (SD)	dB re 1µPa	72.24(1.05)	73.30(1.57)	71.57(2.39)	70.35(1.85)
Received Level @ 20000 Hertz (SD)	dB re 1µPa	72.22(0.93)	72.87(1.55)	71.06(2.31)	70.38(1.62)

Table A.3. Summary statistics of all variables in relation to deployments with the stationary hydrophone (DSG). The names correspond to the date when the deployment/recording was retrieved but also the sampling point (location) is noted. Means and standard deviation (in brackets) are provided except for those marked with "*" which are the values collected on the day of deployment (Continued).

DSG Deployments					
Variables		***May 7th***	***June 3rd***	***June 30th***	***July 5th***
		P157	P171	P245	P245b
Month collected		May	May	June	July
Minutes recorded		1437.50	2652.50	2000.00	1820.00
Hours recorded		23.96	44.21	33.33	30.33
Dolphin presence		1	0	1	1
Depth*	meters	11	22	15	17
Latitude*	decimal	8.84612	8.79147	8.80135	8.80117
Longitude*	decimal	79.60327	79.58564	79.51952	79.5194
Temperature*	ºC	29.3	28.9	28.9	28.6
Salinity*	ppm	28.71	28.71	26.97	27.54
Dissolved Oxygen*	mg/L	4.90	5.80	5.40	4.70
Conductivity*	ms/cm	48.29	47.88	45.40	45.92
Barometric pressure*	mmHg	759.10	756.70	757.90	759.20
Precipitation (SD)	mm	2.71(4.67	7.01(12.35)	19.83(36.52)	11.21(19.54)
min-max		0-14.5	0-33.9	0-91.2	0-52.4
Wind Speed (SD)	km/h	17.96(3.54)	20.47(3.97)	15.70(3.54)	17.05(3.74)
min-max		12.6-22.2	11-25.2	11.1-21.6	14.4-25.2
Distance to coastline*	km	5.2	10.7	12.2	12.2
Distance to buoys*	km	10.3	13.1	9.8	9.8
Distance to anchorage*	km	12.1	12	6	6
Received Level @ 20 Hertz (SD)	dB re 1µPa	82.05(6.00)	81.27(2.41)	84.36(4.15)	81.80(3.40)
Received Level @ 160 Hertz (SD)	dB re 1µPa	85.66(6.34)	87.04(5.32)	89.06(4.07)	85.41(3.20)
Received Level @ 400 Hertz (SD)	dB re 1µPa	70.94(8.57)	78.40(11.78)	79.52(4.79)	81.73(4.02)
Received Level @ 1000 Hertz (SD)	dB re 1µPa	68.58(8.33)	70.13(12.40)	72.98(3.40)	78.75(5.11)
Received Level @ 1600 Hertz (SD)	dB re 1µPa	67.35(6.08)	65.44(10.03)	77.70(1.55)	73.74(4.02)
Received Level @ 5000 Hertz (SD)	dB re 1µPa	71.99(5.27)	66.08(4.22)	83.67(1.52)	79.42(4.40)
Received Level @ 10000 Hertz (SD)	dB re 1µPa	71.27(4.13)	66.18(2.28)	81.96(1.78)	76.84(4.52)
Received Level @ 16000 Hertz (SD)	dB re 1µPa	70.42(3.20)	66.40(1.70)	80.03(1.68)	73.83(4.03)
Received Level @ 20000 Hertz (SD)	dB re 1µPa	70.05(2.93)	66.54(1.55)	78.25(1.46)	73.70(3.93)

Table A.4. Summary statistics of all variables in relation to deployments with the stationary hydrophone (DSG). The names correspond to the date when the deployment/recording was retrieved but also the sampling point (location) is noted. Means and standard deviation (in brackets) are provided except for those marked with "*" which are the values collected on the day of deployment (Continued).

		DSG Deployments			
Variables		***August 12th***	***August 19th***	***October 6th***	***October 19th***
		Pmelones	Ptortolas	P284H	P249
Month collected		August	August	September	October
Minutes recorded		1100.00	2457.50	2517.50	2167.50
Hours recorded		18.33	40.96	41.96	36.13
Dolphin presence		1	1	1	1
Depth*	meters	15	7.5	25	15
Latitude*	decimal	8.81467	8.85861	8.819	8.93645
Longitude*	decimal	79.61057	79.56392	79.48657	79.5129
Temperature*	ºC	28.9	28.9	28.1	27.5
Salinity*	ppm	24.68	24.49	24.40	26.00
Dissolved Oxygen*	mg/L	5.30	5.20	2.60	5.20
Conductivity*	ms/cm	41.82	41.57	40.82	42.68
Barometric pressure*	mmHg	760.20	758.10	758.60	758.00
Precipitation (SD)	mm	10.07(16.29)	7.71(7.95)	10.28(18.94)	9.38(12.19)
min-max		0-41.8	0-25.7	0-48.5	1.5-35.2
Wind Speed (SD)	km/h	16.31(2.32)	13.68(5.87)	23.20(3.86)	17.26(6.06)
min-max		13-18.53	0-18.53	16.2-29.6	9.3-27.8
Distance to coastline*	km	8.1	4.5	12.7	2.8
Distance to buoys*	km	13	5.9	8.7	5.3
Distance to anchorage*	km	13.4	7.8	3.4	10
Received Level @ 20 Hertz (SD)	dB re 1μPa	80.67(0.71)	81.91(2.63)	82.86(3.98)	81.75(1.20)
Received Level @ 160 Hertz (SD)	dB re 1μPa	84.80(2.40)	86.96(5.69)	86.84(4.88)	85.25(1.72)
Received Level @ 400 Hertz (SD)	dB re 1μPa	77.88(8.65)	77.98(10.03)	72.34(7.83)	71.60(5.99)
Received Level @ 1000 Hertz (SD)	dB re 1μPa	68.82(8.69)	69.28(5.48)	68.00(5.98)	70.54(7.35)
Received Level @ 1600 Hertz (SD)	dB re 1μPa	67.63(4.60)	73.00(2.25)	66.21(5.26)	63.90(8.56)
Received Level @ 5000 Hertz (SD)	dB re 1μPa	81.51(1.30)	84.07(1.15)	68.32(4.40)	69.83(7.93)
Received Level @ 10000 Hertz (SD)	dB re 1μPa	79.69(1.14)	80.83(1.31)	68.36(4.16)	70.08(5.06)
Received Level @ 16000 Hertz (SD)	dB re 1μPa	76.56(1.23)	78.64(1.47)	67.84(3.68)	68.34(3.99)
Received Level @ 20000 Hertz (SD)	dB re 1μPa	75.60(1.14)	77.66(1.40)	67.48(3.36)	67.90(3.83)

Table A.5. Summary statistics of all variables in relation to deployments with the stationary hydrophone (DSG). The names correspond to the date when the deployment/recording was retrieved but also the sampling point (location) is noted. Means and standard deviation (in brackets) are provided except for those marked with "*" which are the values collected on the day of deployment (Continued).

DSG Deployments				
Variables		***February 8th***	***February 25th***	***March 17th***
		P224	PN76	PChama
Month collected		February	February	March
Minutes recorded		137.50	1037.50	1115.00
Hours recorded		2.29	17.29	18.58
Dolphin presence		1	1	1
Depth*	meters	14	19	17
Latitude*	decimal	8.77443	8.79546	8.73475
Longitude*	decimal	79.53082	79.51469	79.57883
Temperature*	ºC	24.6	25	23
Salinity*	ppm	28.55	29.64	28.76
Dissolved Oxygen*	mg/L	6.20	2.20	5.70
Conductivity*	ms/cm	43.91	42.20	43.50
Barometric pressure*	mmHg	758.90	757.90	760.70
Precipitation (SD)	mm	0.00	14.06(13)	0.30(0.46)
min-max		0.00	0-26	0-1
Wind Speed (SD)	km/h	18.88	13.07(0.59)	15.81(4.39)
min-max		18.88	12.6-14.8	11.1-24.1
Distance to coastline*	km	14.1	13	18
Distance to buoys*	km	12.9	10.5	18.4
Distance to anchorage*	km	9.3	6.3	15.8
Received Level @ 20 Hertz (SD)	dB re 1µPa	84.75(4.23)	81.05(5.87)	80.33(3.08)
Received Level @ 160 Hertz (SD)	dB re 1µPa	89.71(4.17)	85.31(6.07)	84.70(3.35)
Received Level @ 400 Hertz (SD)	dB re 1µPa	88.59(4.86)	83.03(6.41)	82.33(4.10)
Received Level @ 1000 Hertz (SD)	dB re 1µPa	80.74(8.94)	81.57(8.68)	79.81(5.99)
Received Level @ 1600 Hertz (SD)	dB re 1µPa	66.64(5.53)	78.05(7.13)	75.80(4.71)
Received Level @ 5000 Hertz (SD)	dB re 1µPa	53.88(7.87)	81.21(4.32)	81.13(5.54)
Received Level @ 10000 Hertz (SD)	dB re 1µPa	48.62(7.11)	77.08(3.62)	78.39(5.72)
Received Level @ 16000 Hertz (SD)	dB re 1µPa	47.09(6.01)	74.89(4.02)	77.26(5.28)
Received Level @ 20000 Hertz (SD)	dB re 1µPa	46.83(5.86)	74.59(3.93)	76.69(5.10)

Table A.6. Summary statistics of all Variables in relation to recordings with the boat-based hydrophone (CR55). The labels correspond to the sites where the recordings took place. Means and standard deviation (in brackets) are provided for RL. Other are the values collected on the day of recording. Letters in some of the labels signify the same site was sampled at different events.

CR55 Recordings							
Variables	**N066**	**N088**	**N089**	**N090**	**N091**	**N80**	**N83**
Month	12	3	3	3	3	3	3
Dolphin presence	0	1	0	1	0	0	1
Depth	30.00	16.00	30.00	20.00	19.00	17.00	5.50
Latitude	8.81	8.83	8.59	8.57	8.57	8.73	8.77
Longitude	79.50	79.68	79.59	79.59	79.59	79.58	79.74
Temperature	26.00	21.00	19.80	22.40	20.70	23.00	21.70
Salinity	27.53	29.94	30.78	30.30	30.56	28.76	29.13
Dissolved Oxygen	43.80	44.35	42.88	44.13	43.22	43.50	44.75
Conductivity	1.00	7.60	7.40	7.80	7.60	4.70	6.30
Barometric Pressure	760.30	760.20	760.20	759.70	759.80	760.70	760.40
Precipitation	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Wind Speed	29.60	24.10	24.10	24.10	24.10	18.50	18.50
Distance to coastline	12.40	13.50	13.30	15.00	14.40	18.00	6.00
Distance to buoys	9.90	33.40	34.20	36.10	36.30	18.40	26.80
Distance to anchorage	4.70	30.00	30.80	32.50	41.70	15.80	28.20
Received Level @ 20 Hertz (SD)	106.47(2.41)	90.65(1.38)	97.43(2.61)	97.71(3.12)	95.37(0.68)	94.99(0.75)	87.05(2.06)
Received Level @ 160 Hertz (SD)	100.25(2.47)	93.85(1.50)	93.82(1.95)	94.99(2.58)	90.20(1.11)	88.68(0.81)	90.81(2.07)
Received Level @ 400 Hertz (SD)	103.29(3.43)	93.59(1.33)	93.70(1.04)	95.13(2.01)	92.14(0.65)	81.70(1.74)	84.18(3.38)
Received Level @ 1000 Hertz (SD)	105.42(3.32)	91.39(0.56)	92.19(3.79)	93.13(2.72)	93.61(1.32)	85.24(2.09)	86.24(2.85)
Received Level @ 1600 Hertz (SD)	103.66(3.36)	92.56(0.48)	90.83(0.47)	93.02(1.99)	96.26(0.41)	94.13(0.51)	83.94(3.33)
Received Level @ 5000 Hertz (SD)	98.18(2.04)	87.63(0.24)	95.29(0.28)	90.67(2.54)	96.69(0.59)	93.50(0.25)	88.07(1.61)
Received Level @ 10000 Hertz (SD)	94.54(2.37)	94.35(0.26)	92.48(0.36)	98.41(2.35)	93.65(0.67)	90.35(0.24)	94.64(2.26)
Received Level @ 16000 Hertz (SD)	92.02(2.20)	92.45(0.34)	90.33(0.38)	97.03(2.28)	92.93(0.84)	89.17(0.27)	102.14(1.89)
Received Level @ 20000 Hertz (SD)	NA	NA	NA	NA	NA	NA	NA

Table A.7. Summary statistics of all Variables in relation to recordings with the boat-based hydrophone (CR55). The labels correspond to the sites where the recordings took place. (Continued).

CR55 Recordings							
Site	**NCH1**	**NUR01**	**P102**	**P103**	**P119**	**P120**	**P138**
Month	4	6	3	2	3	2	2
Dolphin presence	1	0	1	1	1	0	0
Depth	13.00	24.00	12.00	14.00	13.00	15.00	17.00
Latitude	8.74	8.78	8.77	8.79	8.77	8.79	8.81
Longitude	79.57	79.53	79.66	79.66	79.64	79.64	79.62
Temperature	28.90	29.40	19.00	25.60	22.50	25.70	24.20
Salinity	28.47	27.29	30.74	28.24	29.91	27.93	29.35
Dissolved Oxygen	47.95	46.04	41.81	44.31	43.93	43.99	44.67
Conductivity	5.60	6.40	4.20	7.00	6.50	7.70	7.30
Barometric Pressure	759.40	769.60	760.40	757.00	760.30	756.10	755.60
Precipitation	0.50	0.00	0.00	0.00	0.00	0.00	0.00
Wind Speed	14.80	11.10	24.10	18.00	24.10	18.00	18.00
Distance to coastline	19.60	12.50	11.70	7.50	13.70	10.30	8.20
Distance to buoys	17.40	11.80	19.90	18.60	18.40	17.10	14.30
Distance to anchorage	15.00	8.50	20.00	19.20	18.20	17.30	14.80
Received Level @ 20 Hertz (SD)	80.29(16.44)	89.21(3.33)	90.54(1.35)	90.30(0.99)	94.08(1.83)	95.00(0.59)	99.07(0.51)
Received Level @ 160 Hertz (SD)	84.74(1.47)	82.90(3.48)	93.25(1.36)	93.22(1.03)	97.06(1.69)	97.84(0.63)	91.82(0.52)
Received Level @ 400 Hertz (SD)	83.68(2.21)	109.09(0.62)	103.98(1.14)	106.99(4.76)	111.10(1.66)	100.15(3.22)	104.76(2.14)
Received Level @ 1000 Hertz (SD)	88.47(6.13)	100.90(2.46)	108.65(1.68)	108.24(5.72)	109.62(1.07)	94.91(3.72)	103.18(2.75)
Received Level @ 1600 Hertz (SD)	78.86(1.89)	103.39(0.45)	101.47(0.52)	98.87(3.59)	103.67(0.93)	90.24(3.30)	91.72(3.24)
Received Level @ 5000 Hertz (SD)	82.30(0.16)	113.60(0.33)	95.48(0.63)	95.71(0.42)	98.82(1.31)	90.89(1.08)	89.66(0.42)
Received Level @ 10000 Hertz (SD)	95.14(0.19)	114.55(0.38)	91.15(0.77)	96.22(0.48)	93.17(1.08)	93.01(0.65)	92.61(0.45)
Received Level @ 16000 Hertz (SD)	NA	109.27(0.37)	91.77(0.76)	97.80(0.39)	94.11(1.21)	94.66(0.70)	94.28(0.32)
Received Level @ 20000 Hertz (SD)	NA	NA	NA	NA	NA	NA	NA

Table A.8. Summary statistics of all Variables in relation to recordings with the boat-based hydrophone (CR55). The labels correspond to the sites where the recordings took place. (Continued).

CR55 Recordings							
Site	**P140**	**P153**	**P158**	**P172**	**P174**	**P175**	**P204**
Month	12	3	12	2	6	12	2
Dolphin presence	0	0	1	1	0	0	1
Depth	8.30	13.00	6.80	15.00	15.00	6.90	17.00
Latitude	8.85	8.77	8.86	8.81	8.85	8.86	8.77
Longitude	79.62	79.60	79.60	79.59	79.59	79.59	79.55
Temperature	24.00	23.60	24.00	25.80	29.50	24.00	24.00
Salinity	28.31	29.53	28.23	27.79	27.38	28.20	28.52
Dissolved Oxygen	44.61	44.43	44.57	43.83	45.64	44.52	44.33
Conductivity	6.10	7.40	5.90	7.50	4.30	5.70	7.20
Barometric Pressure	760.40	760.20	760.20	758.80	759.90	760.30	758.30
Precipitation	0.40	0.00	0.40	0.00	0.80	0.40	0.00
Wind Speed	24.05	24.10	24.05	18.50	11.10	24.05	18.00
Distance to coastline	4.20	17.70	3.00	8.40	4.40	2.30	13.00
Distance to buoys	12.20	15.80	9.60	11.40	8.70	7.70	13.30
Distance to anchorage	14.20	14.70	12.30	11.00	10.20	10.30	10.40
Received Level @ 20 Hertz (SD)	94.30(3.79)	98.51(2.85)	93.07(2.21)	96.89(0.69)	108.33(2.75)	110.25(1.04)	91.98(3.43)
Received Level @ 160 Hertz (SD)	93.88(4.33)	101.37(2.97)	91.92(1.95)	97.26(0.68)	101.19(2.83)	113.17(1.09)	94.84(3.40)
Received Level @ 400 Hertz (SD)	85.49(6.04)	111.80(3.47)	91.91(1.96)	97.67(3.39)	101.49(3.43)	96.48(4.81)	95.01(4.50)
Received Level @ 1000 Hertz (SD)	89.62(7.95)	112.25(4.53)	95.47(5.18)	91.92(4.99)	102.17(4.55)	97.03(6.24)	104.60(5.79)
Received Level @ 1600 Hertz (SD)	91.85(4.21)	104.29(1.39)	99.76(2.04)	93.04(5.96)	94.10(1.55)	98.42(4.20)	95.46(1.51)
Received Level @ 5000 Hertz (SD)	90.05(3.06)	98.16(1.31)	94.51(1.61)	90.15(4.70)	88.00(1.38)	95.61(0.84)	95.04(0.49)
Received Level @ 10000 Hertz (SD)	NA	92.82.(0.85)	NA	86.77(2.31)	82.67(1.02)	96.13(0.81)	93.69(0.36)
Received Level @ 16000 Hertz (SD)	NA	93.06(1.03)	NA	86.61(1.24)	82.95(0.99)	97.72(0.63)	92.89(0.41)
Received Level @ 20000 Hertz (SD)	NA	NA	NA	NA	NA	NA	NA

Table A.9. Summary statistics of all Variables in relation to recordings with the boat-based hydrophone (CR55). The labels correspond to the sites where the recordings took place. (Continued).

CR55 Recordings							
Site	**P209**	**P224a**	**224b**	**P225**	**P244**	**P245**	**P246**
Month	4	2	2	6	12	1	8
Dolphin presence	0	1	0	1	1	1	1
Depth	10.00	16.00	16.00	28.00	27.00	23.00	18.00
Latitude	8.86	8.77	8.77	8.79	8.79	8.80	8.88
Longitude	79.55	79.53	79.53	79.53	79.51	70.52	79.51
Temperature	29.00	24.00	25.50	29.50	26.00	24.00	28.80
Salinity	28.77	28.41	27.45	27.18	27.42	28.10	25.06
Dissolved Oxygen	48.19	43.92	43.12	45.64	43.59	43.00	42.29
Conductivity	NA	6.20	6.90	4.30	0.80	5.80	4.80
Barometric Pressure	758.20	758.80	759.00	759.90	759.40	760.00	759.70
Precipitation	0.00	0.00	0.00	0.80	0.00	0.00	41.80
Wind Speed	13.00	18.50	18.00	11.10	29.60	14.80	13.00
Distance to coastline	4.20	13.90	13.90	11.90	13.00	12.20	6.20
Distance to buoys	4.20	12.90	12.90	10.90	10.90	9.80	1.10
Distance to anchorage	6.40	9.30	9.30	7.60	6.70	6.00	4.30
Received Level @ 20 Hertz (SD)	91.93(2.54)	115.71(2.45)	111.07(2.07)	100.02(2.07)	80.02(2.07)	112.58(1.14)	106.11(1.31)
Received Level @ 160 Hertz (SD)	94.52(2.53)	119.22(2.46)	113.94(2.09)	108.66(1.92)	88.66(1.92)	105.77(1.16)	109.68(1.83)
Received Level @ 400 Hertz (SD)	75.34(3.58)	117.84(5.02)	103.46(1.86)	108.58(2.49)	88.58(2.49)	106.77(0.92)	101.88(6.46)
Received Level @ 1000 Hertz (SD)	81.51(5.63)	117.59(5.90)	102.43(3.39)	101.84(2.35)	91.84(2.35)	102.02(1.77)	88.79(4.32)
Received Level @ 1600 Hertz (SD)	81.58(2.27)	97.59(2.76)	95.56(1.00)	99.47(2.83)	89.47(2.83)	103.25(0.91)	86.53(4.54)
Received Level @ 5000 Hertz (SD)	86.72(2.54)	95.96(0.58)	95.21(0.28)	97.42(1.41)	87.42(1.41)	114.37(0.36)	84.57(4.34)
Received Level @ 10000 Hertz (SD)	85.59(2.68)	93.69(0.45)	93.19(0.35)	NA	NA	111.70(0.36)	82.13(4.38)
Received Level @ 16000 Hertz (SD)	84.73(2.78)	91.88(0.54)	91.57(0.50)	NA	NA	109.60(0.36)	85.86(4.83)
Received Level @ 20000 Hertz (SD)	NA	NA	NA	NA	NA	NA	NA
				*			

Table A.10. Summary statistics of all Variables in relation to recordings with the boat-based hydrophone (CR55). The labels correspond to the sites where the recordings took place. (Continued).

CR55 Recordings							
Site	**P247a**	**P247b**	**P249a**	**P249b**	**P249c**	**P265a**	**P265b**
Month	5	10	4	9	3	6	9
Dolphin presence	0	0	***0***	1	0	1	0
Depth	15.00	11.00	7.30	7.80	9.20	13.00	13.00
Latitude	8.90	8.90	8.94	8.94	8.94	8.92	8.92
Longitude	79.51	79.51	79.51	79.51	79.51	79.49	79.49
Temperature	30.60	27.30	28.80	28.10	26.00	29.50	28.50
Salinity	30.60	26.38	29.15	23.36	29.33	26.59	23.93
Dissolved Oxygen	46.73	43.09	48.53	39.52	47.77	45.28	40.31
Conductivity	6.40	5.00	NA	4.60	6.00	5.20	5.10
Barometric Pressure	758.40	756.90	757.30	759.00	758.60	759.80	758.90
Precipitation	14.50	7.20	36.50	1.50	0.00	0.00	1.50
Wind Speed	12.60	11.10	24.10	16.20	24.50	11.10	16.20
Distance to coastline	4.80	4.80	2.60	5.30	2.60	5.30	5.30
Distance to buoys	1.50	1.70	5.30	5.30	5.30	4.30	4.30
Distance to anchorage	6.10	6.20	10.00	10.00	10.00	7.70	7.70
Received Level @ 20 Hertz (SD)	116.25(1.34)	102.88(9.74)	117.78	115.71	115.26	119.62(2.07)	105.23(1.94)
Received Level @ 160 Hertz (SD)	119.48(0.98)	104.27(9.00)	120.61	118.97	118.87	123.90(2.14)	98.86(0.73)
Received Level @ 400 Hertz (SD)	106.10(6.82)	107.83(8.83)	100.91	103.56	113.84	110.89(5.82)	95.91(1.28)
Received Level @ 1000 Hertz (SD)	108.51(8.30)	102.73(7.84)	102.03	105.63	117.87	102.21(5.33)	91.68(1.11)
Received Level @ 1600 Hertz (SD)	97.52(6.82)	94.01(7.06)	97.52	98.07	114.81	102.45(4.55)	89.87(2.15)
Received Level @ 5000 Hertz (SD)	91.02(7.17)	93.86(7.54)	91.02	92.45	121.46	108.47(3.14)	83.72(1.61)
Received Level @ 10000 Hertz (SD)	99.16(5.07)	NA	90.11	90.82	116.56	107.12(3.30)	NA
Received Level @ 16000 Hertz (SD)	97.44(6.96)	NA	90.43	90.64	111.26	101.31(3.55)	NA
Received Level @ 20000 Hertz (SD)	NA	NA	NA	NA	NA	NA	NA

Table A.11. Summary statistics of all Variables in relation to recordings with the boat-based hydrophone (CR55). The labels correspond to the sites where the recordings took place. (Continued).

	CR55 Recordings						
Site	**P266a**	**P266b**	**P266c**	**P267**	**P284**	**P286**	**P287a**
Month	6	1	3	4	9	10	3
Dolphin presence	***0***	1	0	0	1	***1***	0
Depth	9.50	12.00	9.70	6.00	25.00	14.00	8.80
Latitude	8.94	8.94	8.94	8.95	8.81	8.94	8.95
Longitude	79.49	79.49	79.49	79.49	79.48	79.48	79.48
Temperature	29.50	24.00	25.00	28.80	29.20	27.50	26.00
Salinity	26.59	26.70	29.53	29.15	23.20	26.69	29.46
Dissolved Oxygen	45.28	41.90	47.00	48.50	39.98	43.65	47.78
Conductivity	2.80	5.30	6.70	NA	5.20	5.40	6.20
Barometric Pressure	759.40	760.00	758.98	757.70	756.20	758.20	758.46
Precipitation	0.00	0.00	0.00	36.50	31.60	7.20	0.00
Wind Speed	11.10	14.80	24.50	24.10	25.94	11.10	24.50
Distance to coastline	4.40	4.50	4.50	2.80	14.30	5.70	4.40
Distance to buoys	6.00	6.00	6.00	7.80	10.10	7.10	8.70
Distance to anchorage	9.80	9.80	9.80	11.80	4.70	9.90	11.90
Received Level @ 20 Hertz (SD)	112.65	109.91	108.79	94.18(0.47)	119.68(0.69)	111.07(1.92)	125.88
Received Level @ 160 Hertz (SD)	118.49	114.56	113.23	94.77(0.36)	101.13(1.08)	97.86(1.57)	128.61
Received Level @ 400 Hertz (SD)	108.07	105.94	100.36	102.00(1.11)	94.48(2.32)	91.29(1.14)	103.64
Received Level @ 1000 Hertz (SD)	103.34	108.11	100.23	99.62(1.02)	94.85(1.34)	91.28(2.90)	97.06
Received Level @ 1600 Hertz (SD)	99.88	108.13	105.20	92.21(0.90)	92.81(0.77)	108.63(1.27)	89.83
Received Level @ 5000 Hertz (SD)	105.72	112.55	110.84	92.34(0.27)	85.97(0.71)	92.79(1.79)	85.82
Received Level @ 10000 Hertz (SD)	104.32	112.38	108.04	NA	NA	NA	81.71
Received Level @ 16000 Hertz (SD)	98.41	105.60	101.58	NA	NA	NA	83.58
Received Level @ 20000 Hertz (SD)	NA	NA	NA	NA	NA	NA	NA

Table A.12. Summary statistics of all Variables in relation to recordings with the boat-based hydrophone (CR55). The labels correspond to the sites where the recordings took place. (Continued).

CR55 Recordings							
Site	**P287b**	**P295B**	**P296**	**P297a**	**P297b**	**P30**	**P306**
Month	4	9	11	11	3	3	9
Dolphin presence	1	1	1	0	0	0	1
Depth	8.00	28.00	17.00	13.00	14.00	3.00	27.00
Latitude	8.95	8.81	8.92	8.94	8.94	8.67	8.81
Longitude	79.48	79.46	79.46	79.46	79.46	79.73	79.44
Temperature	28.80	29.00	27.30	27.40	25.00	26.00	29.00
Salinity	28.97	23.94	21.92	22.16	29.55	29.11	24.28
Dissolved Oxygen	48.21	40.73	35.91	36.79	47.65	45.31	41.15
Conductivity	NA	5.20	5.70	6.60	6.50	6.50	5.20
Barometric Pressure	758.00	757.60	760.50	760.80	758.54	761.40	756.90
Precipitation	36.50	31.60	13.50	13.50	0.00	1.00	31.60
Wind Speed	24.10	25.94	18.00	18.00	24.50	11.10	25.94
Distance to coastline	4.40	15.60	8.50	7.40	7.00	3.20	17.20
Distance to buoys	8.70	11.20	7.50	8.60	8.60	33.90	12.50
Distance to anchorage	11.90	5.80	8.70	10.50	10.50	33.10	7.30
Received Level @ 20 Hertz (SD)	122.45	129.43(2.24)	115.88	92.26(3.37)	82.94(3.15)	108.60(3.36)	110.09(1.62)
Received Level @ 160 Hertz (SD)	125.12	111.65(5.53)	103.66	96.25(2.88)	88.03(5.43)	107.35(3.46)	95.18(2.32)
Received Level @ 400 Hertz (SD)	98.23	111.73(6.55)	99.11	92.30(6.25)	76.71(6.22)	102.87(3.43)	97.67(3.69)
Received Level @ 1000 Hertz (SD)	93.84	120.52(3.17)	98.38	94.32(6.72)	76.90(4.33)	103.00(4.21)	96.87(4.42)
Received Level @ 1600 Hertz (SD)	85.99	110.31(7.52)	95.13	84.46(6.29)	72.82(6.88)	96.27(2.86)	96.31(4.14)
Received Level @ 5000 Hertz (SD)	86.68	102.52(8.01)	86.00	72.13(5.45)	69.12(9.21)	91.40(1.76)	91.77(5.66)
Received Level @ 10000 Hertz (SD)	81.91	98.23(12.23)	NA	67.48(4.89)	65.08(3.87)	85.71(1.63)	NA
Received Level @ 16000 Hertz (SD)	83.69	NA	NA	68.00(3.29)	65.16(5.42)	85.65(1.21)	NA
Received Level @ 20000 Hertz (SD)	NA	NA	NA	NA	NA	NA	NA

Table A.13. Summary statistics of all Variables in relation to recordings with the boat-based hydrophone (CR55). The labels correspond to the sites where the recordings took place. (Continued).

	CR55 Recordings						
Site	**P308**	**P45**	**P51**	**P62**	**P63**	**P64**	**P66a**
Month	6	3	3	3	3	3	3
Dolphin presence	1	1	0	0	0	1	1
Depth	30.00	5.00	7.60	17.00	14.00	14.00	13
Latitude	8.85	8.67	8.77	8.67	8.68	8.68	8.73
Longitude	79.44	79.71	79.71	79.70	79.70	79.70	79.69
Temperature	28.80	25.20	24.40	24.50	24.80	23.20	20.7
Salinity	26.75	29.25	29.15	29.37	29.40	29.83	30.44
Dissolved Oxygen	44.87	45.38	44.55	44.91	45.24	44.23	42.8
Conductivity	5.60	6.30	6.50	6.40	6.60	5.40	4.1
Barometric Pressure	758.00	760.90	759.00	760.50	759.60	758.70	758
Precipitation	1.20	1.00	0.00	1.00	1.00	1.00	1
Wind Speed	14.40	11.10	18.50	11.10	11.10	11.10	11.1
Distance to coastline	15.30	2.10	5.80	7.00	6.90	6.30	5.7
Distance to buoys	10.00	32.60	24.80	31.40	29.80	28.30	25.5
Distance to anchorage	5.90	31.60	25.50	30.00	28.70	27.50	25.3
Received Level @ 20 Hertz (SD)	114.14(0.79)	111.73	105.09	111.46	112.78	110.02(4.16)	111.89(1.10)
Received Level @ 160 Hertz (SD)	117.20(0.86)	118.11	115.17	114.25	115.60	112.87(4.23)	113.58(1.08)
Received Level @ 400 Hertz (SD)	112.31(3.10)	112.22	112.21	105.25	111.22	103.07(3.98)	107.82(6.60)
Received Level @ 1000 Hertz (SD)	109.30(2.70)	105.32	99.54	101.11	105.75	98.47(1.76)	102.31(8.99)
Received Level @ 1600 Hertz (SD)	104.60(2.04)	97.58	92.39	95.20	93.51	91.86(0.93)	94.72(5.17)
Received Level @ 5000 Hertz (SD)	103.29(1.84)	92.00	93.64	97.81	89.79	91.08(1.67)	92.99(3.55)
Received Level @ 10000 Hertz (SD)	100.22(2.44)	98.55	92.42	90.72	88.59	90.78(2.41)	92.33(3.51)
Received Level @ 16000 Hertz (SD)	91.74(1.29)	98.19	92.89	87.89	89.51	91.64(2.58)	92.30(1.28)
Received Level @ 20000 Hertz (SD)	NA	NA	NA	NA	NA	NA	NA

Table A.14. Summary statistics of all Variables in relation to recordings with the boat-based hydrophone (CR55). The labels correspond to the sites where the recordings took place. (Continued).

CR55 Recordings						
Site	**P66b**	**P69**	**P75**	**P76Hyd**	**P79**	**P88**
Month	3	3	3	2	3	8
Dolphin presence	0	1	0	1	0	0
Depth	9.70	9.30	10.00	19.00	10.00	6.50
Latitude	8.73	8.79	8.59	8.80	8.95	8.83
Longitude	79.69	79.70	79.67	79.51	79.45	79.68
Temperature	25.00	24.60	28.30	25.00	28.30	29.19
Salinity	29.53	29.11	NA	29.64	NA	24.26
Dissolved Oxygen	47.00	44.67	NA	42.20	NA	41.28
Conductivity	6.70	6.80	NA	2.20	NA	4.30
Barometric Pressure	758.98	757.80	NA	757.90	NA	758.80
Precipitation	0.00	0.00	36.10	0.00	26.20	8.60
Wind Speed	24.50	18.50	24.10	13.00	14.00	18.53
Distance to coastline	5.70	6.60	6.10	13.00	6.60	3.30
Distance to buoys	25.50	22.00	6.80	10.50	10.30	18.50
Distance to anchorage	25.50	23.00	9.40	6.30	12.60	20.30
Received Level @ 20 Hertz (SD)	110.20(1.78)	110.5929195	100.38(4.69)	109.05(1.77)	102.37(0.04)	111.16(0.44)
Received Level @ 160 Hertz (SD)	112.92(1.77)	121.5223684	113.66(6.30)	112.32(1.79)	104.82(0.77)	114.27(0.48)
Received Level @ 400 Hertz (SD)	103.40(5.75)	116.1246265	117.52(4.36)	108.24(5.17)	104.04(2.57)	116.40(1.32)
Received Level @ 1000 Hertz (SD)	103.15(4.94)	110.1756383	114.15(3.82)	104.80(3.57)	103.56(1.47)	111.68(2.69)
Received Level @ 1600 Hertz (SD)	96.95(4.24)	104.5116286	107.30(2.92)	106.86(0.82)	105.23(0.12)	99.39(2.26)
Received Level @ 5000 Hertz (SD)	94.99(5.47)	100.7849234	104.01(4.00)	114.45(0.99)	95.57(0.44)	97.49(0.36)
Received Level @ 10000 Hertz (SD)	92.15(4.89)	98.23248989	103.04(5.10)	113.27(0.77)	95.20(0.51)	97.97(0.49)
Received Level @ 16000 Hertz (SD)	90.97(4.95)	98.09464926	101.28(4.77)	111.51(0.64)	93.84(0.26)	91.33(0.47)
Received Level @ 20000 Hertz (SD)	NA	NA	98.33(5.02)	95.51(7.83)	NA	NA

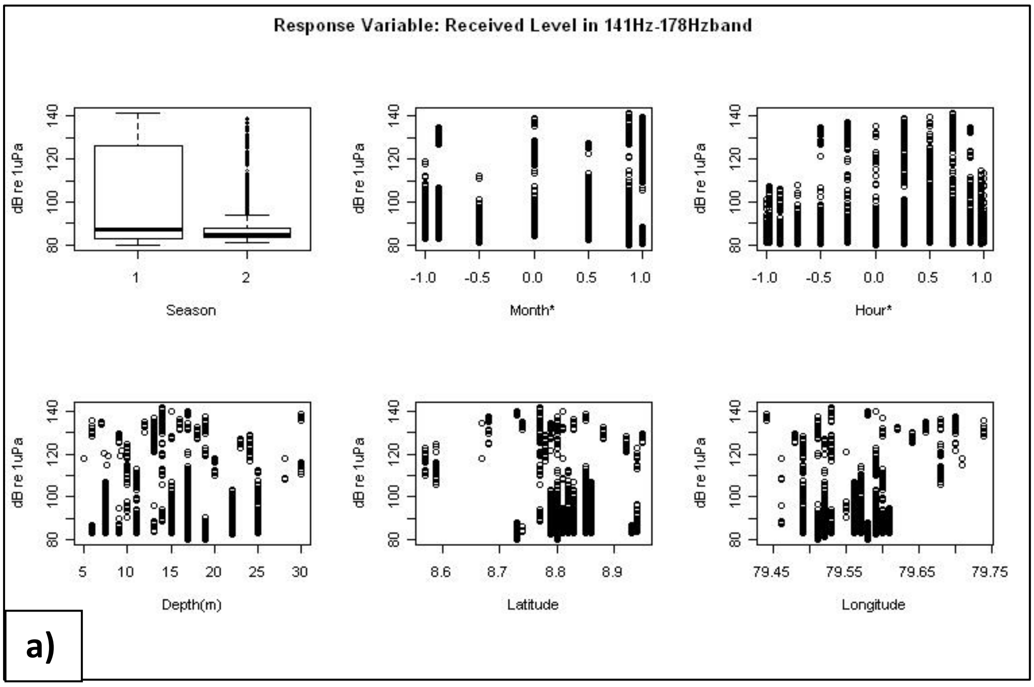
Table A.15a. Correlation Values between all Response and Predictor variables. Correlation is considered to be significant (>0.5,>-0.5).

	wh	presabs	fn	depth	mo	circmo	hrblk	circhrblck	season	temp	sal	do	press	prec	ws
wh	1.0	0.2811	0.0276	0.0173	-0.0366	0.0427	0.0005	-0.0118	-0.0446	-0.0479	0.0333	0.0848	0.0039	0.0223	-0.0161
presabs	0.2811	1.0	0.1015	-0.0017	-0.0617	0.0720	-0.0134	0.0252	0.0524	0.0687	0.0783	0.0131	0.0169	0.0607	-0.0009
fn	0.0276	0.1015	1.0	-0.1456	-0.0209	0.0542	-0.0384	0.0243	0.0580	0.0610	0.0431	-0.1934	0.0410	0.1158	-0.0064
depth	0.0173	-0.0017	-0.1456	1.0	0.0929	-0.1043	-0.0433	0.0120	-0.0867	-0.1667	0.0010	-0.0159	0.0501	-0.1363	0.2229
mo	-0.0366	-0.0617	-0.0209	0.0929	1.0	-0.9542	-0.0023	0.0019	0.5784	0.3496	-0.6418	-0.2584	0.0690	0.1092	0.0037
circmo	0.0427	0.0720	0.0542	-0.1043	-0.9542	1.0	0.0052	-0.0027	-0.4529	-0.2798	0.6966	0.2209	-0.0699	-0.1081	-0.0334
hrblk	0.0005	-0.0134	-0.0384	-0.0433	-0.0023	0.0052	1.0	-0.7827	0.0039	0.0195	0.0088	-0.0311	0.0089	-0.0324	-0.0801
circhrblck	-0.0118	0.0252	0.0243	0.0120	0.0019	-0.0027	-0.7827	1.0	-0.0061	-0.0314	-0.0155	0.0641	-0.0203	0.0203	0.0678
season	-0.0446	0.0524	0.0580	-0.0867	0.5784	-0.4529	0.0039	-0.0061	1.0	0.9050	-0.2384	-0.4308	0.1221	0.1534	0.0106
f20Hz	0.1057	0.0284	-0.2048	0.0345	-0.2312	0.1666	-0.0659	0.0968	-0.4189	-0.4211	0.0705	0.8841	-0.0636	-0.0535	0.0604
f160Hz	0.1065	0.0236	-0.2036	0.0330	-0.2346	0.1664	-0.0636	0.0901	-0.4120	-0.4043	0.0451	0.8586	-0.1036	-0.0597	0.0686
f400Hz	0.0725	0.0298	-0.1298	0.0584	-0.3499	0.2635	-0.0208	0.0418	-0.4638	-0.4149	0.0766	0.6773	-0.1609	-0.0791	0.0432
f1000Hz	0.0832	0.0267	-0.1230	0.1221	-0.3324	0.2696	-0.0173	0.0604	-0.5254	-0.5159	0.1020	0.6950	-0.1650	-0.0739	0.0238
f1600Hz	0.0605	0.0354	-0.1329	-0.0052	-0.3560	0.2502	0.0032	0.0622	-0.4858	-0.4534	0.0785	0.7079	-0.1508	-0.0541	0.0265
f5000Hz	0.0149	-0.0120	-0.0870	-0.2211	-0.2484	0.1152	-0.0179	0.0604	-0.4198	-0.3878	-0.0192	0.6739	-0.1100	-0.0078	-0.0345
f10000Hz	0.0198	-0.0111	-0.1115	-0.1767	-0.2246	0.1012	-0.0279	0.0604	-0.4053	-0.3829	-0.0330	0.7191	-0.1222	-0.0158	-0.0387
f16000Hz	0.0099	-0.0464	-0.1300	-0.1603	-0.2410	0.1231	-0.0227	0.0482	-0.4262	-0.4085	-0.0119	0.6735	-0.1251	-0.0291	-0.0197
f20000Hz	-0.0936	-0.0197	0.1976	-0.1140	0.1738	-0.1727	0.0422	-0.0816	0.3431	0.4285	-0.1882	-0.8839	-0.0918	0.0729	-0.1669
lat	-0.0602	-0.0155	0.1365	-0.4310	0.4275	-0.2941	0.0346	-0.0154	0.5271	0.4351	-0.0608	-0.2174	0.2103	0.1725	-0.2270
lon	0.0128	0.0188	0.0433	-0.0945	0.0632	0.0161	0.0078	-0.0157	0.1062	0.0990	0.0022	-0.1502	-0.0196	0.0211	0.0248
temp	-0.0479	0.0687	0.0610	-0.1667	0.3496	-0.2798	0.0195	-0.0314	0.9050	1.0	-0.2295	-0.4700	-0.0183	0.1409	-0.0697
sal	0.0333	0.0783	0.0431	0.0010	-0.6418	0.6966	0.0088	-0.0155	-0.2384	-0.2295	1.0	0.1954	0.6086	-0.0782	0.1143
do	0.0848	0.0131	-0.1934	-0.0159	-0.2584	0.2209	-0.0311	0.0641	-0.4308	-0.4700	0.1954	1.0	0.0488	-0.0696	0.1159
press	0.0039	0.0169	0.0410	0.0501	0.0690	-0.0699	0.0089	-0.0203	0.1221	-0.0183	0.6086	0.0488	1.0	0.0216	0.1907
prec	0.0223	0.0607	0.1158	-0.1363	0.1092	-0.1081	-0.0324	0.0203	0.1534	0.1409	-0.0782	-0.0696	0.0216	1.0	-0.0331
ws	-0.0161	-0.0009	-0.0064	0.2229	0.0037	-0.0334	-0.0801	0.0678	0.0106	-0.0697	0.1143	0.1159	0.1907	-0.0331	1.0
dcoast	-0.0274	-0.0414	-0.1415	0.6461	-0.1963	0.0584	-0.0532	0.0335	-0.4891	-0.4736	0.0316	0.0868	-0.0142	-0.1678	0.2951
dbuoy	0.0862	-0.0178	-0.1191	0.3312	-0.3909	0.3294	-0.0285	0.0180	-0.6154	-0.6461	0.2886	0.4629	0.0423	-0.1399	0.2698
danch	0.0812	-0.0432	-0.0017	-0.1367	-0.3506	0.3973	0.0066	0.0016	-0.4591	-0.5272	0.3212	0.5033	0.0063	-0.0345	0.1186

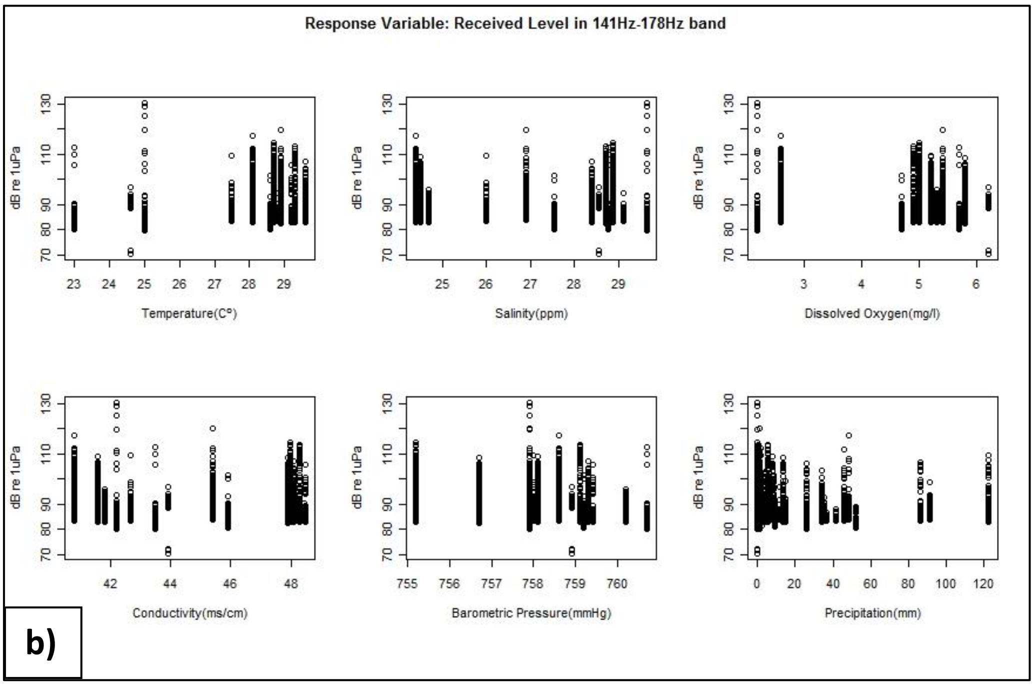
Table A.15b. Correlation Values between all Response and Predictor variables. Correlation is considered to be significant (>0.5,>-0.5).

	f20Hz	f160Hz	f400Hz	f1000Hz	f1600Hz	f5000Hz	f10000Hz	f16000Hz	f20000Hz	lat	lon	dcoast	dbuoy	danch
wh	0.1057	0.1065	0.0725	0.0832	0.0605	0.0149	0.0198	0.0099	-0.0936	-0.0602	0.0128	-0.0274	0.0862	0.0812
presabs	0.0284	0.0236	0.0298	0.0267	0.0354	-0.0120	-0.0111	-0.0464	-0.0197	-0.0155	0.0188	-0.0414	-0.0178	-0.0432
fn	-0.2048	-0.2036	-0.1298	-0.1230	-0.1329	-0.0870	-0.1115	-0.1300	0.1976	0.1365	0.0433	-0.1415	-0.1191	-0.0017
depth	0.0345	0.0330	0.0584	0.1221	-0.0052	-0.2211	-0.1767	-0.1603	-0.1140	-0.4310	-0.0945	0.6461	0.3312	-0.1367
mo	-0.2312	-0.2346	-0.3499	-0.3324	-0.3560	-0.2484	-0.2246	-0.2410	0.1738	0.4275	0.0632	-0.1963	-0.3909	-0.3506
circmo	0.1666	0.1664	0.2635	0.2696	0.2502	0.1152	0.1012	0.1231	-0.1727	-0.2941	0.0161	0.0584	0.3294	0.3973
hrblk	-0.0659	-0.0636	-0.0208	-0.0173	0.0032	-0.0179	-0.0279	-0.0227	0.0422	0.0346	0.0078	-0.0532	-0.0285	0.0066
circhrblck	0.0968	0.0901	0.0418	0.0604	0.0622	0.0604	0.0604	0.0482	-0.0816	-0.0154	-0.0157	0.0335	0.0180	0.0016
season	-0.4189	-0.4120	-0.4638	-0.5254	-0.4858	-0.4198	-0.4053	-0.4262	0.3431	0.5271	0.1062	-0.4891	-0.6154	-0.4591
f20Hz	1.0	0.9579	0.7251	0.7140	0.7180	0.6477	0.6882	0.6679	-0.7699	-0.2293	-0.1462	0.1274	0.3915	0.3628
f160Hz	0.9579	1.0	0.8174	0.7603	0.7470	0.6654	0.7037	0.6961	-0.7312	-0.2593	-0.1372	0.1369	0.3971	0.3624
f400Hz	0.7251	0.8174	1.0	0.8749	0.8190	0.6721	0.6746	0.6411	-0.5484	-0.4012	-0.0885	0.2323	0.4328	0.3558
f1000Hz	0.7140	0.7603	0.8749	1.0	0.8964	0.6362	0.6323	0.5957	-0.5908	-0.3608	-0.0928	0.2547	0.4526	0.3849
f1600Hz	0.7180	0.7470	0.8190	0.8964	1.0	0.8301	0.8088	0.7601	-0.5306	-0.3972	-0.1176	0.2730	0.4111	0.2998
f5000Hz	0.6477	0.6654	0.6721	0.6362	0.8301	1.0	0.9746	0.9000	-0.4182	-0.3276	-0.1506	0.1681	0.3383	0.3042
f10000Hz	0.6882	0.7037	0.6746	0.6323	0.8088	0.9746	1.0	0.9256	-0.4594	-0.3354	-0.1581	0.1761	0.3607	0.3248
f16000Hz	0.6679	0.6961	0.6411	0.5957	0.7601	0.9000	0.9256	1.0	-0.4242	-0.3415	-0.1558	0.1672	0.3769	0.3424
f20000Hz	-0.7699	-0.7312	-0.5484	-0.5908	-0.5306	-0.4182	-0.4594	-0.4242	1.0	0.1575	0.1583	-0.0583	-0.4388	-0.4818
lat	-0.2293	-0.2593	-0.4012	-0.3608	-0.3972	-0.3276	-0.3354	-0.3415	0.1575	1.0	-0.0069	-0.7816	-0.8094	-0.3701
lon	-0.1462	-0.1372	-0.0885	-0.0928	-0.1176	-0.1506	-0.1581	-0.1558	0.1583	-0.0069	1.0	-0.0579	0.0471	0.1050
temp	-0.4211	-0.4043	-0.4149	-0.5159	-0.4534	-0.3878	-0.3829	-0.4085	0.4285	0.4351	0.0990	-0.4736	-0.6461	-0.5272
sal	0.0705	0.0451	0.0766	0.1020	0.0785	-0.0192	-0.0330	-0.0119	-0.1882	-0.0608	0.0022	0.0316	0.2886	0.3212
do	0.8841	0.8586	0.6773	0.6950	0.7079	0.6739	0.7191	0.6735	-0.8839	-0.2174	-0.1502	0.0868	0.4629	0.5033
press	-0.0535	-0.1036	-0.1609	-0.1650	-0.1508	-0.1100	-0.1222	-0.1251	-0.0918	0.2103	-0.0196	-0.0142	0.0423	0.0063
prec	0.0604	-0.0597	-0.0791	-0.0739	-0.0541	-0.0078	-0.0158	-0.0291	0.0729	0.1725	0.0211	-0.1678	-0.1399	-0.0345
ws	0.1274	0.0686	0.0432	0.0238	0.0265	-0.0345	-0.0387	-0.0197	-0.1669	-0.2270	0.0248	0.2951	0.2698	0.1186
dcoast	0.3915	0.1369	0.2323	0.2547	0.2730	0.1681	0.1761	0.1672	-0.0583	-0.7816	-0.0579	1.0	0.5988	0.0080
dbuoy	0.3628	0.3971	0.4328	0.4526	0.4111	0.3383	0.3607	0.3769	-0.4388	-0.8094	0.0471	0.5988	1.0	0.7658
danch		0.3624	0.3558	0.3849	0.2998	0.3042	0.3248	0.3424	-0.4818	-0.3701	0.1050	0.0080	0.7658	1.0

Fig. A.5. Scatterplots showing the correlation between the response variable Received Level (dB re 1uPa) for 141Hz-178Hz band against a) Season (Dry=1, Wet=2), Month (circular month= sine of month as a proportion of a year), Hour (circular hour=sine of hour as a proportion of a year), Depth (m), Latitude and Longitude; b)Temperature (Cº), Salinity (ppm), Dissolved Oxygen (mg/l), Conductivity (mg/cm), Barometric pressure (mmHg) and Precipitation (mm), and c) Wind Speed (km/h), Distance to coast (km), Distance to buoy (km) and Distance to anchorage (km).



a)



b)

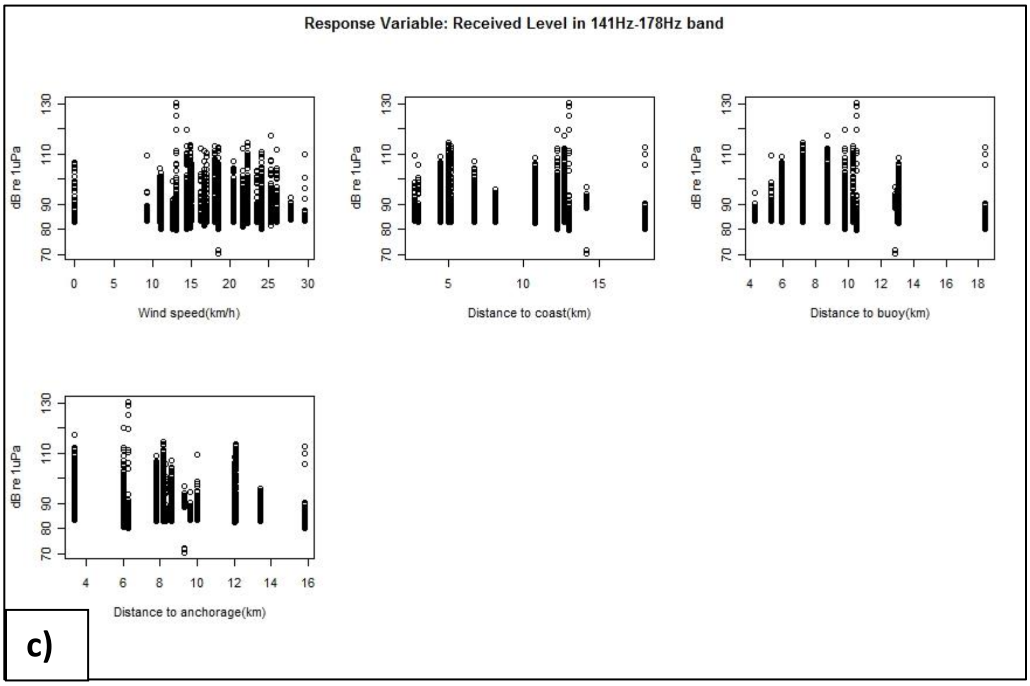
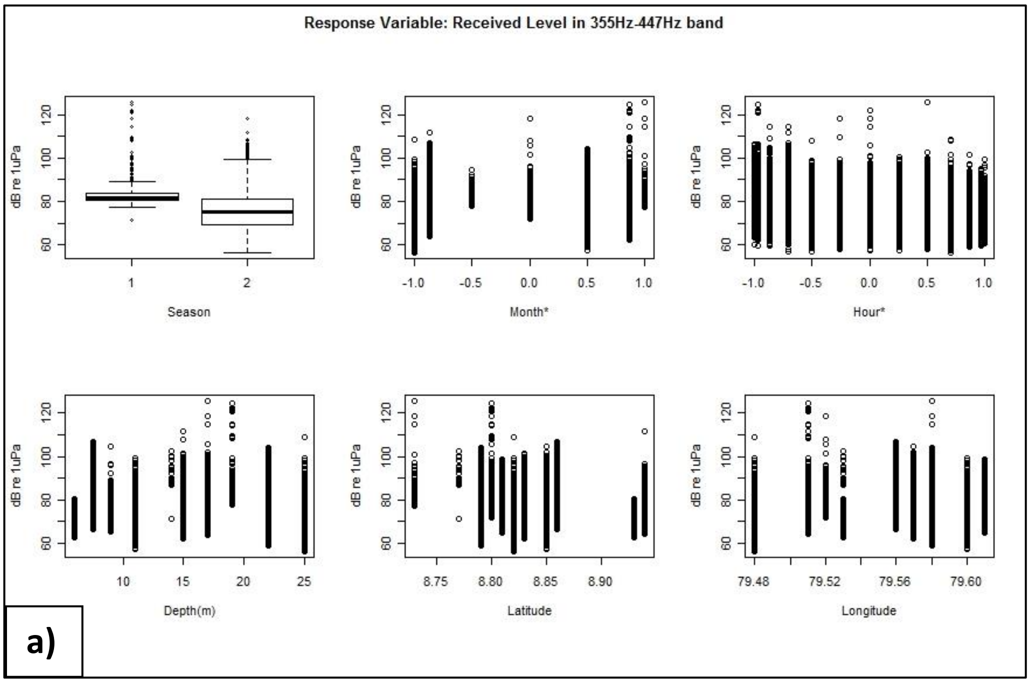
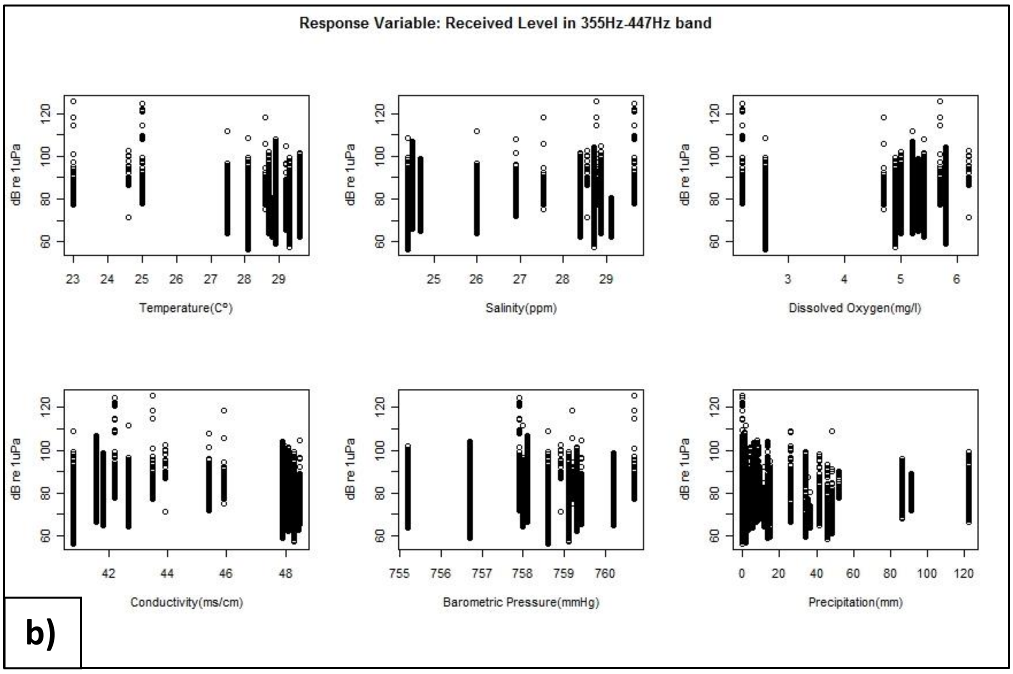


Fig. A.6. Scatterplots showing the correlation between the response variable Received Level (dB re 1uPa) for 355Hz-447Hz band against a) Season (Dry=1, Wet=2), Month (circular month= sine of month as a proportion of a year), Hour (circular hour=sine of hour as a proportion of a year), Depth (m), Latitude and Longitude, b) Temperature (Cº), Salinity (ppm), Dissolved Oxygen (mg/l), Conductivity (mg/cm), Barometric pressure (mmHg) and Precipitation (mm), and c) Wind Speed (km/h), Distance to coast (km), Distance to buoy (km) and Distance to anchorage (km).




Response Variable: Received Level in 355Hz-447Hz band
dB re 1uPa
Temperature(C°)
Salinity(ppm)
Dissolved Oxygen(mg/l)
Conductivity(ms/cm)
Barometric Pressure(mmHg)
Precipitation(mm)
b)

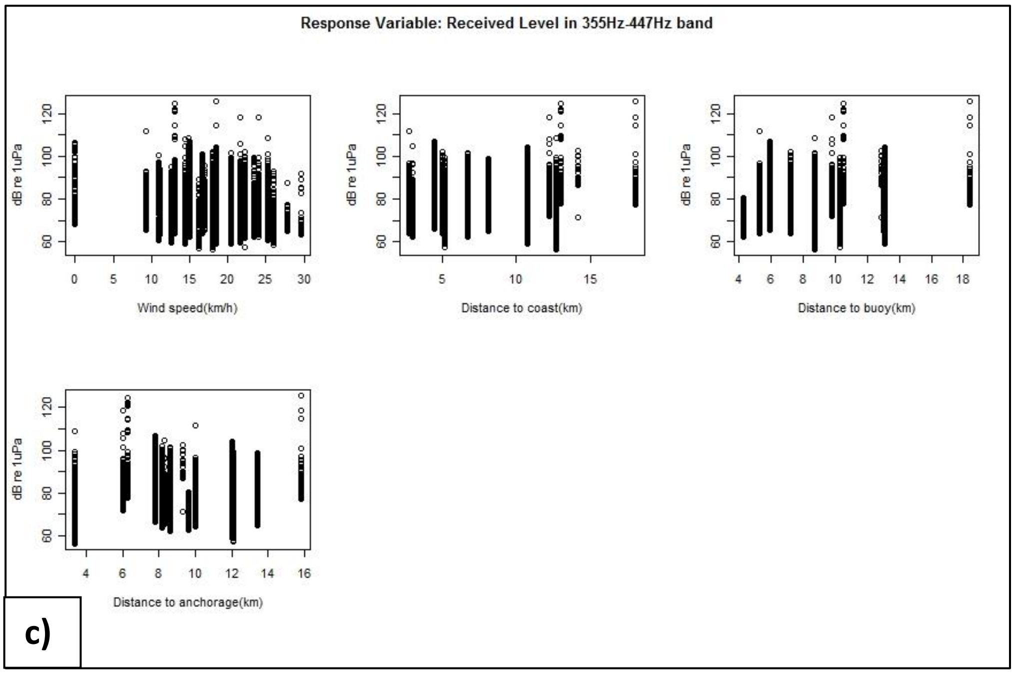
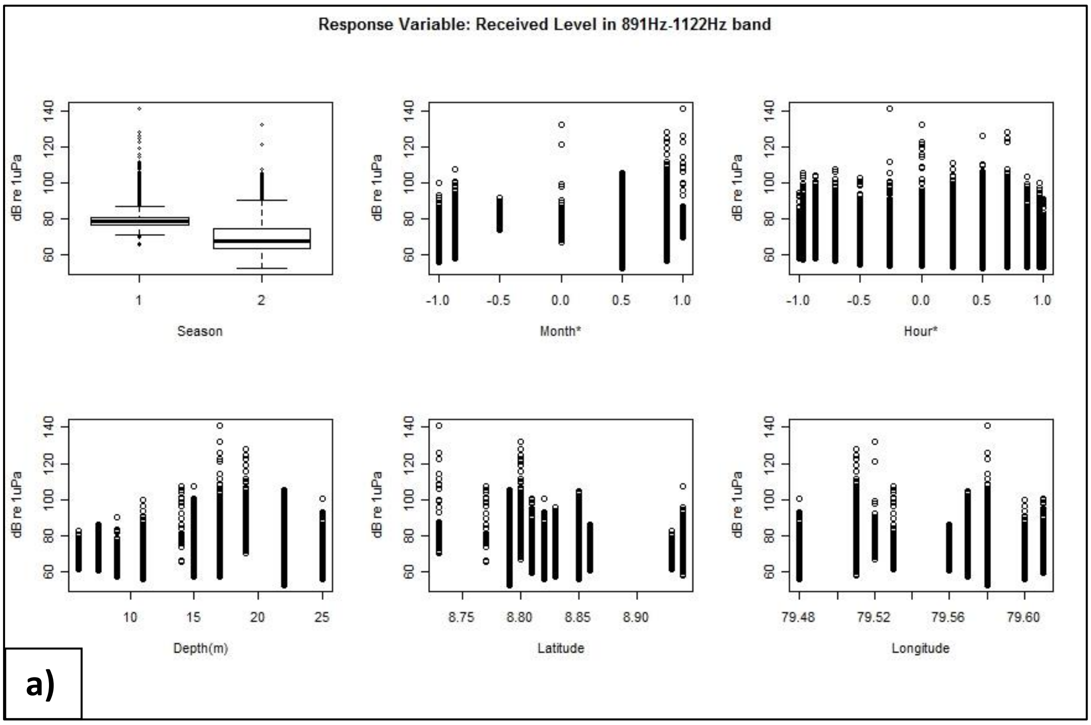
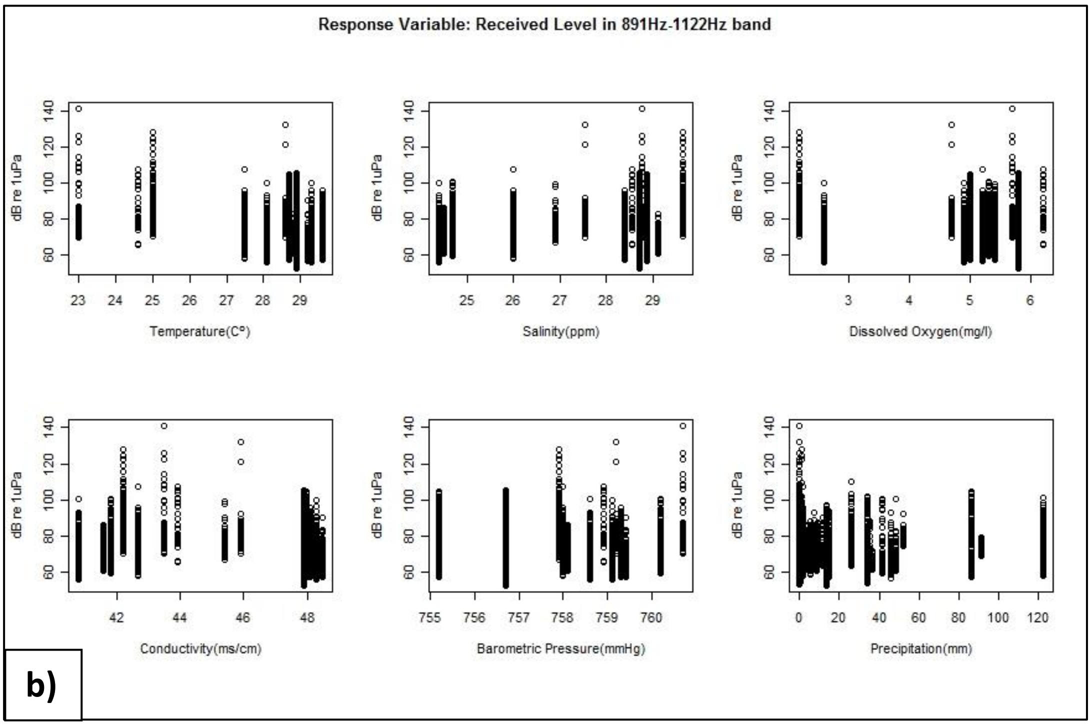

Response Variable: Received Level in 355Hz-447Hz band
dB re 1uPa
Wind speed(km/h)
Distance to coast(km)
Distance to buoy(km)
Distance to anchorage(km)
c)

Fig. A.7. Scatterplots showing the correlation between the response variable Received Level (dB re 1uPa) for 891Hz-1122Hz band against a) Season (Dry=1, Wet=2), Month (circular month= sine of month as a proportion of a year), Hour (circular hour=sine of hour as a proportion of a year), Depth (m), Latitude and Longitude, b) Temperature (Cº), Salinity (ppm), Dissolved Oxygen (mg/l), Conductivity (mg/cm), Barometric pressure (mmHg) and Precipitation (mm), c) Wind Speed (km/h), Distance to coast (km), Distance to buoy (km) and Distance to anchorage (km).





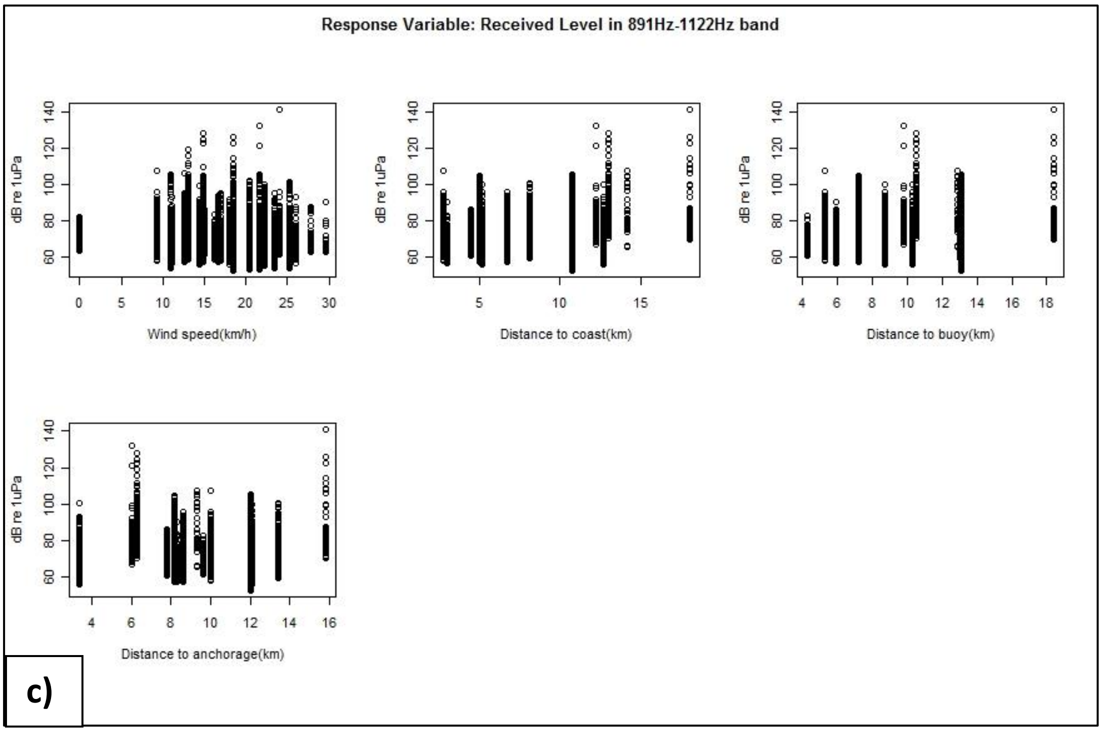
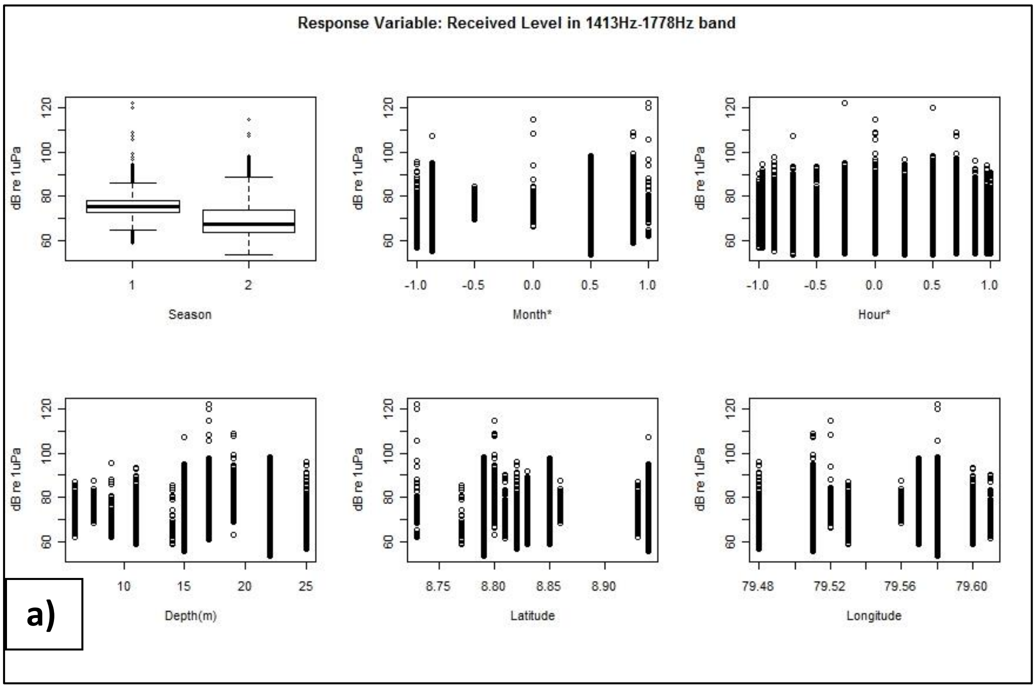
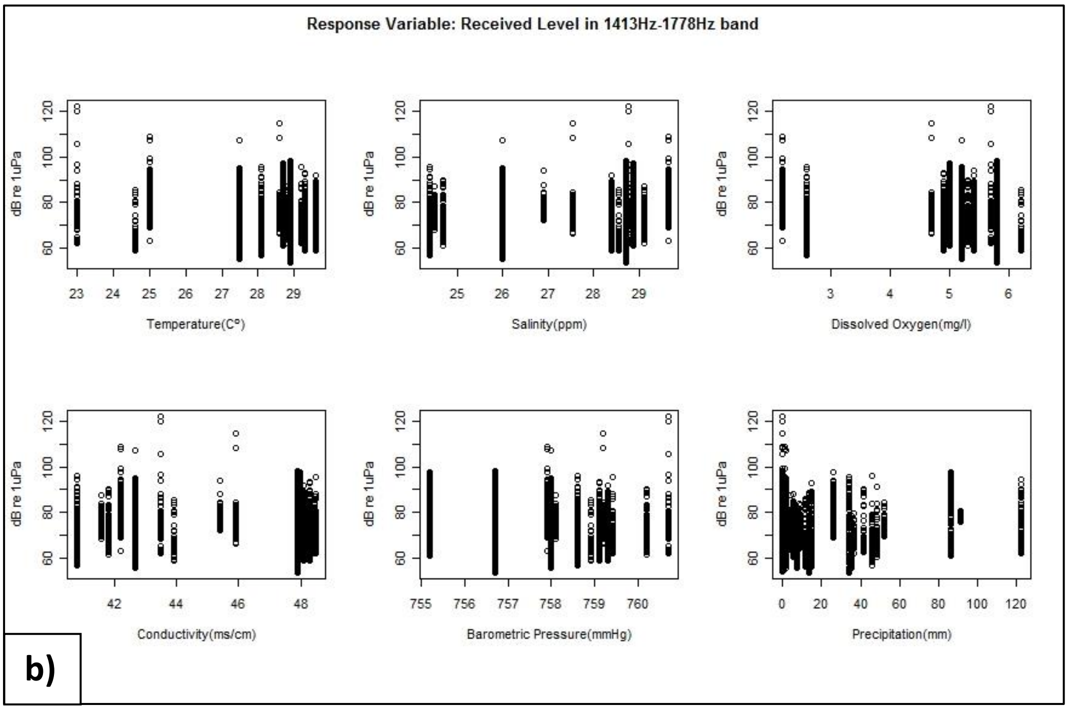
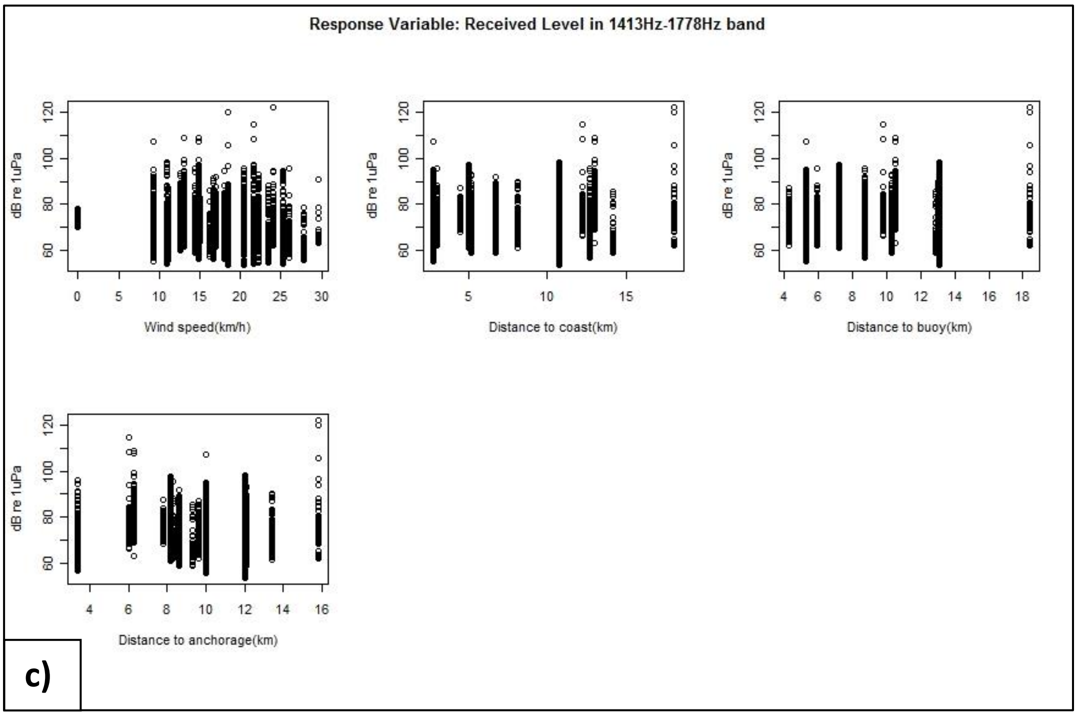


Fig. A.8. Scatterplots showing the correlation between the response variable Received Level (dB re 1uPa) for 1413Hz-1778Hz band against a) Season (Dry=1, Wet=2), Month (circular month= sine of month as a proportion of a year), Hour (circular hour=sine of hour as a proportion of a year), Depth (m), Latitude and Longitude, b) Temperature (Cº), Salinity (ppm), Dissolved Oxygen (mg/l), Conductivity (mg/cm), Barometric pressure (mmHg) and Precipitation (mm), c) Wind Speed (km/h), Distance to coast (km), Distance to buoy (km) and Distance to anchorage (km).



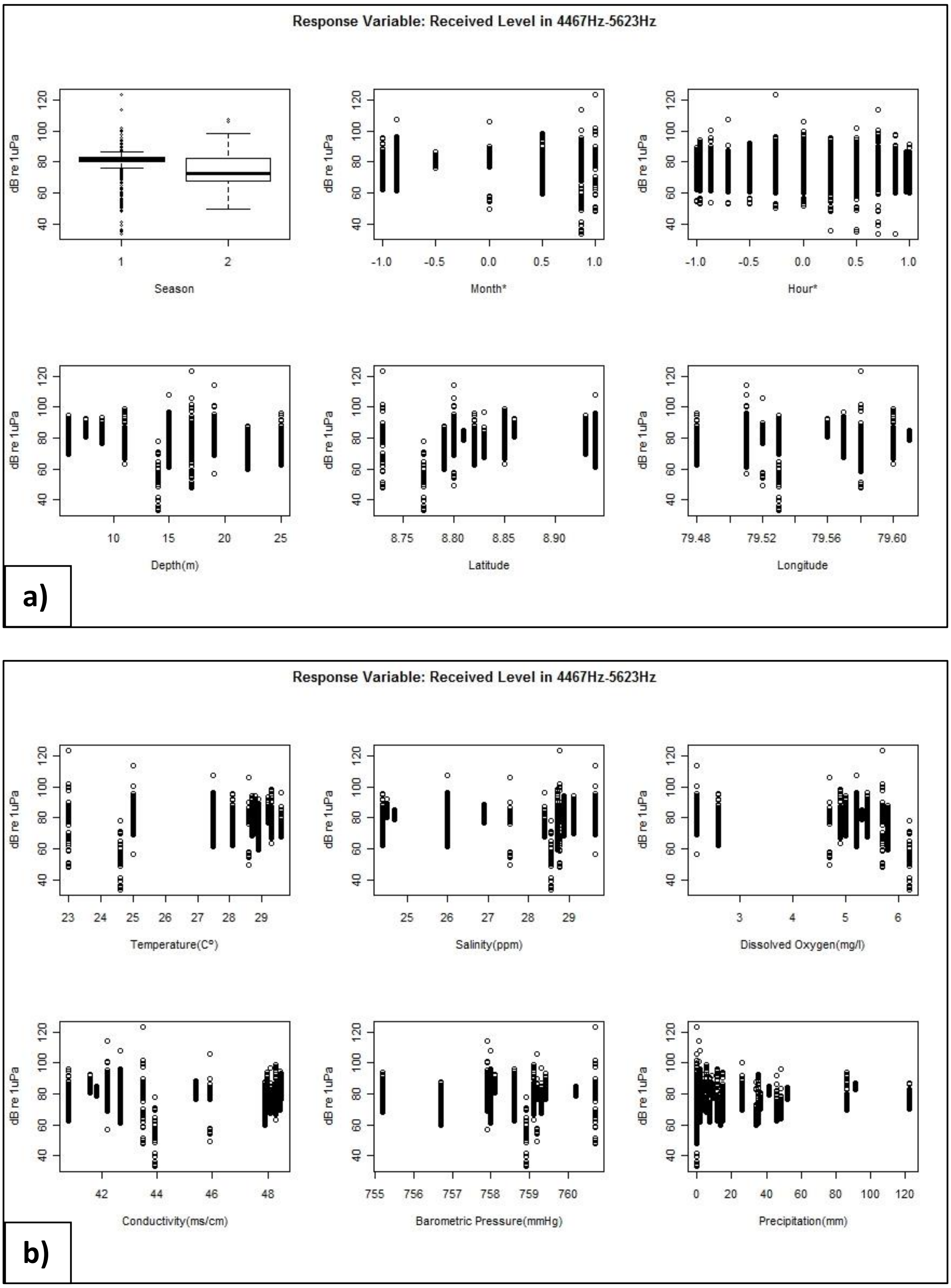

Response Variable: Received Level in 1413Hz-1778Hz band
dB re 1uPa
60
80
100
120
23 24 25 26 27 28 29
Temperature(C°)
25 26 27 28 29
Salinity(ppm)
3 4 5 6
Dissolved Oxygen(mg/l)
42 44 46 48
Conductivity(ms/cm)
755 756 757 758 759 760
Barometric Pressure(mmHg)
0 20 40 60 80 100 120
Precipitation(mm)

b)


Response Variable: Received Level in 1413Hz-1778Hz band
dB re 1uPa
60
80
100
120
0 5 10 15 20 25 30
Wind speed(km/h)
5 10 15
Distance to coast(km)
4 6 8 10 12 14 16 18
Distance to buoy(km)
4 6 8 10 12 14 16
Distance to anchorage(km)

c)

Fig. A.9. Scatterplots showing the correlation between the response variable Received Level (dB re 1uPa) for 4467Hz-5623Hz band against a) Season (Dry=1, Wet=2), Month (circular month= sine of month as a proportion of a year), Hour (circular hour=sine of hour as a proportion of a year), Depth (m), Latitude and Longitude, b) Temperature (Cº), Salinity (ppm), Dissolved Oxygen (mg/l), Conductivity (mg/cm), Barometric pressure (mmHg) and Precipitation (mm), c) Wind Speed (km/h), Distance to coast (km), Distance to buoy (km) and Distance to anchorage (km).



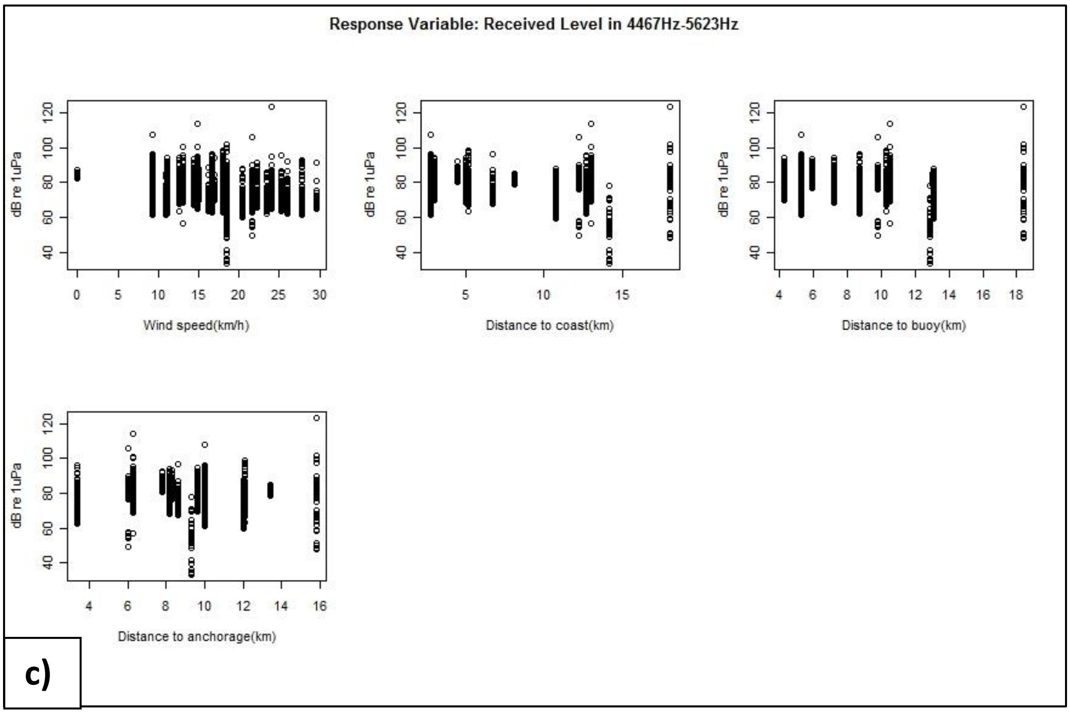
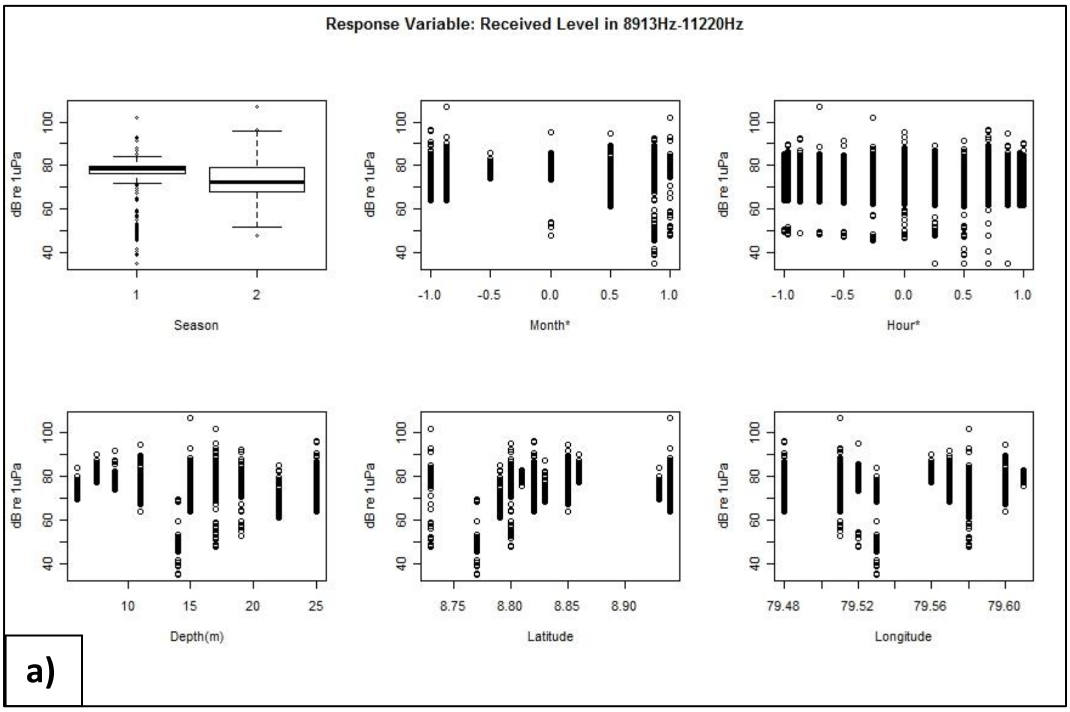
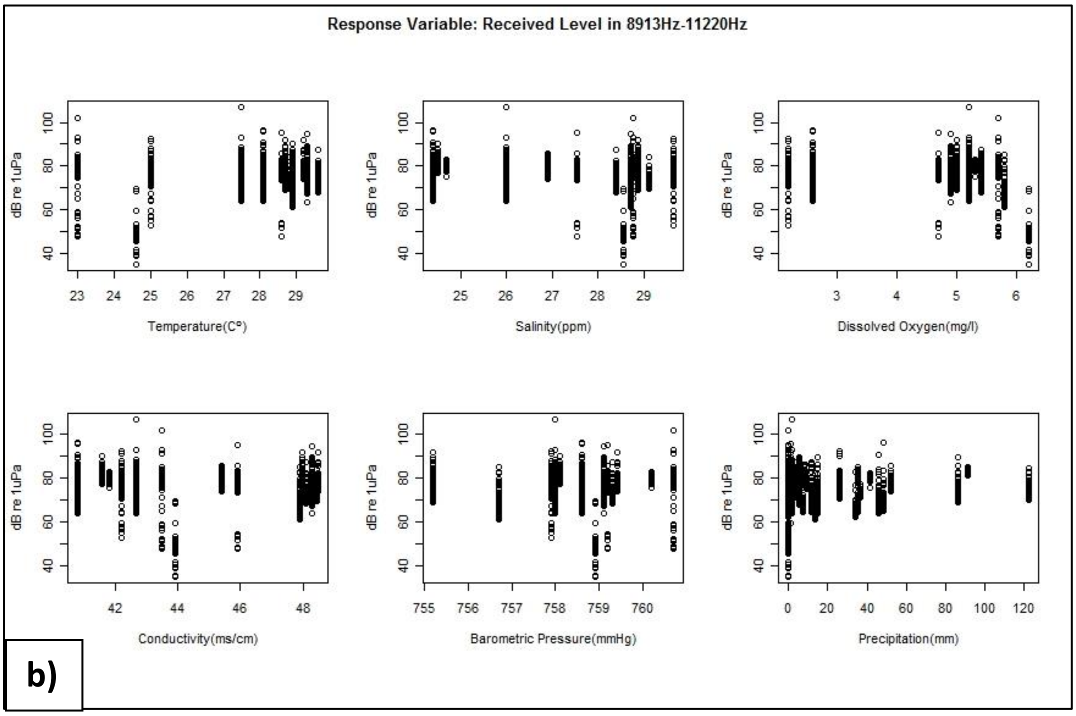
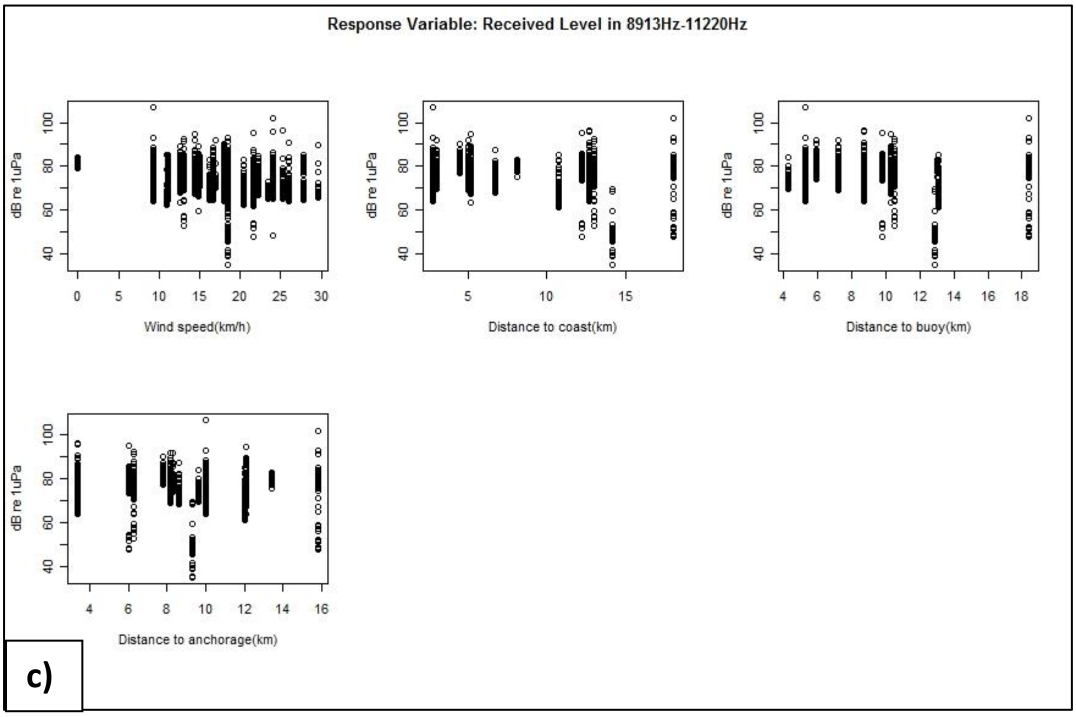


Fig. A.10. Scatterplots showing the correlation between the response variable Received Level (dB re 1uPa) for 8913Hz-11220Hz band against a) Season (Dry=1, Wet=2), Month (circular month= sine of month as a proportion of a year), Hour (circular hour=sine of hour as a proportion of a year), Depth (m), Latitude and Longitude, b) Temperature (Cº), Salinity (ppm), Dissolved Oxygen (mg/l), Conductivity (mg/cm), Barometric pressure (mmHg) and Precipitation (mm), c) Wind Speed (km/h), Distance to coast (km), Distance to buoy (km) and Distance to anchorage (km).



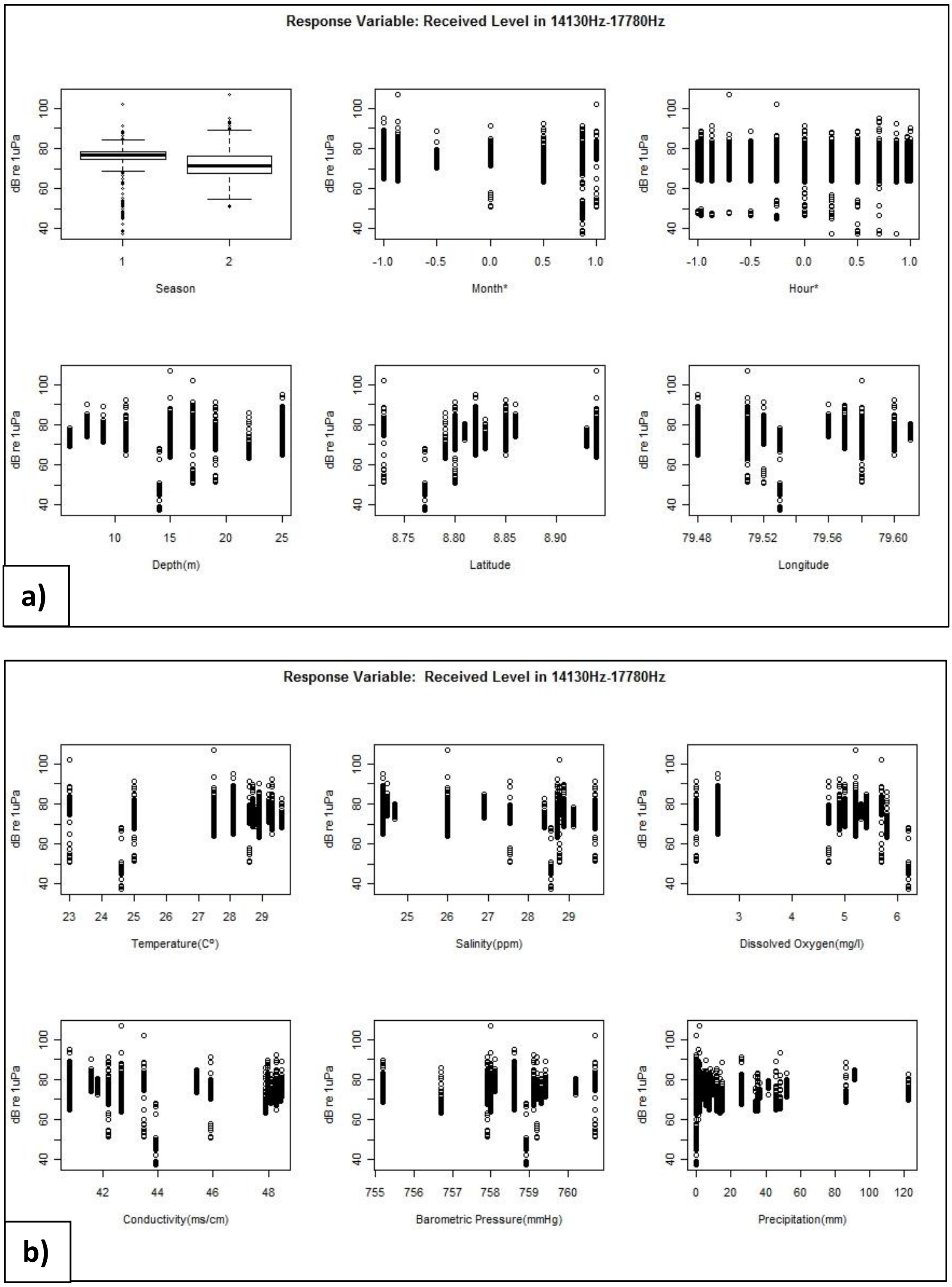

Response Variable: Received Level in 8913Hz-11220Hz
dB re 1uPa
40
60
80
100
Temperature(C°)
23
24
25
26
27
28
29
Salinity(ppm)
25
26
27
28
29
Dissolved Oxygen(mg/l)
3
4
5
6
Conductivity(ms/cm)
42
44
46
48
Barometric Pressure(mmHg)
755
756
757
758
759
760
Precipitation(mm)
0
20
40
60
80
100
120

b)


Response Variable: Received Level in 8913Hz-11220Hz
dB re 1uPa
40
60
80
100
Wind speed(km/h)
0
5
10
15
20
25
30
Distance to coast(km)
5
10
15
Distance to buoy(km)
4
6
8
10
12
14
16
18
Distance to anchorage(km)
4
6
8
10
12
14
16

c)

Fig. A.11. Scatterplots showing the correlation between the response variable Received Level (dB re 1uPa) for 14130Hz-17780Hz band against a) Season (Dry=1, Wet=2), Month (circular month= sine of month as a proportion of a year), Hour (circular hour=sine of hour as a proportion of a year), Depth (m), Latitude and Longitude, b) Temperature (Cº), Salinity (ppm), Dissolved Oxygen (mg/l), Conductivity (mg/cm), Barometric pressure (mmHg) and Precipitation (mm), c) Wind Speed (km/h), Distance to coast (km), Distance to buoy (km) and Distance to anchorage (km).



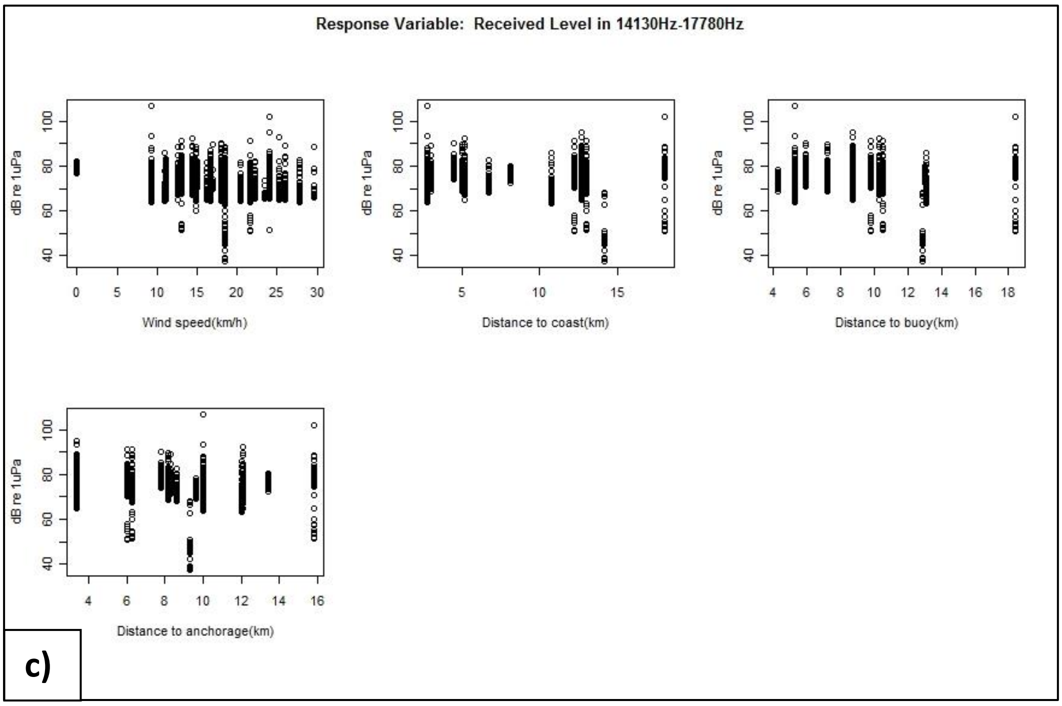
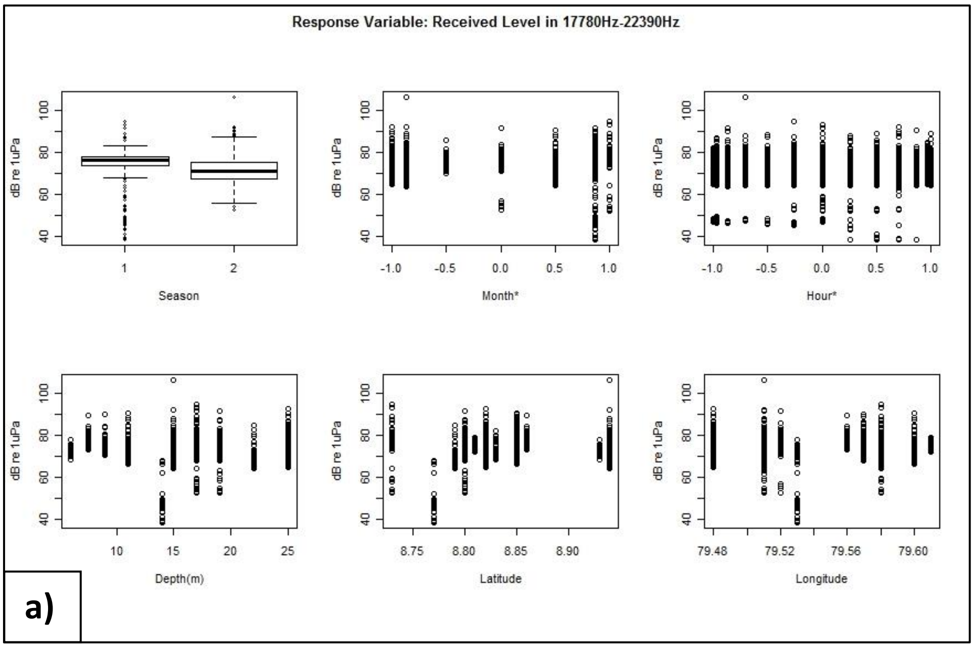
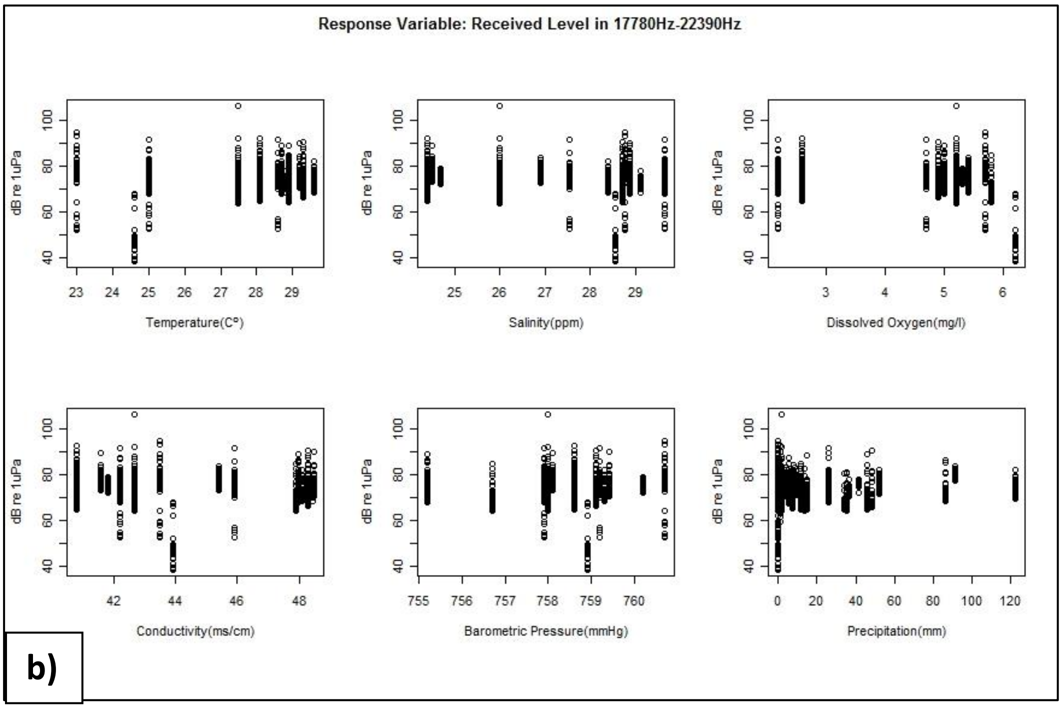
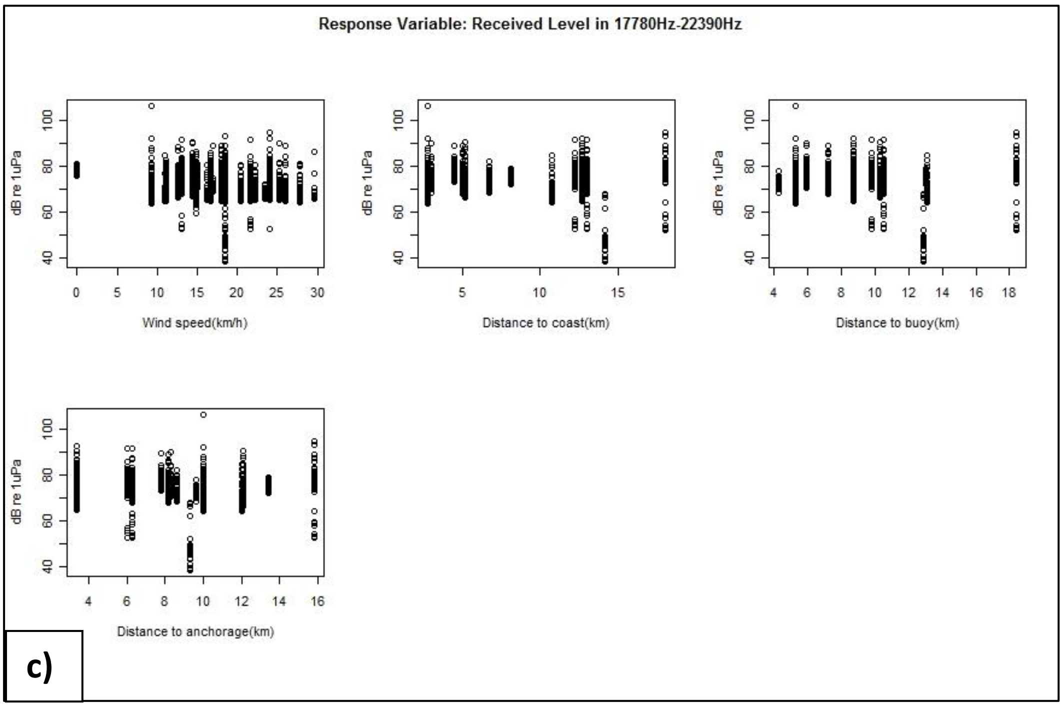


Fig. A.12. Scatterplots showing the correlation between the response variable Received Level (dB re 1uPa) for 17780Hz-22390Hz band against a) Season (Dry=1, Wet=2), Month (circular month= sine of month as a proportion of a year), Hour (circular hour=sine of hour as a proportion of a year), Depth (m), Latitude and Longitude, b) Temperature (Cº), Salinity (ppm), Dissolved Oxygen (mg/l), Conductivity (mg/cm), Barometric pressure (mmHg) and Precipitation (mm), c) Wind Speed (km/h), Distance to coast (km), Distance to buoy (km) and Distance to anchorage (km).




Response Variable: Received Level in 17780Hz-22390Hz
dB re 1uPa
40
60
80
100
23 24 25 26 27 28 29
Temperature(C°)
25 26 27 28 29
Salinity(ppm)
3 4 5 6
Dissolved Oxygen(mg/l)
42 44 46 48
Conductivity(ms/cm)
755 756 757 758 759 760
Barometric Pressure(mmHg)
0 20 40 60 80 100 120
Precipitation(mm)

b)


Response Variable: Received Level in 17780Hz-22390Hz
dB re 1uPa
40
60
80
100
0 5 10 15 20 25 30
Wind speed(km/h)
5 10 15
Distance to coast(km)
4 6 8 10 12 14 16 18
Distance to buoy(km)
4 6 8 10 12 14 16
Distance to anchorage(km)

c)

Table A.16 Mean whistle quantitative parameters obtained with boat-based hydrophone (CR55). Values correspond to each sampled site where whistles were detected. Cells with no data in the cell correspond to data from a site that only provided one whistle. In addition, several sites only provided two readings.

Site	Month	Duration (ms)	Min Duration (ms)	Max Duration (ms)	Min Freq (kHz)	Max Freq (kHz)	Ranges	Mean of min and max Freq (kHz)	Total mean Freq per site (kHz)
P308	June	69.82	-------	-------	18.00	18.43	0.43	18.22	18.22
P246	August	64.00	-------	-------	14.98	15.24	0.26	15.11	15.11
P295B	Sept	188.59	128.00	360.72	8.74	10.98	2.24	9.86	9.97
P306	Sept	183.37	104.54	477.00	4.52	10.85	6.33	7.68	9.57
P296	Nov.	203.64	98.17	407.32	7.70	10.89	3.19	9.34	9.60
P244	Dec.	193.94	151.27	221.09	7.96	10.44	2.48	9.20	10.31
P266	January	71.82	-------	-------	11.37	17.49	6.12	14.42	14.42
P245	January	79.72	-------	-------	21.73	21.97	0.24	21.87	21.87
P224	February	83.40	64.00	104.72	10.42	19.46	9.04	14.94	14.85
P204	February	90.18	72.18	110.55	6.03	10.85	4.82	8.44	8.44
P103	February	76.65	-------	-------	3.02	4.56	1.54	3.80	3.80
P120	February	91.12	-------	-------	5.19	5.51	0.32	5.34	5.34
P138	February	76.53	75.63	104.72	3.01	4.90	1.89	3.96	4.02
P172	February	72.72	69.81	75.63	3.61	21.80	18.19	12.70	12.70
P76	February	108.05	93.09	131.28	3.10	21.96	18.86	12.53	12.90
N80	March	97.43	-------	-------	3.01	3.53	0.52	3.27	3.27
N83	March	92.84	85.14	100.54	3.70	8.87	5.17	6.28	6.60
P85	March	66.90	58.24	74.92	3.01	12.74	9.73	7.88	12.49
P69	March	71.78	75.66	67.89	3.53	13.60	10.07	8.57	8.65
P30	March	69.70	63.77	75.63	3.27	6.80	3.53	5.03	4.85
P45	March	96.99	93.24	101.41	4.04	21.53	17.49	17.80	11.55
P62	March	70.71	63.24	93.09	3.01	17.74	14.73	10.38	4.68
P63	March	90.18	62.89	116.18	3.27	15.50	12.23	9.38	9.45
P64	March	151.15	75.63	1006.55	3.01	21.96	18.95	12.49	10.32
P66	March	66.90	-------	-------	3.10	8.09	4.99	5.60	5.74
N088	March	110.60	-------	-------	4.82	5.00	0.18	4.91	2.58
N090	March	99.78	-------	-------	16.88	17.05	0.17	16.96	8.61
P66	March	122.18	-------	-------	16.71	18.95	2.24	17.83	8.70
MEAN		***102.16***	***84.38***	***213.48***	***7.16***	***13.45***	***6.28***	***10.5***	***9.59***
SD		***42.22***	***25.18***	***240.62***	***5.57***	***6.12***	***6.34***	***5.1***	***4.66***
SE		***7.98***	***6.1***	***58.35***	***1.05***	***1.15***	***1.19***	***0.96***	***0.88***
C.I.		***85.79-118.54***	***71.43-97.33***	***89.76-337.20***	***5.00-9.33***	***11.07-15.82***	***3.82-8.74***	***8.51-12.47***	***7.78-11.40***
C.V.		***41.33%***	***29.85%***	***112.00%***	***77.80%***	***45.53%***	***101.00%***	***48.66%***	***48.59%***