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Passive acoustic monitoring of Antarctic blue and fin whales off the South African west coast

By

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Declaration

I, Senyalo Ishmail Letsheleha, declare that the contents of this dissertation/thesis represent my own unaided work, and that the dissertation/thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions and not necessarily those of the Cape Peninsula University of Technology.

26 November 2020

Signed **Date**

Abstract

Antarctic blue and fin whales were assumed to be common migratory whale species prior to being drastically reduced to almost extinction in the Southern Hemisphere by industrial whaling between 1904, and the mid-1970s. Following the end of commercial whaling some four decades ago, still little is known of their distribution, migrations, current population levels and post-whaling population recoveries. Both of these whale species emit low-frequency, high-intensity calls which are thought to be used for feeding and communication during mating. The development of Passive Acoustic Monitoring (PAM) systems has assisted researchers across the globe to understand the distribution and seasonal abundance of different whale species through the detection of calls from these whales.

Understanding the acoustic ecology of Antarctic blue and fin whales might improve the conservation and management strategies of these highly depleted species. Seasonal acoustic occurrence and behaviour of Antarctic blue and fin whales off the South African west coast were determined using bioacoustic data collected through two autonomous acoustic recorders (AARs) between December 2015 and January 2017. Blue whale Z-calls were detected year-round with a peak in July, while fin whale 20 Hz pulses were detected seasonally with a peak in June by AAR1 deployed at 1118 m water depth. Blue and fin whale calls were detected seasonally with a similar peak in May by AAR2 deployed at 4481 m water depth. The blue whale 27 Hz chorus, and blue and fin whale 28-18 Hz chorus followed a similar trend as the seasonal acoustic occurrence of individual Z-calls and 20 Hz pulses of the two species respectively.

Around AAR1, blue whale Z-call rates peaked during the day in autumn and winter, day and night in spring, and night in summer. Fin whale diel 20 Hz call rates peaked during the day in autumn, and peaked slightly during dawn in winter, with no calls for spring and summer. Around AAR2, blue whale diel Z-call rates peaked during the day in autumn, winter and summer, with no calls recorded in spring. Fin whale diel 20 Hz call rates peaked during the day in autumn, day and night in spring, winter showed no peak differences and no calls were recorded for summer. Results from the ANOVA one-way analysis of variance showed significant differences in both Antarctic blue and fin whale call presence and call rates by month. Diel call occurrence by season for both Z-calls and 20 Hz pulses showed no significant difference in both stations. Diel call rates by season for Z-calls were only significant in winter and spring in AAR1, and only in autumn in the deep station. Diel call rates by season for the 20 Hz pulses showed no significant difference in both stations.

In addition to the detection of the key species of this study, other known biological calls produced by Antarctic minke whales, humpback whales and southern right whales were acoustically detected seasonally in both the shallow and deep stations. Other unknown sounds and anthropogenic sounds were also acoustically detected seasonally in both stations. This study highlights the South African west coast as an important year-round habitat and seasonal breeding or overwintering habitat of these whales. Additionally, the year-round acoustic occurrence in this region supports the notion that blue whale migration patterns are more dynamic than previously perceived. Bioacoustic data allowed us to continue to monitor the seasonal acoustic occurrence and behaviour of blue and fin whales through passive acoustics.

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Chapter 1: Introduction

Modern whaling over the period between 1904 and the mid-1970s resulted in high mortalities (~ 2 million) of whales in the Southern Hemisphere (Clapham and Baker, 2002). Estimates show that over 360, 000 blue whales (*Balaenoptera musculus*), 725, 000 fin whales (*Balaenoptera physalus*), 220, 000 humpback whales (*Megaptera novaeangliae*), 150, 000 southern right whales (*Eubalaena australis*) and 100, 000 Antarctic minke whales (*Balaenoptera bonaerensis*) were caught from across the Southern Hemisphere during that era (Clapham and Baker, 2002; Mori and Butterworth, 2004; IWC, 2006, 2016).

As species of whales were sequentially almost hunted to extinction during the 20th century, various organisations (i.e. the International League of Nations before the International Whaling Commission (IWC) was established) restricted their exploitation at different times (Tønnesson & Johnsen, 1982). Southern right whales were protected from 1935 by the International league of Nations (Best, 1970); while Antarctic blue and fin whales were protected from 1964 (Branch *et al*. 2004), humpback whales were protected from 1963 (Yablokov, 1995; Findlay *et al*. 2011) and Antarctic minke whales were protected in 1985 (Mori and Butterworth, 2004) by the IWC under the International Convention for the Regulation of Whaling. However, illegal hunting of blue and fin whales (along with other baleen whale species such as humpback and southern right whales) continued by four Soviet fleets until the mid-1970s (Zemsky *et al.* 1995; Yablokov *et al.* 1998). Commercial whaling on all whale species and populations was subsequently ceased by the IWC through an international moratorium which took effect from 1985 (IWC, 2006).

Certain whale species (such as blue and fin whale populations) remain greatly depleted to this day, as they are relatively slow reproducing and consequently need a long time to recover from over-exploitation (Branch *et al*. 2004; Best, 2007), compared to other whale species such as the southern right whale and humpback whale which are showing more marked increases of between 6 and 11% per annum (Brandão *et al*. 2013; Cooke, 2018). Similarly, Antarctic minke whale population recoveries have been modelled to be increasing, however estimating the population for this species has been challenging due to its preference for sea ice (Mori and Butterworth, 2004). Population recoveries of coastal migrating species such as southern right whales and humpback whales are far better understood than the more offshore species such as blue or fin whales (Best, 2007), given their accessibility to research and the costs of monitoring wide ranging oceanic species.

Generally, baleen whales are present in almost all marine ecosystems as important secondary consumers (Estes *et al.* 2006). Understanding their ecological roles in various habitats is important to identify and protect these depleted species, to recognise both their roles as top-down and bottom-up drivers of ecosystems (as ecosystem engineers) and their roles in mitigating the effects of anthropogenic activities on such systems, through for example carbon capture and nutrient re-fertilisation (Leaper & Miller, 2011). The significance of the conservation of these species in Southern Ocean and local South African ocean management objectives is highlighted by the fact that the Antarctic blue whale and the fin whale are currently classified as Critically Endangered and Endangered respectively by the International Union for the Conservation of Nature (IUCN) (Reilly *et al*. 2013).

Antarctic blue whales are the largest animals that ever existed on earth, growing to 30 m long and weighing up to 180 tonnes (Best, 2007). They have a broad oceanic distribution and occur seasonally within wide distributions in the Southern Hemisphere. There are currently three internationally recognised blue whale sub-species occurring in different oceans (Best, 2007; Attard *et al.* 2016), including the Northern Hemisphere blue whale *(B. m. musculus*; Linnaeus, 1758), the Antarctic blue whale *(B. m. intermedia*; Burmeister, 1871) and the pygmy blue whale (*B. m. brevicauda*; Ichihara, 1966). Of the large whales in the Southern Ocean, the Antarctic blue whales remain the most depleted (Branch *et al*. 2004). A 1996 population assessment projected that approximately 1% - 3% of the Antarctic blue whale population remains, with an annual increasing rate of about 7% per year (Branch *et al*. 2004). Blue whales have been previously acoustically described to occur seasonally in low latitude areas off the South African west coast (Shabangu *et al*. 2019) and year-round by Thomisch *et al*. (2019) off Namibia and Samaran *et al*. (2010, 2013) and Leroy *et al*. (2016, 2018) in the Indian Ocean.

Fin whales are the Earth's second-largest animal, growing to 24 m and weighing between 60 to 70 metric tons in the Southern Hemisphere (Best, 2007). The sub-specific taxonomy of fin whales is not well understood. Two subspecies are currently recognized namely the Northern Hemisphere subspecies (*B. p. physalus)* and the Southern Hemisphere subspecies (*B. p. quoyi)* which has a relatively larger body size (Reilly *et al.* 2013). Clarke (2004) suggested another subspecies in the Southern Hemisphere, a pygmy form (*B. p. patachonica)* (Burmeister*,* 1865) but this is not generally accepted due to lack of a comprehensive genetic analysis (Reilly *et al.* 2013). Current population levels of fin whales in the Southern Hemisphere are not well understood due to assessments not covering all of their primary summer distribution (Branch and Butterworth, 2001). Using sighting data from subsequent IDCR (International Decade of Cetacean Research) surveys, Branch and Butterworth (2001) estimated fin whale abundance south of 60°S in the Southern Ocean for the period 1991/92–1997/98 at 5,500, an increase from the period 1985/86– 1990/91, during which the population was estimated at 2,100. However, these estimates are not representative of the entire population of fin whales in the Southern Hemisphere as the entire range is not surveyed (Clarke, 2004). The recovery rate of this species is also currently unclear, however it is suspected to be increasing (Cooke, 2018). Fin whales have been acoustically described to occur seasonally in low latitude areas such as off south-west of South Africa (Shabangu *et al*. 2019) and Namibia (Thomisch *et al*. 2019).

1.1. **Migration patterns**

Most baleen whales are traditionally thought to migrate seasonally between summer high-latitude feeding grounds and winter breeding grounds in low-latitude warmer waters where they mate and calve, however the precise locations of breeding grounds remain unknown (Mackintosh, 1966; Branch *et al*, 2004, 2007; Best, 2007; Samaran *et al*. 2013). For blue and fin whales this also appears to be the case, based on commercial whaling records in the Benguela ecosystem were blue whales are mostly abundant in winter from May to August and fin whales from May to November (Best, 1998; 2007). However, recent evidence shows that the migratory behaviour of these species is more dynamic than initially thought, as these species have been reported to acoustically occur year-round in both high and low latitude areas (Branch *et al*. 2007). The migratory behaviour of baleen whales is hypothesised to be influenced by ecological aspects such as predation, habitat conditions, prey resources, continental slopes of Southern Hemisphere continents and competition, but seasonal variation in resources is mostly the main reason for long distance migrations (Corkeron and Conner, 1999; Alerstam *et al*. 2003).

An important aspect in identifying migration patterns is that of the modality of seasonal abundance by latitude (see Figure 1 for hypothetical patterns). Migrations comprise a series of waves by latitude, and (Figure 1) hypothetically identifies these waves as:

A - Peak austral summer unimodal distribution in the polar feeding ground.

B- Peak austral winter unimodal distribution on low latitude breeding grounds. An animal migrating from summer Antarctic feeding grounds to winter low latitude breeding grounds would be expected to show unimodal summer modality and unimodal winter modality on these feeding grounds and breeding grounds respectively. Migrations would be shown by bimodal modalities with a northward migration shown by a first peak earlier in the year, and a return southward migration shown by a second peak later during the year. The spacing between the bimodal peaks would be latitude dependent with the bimodal distribution converging to unimodality as the latitudes of the breeding ground is approached.

M1 and M2 Migration Streams - bimodal peaks of the northward and southward migration streams – with timing between the migration peaks reflecting the latitude of the migrations.

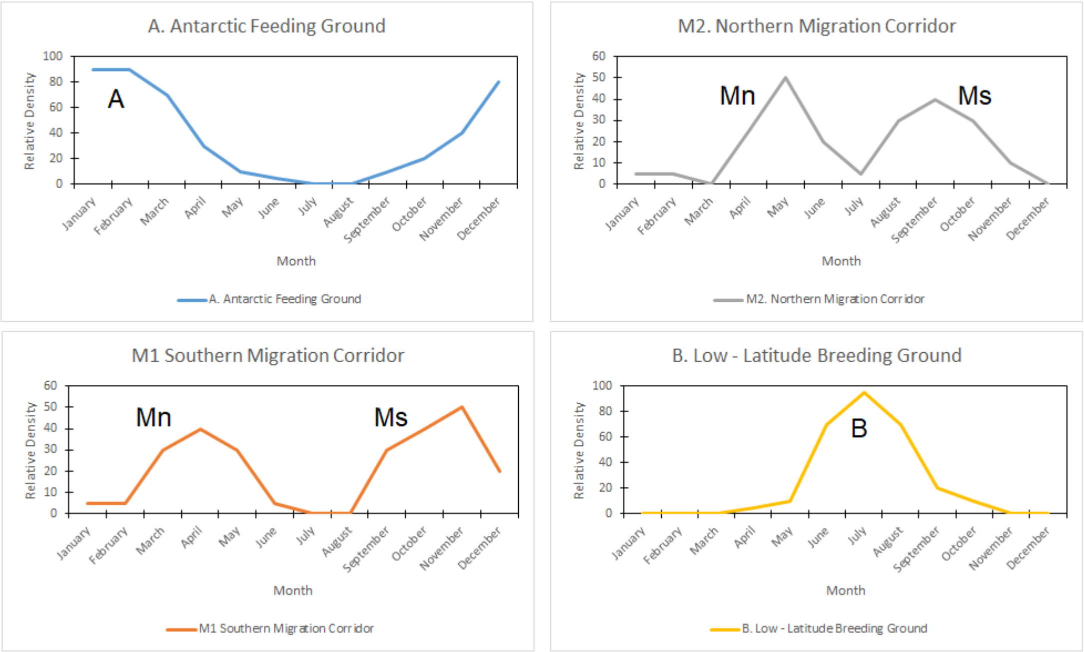

Figure 1: Hypothetical seasonalities of whale migrations by latitude. The Figure is provided for the discussion of the acoustic presence of species in relation to seasonal densities and migration pathways. A unimodal winter distribution of acoustic presence is evidence of a breeding ground, a unimodal summer distribution of acoustic presence is evidence of a feeding ground, while bimodal seasonalities are evidence of migration pathways. A single unimodal migration distribution in autumn or spring may be evidence of longitudinal shifts in migration corridors. [adapted from Findlay and Best (2016)]

In high latitudes of the Southern Ocean, a year-round acoustic occurrence of blue whales has been recently recorded (Širovic´ *et al*. 2004, Thomisch *et al*. 2016). Alternatively, in low latitudes, Thomisch *et al*. (2019) off Namibia and Samaran et al. (2010, 2013) and Leroy *et al*. (2016, 2018) in the Indian Ocean, found a year-round acoustic presence of Antarctic blue whales which counters the traditional migration hypothesis that largely originates from historic whaling seasonality. The prolonged year-round presence of blue and fin whales in high latitude feeding areas in mid-winter has been thought to be influenced by the magnitude of Antarctic ice sheet which possibly limits migrations of some populations of these species to low latitude overwintering areas (Thomisch *et al*. 2016). This essentially means that part of the population populations may use this area to also overwinter as opposed to migrating to low latitude areas. Another possibility is that the non-migratory population of these species is composed of sexually immature individuals, which choose to stay on the feeding grounds for growth and increased body size (Brown *et al*. 1995). It is further possible that pregnant females, avoid migration to low latitude areas due to its costly energy obligation and rather remain in the feeding grounds (Brown *et al*. 1995).

The Benguela region serves as an important over-wintering area for various baleen whale species (blue, fin, right, humpback etc.) due to the occurrence of these species in these waters based on whale catch data (Best, 1998; 2007) and acoustic data (Shabangu *et al*. 2019; Thomisch *et al*. 2019). Regardless of this importance, little is still known of locations of the migration dynamics of these particular species. The continued research and multi-year population monitoring of these species in this area is therefore crucial to increase our knowledge of these species migration dynamics. This has become increasingly crucial since blue and fin whales also face other threats such as increased anthropogenic activities including climate-induced range shifts (Record *et al*. 2019).

1.2. Whale Population Monitoring

Populations of animals may vary in size and distribution over a period of time due to a number of direct and indirect factors. Currently, whale populations depleted by whaling face a range of new anthropogenic threats to their recoveries. The most important direct threats include incidental entanglement in fishing gear and ship-strikes (Rolland *et al*. 2012; Reilly *et al*. 2013). Indirect threats may comprise of recreational and commercial utilization of favourable habitat by humans, pollution, rise in ocean noise and reduction in habitat and prey availability due to climate change, ocean acidification or fisheries competition (Rolland *et al*. 2012; Roman *et al*. 2014). It is consequently deemed essential to conduct multidisciplinary research on the abundance, distribution and stock structure of whale populations to define the status of population-based units for management and conservation purposes (Van Parijs *et al*. 2009). Parameters of interest in such monitoring initiatives could include the following:

- Spatial and temporal variation in relative or absolute cetacean abundance which is crucial to decide the necessary management actions to be implemented and the efficacy of any actions that are implemented (Hammond, 1987; Mikhalev, 2020). The integration of these data with other data such as the structure of the population, direct (incidental capture in fishing gear) and indirect (pollution) anthropogenic factors is important to obtain an accurate interpretation of the status of cetacean populations (Hammond, 1987; 1995; Thomas *et al*. 2016; Mikhalev, 2020; Pérez-Jorge *et al*. 2020).
- Abundance trends (usually measured as relative rather than absolute abundance) are mostly suitable for determining populations of concern and for monitoring the efficacy of management actions (Hammond, 1995; Thomas *et al.* 2016).
- Geographical and temporal distribution patterns determine predictable regions and periods of concentration (whereby density is a metric of interest) that may assist with directing conservation measures associated to human activities (e.g. tourism, by-catch minimization actions; threats posed by shipping,) (Hammond *et al*. 2013; Halpern *et al*. 2019). Such information may also clarify periods and regions of notable importance for different life cycle stages, such as mating or calving (Hammond, 1987; Mikhalev, 2020).

This information is especially crucial in relation to Antarctic blue and fin whales since the locations of breeding areas are poorly understood (Best, 2007; Branch *et al*. 2007).

There are a variety of methods that are utilized for monitoring of marine mammals, each having their own advantages and disadvantages.

1.2.1. Visual surveys

Visual surveys are considered the traditional method used for monitoring of cetacean populations (Buckland and York, 2002; Zimmer, 2011). These surveys are typically conducted from ship-based, aerial or land-based survey platforms using dedicated human observers (Zimmer, 2011). During visual line-transect surveys, observers search the survey area for cetaceans along predetermined transect lines (Buckland *et al*. 2001; Angliss *et al*. 2018). In order to estimate densities, the observers note the distance of the cetacean group from the transect line, species, location (latitude and longitude), group size and composition (Buckland *et al*. 2001). Data from the sightings are analysed at a later stage using distance sampling statistical models to estimate search widths for abundance estimation, whilst positional data are used in geographic information system (GIS) for spatial analysis (Rankin *et al*. 2005; Angliss *et al*. 2018). Major advantages of visual surveys are that they can be used to discriminate among certain species (although Antarctic blue whale are difficult to discriminate from pygmy blue whales at sea) and also provide a direct count of animals (Zimmer, 2011). However, daylight and relatively good weather conditions are also a major limiting factor, and sightings may be missed as whales spend much of the time underwater (Buckland and York, 2002). Such missing of whales on the survey track line when animals are diving reduces the availability of whales for counting, and is usually ignored in the analyses by assuming the probability of encounter is definite (that g (0)) is one) (Zimmer, 2011). Collections of records of recognisable cetaceans may also be used for abundance estimation. Photo-identification of distinguishable traits that enable identification of individuals allow the cataloguing of encounter histories which can be used within a mark -recapture framework to estimate population abundance and survival parameters (Hammond, 1986; Buckland and York, 2002; Rankin *et al*. 2005). Whilst genetic markers collected through biopsy techniques may be used to address evolutionary, behavioural and demographic topics which can provide a detailed understanding of population dynamics and delineations (Amos *et al*. 1993).

Limitations for visual surveys include logistical constraints since trained observers, and numerous hours of operating costly vessels are needed (Mellinger *et al*. 2007; Thomas and Marques, 2012). Consequently, the current understandings of whale abundance and distribution may be limited due to animal mobility, pelagic lifestyles and often remote habitat (Stafford *et al*. 2001; Leroy *et al*. 2018), and the associated costs of research in remote and offshore habitats (Kelly *et al*. 2012). Novel and innovative research methods are therefore critical to obtain data required for addressing research on population status.

One such novel methodology is the use of PAM surveys of whale vocalisations (introduced in detail in Section 1.2.4 below). Prior to introducing these methods, brief introductions to underwater sound and baleen whale vocalisations are provided. For example, prior to Shabangu *et al*. (2019), post whaling records of blue or fin whales in South African waters were limited to a handful, yet Shabangu *et al*. (2019) have identified extensive seasonal distributions of both species through PAM surveys.

1.2.2. Underwater sound

Sound is produced through a mechanical disturbance that travels through a medium as vibration of particles in that medium (Etter, 2003). In contrast to light which penetrates only a few hundred meters into the ocean, sound can propagate long distances in underwater environments (Zimmer, 2011). The hearing of sound waves is consequently the primary sense used by marine mammals to detect their prey, communicate, and to navigate underwater (Zimmer, 2011; Usman *et al.* 2020).

Zimmer (2011) outlines important characteristics of sound as “(a) its frequency which is defined as the number of complete oscillations per second and is measured in Hertz (Hz), (b) its period (the duration of an oscillation cycle in seconds (s), (c) its wavelength (defined as the length of a single oscillation in metres), and (d) its sound intensity which is defined as the sound power of a unit area and is commonly defined using a logarithmic scale in decibels (dB)”. The dB unit is not representative of a unit of measure, but a relative pressure value expressing a ratio between the measured pressure and a reference pressure (Zimmer, 2011; Usman *et al.* 2020). In underwater acoustics a reference pressure of 1 µPa is commonly used (Etter, 2003; Kuperman & Roux, 2007). The speed of a sound wave is defined as the rate (distance travelled per unit time) at which oscillations propagate through the medium (Urick, 1983; Kuperman & Roux, 2007). The speed of sound in water is much faster (1500 m/s) than in air (about 340 m/s) due to the higher density of water (Etter, 2003; Zimmer, 2011). The speed of a sound wave that moves through a medium is not a constant, but is dependent on the medium density which may therefore result in sound not travelling along straight paths (Simmonds and MacLennan, 2005; Zimmer, 2011) as it is reflected or refracted across density interfaces. As sound waves propagate through the ocean, they refract due to sound speed changes, and reflect off of interfaces at both the sea surface and seafloor, causing waveguides at various ocean depths (Zimmer, 2011). Propagation of sound to a region of minimal sound velocity from its source is inclined to occur when sound is transmitted in upward and downward angles, whilst refracts to the depth of its source after striking the surface and bottom borders (Urick, 1963; Au and Hastings, 2008).

The speed of sound through water primarily depends on temperature, pressure (or depth) and salinity (Au and Hastings, 2008), all of which influence the water density. In the upper ocean layers, the speed of sound is greatly affected by the water temperature, whilst pressure drives sound speeds in the deeper ocean layers (Etter, 2003; Kuperman & Roux, 2007; Zimmer, 2011). The sound speed decreases with depth as temperature decreases with depth (Simmonds and MacLennan, 2005; Kuperman & Roux, 2007; Zimmer, 2011). At the interface of the thermocline (a region of rapid change in temperature with depth) and the isothermal (uniform temperature) depths, a region of minimal speed of sound can be identified (Etter, 2003; Usman *et al.* 2020). This interface creates the deep sound channel in the oceans that permits low frequency sound to propagate for great distances (Au and Hastings, 2008). This channel, called the sound fixing and ranging channel (SOFAR), was first discovered by Ewing and Worzel (in Urick, 1963) during World War II. In high latitudes the SOFAR channel is usually found at shallower depths, whereas in low latitudes it is found at deeper depths (Au and Hastings, 2008; Zimmer, 2011). Whales appear to use this channel for transmission of sound for great distances (Samaran *et al*. 2010). Acousticians also take advantage of the properties of SOFAR by placing hydrophones at the axis of the channel seeing that the sound at this axis experiences minimal geometric spreading loss in contrast to surface or bottom reflection (Samaran *et al*. 2010; Zimmer, 2011).

1.2.2.1. Sound propagation

When an underwater sound propagates in the ocean, the signal becomes delayed, distorted and weakened (Urick, 1983; Au and Hastings, 2008). Consequently, when a whale vocalizes in the marine environment, the received signal is an altered version of the original waveform produced by the marine mammal due to such transmission loss (TL). Factors such as temperature, salinity, pressure, bathymetry and ocean bottom properties can contribute significantly to the TL (Etter, 2018). Propagation effects in the ocean are also influenced by temporal and spatial fluctuations which may change over time because of changes in the water column, resulting in the overall change in the sound velocity profile (Etter, 2003). To ensure accurate estimates various models (e.g. BELLHOP) have been used to model sound propagation in the ocean using environmental parameters (sound velocity profiles, and surface, bottom and water volume properties) (Porter and Bucker, 1987; Porter and Liu, 1994; Porter, 2011). The choice of the model is however highly dependent on frequency, depth and range (Kuperman & Roux, 2007; Küsel *et al*. 2011).

The detection of an underwater sound signal is a function not only of the properties of the received signal (determined by source level and TL components), but also of the received level against the ambient noise (André *et al*. 2011). Ambient noise includes physical, biological and anthropogenic sea noise which essentially exhibits considerable variability in space and time (Andre *et al*. 2011)

Physical sea noise commonly arises from ocean turbulence, wind dependent noise from bubbles and spray resulting from surface agitation (amongst others) or other sources such as rain, seismic events or ice noise (Wenz, 1962; Andre *et al*. 2011) (Figure 2). The dominant source of physical sea noise typically occurring at (1 Hz to 100 kHz) is mostly due to ocean surface waves produced by the wind exerting stress on the sea surface (National Research Council, 2003).

Biological sound sources make a noticeable contribution to ocean noise (Southall *et al*. 2020). The prime areas of biological sound production are marine mammals and fish, however, crustacean also produce high sound energy into the ocean (Pieretti *et al*. 2020; Southall *et al*. 2020). For example, snapping shrimp occurring along reefs and in rocky bottom areas in warm shallow waters are known to produce natural noise ranging from a few Hz to over 100 kHz (National Research Council, 2003).

Anthropogenic noise mainly arises from a wide range of commercial activities such as; ship traffic, seismic surveys and construction activities (Hatch *et al*. 2008). The frequency of these activities range from few Hz to hundreds of kHz (National Research Council, 2003; Melcon *et al*. 2012). Seismic surveys typically output one of the loudest anthropogenic ocean noise usually occurring at the 10 to 200 Hz band (Hatch *et al*. 2008). Underwater noise from ship's propeller cavitation in particular, typically reach 50–150 Hz, however can further increase up to 10 000 Hz (Roland *et al*. 2012). Overall, the increasing contribution of anthropogenic activities to the ambient ocean noise poses a threat to certain marine mammal (particularly large whale) and crustaceans due to interfering with crucial communication frequencies (10 to 1000 Hz), which makes it challenging for these species to retain acoustic contact with other species (Hatch *et al.* 2008; Zimmer, 2011).

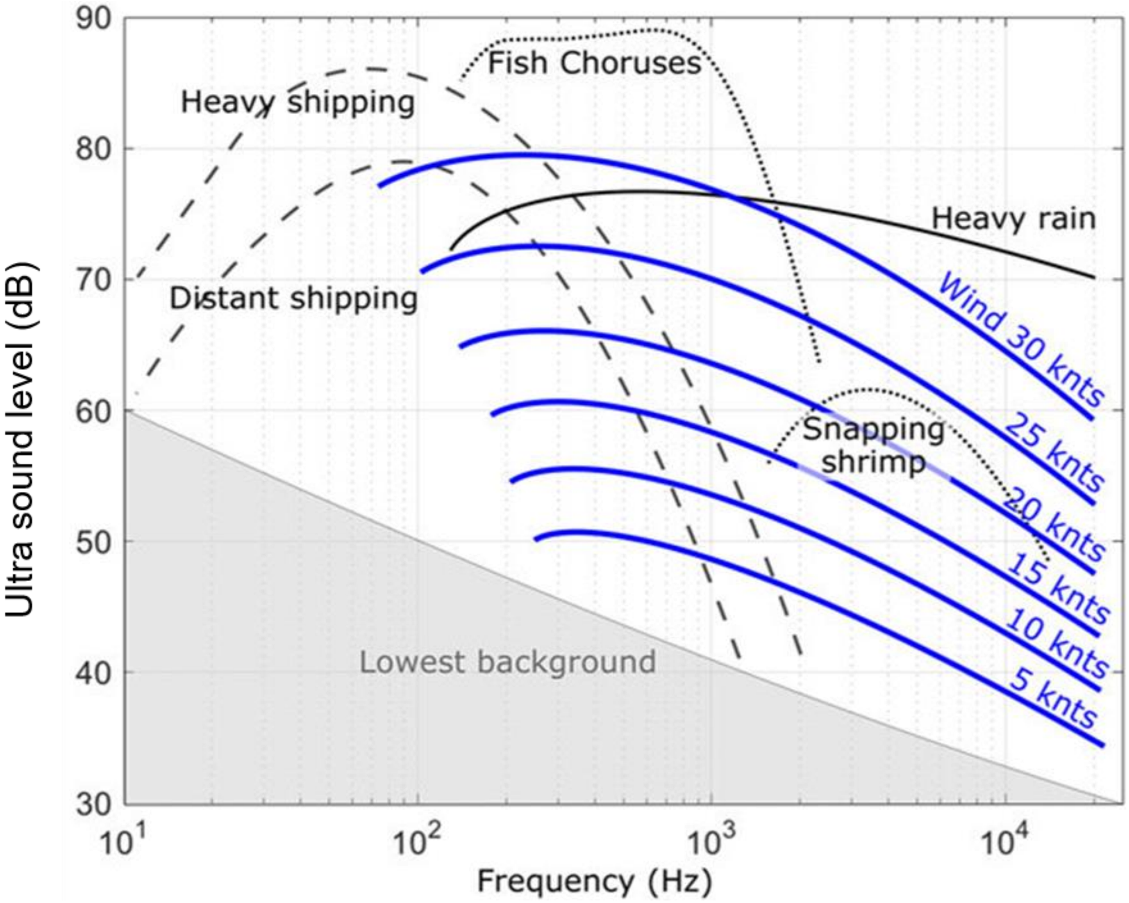

Figure 2: Shows Frequency (Hz) and ultra sound level (dB) of various underwater ambient noise sources found in the ocean, anthropogenic (dashed), biological (dotted), and physical (solid) sources [adapted from Wenz (1962)].

1.2.2.2. The Sonar Equation

A particular ocean sound can be characterised using the passive sonar equation which relates the characteristics of the source, the receiver and the acoustic environment (Urick, 1983). This equation was originally developed during World War II for determining the maximum range of sonar equipment and has been utilised in PAM studies to estimate whale call range propagations thereafter (Urick, 1983).

The sonar equation models a sound emitted at source level (SL-usually defined at a reference distance of 1 m from the source) which is received (by an animal or a hydrophone system) at a lower signal level (received level, RL) at some distance from the source due to TL through the sound path and estimated from a propagation model (Urick, 1983; Zimmer, 2011). The model can be represented in the equations below:

$$RL=SL-TL \qquad (1)$$

The ambient noise, N, of external environmental noise at a single hydrophone is subtracted from equation [1] to get the signal-to-noise ratio (SNR) at a single hydrophone receiver.

$$SNR = SL - TL - N \qquad (2)$$

Sonar systems usually comprise of an array of hydrophones, which enhance signal to noise through a beamforming process. The dB is used to quantify this process by array gain (AG) that is hence added to the single hydrophone SNR.

$$SNR = SL - TL - N + AG \qquad (3)$$

Due to additional factors that may influence detection it is crucial to obtain a detection threshold (DT) which is at a level greater than the SNR. The difference between these two quantities is known as signal excess (SE).

$$SE = SL - TL - N + AG - DT \qquad (4)$$

Each parameter in the sonar equation will have some uncertainty due to variability in either the property itself or as a result of measurement or estimation, so that each should therefore be more properly represented using a probability of distribution (Kuperman & Roux, 2007). This is particularly true for environmental variables, although other variables such as array gain may be quantified through calibration (Cato *et al*. 2006).

As a result of the statistical distribution associated with some of the variables, results are described statistically as function of probability of detection (Cato *et al*. 2006), and probability of detection is the basis for analysis of sonar performance (Kuperman & Roux, 2007). For PAM, the probability of detection is crucial in the estimation of whale abundance (Kuperman & Roux, 2007). It is therefore essential that PAM studies are combined with sonar performance assessments to understand the probability of detection function over a range of environmental and ocean noise conditions (Cato *et al.* 2006; Kuperman & Roux, 2007).

1.2.3. Vocalisations

1.2.3.1. Antarctic blue whales

Antarctic blue whales produce some of nature's loudest biological calls (at 186 to 189 dB re 1 µPa at 1m (McDonald *et al.* 2001; Širovic *et al*. 2007; Leroy *et al*. 2016), that have been suggested to be detectable at distances of 200 to 1,700 km (Clark *et al*. 1995; Širovic *et al*. 2007; Samaran *et al*. 2010; Shabangu *et al*. 2020a). Call rates are the acoustic behaviour (i.e. call production per unit time) in which singular, transient sounds are produced irregularly or as calls and counter-calls between various individuals (McDonald *et al*. 2006). Whilst a number of different blue whale calls have been recorded worldwide, Antarctic blue whales make two different call types, namely a stereotyped Z call and a D call (Oleson *et al*. 2007; Leroy *et al*. 2016, 2018). Z-calls have three components that are frequency modulated and are up to 18 to 26 seconds in duration (Rankin *et al*. 2005; Leroy *et al*. 2018). The first component occurs at frequency ~27 Hz (Leroy *et al*. 2016; Shabangu *et al*. 2019) and is 8-12 s in duration (Rankin *et al*. 2005; Shabangu *et al*. 2020a), the second component's frequency downsweeps from ~27 Hz to 20 Hz and is 2 s in duration, and the third component is somewhat frequency modulated from 20 to ~18 Hz (Rankin *et al*. 2005) and is 8-12 s in duration. These Z-calls may sometimes occur as either all three components, the first and second component, or just one component comprising of the first component. The frequency of the first component of the Z call seems to have been declining in the last decades from 28 Hz to around 26 Hz for an unknown reason but hypothesized to be possibly due to anthropogenic and climate change (amongst others) (McDonald *et al*. 2009; Ward *et al*. 2017; Leroy *et al*. 2018). Z-calls are repeatedly produced in long bouts (as songs) that form a recognisable pattern in time, and whilst produced year-round are believed to be a male reproductive display (McDonald *et al*. 2006; Oleson *et al*. 2007; Širovic *et al*. 2009).

Conversely, D-calls are signals that are variable and somewhat frequency modulated between 22 and 106 Hz and can last between 1 and 4 seconds (Thompson *et al*. 1996; Rankin *et al*. 2005; Oleson *et al*. 2007). D-calls are believed to be produced during feeding behaviour by both sexes (Oleson *et al.* 2007; Samaran *et al*. 2010; Lewis *et al*. 2018). However, Schall *et al*. (2020) found from D-tags that D-calls are also produced during mating displays. Leroy *et al.* (2017) have recently described two unknown calls that could possibly be whale calls, the first one is termed "P call" and is centred at a frequency near the 27 Hz component of the Z call with a duration of 10 s, but can also be confused with the first component of the Z-call. Similarly, to the first component of the Z call, the P call has also shown to be declining in frequency over the past five years (McDonald *et al*. 2009; Leroy *et al.* 2017, 2018). The second call is termed the "M-call" and it is a single component which occurs ~22 Hz and lasts for approximately 10 s (Leroy *et al*. 2017).

1.2.3.2. Fin whales

Fin whale calls have been extensively studied in the Northern Hemisphere (McDonald *et al*. 1995; Castellote *et al*. 2012; Pereira *et al*. 2020). Like blue whales, fin whales produce low frequency and high intensity calls which means they are well suited to PAM. Fin whales across the Northern Hemisphere oceans produce short (~1s) repetitive pulses between 15 and 40 Hz (Thompson *et al*. 1992; Castellote *et al*. 2012). Similar frequency sounds have been reported from the Southern Ocean and have been used to acoustically monitor fin whales in the Southern Hemisphere (Širovic *et al*. 2004, 2007; Shabangu *et al*. 2019, 2020a). These sounds include two different types of calls, namely a 20 Hz pulse (downsweeps from 28 Hz to 15 Hz), with a simultaneous higher frequency component at 89 Hz from the Western Antarctic Peninsula region and at 99 Hz in Eastern Antarctica (Gedamke, 2009; Širović *et al.* 2009). Fin whales also produce a less common short duration pulse that downsweeps from 70 Hz to 40 Hz (Širović *et al.* 2013), termed the 40 Hz pulse. Although the 40 Hz pulse can sometimes be confused with blue whale D calls, these are much shorter in duration than the D-calls (Rankin *et al.* 2005; Širović *et al*. 2013).

The South African Blue Whale Project (SABWP) has been using both PAM (off South Africa and Antarctica) and sighting surveys (off Antarctica) to investigate the distribution and relative abundance of Critically Endangered Antarctic blue whales over a range of spatial and temporal scales (Shabangu and Findlay, 2014; Shabangu *et al*. 2019). Although, PAM methodology is not as mature as sighting surveys due to low levels of PAM research conducted, the work of the SABWP has identified the seasonal occurrences of Antarctic blue whales in South Africa and Antarctica (Shabangu *et al.* 2017, 2019; Shabangu, 2018) and has identified significant blue whale distributions off the South African west coast. This research also provides information on other baleen whale species such as fin whales, minke whales and southern right whales (e.g. Shabangu *et al.* 2019; 2020a).

1.2.4. Passive Acoustic Monitoring (PAM) Surveys

As discussed above, baleen whales are vocal animals and their social interactions as well as successful orientation and feeding depends on their production and reception of sound (Balcazar *et al*. 2017). They can consequently be monitored in time and space through PAM (Mellinger and Clark, 2003; Mellinger *et al*. 2007). Analyses of whale call recordings may provide important information about the relative abundance, behaviour and distribution (amongst other characteristics) of baleen whales (Evans and Chapell, 1994; Van Parijs *et al*. 2009). PAM is increasingly being used as an alternative research methodology to visual surveys throughout the marine mammal research community (Thomas *et al*. 2012; Leroy *et al*. 2016; Thomisch *et al*. 2019; Shabangu *et al*. 2019, 2020a, 2020b;). Researchers across the globe have used PAM to understand the distribution and seasonal abundance of different whale species (Širović *et al*. 2004; Stafford *et al*. 2004; Mellinger *et al.* 2007; Samaran *et al*. 2010; Gavrilov *et al*. 2012; Morano *et al*. 2012; Nieukirk *et al*. 2012; Sousa-Lima *et al*. 2013; Balcazar *et al*. 2017; Shabangu *et al*. 2017), including density estimation (McDonald and Fox, 1999), geographic variability (Stafford *et al*. 2001; Mellinger and Clark, 2003; McDonald *et al*. 2006), seasonality (Moore *et al*. 1998; Clark *et al*. 2004; Shabangu *et al*. 2019; Thomisch *et* *al*. 2019), occurrence and behaviour of whales in relation to environmental conditions (Shabangu *et al*. 2017) and migratory behaviour of whales (Stafford *et al*. 1999; Clark and Ellison, 2000).

PAM systems may comprise (a) mobile ship-towed array systems where hydrophones are towed behind a vessel (Hastie *et al*. 2003; Mellinger *et al*. 2007; Gillespie *et al*. 2009); (b) fixed location systems utilising autonomous acoustic recorders (AARs) moored within the ocean water column or on the ocean floor (Shabangu *et al.* 2019) (c) drifting recorders deployed close to a research vessel such as sonobuoys (Miller *et al*. 2012, 2016; Shabangu *et al.* 2017) (d) Acoustic tags attached on whales to record sound (Risch *et al*. 2014) or e) more recently, systems employed on ocean gliders (Moore *et al*. 2007; Baumgartner *et al*. 2013, 2014). Incoming sounds are filtered (usually by the sampling frequency bandwidth) and only certain ranges of interest are stored/archived in the internal memory of the AAR, computers (towed arrays) or transmitted via very high frequency back to ship (sonobuoys) (Miller *et al*. 2012, 2013). The sampling frequency bandwidth is selected dependent on the species calls of research interest (Mellinger and Clark, 2003; Mellinger *et al*. 2007) as there remains a trade – off between sampling frequencies and battery life. Data archived on systems include amplitude, frequency and duration of particular calls and/or song as a combination of calls or themes (Van Parijs *et al*. 2009; Zimmer, 2011). AARs moored in the ocean water column or on the ocean floor are the most common PAM systems used to record cetacean vocalizations for weeks, months or even years at a time, and can be extended further by duty cycling the data acquisition so that subsampling occurs (Van Parijs *et al*. 2009; Van Opzeeland and Hillebrand, 2020). Such data collection enables determination of diurnal or seasonal patterns of relative presence in an area (Van Opzeeland and Hillebrand, 2020) on the assumption that there are no diurnal or seasonal call rate biases. AARs moored on the ocean floor are considered a cost effective alternative compared to visual sightings since they may be deployed for long periods of time at sea requiring much less expensive vessel time and human involvement (Van Parijs *et al*. 2009; Van Opzeeland *et al*. 2013). They are also able to detect whales from long distances, regardless of the time of day, and in any form of sea-state or weather (Baumgartner *et al*. 2013, 2014), thus overcoming some of the identified limitations of visual surveys.

The detection of whale calls from archived acoustic recordings is commonly carried out through automated detection algorithms (Baumgartner *et al*. 2011; Balcazar *et al*. 2017). A variety of methods involving classification and detection of marine mammals have been developed; including methods of spectrogram correlation (Mellinger and Clark, 2000; Mellinger, 2001), neural networks (Knight *et al*. 2017; Kirsebom *et al*. 2020), binary point matching (Towsey *et al*. 2012; Hafner & Katz, 2018), Markov models (Brown & Smaragdis, 2009; Buchan *et al*. 2020), band-limited energy detection (Figueroa, 2012; Bioacoustics Research Program, 2015) amongst others. However, the selection of the method depends on the SNR which differs according to the range of the calling marine mammal species, types of calls, noise conditions and other biological and instrumentation factors (Simard *et al*. 2019). The most commonly used energy detection algorithms for spectrogram correlation of blue and fin whales, include Ishmael (Mellinger and Clark 2000; Mellinger, 2001), the custom-designed MATLAB driven eXtensible BioAcoustic Tool (Xbat; Figueroa, 2006) or a more recent open-source software package written in R “monitoR” (Hafner & Katz, 2018). The numbers of detected calls (above a custom-selected threshold) pooled over a specified period (day, month or season) are commonly used to identify the presence of the whale species at the acoustic sampling station (Mellinger, 2001; Figueroa, 2012). Real-time verifications of a subset of algorithm detections are an important component of these analyses as challenges with spectrogram correlation include both the detection of distant calls above the background chorus of distant callers (where low amplitude individual calls cannot be identified), the number of individual calls that may be detected within recordings as well as other background sound such as ship noise (Sirovic *et al.* 2015; Leroy *et al*. 2016; Balcazar *et al*. 2017).

Despite the benefits of the automated detection methods, detected signals can be either false positive (automated detections that were not target whale calls) or false negatives (missed true target whale calls) (Mellinger and Clark, 2000). In the absence of human aid, computer-automated methods usually generate undesirable false detections, which can classify non-target noise as calls of species of interest (Acevedo *et al*. 2009). The rate of false detection primarily depends on a number of factors such as; the particular automated detection method used (Bravo *et al*. 2017), call characteristics produced by the target species (Towsey *et al*. 2012), the amount of training data which reflects the performance of the automated algorithm particularly for neural networks (Knight and Bayne, 2018) and choice of detection thresholds (herein defined as the lowest percentage of detectable similarity between an automated template for detection and true call) in order to test the efficacy of the spectrogram cross-correlation automated detectors (Knight *et al*. 2017). This study addresses the efficacy of the utilised blue and fin whale automated call detection template based on variable detection thresholds in the following chapter.

Currently, PAM only provides relative indices of animal presence/absence in the form of counts of vocalizations that can be used to estimate trends when constant parts of the vocalising population are estimated per annum (Buckland and York, 2002; Zimmer, 2011; Etter, 2018). The use of relative index values, however, has its own challenges as it will only (at best) inform on the direction and magnitude of any changes in the absolute abundance, or actual population size (Anderson, 2001; Zimmer, 2011). PAM and visual line methods are currently being used in conjunction, to develop methods that can convert cost-efficient and objectively sampled PAM data to absolute animal densities (Balcazar *et al*. 2017). However, there are various concerns which need to be addressed such as optimal sampling rates and schemes of the AAR (Thomisch *et al.* 2016; Shabangu *et al.* 2020a), the estimation of the distance to the vocalising animal (in order to estimate densities) and how to assess group size issues in the translation of call rates to group size (Mellinger *et al*. 2007). Nevertheless, various propagation models such as BELLHOP (Porter, 2005) and Monte Carlo Simulations (Küsel *et al*. 2011) have assisted with challenges in the estimation of distance to the vocalising animal if source levels are known

This study utilises PAM data collected using AARs deployed on oceanographic moorings off the South African west coast between December 2015 and January 2017. Results from this study allow a better understanding of the seasonal occurrence and calling behaviour of Antarctic blue and fin whales off the South African west coast.

1.3. Research questions

This study aims to address the following research questions:

- Can the seasonal occurrence and behaviour of Antarctic blue and fin whale calls be detected in acoustic recordings from 2015 through early 2017 using automated detection algorithms?
- Which detection thresholds provide the optimum detection of whale calls?
- Is there a difference in call occurrence and call rates at the two deployment stations (AAR1 and AAR2) for blue and fin whale calls?
- Is there a diel variability in call occurrence and call rates for blue and fin whales?
- Is there a seasonal variability in call occurrence and call rates for blue and fin whales?

1.4. Research Objectives

The overall aim of this study is to determine the seasonal occurrence, and possible migratory behaviour of blue and fin whales off the South African west coast, southeast Atlantic Ocean using PAM. The objectives of this study therefore include:

- To determine the seasonal occurrence of Antarctic blue and fin whale calls in acoustic recordings data sets using different threshold levels.
- To explore which detection threshold can be used to obtain optimum number of calls.
- To compare call occurrence and call rates of blue and fin whale according to time of day.
- To compare call occurrence and call rates of blue and fin whale according to the season.
- To compare call occurrence and call rates of blue and fin whale between the deployment stations.

1.5. Thesis structure

The thesis is structured as follows:

Chapter 1 is an introductory chapter and provides a literature review on the history and acoustics research of baleen whales in particular Antarctic blue and fin whales. The chapter reviews the current methodologies used for monitoring of blue and fin whales with the primary focus being PAM. This chapter provides a brief introduction to the principles of sound propagation in water including vital parameters of underwater sound, together with the way in which sound propagation influences the results of this study.

Chapter 2 outlines a brief description of the study area, materials and methods and the statistical analyses applied to the collected data.

Chapter 3 presents and describes the results which include seasonal and diel call occurrence, and seasonal and diel call rates for blue and fin whales in both stations. Other recognized and unrecognized calls within the recorded dataset are also described.

Chapter 4 details the discussion and interpretation of the results obtained, and further compares this with similar research conducted across the globe. Variability in seasonal and diel call patterns, call variability at different stations are also be discussed for blue and fin whales, providing some information on the relative abundances and therefore migration characteristics. Such migration characteristics are to the most extent unknown for the region. The chapter also discusses other recognized and unrecognized calls detected during the analyses.

Chapter 5 concludes the thesis and makes general recommendations.

Chapter 2: Methods

2.1. Study area

The Benguela Upwelling System (BUS) is the Eastern Boundary Current System of the southeast Atlantic Ocean and extends from the south coast of South Africa to the southern boundary of Angola (Shannon *et al*. 1985; Blanke *et al*. 2005) (Figure 3). It is included as one of the four major upwelling systems in the world (Parrish *et al*. 1983), and one of the world's most productive oceanic regions (Shannon *et al*. 1985; Hutchings *et al*. 2009). The BUS is characterised by the Benguela Current, a cool, shallow and broad surface current along the South African west coast that flows towards the north from east of the Cape of Good Hope (South Africa) equator-wards to southern Angola (Hutchings *et al*. 2009), feeding warm waters by the Agulhas Current leakage through Agulhas Rings (Gordon *et al*. 1992; Lutjeharms and Cooper, 1996).

The Benguela Current is mainly driven by prevailing south easterly trade winds which produce nutrient-rich coastal upwelling brought about by Ekman pumping (as a result of offshore wind stress curl) and Ekman transport (as a result of alongshore winds) (Wedepohl *et al*. 2000). This results in highly productive areas that are rich in marine biodiversity and crucial for coastal fisheries (Bakun *et al*. 2010; Leduc *et al*. 2010). This subsequently also contributes to the presence of top marine predators in this particular region (Sirovic *et al*. 2004). The Benguela system's bathymetry, hydrography, chemistry, geographical location and proximity to the warm-water boundaries of the Agulhas Current and the Angola Current makes it unique among other major upwelling systems (Brown *et al*. 1991; Hutchings *et al*. 2009). From the north at 14° and 17°S, the Benguela region is influenced by the Angola Current (Shannon and Nelson, 1996). From the Indian Ocean, the Agulhas Current flows towards the west around South Africa and retroflects south of Cape Town at the Agulhas (approximately 37°S) (Shannon *et al*. 1985; Shannon and Nelson, 1996; Hutchings *et al*. 2009). However, Agulhas Current Rings are formed at the retroflection and resultantly transfer heat, salt and energy to the South Atlantic Ocean (Shannon and Nelson, 1996; Hutchings *et al*. 2009)

The persistence and strength of upwelling in the BUS depends on latitude, and several upwelling cells can be distinguished (Shannon and Nelson, 1996). Areas of intense upwelling are located off Lüderitz (26.4°S), where upwelling occurs throughout the year (Shannon and Nelson, 1996). The Lüderitz upwelling cell divides the BUS itself into two subsystems: the northern and the southern BUS (Nelson and Hutchings, 1983; Hutchings *et al*. 2009) (Figure 3). In the southern Benguela, upwelling takes place along the coast, though it ranges further away from the coast in the northern Benguela (Fennel *et al*. 2012). Both upwelling system are immensely seasonal (Tim *et al*. 2015). Upwelling is more intense in the north during austral winter and spring, particularly when the subtropical high (system of high atmospheric pressure; latitudes 30° N and S) is positioned farthest in the north (Chavez & Messié, 2009) and the trade winds are strongest in this region (Lutjeharms and Meeuwis, 1987; Hutchings *et al*. 2009). Alternatively, upwelling is more intense in the south during austral summer when the subtropical high has positioned farthest in the south (Chavez & Messié, 2009) and trade winds in the southern region are upwelling-favourable (Hutchings *et al*. 2009).

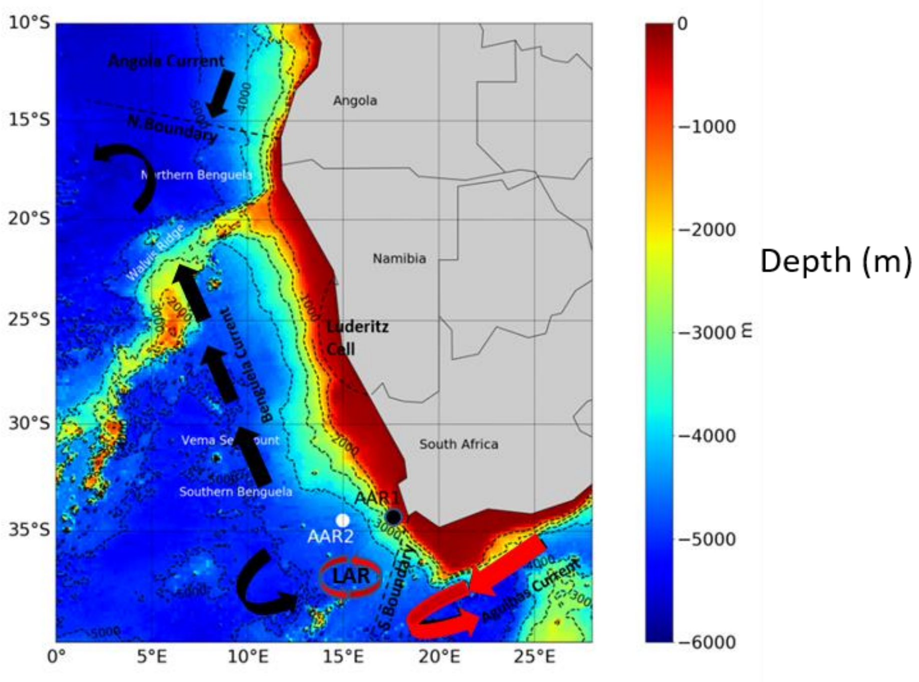

Figure 3: Position of AARs (1 and 2) off the South African west coast in the Benguela Upwelling System, Atlantic Ocean. The Benguela Current extends from South Africa to Angola with the strongest upwelling cell (the Luderitz cell) located in its middle. The cool Benguela Current's flow path is indicated by the black arrows and the red arrows indicate the flow of the warm Agulhas Current. The northern and southern boundaries of the Benguela Current are represented by the dashed broken lines. LAR represents the Agulhas Current leakage through Agulhas Rings that feed warmer waters to the Benguela ecosystem. Data on bathymetry were accessed from the ETOPO1 dataset (Amante and Eakins, 2009).

2.2. Data collection

Single autonomous acoustic recorder (AARs) instruments; Autonomous Underwater Recorder for Acoustic Listening (AURAL M2 version 04.1.3, Multi-Electronique, Inc., Rimouski, QC, Canada) were used to collect data on the acoustic environment at each of two PAM stations (Figure 3). These AARs were deployed opportunistically on the South Atlantic Meridional Overturning Circulation Basin-wide Array (SAMBA) oceanographic moorings (Figure 4) located in the southeastern Atlantic Ocean (Ansorge *et al*. 2014). The SAMBA project includes a hydrographic mooring and instrument transect that forms part of the South Atlantic Meridional Overturning Circulation (SAMOC) project aimed at understanding the Benguela Jet, and the water leakage from the Indian Ocean into the South Atlantic Ocean through Agulhas rings and the salt and heat exchange of thermohaline circulation in the region (Ansorge *et al*. 2014).

Both AAR mooring deployments were carried out on 04 December 2015 using the RV *Algoa* during a SAMBA mooring refurbishment cruise. The first mooring (AAR1) was positioned on the shelf edge at 34° 23.6357' S; 17° 35.6644' E in a water depth of 1,118 m, and the second mooring (AAR2) was deployed at 34° 30.36'S 14° 58.81'E in a water depth of 4,481 m (Figure 3). The AARs 1 and 2 instruments were positioned at 300 m and 200 m respectively below the sea surface, both of which approximates the SOFAR channel in the BUS. AAR1 was located approximately 75km from the nearest coastline and AAR2 was located further offshore at approximately 240 km from AAR1 (Figure 3) or 315 km from the coast. AAR1 and AAR2 stopped recording on 1 January 2017 and 13 January 2017 respectively due to depletion of battery power. Both AARs were recovered in April 2017 and were not redeployed due to project financial constraints.

Both AARs were equipped with HTI-96-MIN hydrophones (High Tech, Inc., Long Beach, MS, USA) with a sensitivity of -164.10 dB re 1 V/µPa for AAR1 and -164.20 dB re 1 V/µPa for AAR2. An amplification level gain of 22 dB was applied for both AARs, and the sampling rate at 8192 Hz was used for an effective monitored bandwidth range of 10 to 4,096 Hz (i.e. the Nyquist frequency- the maximum-recorded frequency at half the sampling rate) to sample the low frequency sounds of baleen whales. All recordings were archived in hard drives within the instruments. Both AARs were programmed to record for 25 minutes of every hour of the day as a sampling duty cycle over the duration of the deployment to maximise battery lifespan. Upon recovery of the instrument, the archived acoustic data were retrieved from both AARs and stored on portable hard drives for analyses.

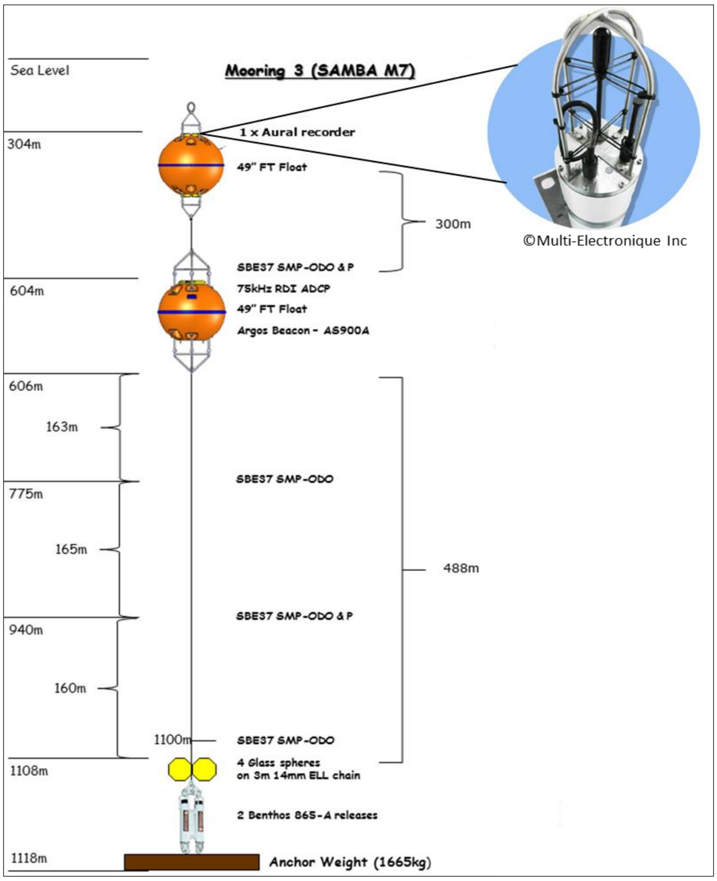

Figure 4: The design of the SAMBA oceanographic moorings. The position of the AAR1 instrument is on the top buoy/float. The inset provides a magnified view of the hydrophone and protective bars on the AAR head. Other oceanographic instruments (Acoustic Doppler Current Profiler (ADCP)), were attached at different depths of the mooring below the top buoy. Schematic diagram adapted from Shabangu *et al*. (2019).

2.3. Acoustic analyses

2.3.1. Retrieval and preparation of data

Prior to importing of data for analyses, the archived acoustic data recordings were prepared to align with specific formats that the analyses software can interpret. The retrieved acoustic data had been archived in 1hr 15 minute bins by the AAR archival software, which comprised three recording intervals (that correspond to recording bouts of 25 minutes each). These required separations into discrete 25-minute recording bouts for the data analyses.

The software package Raven Pro (Bioacoustics Research Program, 2015) was used as the preliminary means to investigate and characterise the data using visual verification. This visual verification method entails visually identifying signals based on their species-specific/characteristic call. The archived acoustic data with presence of whale calls were split into three 25-minute separate files using Sound eXchange (Sox 14.4.2, 2015). Those split acoustic data files with presence of whale calls were then down-sampled to 1024 Hz using a custom driven script on MATLAB R2014a platform (MathWorks Inc, 2014) to assist with the visual analysis of low frequency blue and fin whale vocalizations, and to further improve the frequency resolution and the fast Fourier transform (FFT) length. This resulted in new sound files with a Nyquist frequency of 512 Hz, which was sufficient to show all low frequency fin and blue whale vocalizations, and also sufficiently low to eliminate undesirable higher frequency noise.

2.3.2. Automated call detection

The automated discrimination of animal vocalizations is an effective and accepted methodology for expediting analyses of acoustic data and generating more reliable results in contrast to visual discrimination (manual) of sounds by humans (Mellinger and Clark, 2000; Širović, 2016). In this study, the automatic detection of blue and fin whales was conducted through spectrogram correlation (Mellinger and Clark, 2000; Mellinger, 2001), using a MATLAB driven eXtensible BioAcoustic Tool (Xbat) which uses automatic detection templates (Figueroa, 2006). This method cross-correlates the spectral characteristics of sounds of interest with an artificial kernel that represent whale calls using a similarity level above a defined threshold (Mellinger, 2001).

Blue and fin whale calls with high SNR calls were chosen visually from the acoustic data, and used as templates for the automatic detection of calls. A complete Z-call (Figure 5a) with all the three units were used as the blue whale primary detection templates due to comprising of most of the energy of these calls. As some Z-calls did not consist of the three components of the call (as used in the full Z-call template), additional templates which contained either one or two of the three-component Z-call were also used in analyses. Such additional templates significantly improved accuracy of the automated detection template method. Call choruses 27 Hz (Figure 5b) and 28 -18 Hz chorus are typically produced by distant Antarctic blue and fin whales in bands of continuous calling and often associated with a high species call rate (Thomisch *et al*. 2016, 2019). The presence of these chorus as a “background” essentially makes it difficult to detect faint individual Z-calls and fin whale 20 Hz pulses. The presence of choruses has been previously computed as a blue whale index (BWI) which quantifies the period were the acoustic energy of the chorus is higher than the ambient noise (Thomisch *et al*. 2016; 2019). However, for this study the presence of both choruses was noted using the visual verification method.

The short frequency modulated downsweeps of the 28-15 Hz tone (defined as the 20 Hz pulse) (Figure 5b) were used for automated detection of fin whale calls since it is the most frequent occurring and reliably detected sound of fin whales. All blue and fin whale call detections were finally verified by a manual (visual) verification method. Other identified biological and unknown calls “including M-calls” were detected only with the manual (visual) verification method (without any automated detector) due to the variability of the calls (i.e. humpback whale calls).

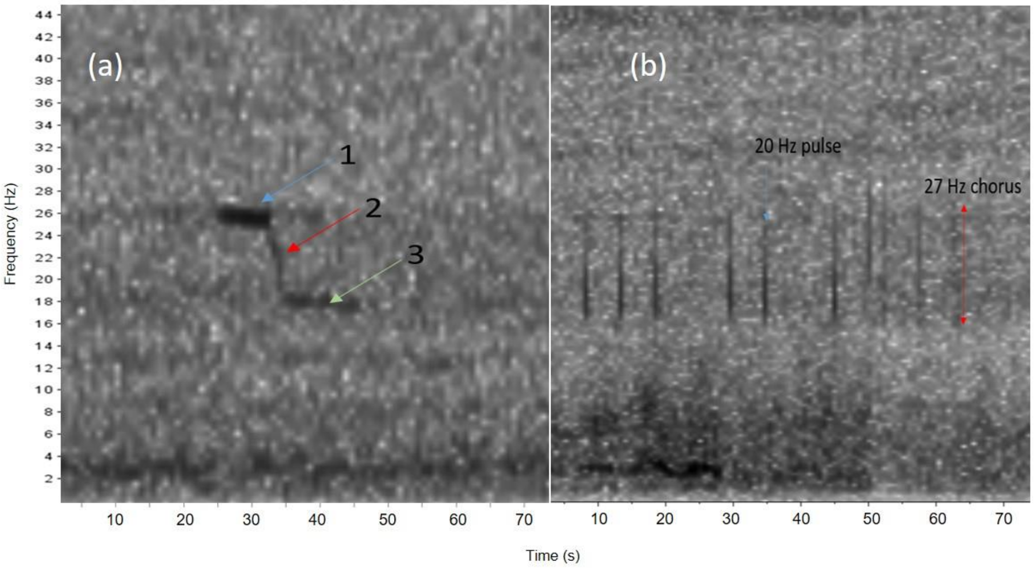

Figure 5: Spectrogram showing frequency modulated (27 to 18 Hz) Antarctic blue whale Z-calls (a), fin whale 20 Hz pulse and 27 Hz chorus (b) Coloured arrows show the different three components (1, 2 and 3) of Z-calls. Spectrogram parameters: (a) 6803 hop size, 50% overlap, DFT size 16,384 samples, Hann window.

2.3.3. Threshold testing

To assess the effectiveness of the automated detectors, each of the automated detectors were tested based on variable detection thresholds (i.e. The lowest percentage of detectable similarity between an automated template for detection and true call). Results of the threshold tests are included in this methodology section as they represent preliminary exploration on the optimum threshold for automated detection of blue and fin whale calls to be utilised in the final analyses.

Randomly selected 20% blocks (chunks) of the data with presence of each of the target whale calls were chosen as a representative subsample from each station. Three thresholds (10%, 15% and 20%) were applied to these subsample data, and visually reviewed for the estimation of the number of false positives (automated detections that were neither blue or fin whale calls) and false negatives (missed true blue and fin whale calls by the automated detector). During the threshold testing, the 10% detection threshold was not used for fin whales in both stations as it yielded higher false positives.

Overall, the 10% and 15% detection thresholds were best suited for blue and fin whales respectively in both AAR's as they produced the fewest missed calls (false negatives). For AAR1, the 10% detection threshold yielded 7% false negative rate for the blue whale Z-call, and 15% threshold yielded 0.6% false negative rate for fin whale 20 Hz pulse (Figure 6). Hence, 93% and 99.4% true positives (blue or fin whale calls that were correctly identified) for blue whale Z-call and fin whale call respectively. For AAR2, the 10% detection threshold yielded 24% for the blue whale Z-call, and 15% threshold yielded 0.5% for the fin whale 20 Hz pulse (Figure 6). Hence, 76% and 99.5% true positives. Following the results of the threshold testing, the chosen thresholds was applied on the entire acoustic dataset for the analysis of blue and fin whale calls. Low thresholds are generally used for examining large data sets such as the one used in this study (Mellinger and Clark, 2000). Visually identified detections of false positive calls were manually excluded from further data analyses. Visually identified false negative detections were manually incorporated into the calculations of the final total call number and rates.

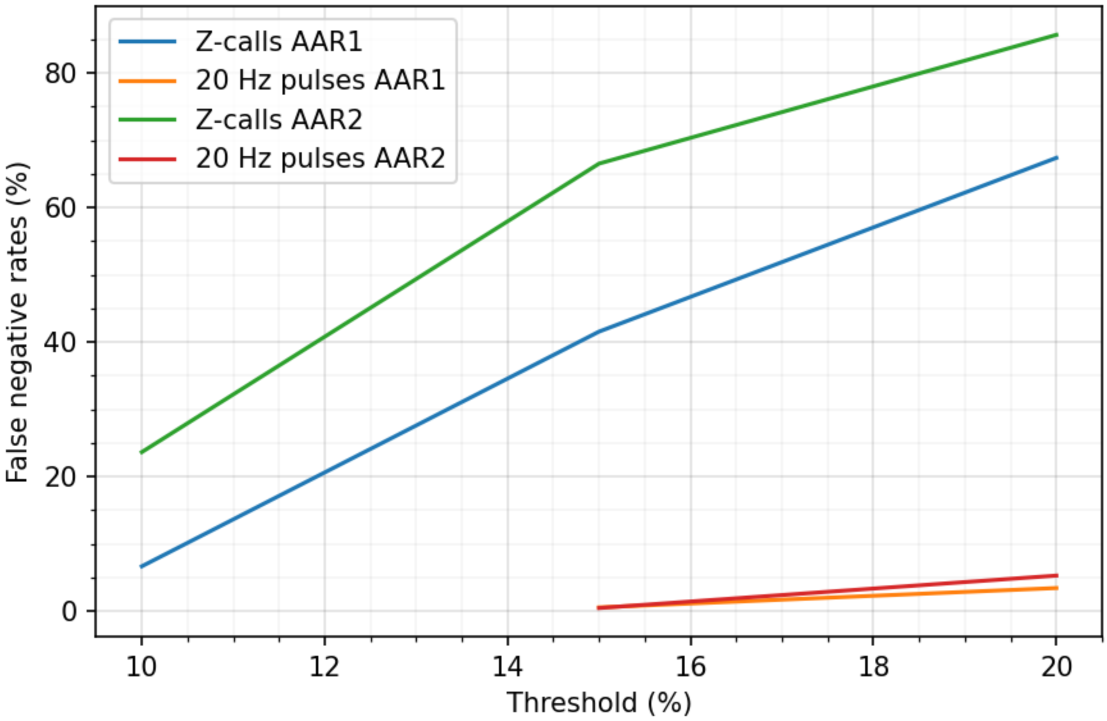

Figure 6: False negative rates at different thresholds (10, 15, 20 percent) for Z- calls and 20 Hz pulses at AAR1 and AAR2.

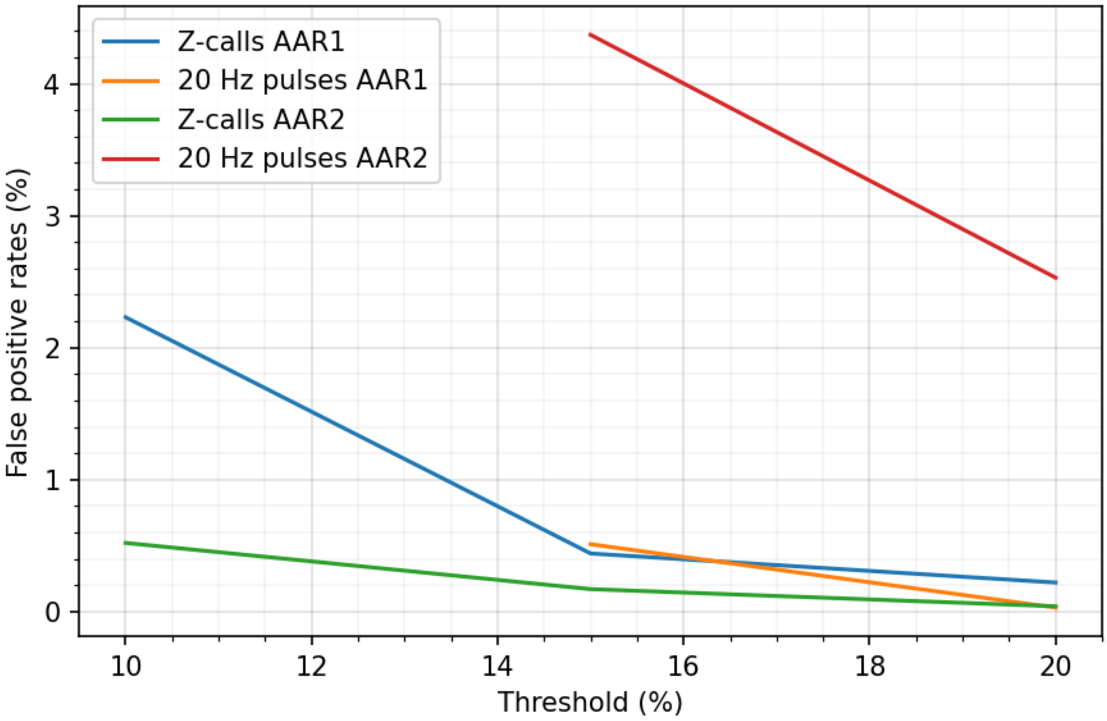

Figure 7: False positive rates at different thresholds (10, 15, 20 percent) for Z- calls and 20 Hz pulses at AAR1 and AAR2.

2.4. Seasonal occurrence

In this study, acoustic occurrence of blue and fin whale calls represent instances when one or more calls of either whale species were detected within a 25-minute sampling interval. Acoustic absence represents the lack of blue or fin whale calls within such a sampling interval. In order to determine the acoustic occurrence of blue and fin whale, the Z-call and the 20 Hz pulse were used since they were the most dominant call types in the data. Species occurrence was obtained as a percentage by calculating number of sampling intervals that contained calls divided by the total number of sampling intervals per month. To investigate seasonal occurrence, the data were parsed into the Southern Hemisphere (austral) seasons of the year by month: autumn (March to May), winter (June to August), spring (September to November) and summer (December to February). Seasonal differences in occurence of calls between the stations was further compared to infer the migratory call behaviour of blue and fin whales. Similarly, the seasonal acoustic occurrence of blue whale 28-18 Hz chorus, other identified and unidentified sounds were calculated using the methods described above.

2.5. Diel call occurrences

To investigate diel call occurrence, different light regimes [dawn [nautical twilight], daytime, dusk [nautical twilight] and night time] were classified over different seasons in accordance with the altitude of the sun by averaging hourly sun altitudes over the austral seasons. Sun altitudes were retrieved from the United States Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil). The time of twilight between nautical twilight start and sunrise was defined as dawn, the time of twilight between sunset and nautical twilight end was defined as dusk. The time between nautical twilight and sunrise was defined as night, the time between sunrise and sunset was defined as day. It should be noted that times presented in this study are in the format Coordinated Universal Time (UTC). The divisions of light regimes per hour is shown in the **Appendix** Table 1 and 2.

2.6. Call Rates

To obtain the call rates, the recording time of sampling (25 minutes per hour sampling duty cycle) for both stations (AAR1 & AAR2) was converted to hourly rates. Call rates (described as calls per hour) of both species were calculated as the total number of calls recorded within a sampling interval divided by the duty cycle (of 0.416 hours) for both stations. Call rates generally describe the acoustic behaviour of whales of a particular area (i.e. South African west coast in this study) by showing the amount of calls produced by an animal within a given period of time, which could indicate their interaction with their conspecifics. It should also be noted that the whale call rates denote to the overall call detection rate per unit time, and not the number of whales as the call rates per individual remains unknown for this study. Mean monthly call rates were calculated as an average of call rates per month. Mean daily call rates were calculated as an average of call rates per day. As time of day is a circular variable, smoothed means of the diel call rate patterns per season were calculated using penalized cyclic cubic regression splines (Wood, 2017) in R (R Core Team, 2016).

2.7. Statistical analysis

Comparisons among months and diel period were made using one-way analysis of variance (ANOVA, $\alpha=0.05$) for both call occurrences and rates. All assumptions of ANOVA were met for months and diel period. Tukey's HSD was used as a post-hoc one-step pairwise comparison technique to test for differences between each of the months and diel periods for both call occurrence and rates. This is crucial for adjusting for Type I error rate that may arise across multiple comparisons. All statistical analyses were performed using ‘R’ version 1.1.456 (R Core Team, 2016). Graphics were produced in R using the ggplot2 package (Wickham, 2009).

Chapter 3: Results

3.1. Sampling Effort

A total of 3,982 hours (9,480 sampling intervals) of acoustic data from 25 minute sampling intervals were recorded at AAR1. Of these, 1,353 hours (3,221 sampling intervals) contained Antartic blue whale Z-calls and 202 hours (480 sampling intervals) contained fin whale calls. The blue whale 27 Hz chorus was detected in 772 hours (1,855 sampling intervals) and Antarctic blue and fin whale 28-18 Hz chorus were detected in 124 hours (297 sampling intervals) from AAR1.

A total of 4,098 hours (9,756 sampling intervals) of acoustic data from 25 minute sampling intervals were recorded at AAR2 . Only 377 (897 sampling intervals) hours contained Antartic blue whale Z-calls and 139 hours (330 sampling intervals) contained fin whale calls. The blue whale 27 Hz chorus was detected in 74 hours (177 sampling intervals) whereas the Antarctic blue and fin whale 28-18 Hz chorus was detected in 11 hours (26 sampling intervals) from AAR2. M-calls were detected in 12 hours (29 sampling intervals) and 40 hours (96 sampling intervals) from AARs 1 and 2 respectively.

3.2. Call detections

The total number of calls computed for the two species from the AAR1 shallow station were 88,859 Antarctic blue whale Z-calls and 28,697 fin whale 20 Hz calls**.** The total number of calls computed for the two species from AAR2 were 23,190 Antarctic blue Z-calls and 23,403 fin whale 20 Hz calls. Antarctic blue whale feeding D-calls were not detected at either station.

3.3. Monthly acoustic occurrence

There were differences between the two stations in the seasonal call occurrence of both blue and fin whales. It should be noted that only a single day was sampled in January 2017 around AAR1, and 13 days were sampled in January 2017 around AAR2.

Around the AAR1 recordings, Z-calls were detected each month from December 2015 through December 2016 (Figure 8a). The blue whale 27 Hz chorus was recorded each month from December 2015 to October 2016, and again in December 2016; no chorus was detected in November (Figure 8a). The blue and fin whale 28-18 Hz chorus was detected only in March and from May to September 2016. Fin whale 20 Hz pulses were recorded seasonally from May through August 2016 (Figure 8a). The peak monthly occurrence for Z-calls (95%) was recorded in late winter i.e. July 2016, while peaks for both 27 Hz (72%) and 28-18 Hz (25%) choruses were detected in June 2016 i.e. mid-winter (Figure 8a). The peak monthly acoustic occurrence for fin whales (30%) was recorded in June 2016 i.e. mid-winter (Figure 8a). There was a significant difference in the monthly acoustic occurrence of Z-calls (ANOVA, $F_{13,9466}$= 1018, $p<0.05$) and fin 20 Hz pulses (ANOVA, $F_{13,9466}$= 188.7, $p<0.05$) around AAR1.

Around the AAR2 recordings, Z-calls were detected seasonally between December 2015 and July 2016, and again in December 2016 (Figure 8b). The 27 Hz chorus was recorded between January and July 2016, while the 28-18 Hz chorus was recorded between April and June 2016 (Figure 8b). Fin whale 20 Hz pulses were recorded seasonally between April 2016 and July 2016, and again in September 2016 (Figure 8b). The peak in monthly acoustic occurrence of Antarctic blue whale Z-calls (75%), 27 Hz chorus (18%), and 28-18 Hz chorus (3%) within the AAR2 recordings, were all recorded much earlier in the year (May 2016) than in June within the AAR1 recordings (Figure 8b). Similarly, the peak monthly percentage (24%) of acoustic occurrence of fin whale 20 Hz pulses was detected in May 2016 (late autumn), which is also much earlier in the year than recorded by AAR1. There was a significant difference in the monthly acoustic occurrence of Z-calls (ANOVA, $F_{13,9741}$= 632.8, $p<0.05$) and fin 20 Hz pulses (ANOVA, $F_{13,9741}$= 115.7, $p<0.05$) around AAR2.

See (**Appendix** Table 3) for Tukey’s HSD multiple comparisons results for monthly call occurrence around AAR1 and AAR2.

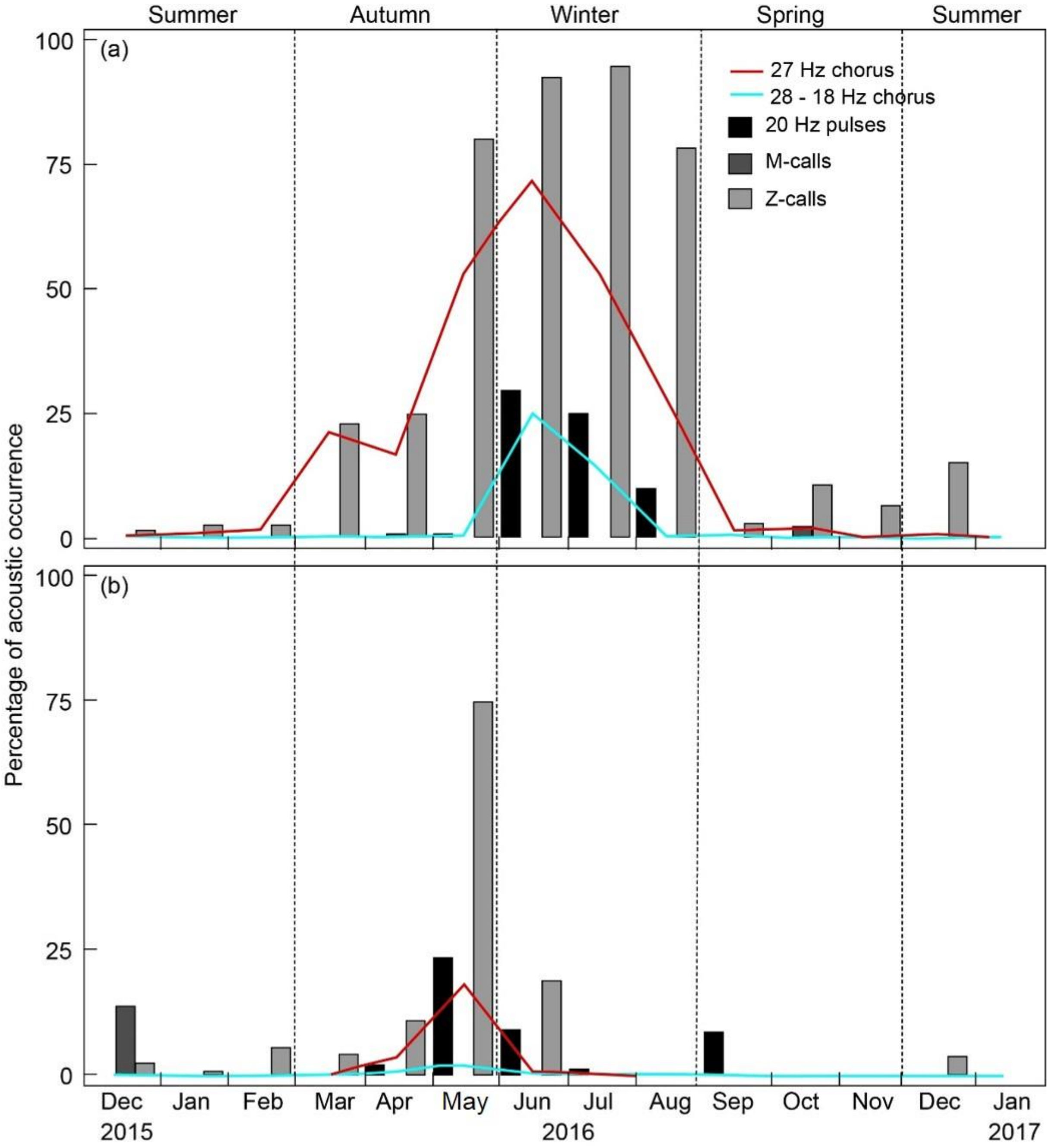

Figure 8: Monthly percentages of acoustic occurrence of Antarctic blue, fin whale calls, M-calls, 27 Hz blue chorus and 28-18 Hz Antarctic blue and fin whale chorus from AARs 1 (a) and 2 (b).

3.4. Call rates by month and day

As mentioned on the previous chapter, monthly call rates refer to average of call rates per month and mean daily call rates refer to average of call rates per day. It should be noted that only a single day was sampled in January 2017 around AAR1, and 13 days were sampled in January 2017 around AAR2.

There were differences between the two stations in the monthly call rates of blue and fin whales. Around AAR1, higher monthly blue whale Z-call rates were observed from May to August 2016 than other months, and June 2016 had the highest median Z-call rate of 76 calls per hour (Figure 9). Overall the highest mean daily rate for Antarctic blue whale Z-calls was in June 2016 with 223 calls per hour (Figure 10). Fin whale 20 Hz monthly call rates were highest in June 2016 (Figure 11), and the highest mean daily rate was recorded in July 2016 with 386 calls per hour (Figure 12). There was a significant differnce in the monthly call rates of blue whale Z-calls (ANOVA, $F_{13,9466}$= 440.3, $p<0.05$) and fin whales (ANOVA, $F_{13,9466}$= 146.4, $p<0.05$) around AAR1.

Around AAR2, the highest monthly blue whale Z-call rates and median were observed in May 2016 with 65 calls per hour (Figure 13). The highest mean daily rate for Z-calls was also in May 2016 with 214 calls per hour throughout the day (Figure 14). Fin whale 20 Hz monthly call rates medians and interquartile widths were zero for all months (Figure 15). However, the highest mean fin whale 20 Hz pulse daily call rate was recorded in May 2016 with 437 calls per hour (Figure 16). Similarly, there was a high significance in the monthly call rates of Z-calls (ANOVA, $F_{13,9741}$= 680.3, $p<0.05$) and fin 20 Hz pulses (ANOVA, $F_{13,9741}$= 79.98, $p<0.05$) around AAR2.
See (**Appendix** Table 4) for Tukey's HSD multiple comparisons results for monthly call rates around AAR1 and AAR2.

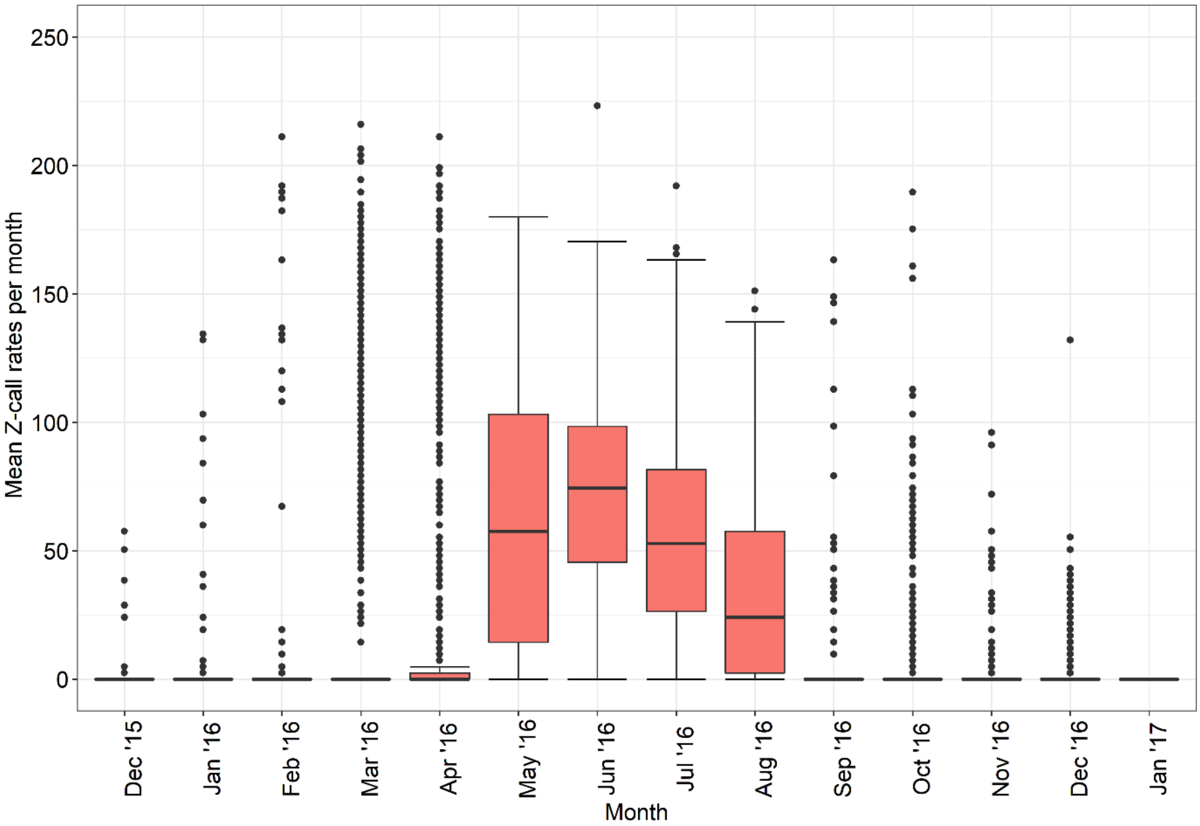

Figure 9: Monthly call rates of Antarctic blue whale Z-calls from AAR1 (shallow station) off the South African west coast. The box shows the interquartile range (denoted by upper and lower

quartiles), and the horizontal line in the box represents the median. The whiskers are denoted by the lines that extend outside the box and range from the lowest to the highest observations, and the closed circles are observations which fall beyond the range covered by the whisker.

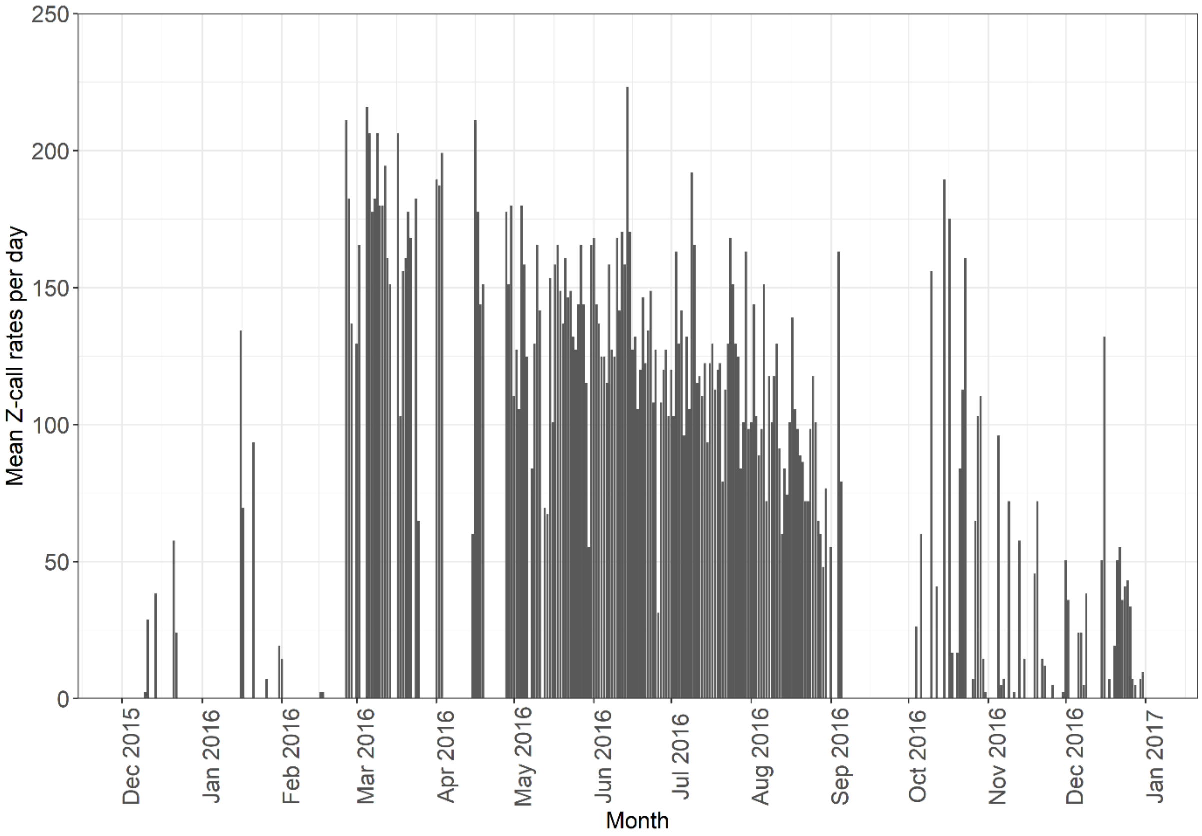

Figure 10: Mean daily call rates of Antarctic blue whale Z-calls from AAR1 (shallow station) off the South African west coast.

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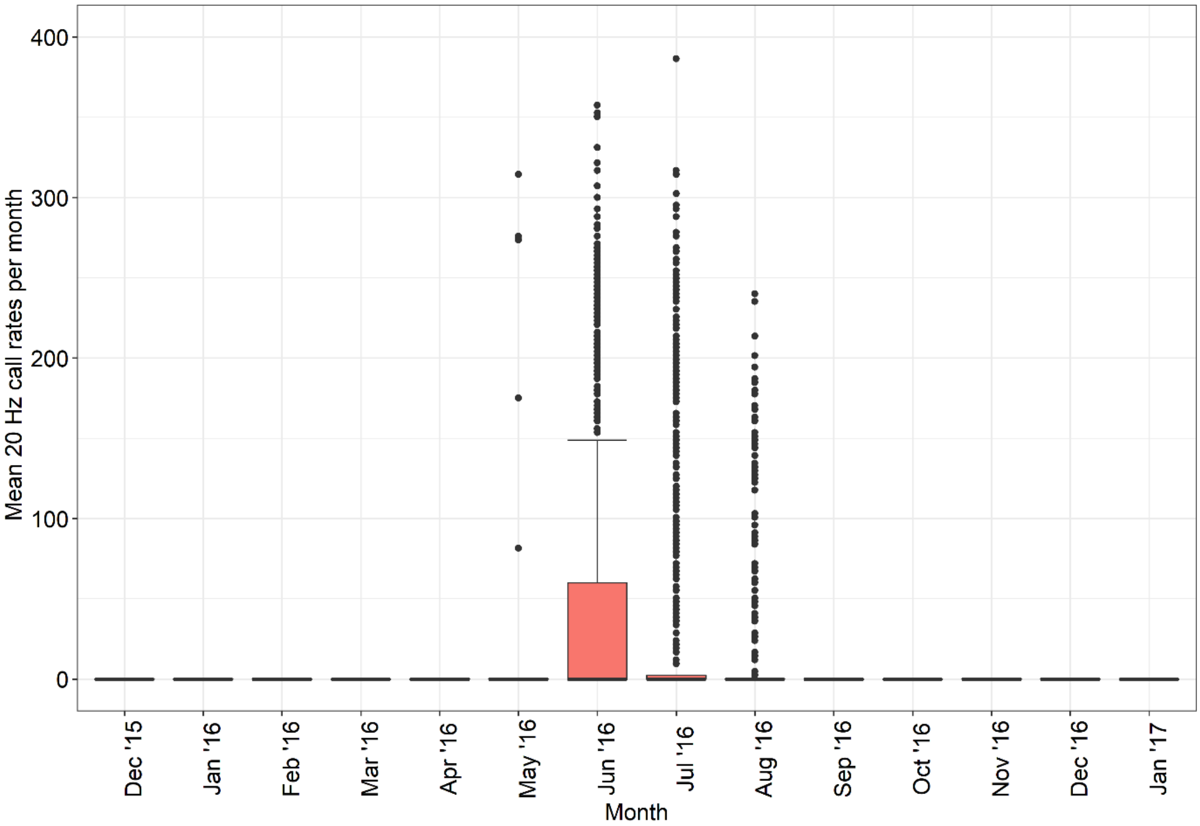

Figure 11: Monthly call rates of fin whale 20 Hz calls from AAR1 (shallow station) off the South African west coast. The box shows the interquartile range (denoted by upper and lower quartiles), and the horizontal line in the box represents the median. The whiskers are denoted by the lines that extend outside the box and range from the lowest to the highest observations, and the closed circles are observations which fall beyond the range covered by the whisker.

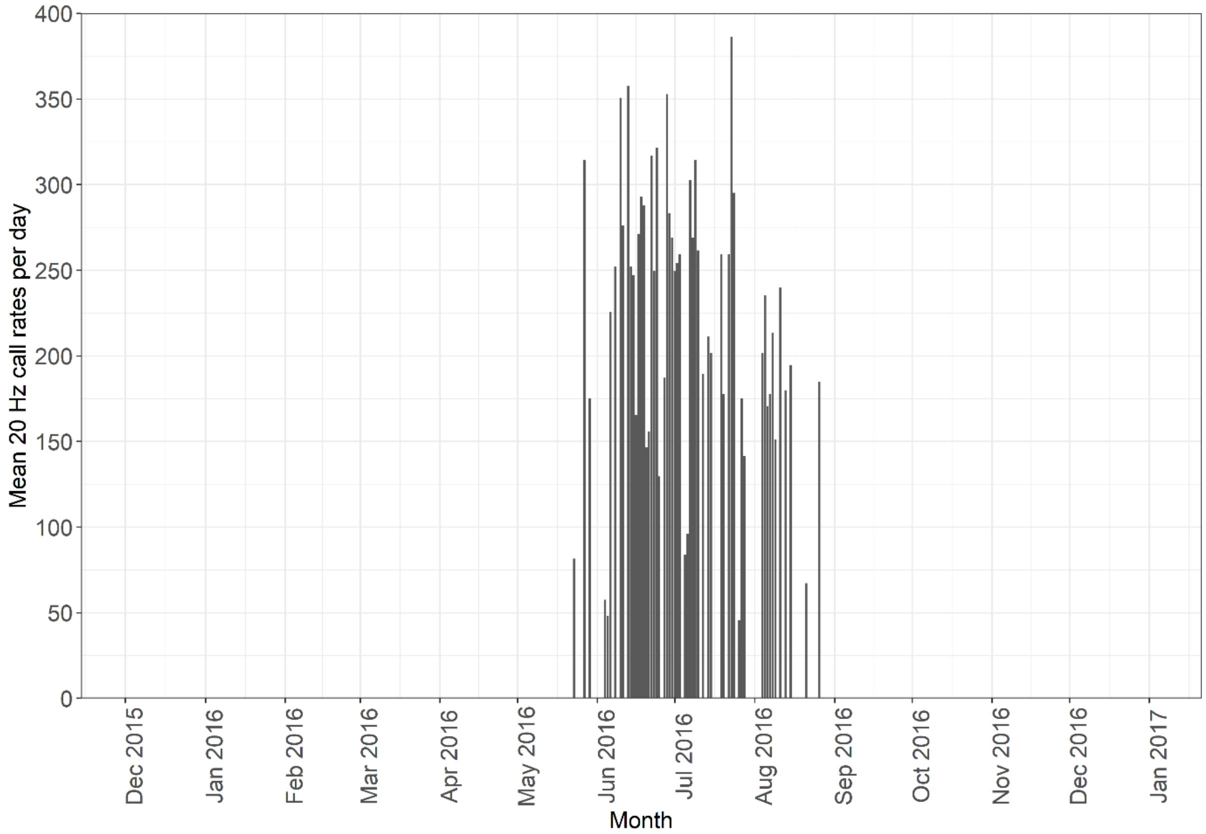

Figure 12: Mean daily call rates of fin whale 20 Hz calls from AAR1 (shallow station) off the South African west coast.

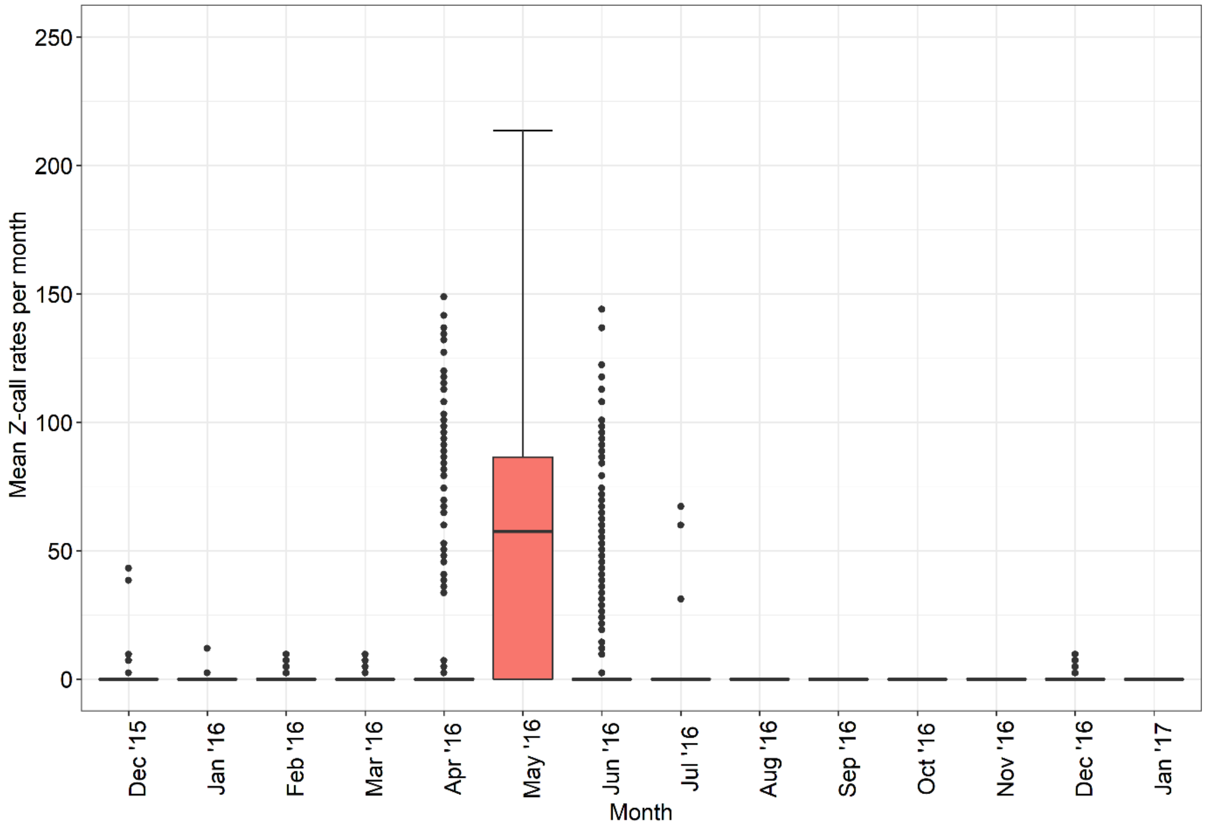

Figure 13: Mean monthly call rates of Antarctic blue whale Z-calls from AAR2 (deep station) off the South African west coast. The box shows the interquartile range (denoted by upper and lower

quartiles), and the horizontal line in the box represents the median. The whiskers are denoted by the lines that extend outside the box and range from the lowest to the highest observations, and the closed circles are observations which fall beyond the range covered by the whisker.

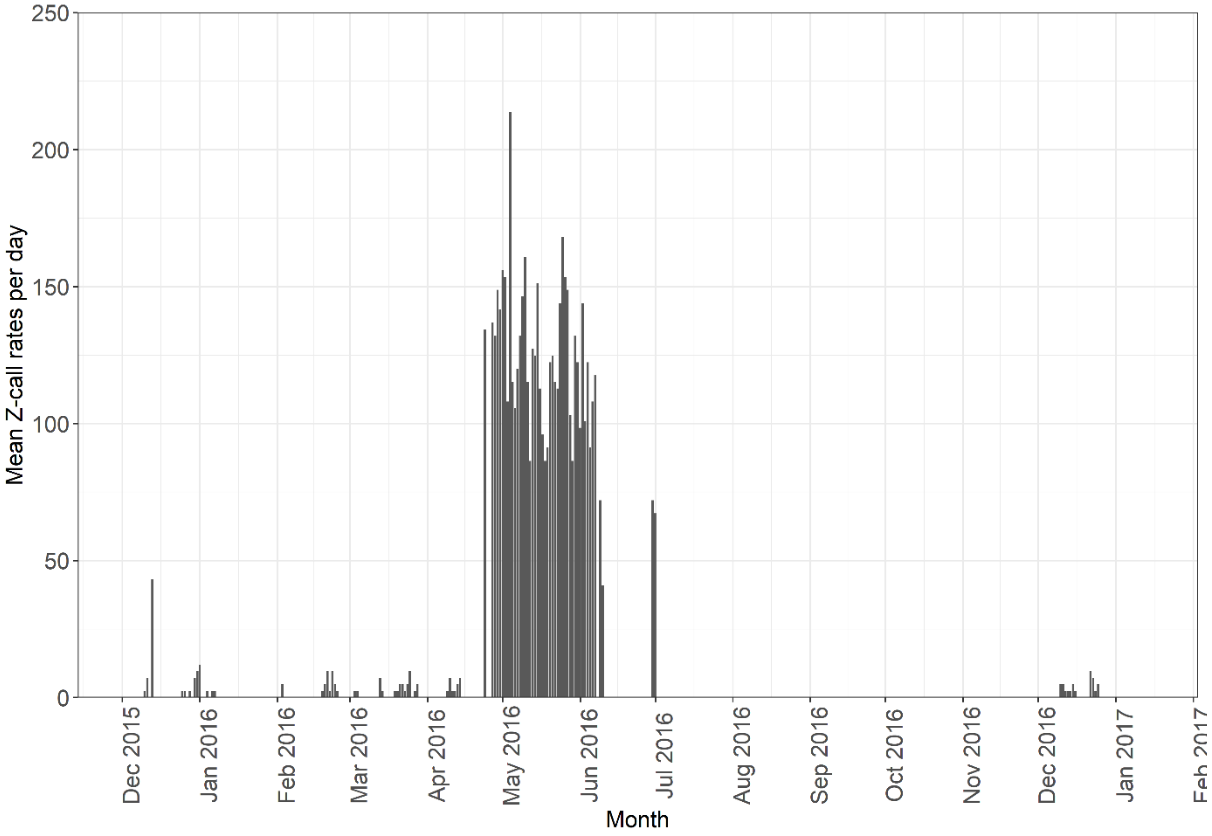

Figure 14: Mean daily call rates of Antarctic blue whale Z-calls from AAR2 (deep station) off the South African west coast.

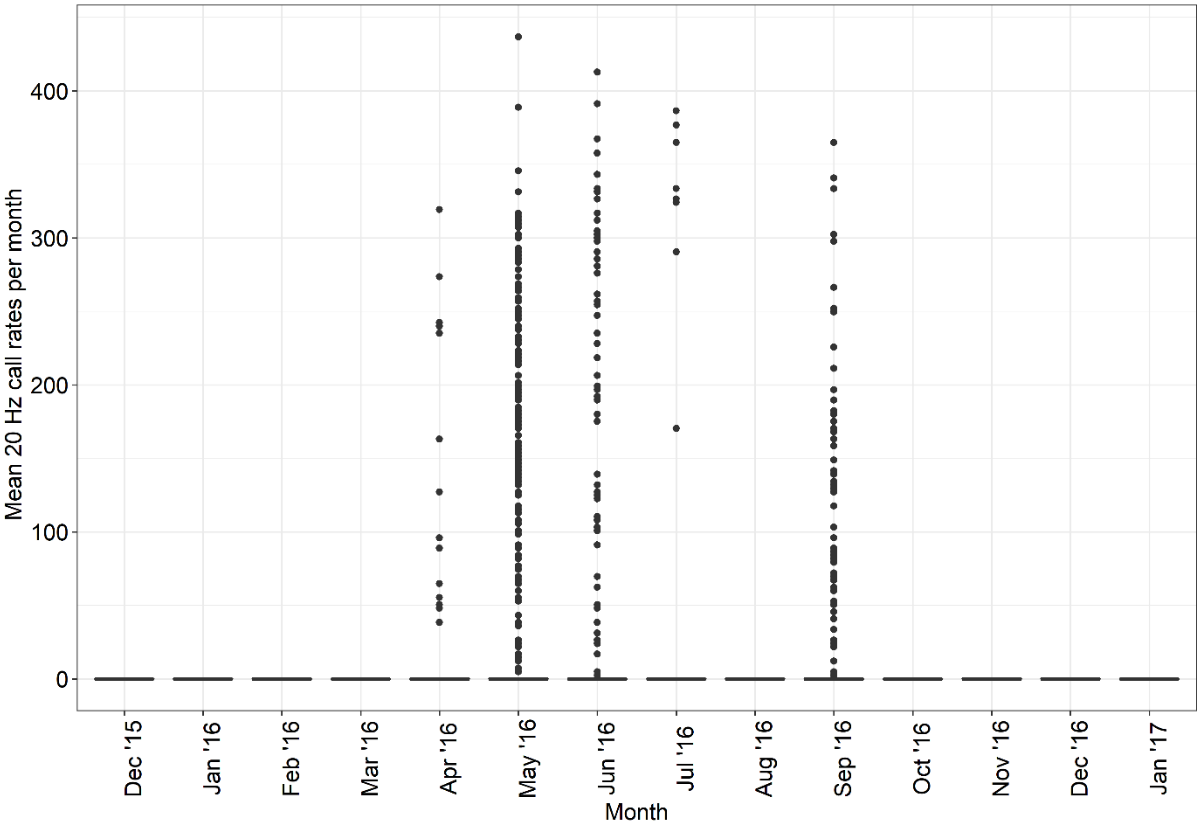

Figure 15: Mean monthly call rates of fin whale 20 Hz calls from AAR2 (deep station) off the South African west coast. The box shows the interquartile range (denoted by upper and lower quartiles), and the horizontal line in the box represents the median. The whiskers are denoted by the lines that extend outside the box and range from the lowest to the highest observations, and the closed circles are observations which fall beyond the range covered by the whisker.

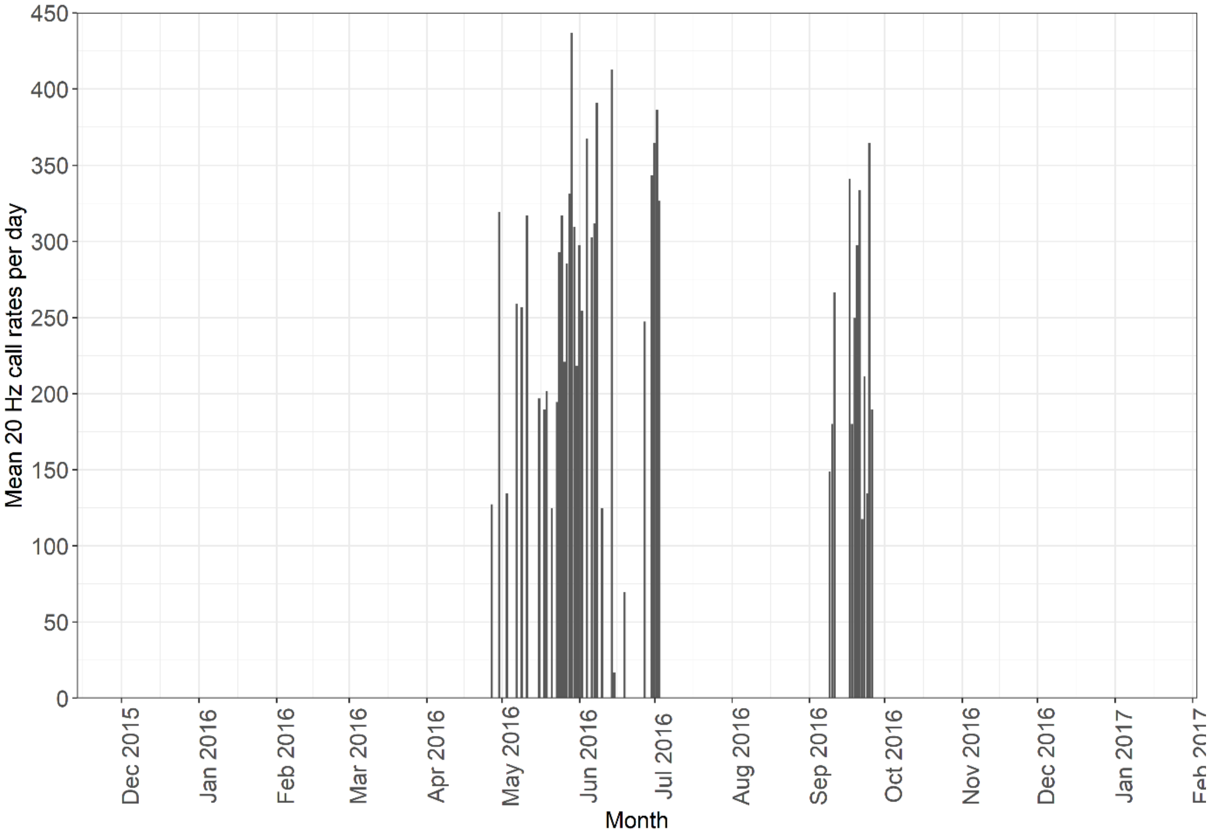

Figure 16: Mean daily call rates of fin whale 20 Hz calls from AAR2 (deep station) off the South African west coast.

3.5. Diel call occurrence by season

Around AAR1, the proportion of call occurrence for Antarctic blue whales slightly peaked at dawn in summer, during the day in autumn and spring, and at dusk in winter (Figure 17). Overall the mean diel seasonal blue whale Z-call occurrence for the light regimes was highest during dusk in autumn, winter and spring, while in summer, dawn had the highest mean (Table 5). The proportion of call occurrence for fin whales peaked during the day for both winter and autumn (Figure 18). Overall the mean seasonal fin whale 20 Hz call occurrence for the light regimes was highest during the day in autumn and at dusk in winter (Table 5). There was no significant difference in the diel call occurrence of blue whale Z-calls in all seasons; autumn (ANOVA, $F_{3,2204}$= 0.301, p>0.05), winter (ANOVA, $F_{3,2204}$= 0.529, p>0.05), spring (ANOVA, $F_{3,2180}$= 0.213, p>0.05) and summer (ANOVA, $F_{3,2876}$= 0.393, p>0.05). Similarly, fin whale 20 Hz pulses indicated no significant difference in the diel call occurrence; autumn (ANOVA, $F_{3,2204}$= 2.342, p>0.05) and winter (ANOVA, $F_{3,2204}$= 0.494, p>0.05). Overall very little diel patterns were found in the call occurrence of blue and fin whales around AAR1.

Around AAR2, the diel proportion of call occurrence for Antarctic blue whales peaked during the night and at dawn in summer, at dusk in autumn and during the day in winter (Figure 29). Overall the mean blue whale Z-call seasonal call occurrence for the light regimes was highest during dusk in autumn, dusk and night in summer, and during the day in winter (Table 6). The proportion of call occurrence for fin whales peaked during the day for autumn, dusk and night for both winter and spring (Figure 20). Overall the mean fin 20 Hz diel seasonal call occurrence for the light regimes was highest during dusk in autumn, dawn in spring, and dusk in winter (Table 6). There was no significant difference in the diel call occurrence of blue whale Z-calls in all seasons; autumn (ANOVA, $F_{3,2204}$= 0.944, p>0.05), winter (ANOVA, $F_{3,2204}$= 1.029, p>0.05), and summer (ANOVA, $F_{3,3151}$= 0.082, p>0.05). Similarly, fin whale 20 Hz pulses indicated no significant difference in the diel call occurrence; autumn (ANOVA, $F_{3,2204}$= 0.782, p>0.05), winter (ANOVA, $F_{3,2204}$= 0.107, p>0.05) and spring (ANOVA, $F_{3,2180}$= 0.294, p>0.05). Overall very little diel patterns were found in the call occurrence of blue and fin whales around AAR2. See (**Appendix** Table 7) for Tukey's HSD multiple comparisons results for diel call occurrence by season around AAR1 and AAR2.

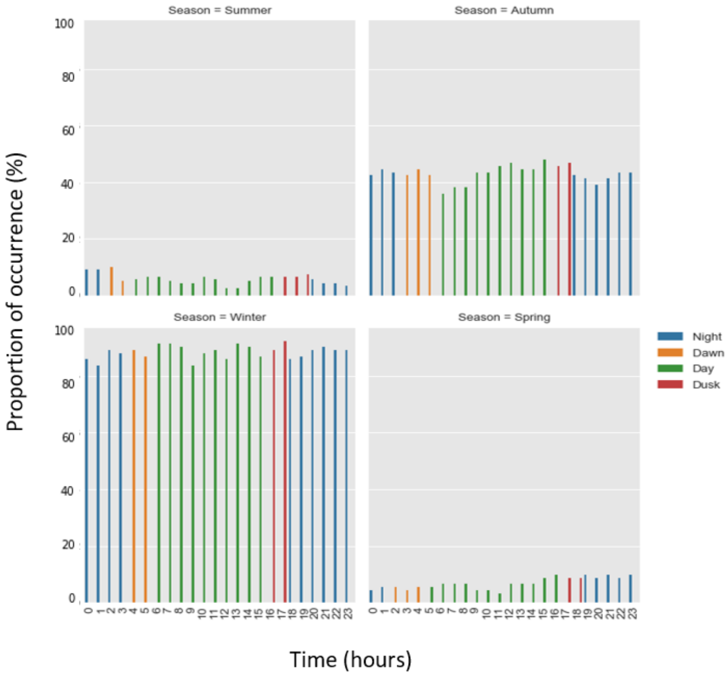

Figure 17: Diel proportion of call occurrence per season and per hour for blue whale Z-calls from AAR1 (shallow station) off the South African west coast. It should be noted that times presented in this study are in UTC format.

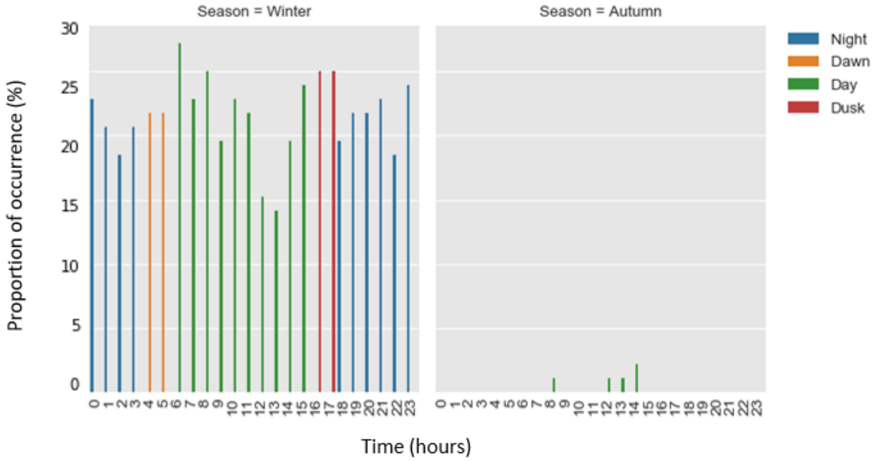

Figure 18: Diel proportion of call occurrence per season and per hour for fin whales 20 Hz calls from AAR1 (shallow station) off the South African west coast. No calls were recorded in summer and spring. It should be noted that times presented in this study are in UTC format.

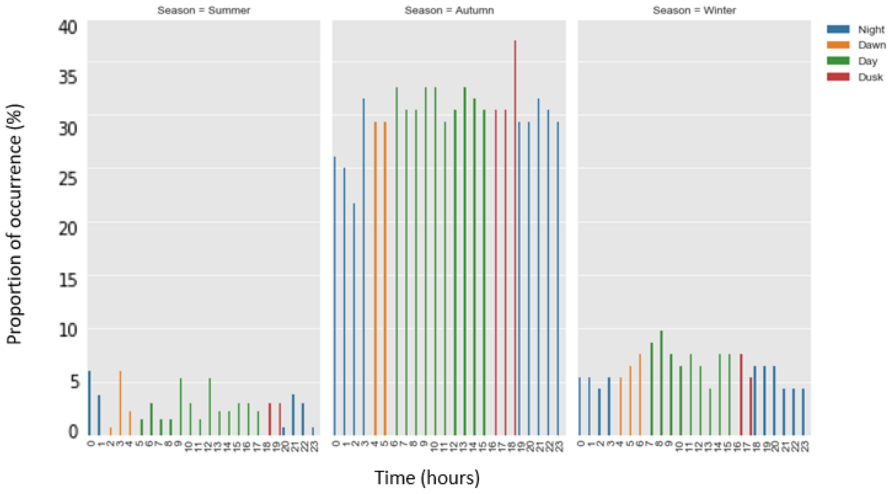

Figure 19: Diel proportion of call occurrence per season and per hour for blue whale Z-calls from AAR2 (deep station) off the South African west coast. No calls were recorded in spring. It should be noted that times presented in this study are in UTC format.

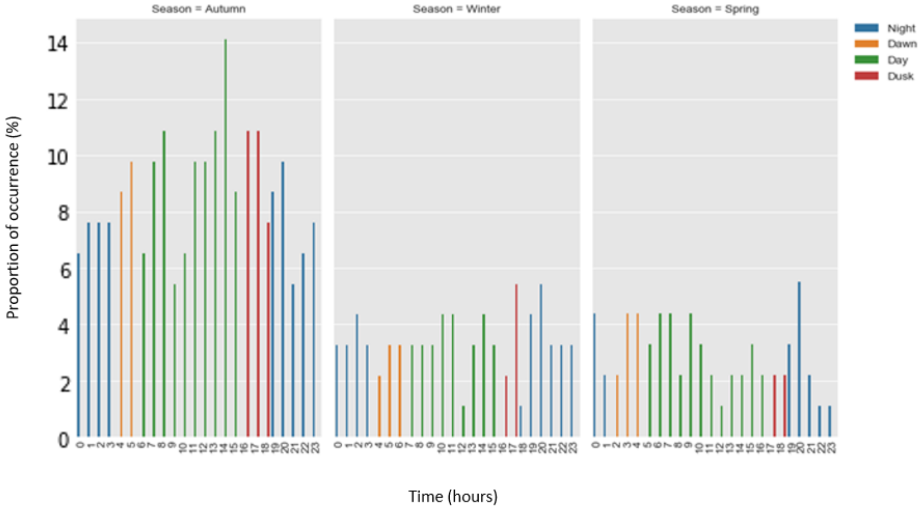

Figure 20: Diel proportion of call occurrence per season and per hour for fin whales 20 Hz pulse from AAR2 (deep station) off the South African west coast. No calls were recorded for summer. It should be noted that times presented in this study are in UTC format.

3.6. Diel call rates by season

From AAR1, blue whale diel Z-call rates peaked during the day and night in spring, day in autumn and winter and night in summer (Figure 21). There was a temporal stratification of diel call rate peaks in spring and winter. Overall the mean blue whale diel Z-call seasonal call rates for the light regimes was highest during dusk in autumn, night in spring, and dawn in both summer and winter (Table 8). Fin whale 20 Hz call diel call rates peaked during the day in autumn, and peaked slightly during dawn in winter, with no calls for spring and summer (Figure 22). Overall the mean fin whale 20 Hz seasonal call rates for the light regimes was highest during the day in autumn and during dawn in winter (Table 8). There was a significant difference in the diel call rates by hour of blue whale Z-calls only in winter (ANOVA, $F_{3,2204}$= 5.532, $p<0.05$) and spring (ANOVA, $F_{3,2180}$= 2.73, $p<0.05$). Autumn (ANOVA, $F_{3,2204}$= 0.919, $p>0.05$) and summer (ANOVA, $F_{3,2876}$= 1.904, $p>0.05$) did not show any significant differences in the diel call rates by hour of blue whale Z-call rates. Fin whale 20 Hz pulses indicated no significant difference in the diel call rates by hour in autumn (ANOVA, $F_{3,2204}$= 2.047, $p>0.05$) and winter (ANOVA, $F_{3,2204}$= 0.338, $p>0.05$).

From AAR2, diel blue whale Z-call rate peaked during the day in autumn, winter and summer, with no calls recorded in spring (Figure 23). Overall the mean diel blue whale Z-call seasonal call rates for the light regimes were highest during day in both autumn and summer, but highest in dusk for winter (Table 9). The diel fin whale 20 Hz call rates peaked during the day in autumn, and both night and day in spring and no difference in the light regimes call rates for winter. No calls were recorded for summer. There was a strong temporal stratification of diel call rate peaks in spring (Figure 24). Overall the mean fin whale 20 Hz seasonal call rates for the light regimes were highest during dusk in autumn and winter, but highest during dawn for spring (Table 9). There was a significant difference in the diel blue whale Z-call rates only in autumn (ANOVA, $F_{3,2204}$= 3.571, $p<0.05$). Winter (ANOVA, $F_{3,2204}$= 1.295, $p>0.05$) and summer (ANOVA, $F_{3,3151}$= 0.273, $p>0.05$) did not show any significant differences in the diel call rates. No significant seasonal difference was found in the diel fin whale 20 Hz call rates; autumn (ANOVA, $F_{3,2204}$= 1.495, $p>0.05$), winter (ANOVA, $F_{3,2204}$= 0.108, $p>0.05$) and spring (ANOVA, $F_{3,2180}$= 0.773, $p>0.05$).

See (**Appendix** Table 10) for Tukey's HSD multiple comparisons results for diel call rates by season around AAR1 and AAR2.

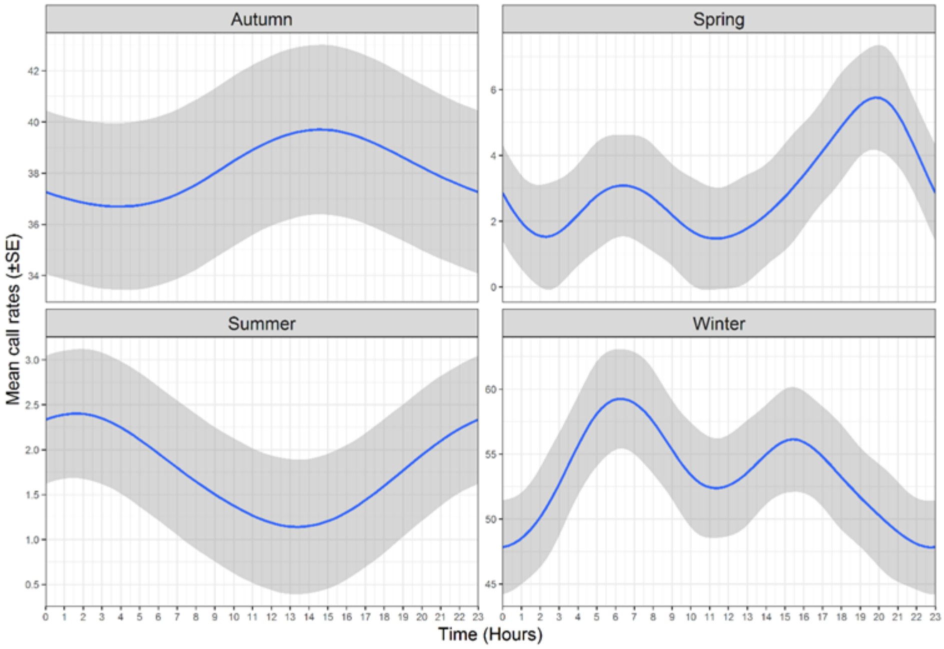

Figure 21: Seasonal circular smoothed mean diel call rates for Antarctic blue whale Z-calls from AAR1 (shallow station) off the South African west coast. The grey shaded areas of the line plot show the standard error (SE) of the smoothed mean line.

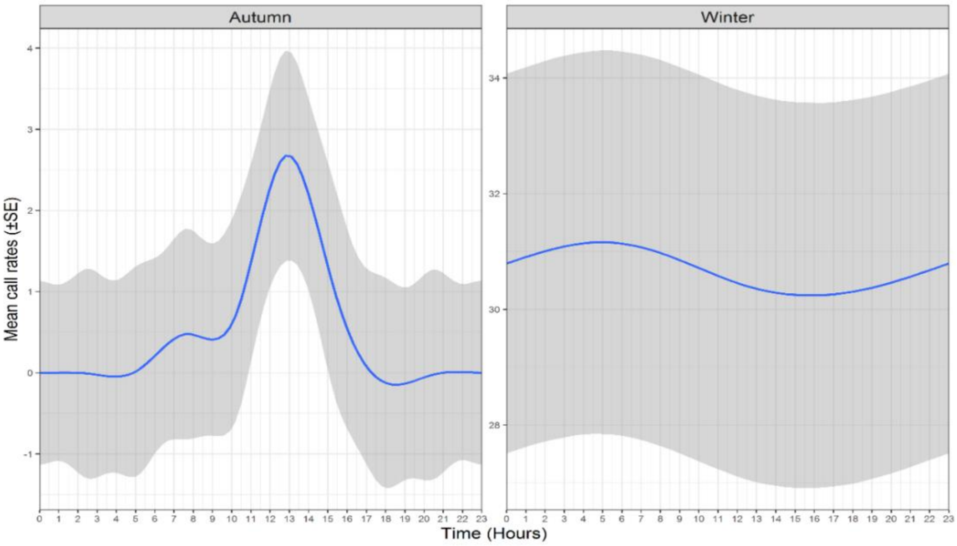

Figure 22: Seasonal circular smoothed mean diel call rates for fin whale 20 Hz calls from AAR1 (shallow station) off the South African west coast. The grey shaded areas of the line plot show the standard error (SE) of the smoothed mean line. No calls were recorded for summer and spring.

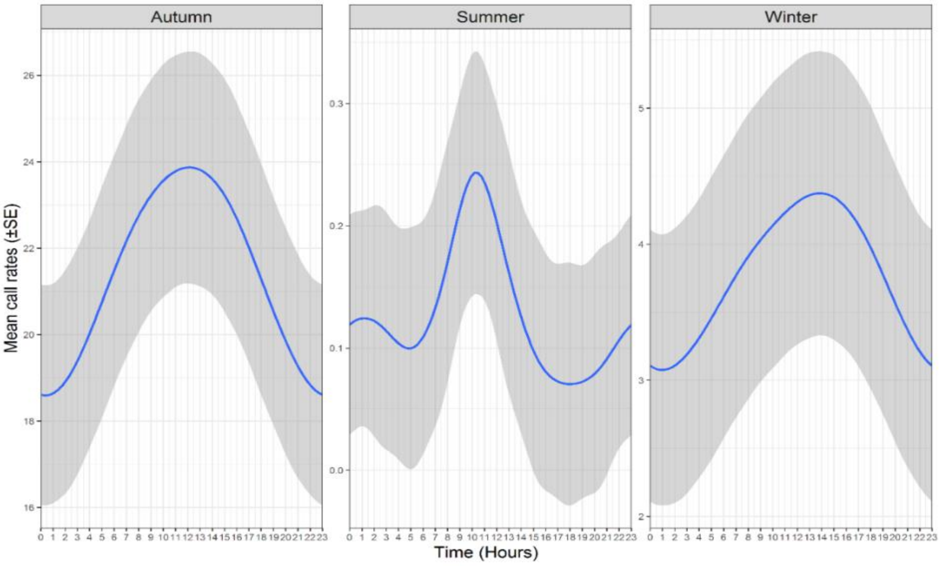

Figure 23:Seasonal circular smoothed mean diel call rates for Antarctic blue whale Z-calls from AAR2 (deep station) off the South African west coast. The grey shaded areas of the line plot show the standard error (SE) of the smoothed mean line. No calls were recorded for spring.

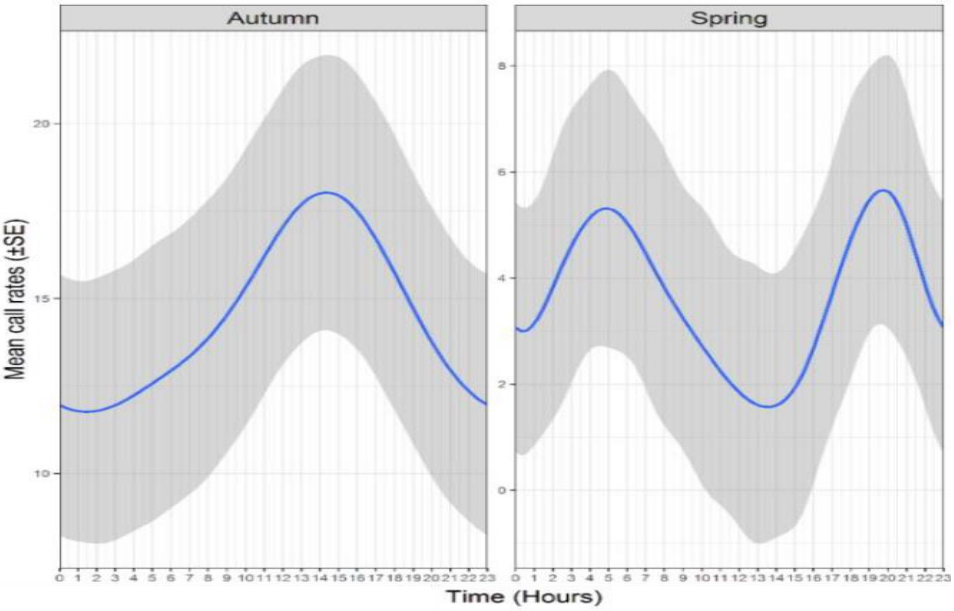

Figure 24: Seasonal circular smoothed mean diel call rates for fin whale 20 Hz calls from AAR2 (deep station) off the South African west coast. The grey shaded areas of the line plot show the standard error (SE) of the smoothed mean line. There was no difference in the light regimes call rates by hour for winter. No calls were recorded in summer.

3.7. Other identified biological signals

Calls of other baleen whale species recorded in the southern Benguela Upwelling System in this study included those from Antarctic minke whales, humpback whales and southern right whales around both AAR1 and AAR2.

Antarctic minke whales have recently been recognised by their ‘bioduck’ call signal which had been recorded but remained unidentified in the Southern Ocean for decades (Risch *et al*. 2014). These vocalisations are characterised by their highly rhythmic pattern which consists of bouts of short (0.1 s) pulses, which frequently occur at regular intervals (Matthews *et al*. 2004, Risch *et al*. 2014). Antarctic minke whale bioduck calls found in this study are consistent with those found in previous studies (Risch *et al*. 2014; Dominello and Širović, 2016; Shabangu *et al*. 2020b) (Figure 25). Antarctic minke whale ‘bioduck’ calls were detected seasonally in AAR1 and AAR2 particularly in austral spring of 2016 (September & October) and austral summer of 2015 (December) respectively in this study.

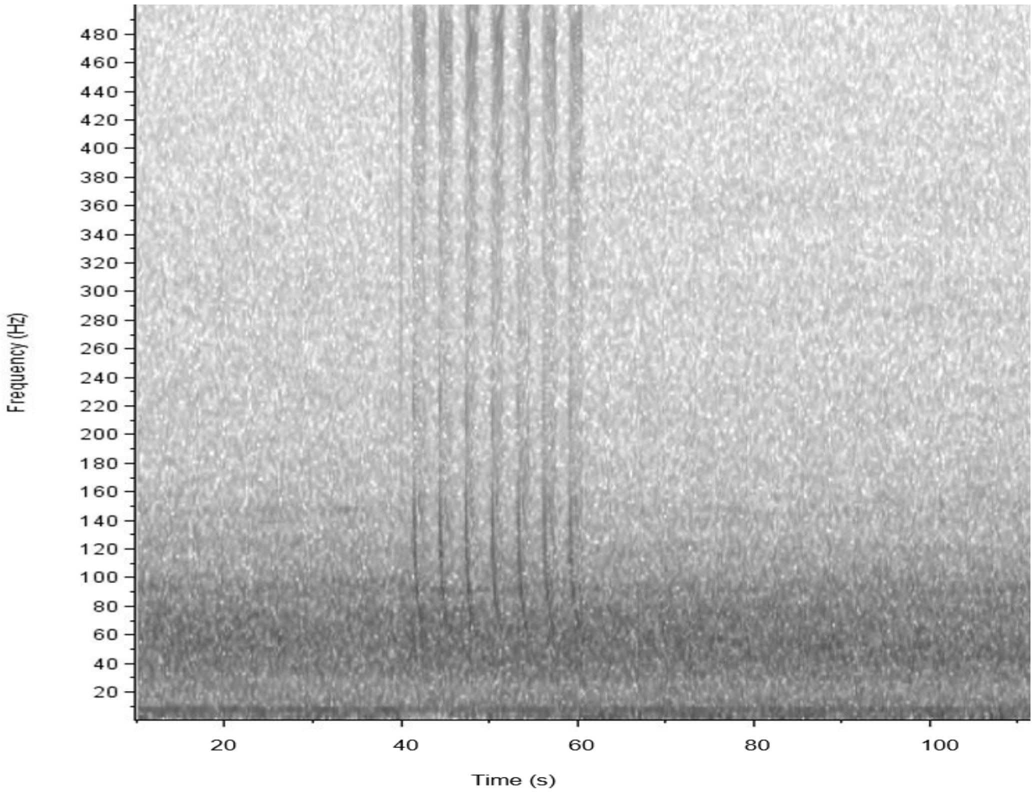

Figure 25: Spectrogram of Antarctic minke whale bioduck call sequence recorded from AAR 1 off the South African west coast ; Spectrogram parameters (16,384-point FFT, 50% overlap, 4751 hop size, Hanning window).

Humpback whales typically produce a variety of complex vocalisations (this includes up-calls, down-sweeps, tonal sounds and a combination of up- and down-sweeps) with main frequencies below 4 kHz (Payne and Payne, 1985). The different vocalisations either occur as a) single signals, b) in short sequences with no noticeable structure or c) structures into phrases/themes, which sequentially are organized into a pattern that recurs in a steady order to make up what is known as a humpback song (Payne *et al*. 1983). The common sound units within humpback songs typically last from 0.1 to 10 seconds (Payne and Payne, 1985) but song can last for 5 and 20 minutes before the structured sequence is repeated (Cholewiak *et al*. 2013). In this study only humpback songs were detected in both AARs.

Humpback whale songs detected around AARs1 and 2 off the South African west coast were variable in the spectrogram frequency range, duration and repetition rate (Figure 26). The basic sound units occurred from 2-8 seconds, while songs occurred up to 20 minutes with medium to high frequency (200 Hz to 4 kHz). Around AAR 1, humpback vocalisations occurred in winter (June, July, August) and spring (September, October, November) of 2016. Around AAR2, humpbacks occurred in summer (December) of 2015, autumn (May), winter (June, July) and spring (September, October, November) of 2016.

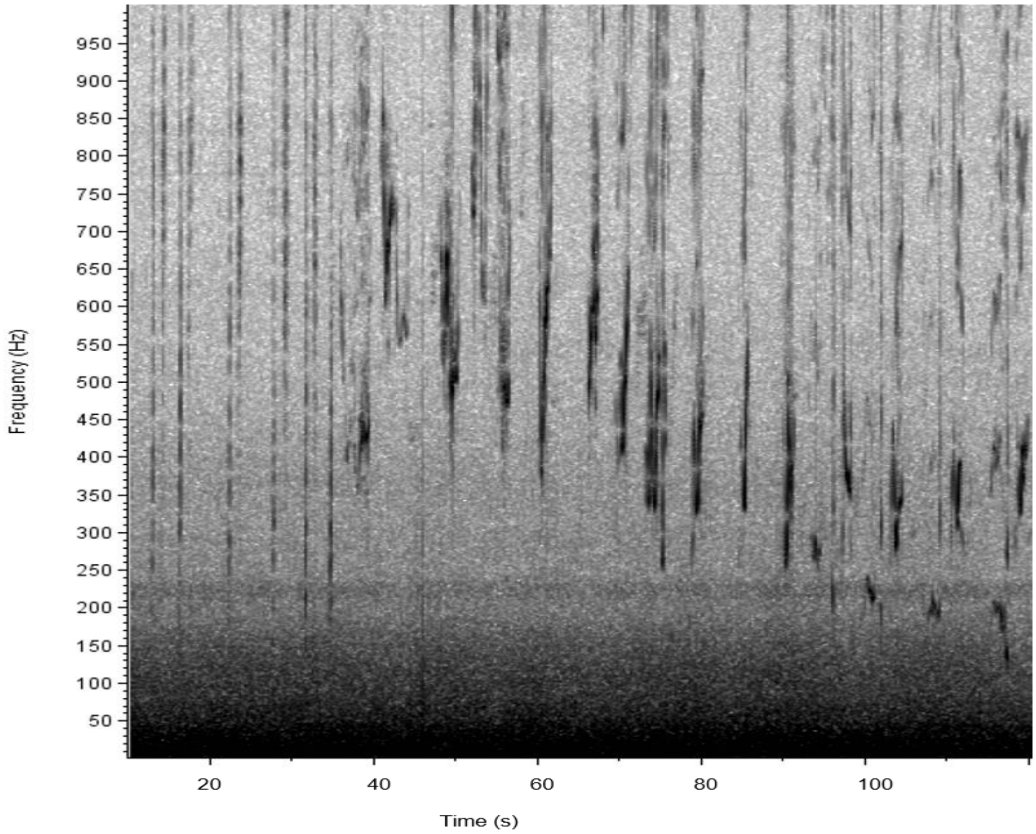

Figure 26: Spectrogram of humpback song recorded from AAR 2 (deep station) off the South African west coast; Spectrogram parameters (8,192-point FFT, 50% overlap, 3350 hop size, Hanning window).

Southern right whales are known to have an extensive acoustic repertoire with frequencies between 50 and 500 Hz (Cummings *et al*. 1972, Clark, 1982). Additionally, southern right whales produce a short, distinctive broadband explosive sound termed the gunshot sound (Hofmeyr-Juritz & Best, 2011; Shabangu *et al*. 2021). In this study, a few gunshot sounds were detected in AAR2 on single days in February, May, November and December 2016 (Figure 27).

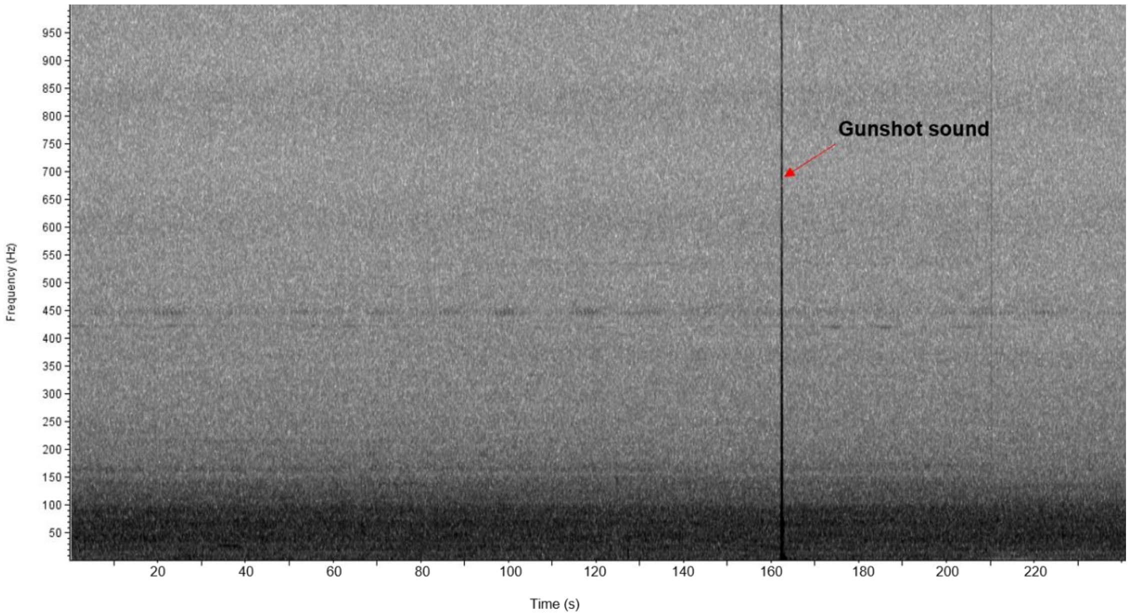

Figure 27: Spectrogram of southern right whale gunshot sound recorded from AAR 2 (deep station) off the South African west coast; Spectrogram parameters (8,192-point FFT, 50% overlap, 3350 hop size, Hanning window.

3.8. Unidentified signals

Several unidentified and assumed to be biological signals were found in the passive acoustic data at both the shallow and deep stations. Most of these signals occurred only once or twice (See **Appendix** Figures 32-36), However, three signals were found to occur frequently in this study and are described below. Sample spectrograms of other unidentified signals are attached as appendices for further reference.

The first unidentified sound consisted of a single tonal near 22 Hz and is denoted as the M-call in this study. The call lasted approximately 8 to 10 seconds, and occurred in long sequences, at recurring intervals of about 2.2 minutes (Figure 28). Around AAR1 (shallow station), the M-call occurred sporadically during 2016 in autumn (April), winter (July) and spring (October & November) (Figure 8a). Around AAR2 (deep station), the M-call occurred sporadically in summer of December 2015 and autumn of May 2016 (Figure 8b).

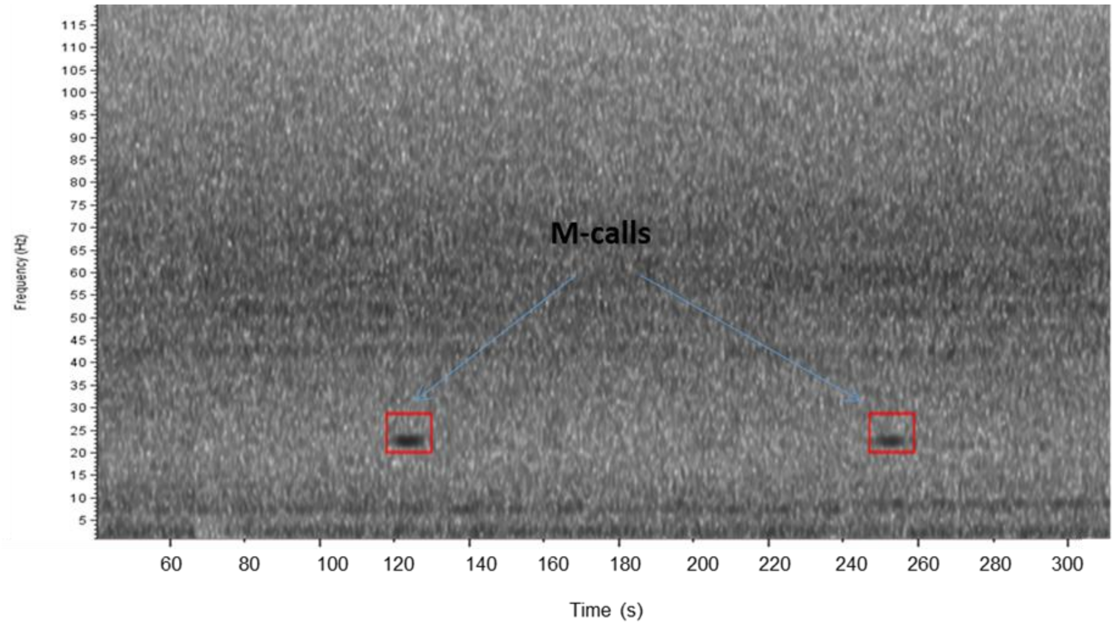

Figure 28: Spectrogram of M-call recorded from AAR 1 (shallow station) off the South African west coast; Spectrogram parameters (16,384-point FFT, 50% overlap, 4105 hop size, Hanning window.

The second unidentified sound (hereinafter referred to as unidentified sound two) composed of rapid series of frequency modulated pulses between 600 to 800 Hz which could not be assigned to any species in the acoustic analysis (Figure 29). This sound occurred in autumn (May) of 2016 only from AAR 2 (deep station).

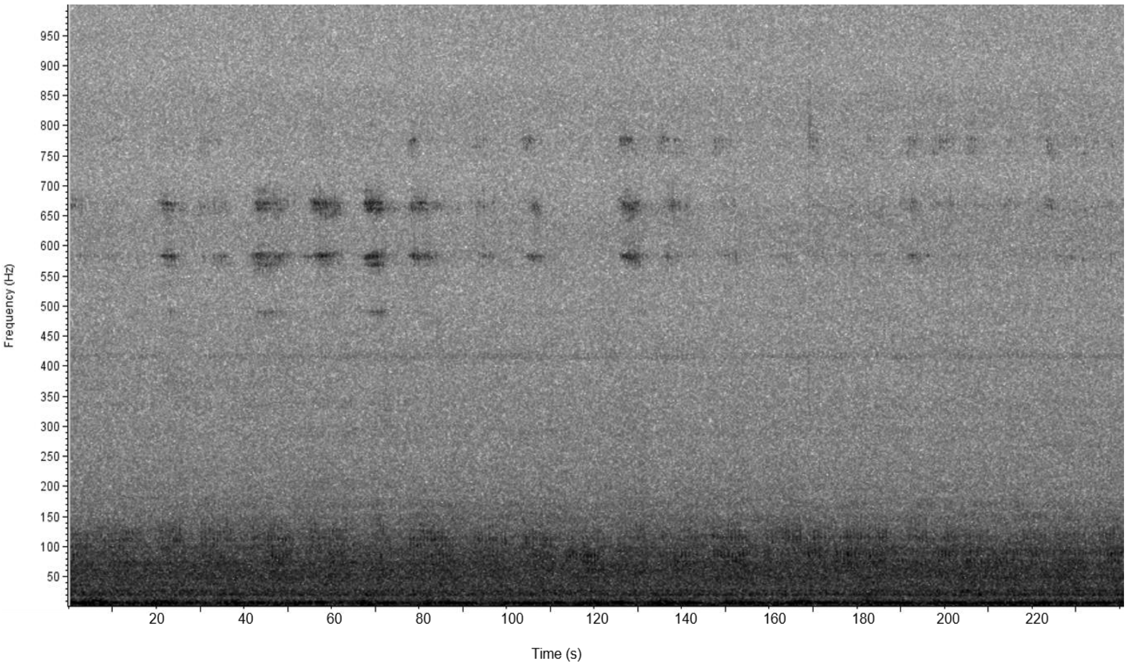

Figure 29: Spectrogram of unidentified sound two recorded from AAR2 (deep station) off the South African west coast; Spectrogram parameters (16,384-point FFT, 50% overlap, 5496 hop size, Hanning window).

The third unidentified sound (hereinafter referred to as unidentified sound three) comprised regularly repeated pulses at low frequencies (define) which could not be assigned to species-level in the acoustic analysis (Figure 30). This sound occurred sporadically from AAR 1 (shallow station) in October, November, December of 2016. From AAR2 (deep station), it only occurred in January of 2017.

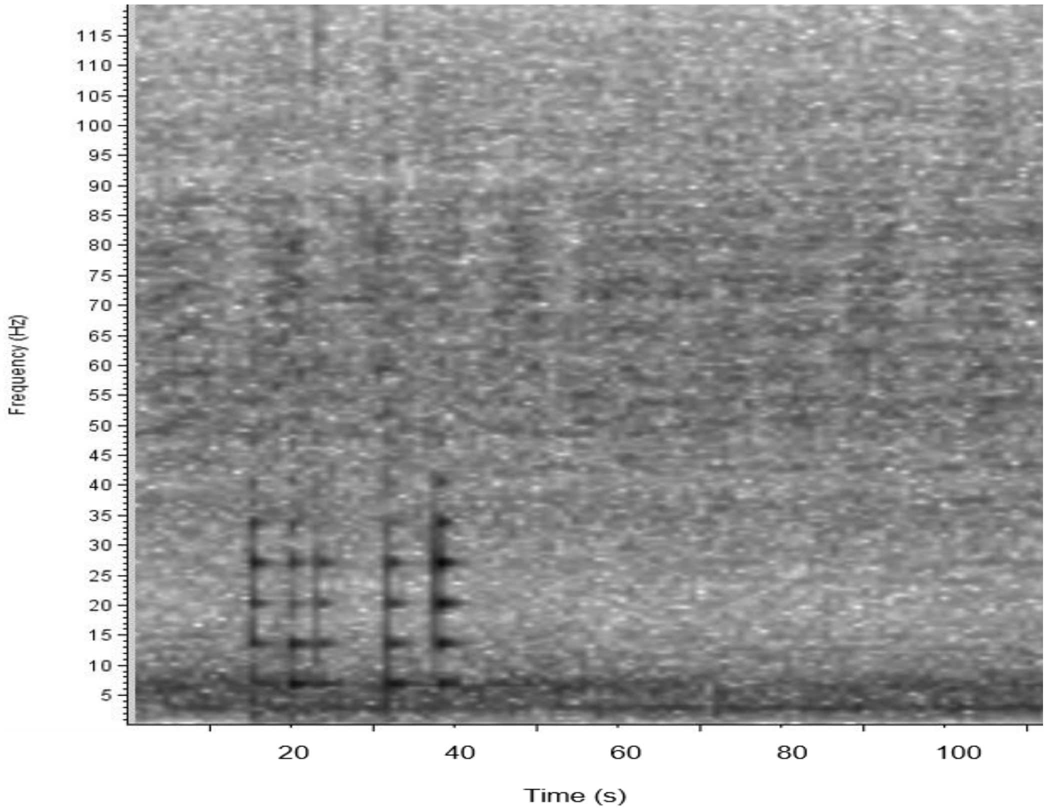

Figure 30: Spectrogram of unidentified sound three recorded from AAR1 (shallow station) off the South African west coast; Spectrogram parameters (16,384-point FFT, 50% overlap, 4100 hop size, Hanning window).

3.9. Anthropogenic signals

Other acoustically detected signals present during the recording period in both the shallow and deep station included anthropogenic sources such as shipping / vessel activity. Vessels produced narrow-band lines at low frequencies lower than 1 Hz (Figure 31). Although vessel noise occurrence was sporadically detected from both AARs over the recording period, vessel noise was more frequent from AAR 2 (deep station), with peaks in the austral autumn (May) and the austral winter (June).

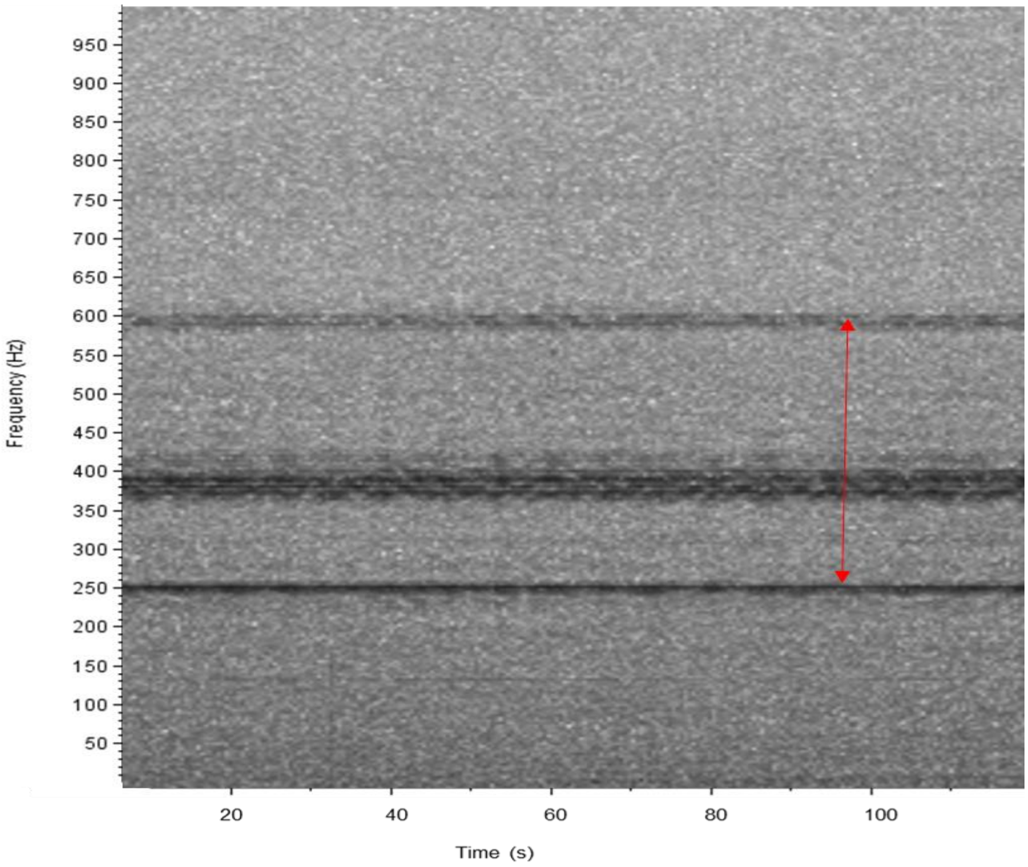

Figure 31: Spectrogram of vessel noise (denoted by red arrow) recorded from AAR 2 (deep station) off the South African west coast; Spectrogram parameters (16,384-point FFT, 50% overlap, 6803 hop size, Hanning window)

Chapter 4: Discussion

Antarctic blue and fin whales have a broad-based, highly seasonal migratory distribution and are widely distributed in the Southern Hemisphere. Populations undertake seasonal migrations between high latitude feeding grounds in summer and low latitude breeding grounds in winter (Mackintosh, 1966; Best, 2007). However, no clear migratory behavior has been described for these whale populations, and locations of respective breeding areas are still uncertain (Branch *et al*. 2004; Best, 2007; Samaran *et al*. 2013; Thomisch *et al*. 2016).The temporal and spatial presence both in the Southern and the Northern Hemisphere have been acoustically described in various regions worldwide such as the Antarctic (e.g. Širović *et al*. 2004, 2007), South Indian Ocean (Samaran *et al*. 2010, 2013; Leroy *et al*. 2016; Balcazar *et al*. 2017), South-east Pacific (Stafford *et al*. 2001, 2005), North Atlantic (Mellinger and Clark, 2003), west coast of Africa (Best, 1998; Figueiredo and Weir, 2014; Shabangu *et al*. 2019; Thomisch *et al*. 2019), Equatorial Atlantic (Haver *et al*. 2017; Samaran *et al*. 2018) and North Pacific (Oleson *et al*. 2007, 2014). Passive acoustic monitoring here enabled the study of seasonal acoustic occurrence and behaviour of Antarctic blue and fin whales in a low latitude region, which expands our knowledge of these species that was previously limited given their visual sighting and dated historical information.

4.1. Acoustic occurrence

Off the South African west coast, blue and fin whales were acoustically detected based on their characteristic calls in the passive acoustic data of both AAR1 and AAR2. It should be emphasised that an absence of acoustic detections does not essentially mean that whales are not present, just that they are not vocalizing. The results showed that AAR1 (1,118 m) had a year-round acoustic occurrence (with a strong peak across the May-August period), and also a higher number of blue whale Z-calls (88,859) than AAR2. Conversely, AAR2 (4,481 m) showed a more marked seasonal acoustic occurrence (centred in May as a Mn peak) and a lower number (23,190) of blue whale Z-calls, with no call occurrence in spring (an Ms peak) and a slight increase in December. The year-round acoustic occurrence of blue whales off the west coast of South Africa contrasts the traditional migration theory that all blue whales are distributed at higher latitudes during the austral summer (Brown, 1954; Best, 1998;2007), suggesting that their migration behaviour is more complex and not obligate (Thomisch *et al*. 2016).

Similar year-round acoustic occurrence of blue whales has also been reported in the Equatorial Atlantic (Haver *et al*. 2017; Samaran *et al*. 2018), Indian Ocean (Samaran *et al*. 2010, 2013; Leroy *et al*. 2016) and more recently off Namibia (Thomisch *et al*. 2019). Equally, Thomisch *et al*. (2019) suggested this year-round presence to be heavily influenced by availability of prey in high-productive waters of the Benguela region and the associated high-turbulence eddy regime. Eddy regimes are important as they serve as retention zones and resultantly affect the distribution of nutrients (Hutchings *et al*. 1995). However, it is intriguing that the blue whale feeding associated D-calls were not detected from our data with year round acoustic occurrence since these were detected in the year with seasonal blue whale acoustic occurrence (Shabangu *et al*. 2019). The absence of D-calls during this year-round blue whale presence could be because this call type is rarely produced and it has a short detection range given its slightly higher frequency (Oleson *et al*. 2007). Best (1967) observed stomachs of blue whales whaled off the west coast of South Africa to contain crab larvae (megalopa), indicating that these whales were feeding in South African waters. The year-round occurrence of blue whales in AAR1 supports the notion that these animals can possibly sustain themselves year-round through opportunistic feeding hence the detection of presumed feeding associated blue whale D-calls by Shabangu *et al*. (2019) off the west coast of South Africa.

The higher calls detected around AAR1 likely indicates that blue whales could be preferring water depths around 1000 m that are associated with biological productive conditions (Best, 1998). An earlier study of blue whales off the west coast of South Africa by Shabangu *et al*. (2019) also seasonally detected more calls (no occurrence of calls in the summers of 2014 and 2015) around 1000 m water depth than at 850 m, further supporting this water depth to be important for blue whales. Fin whales 20-Hz pulses showed a seasonal acoustic occurrence at both AARs, with the highest number of calls around AAR1 (28,697) than AAR2 (23,403). Shabangu *et al*. (2019) also seasonally detected higher fin whale 20 Hz pulses (53,964) in waters at 1,118 m. Similarly, more sounds of Antarctic minke whales *B. bonaerensis* and sperm whales *Physeter macrocephalus* were also detected around water depths of 1000 m (Shabangu *et al*. 2020b, Shabangu and Andrew, 2020), further supporting the idea of the importance of this water depth for various baleen whales.

The 27 Hz blue whale and 28-18 Hz blue and fin whale choruses were higher in AAR1 than AAR2, further supporting the idea of the importance of this depth to these animals. These 27 Hz choruses have also been recently described in both high latitudes off Antarctica (Shabangu *et al*. 2020a) and low latitudes off the Namibian coast (Thomisch *et al*. 2019) and the Equator in the Atlantic Ocean (Samaran *et al*. 2018). The 27 Hz choruses are often associated with an overlay of individual Z-calls in continuous bands particularly when the call rate of the species is high and the animals are distant to the recorder. Shabangu *et al*. (2019) did not detect any choruses in both AARs, suggesting an increase in the blue whale population in the area for some years, as seen in the recent increase in the recording of this call by various researchers worldwide (Leroy *et al* 2016; Thomisch *et al*. 2019). Both the 27 Hz and 28-18 Hz chorus detected in this study generally follow a similar trend as the seasonal variations of call numbers. This trend has also been observed for the 27 Hz chorus by Thomisch *et al*. (2016), Leroy *et al*. (2016) and Shabangu *et al*. (2020a). Although Thomisch *et al*. 2016 and Leroy *et al*. (2016), quantified this as the proportion of time when the chorus energy was higher than the ambient noise, and termed it the blue whale index (BWI) and chorus to noise-without-chorus ratio (CNR) respectively. The 27 Hz and 28-18 Hz chorus typically present difficulty in delineating individual Z-calls and 20 Hz pulses as a result of high species call rate. As such, the automated detector could possibly have introduced bias in the numbers of Z-calls and 20 Hz pulses in this study.

Generally, vocalizing animals in a given area may change on a yearly basis, since the number of annual detections changes between years at a particular station and suggests non-homogeneity among stations (Sirovic *et al*. 2004, 2013; Leroy *et al*. 2016). This inter-annual variability essentially suggests that individuals in a population may alter migrations between years or seasons, as observed during commercial whaling (Stafford *et al*. 2004). Factors such as water depth, month of the year, environmental conditions, AAR deployment, and changes in AAR seasonal detection ranges may cause this inter-annual variability. In this study, both AAR1 and AAR2 had similar sampling configurations and deployment periods, yet AAR1 had significantly higher numbers of Z-calls (88859). This is also significantly higher than what Shabangu *et al*. (2019) detected in both AAR1 (2602) and AAR2 (6114) off the west coast of South Africa, although sampling configurations and deployment periods differed from this study.

Detection range estimations of whale long range calls are affected by factors such as the surrounding conditions of the acoustic recorder, the source level, background noise level, bathymetry and the depth of the vocalizing whale (Sirovic *et al*. 2015). These parameters are not well understood and minor differences in their estimation may significantly influence the detection range. In the Indian Ocean, Samaran *et al*. (2010) detected blue whale Z-calls at a range of approximately 200 km (hydrophone placed within the sound channel). Sirovic *et al*. (2007) estimated a maximum of 1300 km in the Southern Ocean (hydrophone positioned on the seafloor), and Thomisch *et al*. (2016) estimated a maximum range of 700 km in the Wedell Sea of the Southern Ocean. Fin whale call detection ranges in the Southern Ocean varied with the levels of ambient noise from 10 km–100 km (Širović *et al*. 2007). In the northern Benguela, Thomisch *et al*. (2019) found a detection range of 200 km off the Namibian coast. However, Shabangu *et al*. (2019) found significantly less detection ranges of 60 km in the shallow waters off the South African west coast, possibly due to factors including but not limited to; background noise, sea state conditions, bathymetric properties, recorder types and source levels. In this study, it is assumed that the distance at which blue and fin whale calls can be detected was similar to the range as found by Shabangu *et al*. (2019) for AAR1 However, this detection range may have been larger for this study given the occurrence of 27 Hz and 28-18 Hz choruses (i.e. previously not detected by Shabangu *et al*. 2019), which generally have larger detection range than individual Z-calls and fin 20 Hz calls (Leroy *et al*. 2016). For the AAR2, it is generally assumed that the receiver would have a greater detection range than in the AAR1 because of the increased water depth that allows for better sound propagation with bathymetric influence. Conversely, the AAR1 detection ranges would be limited due to the shallower environment, higher noise levels because of elevated inshore ship's traffic, and acoustic properties of the bottom could be crucial for range estimates, although detection ranges could possibly also extend further offshore. Regardless of these limitations, the location and placement of the acoustic recorders used in this study were chosen to ensure the maximum probability of detection in both AARs.

4.2. Comparability of the acoustic seasonality to seasonality recorded in whaling data.

Previous understandings of blue whale migrations and seasonal abundances have been heavily based on historic catch data. Prior to 1913, Olsen (1914) found blue whales to be present off the Cape Province from May to June. Catches from the Saldanha Bay stations on the west coast of South Africa between 1922 and 1928 showed bimodal seasonality centred on May to July and August to October peaks (Harmer, 1931; Best, 2007). Off both Namibia and Angola catches (1924 to 1927) showed a single unimodal seasonality in July and August respectively (Harmer, 1931; Best, 2007). Fin whales were mostly abundant from May to November in the northern and southern Benguela ecosystem (Best 1998 ,2007). In AAR1, the highest proportion of blue whale call occurrence and rates was in May through August with a peak in July. The highest proportion of fin whale 20 Hz pulse occurrence and rates in AAR1 was in June. Alternatively, the highest proportion of blue and fin whale call occurrence and rates occurrence in AAR2 was much earlier in May, and increased again in September only for fin whales. This suggests that the majority of the vocalizing part of the blue and fin whale population gradually reaches AAR2 earlier in autumn as calls increase progressively, leaves in late winter (as calls decrease) to preferable overwintering areas closer to AAR1 or to areas further north, hence the significant call peak later in June and July for blue and fin respectively in AAR1.

Thomisch *et al*. (2019) detected Antarctic blue whale Z-calls from November 2011 to August 2012, and from November 2012 to May 2013 with significant increase of calls from autumn through winter, suggesting similarities in the arrival of whales in the southern African sub-region in the two sets of data. Shabangu *et al*. (2019) also detected an increase in blue whale Z-calls from late autumn through winter and peaks in winter off the South African west coast, although no calls occurred in summer and also no-choruses were detected. Similar peaks have also been observed in in the Indian Ocean in autumn and winter (Samaran *et al*. 2010, 2013; Leroy *et al*. 2016). This essentially shows that regardless of the inter-annual variation in the occurrence in Z-calls, these seasonal patterns are steady across the years as seen in historical catch data (Mackintosh and Wheeler, 1929; Best, 1998). In contrast, Sirovic *et al*. (2009) in the Southern Ocean detected a peak in call numbers from late summer through autumn followed by a decrease in call numbers in winter; then call numbers increasing yet again during late spring. Shabangu *et al*. (2020a) found increased proportion of blue whale occurrence above 81% from mid-January to mid-September in the Southern Ocean.

The decreased Z-calls in spring and summer possibly means that most of the vocalising population leaves these grounds to go north or south, while some populations choose to remain in this area. Mackintosh and Wheeler (1929) suggested that non-migratory whales could possibly be juvenile individuals. Off Namibia, juveniles with impoverished body states prevailed in winter catches, suggesting that these particular juveniles could possibly have not undertaken a southward migration during the previous summer but chose to overstay in wintering areas (Mackintosh and Wheeler, 1929; Thomisch *et al*. 2019). This suggests that these sexually immature individuals possibly choose to stay on the productive breeding areas for growth and increased body size (Brown *et al*. 1995). In the Southern Ocean, some adult whales are hypothesized to not undertake in the annual migration but rather stay in high latitude areas to feed, hence the year-round catches in this region (Sirovic *et al*. 2004, 2009).

Shabangu *et al*. (2019) detected fin whale calls off the South African west coast from late autumn (May) until end of spring (November) with a peak occurrence in winter (July). This peak in winter is consistent with this study, however the absence of fin whales in spring and summer for AAR1 could mean that the population could have already migrated to the south, (or offshore where the deep water peak is observed) in contrast to some blue whale population which are present year-round. This could possibly be attributed to prey limitations, and the migratory behaviour of this species as seen with other studies (Sirovic *et al*. 2013; Shabangu *et al*. 2019). Širović *et al*. (2009) recorded a small number of fin whale calls in the Antarctic by the late summer through autumn (peaking in autumn) and no calls detected for the rest of the year. Recent detection of the fin whale 99 Hz chorus indicates that whales might be present in Antarctica during periods of high sea ice concentration in winter (Shabangu *et al*. 2020a).

These complimentary patterns are consistent with the notion that the vocalizing blue and fin whales that make up the majority of the acoustic detections are migrating between summer feeding grounds off the Antarctic in summer and wintering grounds off the low-latitudes in winter. However, this is not always the case since animals also maintain year round presence in both latitudes. Furthermore, the intermittent vocal occurrence of blue whale and fin whales is consistent with suggestions of blue and fin whale migration as a gradual movement of the animals from Antarctic waters, as opposed to a bulk movement (Sirovic *et al*. 2004, 2009). The year-round (through bi-modal peaks) and seasonal occurrence of blue and fin whale occurrence possibly implies that the South African west coast may probably serve as a wintering ground and migration corridor to areas further north such as Namibia and Angola where occurrences of these species have been previously recorded (Thomisch *et al*. 2019; Figueiredo and Weir, 2014).

4.3. Diel patterns

Blue whale socialising Z-call type calls are known to follow a diel trend with higher calls emitted during the day than during the night (Stafford *et al*. 2004; Oleson *et al*. 2007; Leroy *et al*. 2016). This periodicity may be due, in part, to an energy reserving behavioural mechanism where animals socialize when their prey is at deeper waters during the day, but feed when the prey is located towards the sea surface due to diel vertical migration during the night (Stafford *et al*. 2005). However, studies by Tripovich *et al*. (2005), Stafford *et al*. (2005) and Wiggins *et al*. (2005) detected more blue whale Z-calls at night than during the day in the Australian coast and the eastern tropical Pacific, possibly to avoid feeding competition with other baleen whales. Shabangu *et al*. (2020a) further showed that diel calling pattern change with season which essentially shows variability in diel calling behaviour of animals.

Blue whales socializing in AAR1 showed peak Z-calling rates during the day in autumn, and two peaks also during the day in winter. Spring showed peak calling rates during the day and night, and summer showed peak calling rates during the night. This suggests that for autumn and winter when the blue whale where most abundant, these animals followed the known diel trends. However, these essentially differ for summer and spring possibly due to limited competition since there are fewer whales present during this period. In AAR2, peak blue whale socialising Z-call rates were observed during the day for autumn, summer and winter according to current known diel pattern trends. This is consistent with Shabangu *et al*. (2019) were higher blue whale Z-call rates were detected during the day than at night in winter off the South African west coast. In the Indian Ocean, Leroy *et al*. (2016) also detected higher blue whale Z-call rates during the day than the night suggesting higher vocal activity during this period. The rarely produced blue whale feeding associated D-calls were not detected in this study, However, Shabangu *et al*. (2019) detected a low number of these calls from dusk to midnight for the 2014 and 2015 acoustic data off the South African west coast. Similarly, Samaran et al. (2013) detected these calls at night in the Indian Ocean suggesting more feeding during this period. Although this study did not detect these calls, the year-round acoustic occurrence of blue-whale Z-calls in the AAR1 suggests some opportunistic feeding occurrence off the South African west coast as whales will need to sustain themselves during such long overstays in low latitudes, assuming these are the same whales that are calling throughout the year.

Fin whales in AAR1 showed peak calling rates during the day in autumn and peaked slightly during dawn in winter. Fin whales in AAR2 showed peak calling rates during the day in autumn, spring showed two peak calling rates during the day and night. Winter showed no difference in diel calling rate patterns. These results are also consistent with studies by Shabangu *et al*. (2019) off the South African west coast which observed that most fin peak calling rates occurred during the day in winter and autumn. Fin whale calls have no confirmed associated feeding call, but are also believed to exhibit similar feeding behaviour to blue whales. This is primarily due to the absence of temporal separation between blue and fin whales diel call rate peaks in autumn and winter, which essentially shows that both species vocalise and occur simultaneously in the Benguela ecosystem. Although there are some differences in spring and summer primarily due to a low number of blue whale calls which are generally not comparable. Sirovic *et al*. (2013) suggests that the 40 Hz pulse might be used for foraging, however this has not been widely accepted. Similarly, to Shabangu *et al*. (2020a), the results of this study show a change in diel calling pattern of blue and fin whales with season which essentially shows variability in diel calling behaviour of these animals possibly due to food availability etc. Overall, these results when grouped by time of day showed no significant diel trend in blue and fin whale calling rates for both stations. However, when the results were grouped by light regimes, AAR1 showed a significant diel trend in blue whale calling rates only in spring and winter. In AAR2, a significant diel trend in blue whale calling rates was only observed in autumn. Fin whales showed no significant diel trend calling rates in both the shallow and AAR2 across all seasons. Although significant diel call rate patterns were observed for blue whales in some seasons, these are not as clear as overall seasonal occurrence patterns suggesting that time of the day is not a reliable predictor of the vocalisation of these whales. Such a result has importance in the determination of diel duty cycling of acoustic recorders in future studies.

The continued occurrence of blue whale Z-calls and fin whale calls in both stations, the consistency of this occurrence over the years as seen in studies of Shabangu *et al*. (2019) and Thomisch *et al*. (2019), and the number of detected calls extends our knowledge of the importance of the Benguela ecosystem as a wintering area for the blue and fin whale population as previously suggested (True 1904; Mackintosh, 1966; Best, 2007). The sympatric occurrence of blue and fin whales in both stations, suggest they utilize the same geographical area for breeding purposes and that their breeding activities coincide, even though some blue whales were observed to remain much longer particularly in AAR1. Antarctic blue whale calls recorded in this study might possibly belong to some of the three recently genetically identified Antarctic blue whale populations that aggregate in Southern Ocean feeding grounds but not in the unique Southern Hemisphere winter breeding grounds (Attard *et al*. 2016). Only calls of the eastern Antarctic fin whale population were detected in both stations, suggesting longitudinal isolation between the eastern and western Antarctic fin whale populations (Širović *et al*. 2009).

4.4. Other biological signals

In addition to the detection of the key species of this study, other biological signals of Antarctic minke whales, humpback whales and southern right whales were identified by means of their distinct, species-specific calls in the passive acoustic data off the South African west coast.

Antarctic minke whales occur mainly in the Southern Hemisphere. Their acoustic presence has been detected in the Antarctic (Risch *et al*. 2014; Dominello & Sirovic, 2016; Shabangu *et al*. 2020b), South Pacific (Matthews *et al*. 2004), Atlantic (Shabangu *et al*. 2020b), Indian Ocean (Cerchio *et al*. 2018) and North Atlantic Ocean (Risch *et al*. 2013). Although their acoustic behaviour has been less studied due to their offshore distribution, minke whales are known to produce two types of calls: bioduck calls and downsweeps (Risch *et al*. 2014; Dominello & Sirovic, 2016). In this study, few Antarctic minke whale 'bioduck' calls were detected seasonally in AAR1 and AAR2 particularly in spring of 2016 (September & October) and summer of 2015 (December) respectively, with no occurrence in other seasons. However, off the South African west coast, Shabangu *et al*. (2020b) detected Antarctic minke whales seasonally in late winter, spring and summer (2014 to 2015). Similarly, Thomisch *et al*. (2019) also detected Antarctic minke whale calls from late winter through summer (2011 to 2013) in Namibia. Such seasonalities concur with whaling and sighting survey records on the Durban whaling ground on South Africa's east coast (Findlay and Best, 2016). This annual variation in the acoustic detection of these species might imply that they move to different sites each year (as seen with blue and fin whales), particularly due to food availability in the area, or that only a minor population of vocalising animals was detected within the radius of the recorder. In the Antarctic, an extended detection (January through September) and high 'bioduck' calls during winter were observed (Dominello and Sirovic, 2016; Shabangu *et al*. 2020). This suggests that most minke whale population use this area year round since they are known to prefer heavy sea ice-covered areas (Lee *et al*. 2017), while some proportion of the population migrates seasonally to productive low latitudes such as the Benguela ecosystem (Best, 1982).

Humpback whales occur worldwide in all ocean basins and produce highly variable calls with a range of frequencies (Best, 1998;2007; Findlay *et al.* 2011). Like most baleen whales, humpback whales typically migrate between high latitude feeding grounds in summer to low latitude breeding grounds in winter based on both historical catches and acoustic methods (Mackintosh, 1942; Best, 2007). In this study, humpback whales were detected seasonally in winter (June, July, August) and spring (September, October, November) for AAR1. At AAR2, acoustic detection of these species occurred in summer (December 2015), late autumn (May 2016), winter (June, July) and spring (September, October, November). Thomisch *et al*. 2019 similarly found a seasonal occurrence of this species in winter (June, July, August), spring (November) and summer (January, December) in Namibia. These results are in line with historical catch data which indicated clear seasonal peaks of abundance, thought to relate with the northward (July/August) and southward (October/November) migration of humpback whales in the breeding/calving grounds (Best *et al*. 1995). Furthermore, Findlay *et al*. (2017) describes humpback whale feeding aggregations off the South African west coast in October and November. However, Barendse *et al*. (2010) sighted humpback whales year-round around the nearshore waters off the South African west coast. This variability possibly suggests that humpbacks that occur off the South African west coast utilize various areas each year, possibly due to prey availability as seen with blue and fin whales.

Southern right whales have a cosmopolitan distribution in the Southern Hemisphere and are also known to migrate between high latitude feeding grounds in summer to low latitude breeding grounds in winter (Best, 1998; 2007). Southern right whales are known to have an extensive acoustic repertoire. In the South African coastal waters, twelve call-types of southern right whales have been defined (Hofmeyr-Juritz, 2010; Hofmeyr-Juritz & Best, 2011). In this study, a few gunshot sounds were detected only in the deep station on single days in February, May, November and December 2016. Shabangu *et al*. (2021) detected high right whale gunshot sounds in the shallower areas (deployed in 855 m water depth) of the South African west coast from August through December 2014, and the sound occurrence peak was in October 2014. Hofmeyr-Juritz (2010) also observed increased southern right whale call rates around September/October off the coastal water waters of the southwest coast of South Africa in the Walker Bay area. This further reinforces the importance of the productive shallower inshore component of the South African west coast for right whales and other baleen species as they use this area from winter through summer for overwintering, feeding and breeding ground. The occurrence of the few gunshot sounds in February, May, November and December 2016 in the deep station could indicate utilization as a migratory route to locations closer to the shore or southwards to the Antarctic (Best, 2000;2007).

4.5. Unknown signals

Three unknown signals were detected frequently in this study ("M-call", unidentified sound two and unidentified sound three).

In AAR1, the M-call occurred sporadically in April, July and October & November of 2016. In AAR2, the M-call occurred sporadically in December 2015 and May 2016. A similar call was also detected in the southeast Atlantic Ocean, Namibia (Thomisch *et al*. 2019) and in the southern Indian Ocean where it was defined as an "M-call" (Leroy *et al*. 2017). Its first tonal unit occurs at a lower frequency (22 Hz) than blue whale Z-calls and may be confused to the first unit of a blue whale Z-call. The temporal pattern in the acoustic occurrence of this signal is observed to be similar to other baleen whales hence it is hypothesized that it could possibly belong to a mysticete species. Leroy *et al*. (2017) hypothesized that the M-call could possibly be produced by a blue whale subspecies, perhaps produced by pygmy blue whales. Stafford *et al*. (2001) also reported similar blue whale calls in the central North Pacific Ocean, which possibly suggests that it could be produced by a blue whale subspecies. Macdonald *et al*. (2006) also found a similar call off New Zealand which was attributed to Brydes whale calls, however there has not been any conclusive evidence to support this finding. The occurrence of this call off the South African west coast and Namibia (Thomisch *et al*. 2019), further indicates the importance of the Benguela region as an overwintering ground for various baleen whales as previously suggested.

Unidentified sound two occurred at medium to high frequencies and was sporadically detected only during May in AAR2. Unidentified sound three occurred in low frequencies and was sporadically recorded in AAR1 (October, November, December) of 2016 and AAR2 (January 2017). Both these signals could possibly originate from humpback whales as they also produce highly variable calls with low to high frequencies. Alternatively, the signal could possibly be produced by an anthropogenic source, although the pulsed characteristics of the signals suggest a more biological origin.

4.6. Anthropogenic activity

Anthropogenic noise mainly arises from a wide range of commercial activities such as ship traffic, seismic surveys and construction activities (Hatch *et al*. 2008). The frequency ranges of these activities range from few Hz to hundreds of kHz (Melcon *et al*. 2012). Seismic surveys are known to produce some of the loudest anthropogenic noise in the ocean in the 10 to 200 Hz band. Underwater noise from ship's propeller cavitation in particular, is suggested to range from 50–150 Hz but can extend up to 10, 000 Hz (Roland *et al*. 2012). In acoustic recorders, noise with frequency varying levels particularly from shipping traffic might decrease the signal detection range of whale calls at a given site (e.g., Shabangu *et al*. 2019).

Noise emitted by anthropogenic activities may affect marine mammals in several ways (Cox *et al*. 2006; Richardson *et al*. 2013). Firstly, it can interfere with the vocalizations of marine mammal which essentially make it difficult for marine mammals to maintain acoustic contact and affects the chances of identifying prey and possible predators (Hatch *et al.* 2008). Secondly, it might cause behavioural responses, such as avoidance reactions, vocal activity alterations, or irregular migratory routes (Di Iorio & Clark, 2010; Castellote *et al.* 2012; Blackwell *et al.* 2015). Thirdly, it may result in modifications in hearing (temporal or permanent) (Finneran, 2015). Finally, anthropogenic noise might lead to injury or ultimately the mortality of marine mammals (Zimmer and Tyack, 2007; Finneran, 2015).

Vessel noise occurrence was sporadically detected in both AARs over the recording period. However, vessel noise was more frequent in AAR2, with peaks in May and June. This study did not investigate any correlation between anthropogenic noise and the acoustic occurence of the baleen whale species in the South African west coast. However, general assumptions can be made based on other studies that anthropogenic noise does influence the vocal behaviour of whales (Melcón *et al*. 2012). Further research is needed to understand the effects of noise pollution on marine mammals in the Benguela ecosystem using Automatic Identification System (AIS) data, which relays information on vessel activity (position, speed, course) within an area and can possibly be integrated to acoustic data (Haver *et al*. 2017) to model sound input in the ocean (see Figure 2). AIS data can possibly inform resource managers on estimated sound level effects from anthropogenic sources such as shipping, which produce tonal sounds that can negatively affect baleen whales and can resultantly be difficult to quantify (Haver *et al*. 2017). This will essentially help in understanding the acoustic behaviour and distributions of baleen whales particularly in the South African west coast which is associated with busy shipping lanes. The integration of this AIS data and passive acoustics data can overall help conservative management efforts in strives to protect the critical habitats/migration routes of the highly depleted whale species and also developing effective strategies to manage the growing ocean noise levels.

Chapter 5: Conclusion and recommendations

Bioacoustic data allowed us to continue to monitor the seasonal acoustic occurrence and behaviour of blue and fin whales through passive acoustics. These species are rarely sighted in the Benguela ecosystem. The year-round acoustic occurrence and higher number of blue whales calls in the vicinity of AAR1 (albeit at different densities), suggests that the southern Benguela ecosystem provides suitable and favourable environmental conditions throughout the year for this species. On the other hand, the seasonal acoustic occurrence of blue whales around AAR2 and of fin whales around both AARs indicates that that region is a seasonal habitat used for overwintering, breeding/calving and/or migration. Blue and fin whale acoustic occurrence was high in autumn and winter suggesting this as a period when most of these whales are in the Benguela ecosystem or have an increasing calling rate. Call rates of both whale species were high during the day for most seasons as most whales were vocally active during the day. Results from the ANOVA statistical tests showed significant differences in both Antarctic blue and fin whale call occurrence and call rates by month. However, significant differences for diurnal call rates were only observed in some seasons only for Antarctic blue whale, this suggests that time of the day is a not an informative predictor of the vocalisation of these whales, but can be of importance in the determination of diel duty cycling of acoustic recorders in future studies.

This study highlights the ecological importance of the South African west coast as a year-round and seasonal habitat/migration corridor of Antarctic blue whales, fin whales and other whale species (namely, humpback whales, minke whales, southern right whales). However, in order to understand seasonal variation in relation to environmental conditions between various stations, it is crucial to conduct a multi-disciplinary study to include analyses of environmental data such as depth, sea surface temperature, chlorophyll etc. of the particular area to investigate environmental drivers of whale distributions and seasonal abundance. Furthermore, a more enhanced analysis on the detection range estimations using various model parameters (source level, background noise level, bathymetry and the depth) would help better understand the acoustic transmission conditions of an area.

Despite the importance of the South African west coast as a habitat for various baleen whales, it is also threatened by anthropogenic factors such as shipping, fisheries, oil and gas explorations etc. The integration of AIS shipping and passive acoustics data would also assist conservative management efforts in protecting the critical habitats/migration routes of whales and developing strategies to manage increasing ocean noise levels.

Lastly, this study like others, further confirms that these Antarctic baleen whales can be monitored effectively through bioacoustics in the low latitudes such as the west coast of South Africa.

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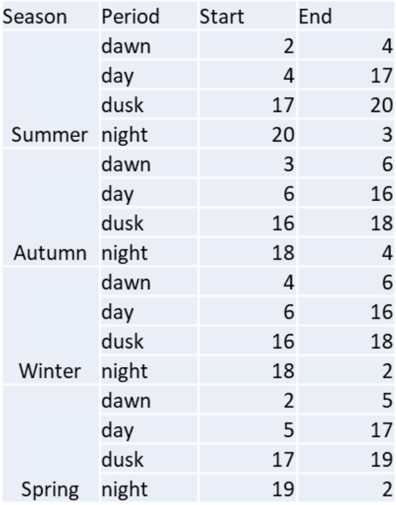
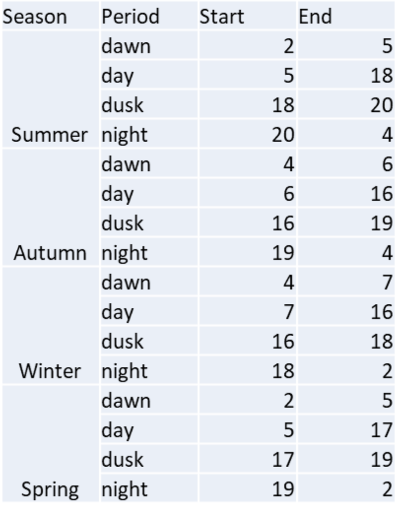
5.2. Appendix

Table 1: Start and end times for diel periods (dawn, day, dusk, night) per season around AAR1. It should be noted that times presented in this study are in UTC format.



Season	Period	Start	End
Summer	dawn	2	4
	day	4	17
	dusk	17	20
	night	20	3
Autumn	dawn	3	6
	day	6	16
	dusk	16	18
	night	18	4
Winter	dawn	4	6
	day	6	16
	dusk	16	18
	night	18	2
Spring	dawn	2	5
	day	5	17
	dusk	17	19
	night	19	2

Table 2: Start and end times for diel periods (dawn, day, dusk, night) around AAR2. It should be noted that times presented in this study are in UTC format.



Season	Period	Start	End
Summer	dawn	2	5
	day	5	18
	dusk	18	20
	night	20	4
Autumn	dawn	4	6
	day	6	16
	dusk	16	19
	night	19	4
Winter	dawn	4	7
	day	7	16
	dusk	16	18
	night	18	2
Spring	dawn	2	5
	day	5	17
	dusk	17	19
	night	19	2

Table 3: Tukey's HSD multiple comparisons for monthly call occurrence in the shallow (AAR1) and deep station (AAR2) off the South African west coast.

Shallow		Deep	
Blue	Fin	Blue	Fin
May	May	March	April
June	June	April	May
July	July	May	June
August	August	June	September

Table 4: Tukey's HSD multiple comparisons for monthly call rates in the shallow (AAR1) and deep station (AAR2) off the South African west coast.

Shallow		Deep	
Blue	Fin	Blue	Fin
March	May	March	April
April	June	April	May
May	July	May	June
June	August	June	September

Table 5: Mean of diel seasonal call occurrence for the light regimes in both blue (BWP) and fin (FWP) whale calls from AAR1 (shallow station).

	BWP				FWP			
Season	Dawn	Day	Dusk	Night	Dawn	Day	Dusk	Night
Autumn	0.43	0.43	0.46	0.42	0.00	0.54	0.00	0.00
Spring	0.05	0.06	0.09	0.08	0.00	0.00	0.00	0.00
Summer	0.08	0.05	0.07	0.06	0.00	0.00	0.00	0.00
Winter	0.88	0.89	0.91	0.88	0.22	0.21	0.25	0.21

Table 6: Mean of diel seasonal call occurrence for the light regimes in both blue (BWP) and fin (FWP) from AAR2 (deep station).

	BWP				FWP			
Season	Dawn	Day	Dusk	Night	Dawn	Day	Dusk	Night
Autumn	0.29	0.31	0.33	0.28	0.09	0.09	0.10	0.07
Spring	0.00	0.00	0.00	0.00	0.04	0.03	0.02	0.03
Summer	0.03	0.03	0.03	0.03	0.00	0.00	0.00	0.00
Winter	0.07	0.07	0.07	0.05	0.03	0.03	0.04	0.03

Table 7: Tukey's HSD multiple comparisons for diel seasonal call occurrence in the shallow (AAR1) and deep station (AAR2) off the South African west coast.

	Shallow		Deep	
Season	Blue	Fin	Blue	Fin
Spring	$p > 0.05$	No calls	No calls	$p > 0.05$
Winter	$p> 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$
Autumn	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$
Summer	$p > 0.05$	No calls	$p > 0.05$	No calls

Table 8: Mean of diel seasonal call rates for the light regimes in both blue (BWZH) and fin (FWH) from AAR1 (shallow station).

	BWZH				FWH			
Season	Dawn	Day	Dusk	Night	Dawn	Day	Dusk	Night
Autumn	38.31	38.36	43.75	36.44	0.00	1.22	0.00	0.00
Spring	1.40	2.50	3.82	4.21	0.00	0.00	0.00	0.00
Summer	3.00	1.36	1.60	2.38	0.00	0.00	0.00	0.00
Winter	58.11	55.46	57.01	49.29	34.55	30.73	32.71	29.46

Table 9: Mean of diel seasonal call rates for the light regimes in both blue (BWZH) and fin (FWH) from AAR2 (deep station).

	BWZH				FWH			
Season	Dawn	Day	Dusk	Night	Dawn	Day	Dusk	Night
Autumn	20.48	24.03	22.12	18.13	16.84	15.69	17.48	11.32
Spring	0.00	0.00	0.00	0.00	5.04	2.99	2.80	4.46
Summer	0.12	0.14	0.08	0.11	0.00	0.00	0.00	0.00
Winter	3.44	4.29	5.02	3.08	6.46	7.78	8.61	7.23

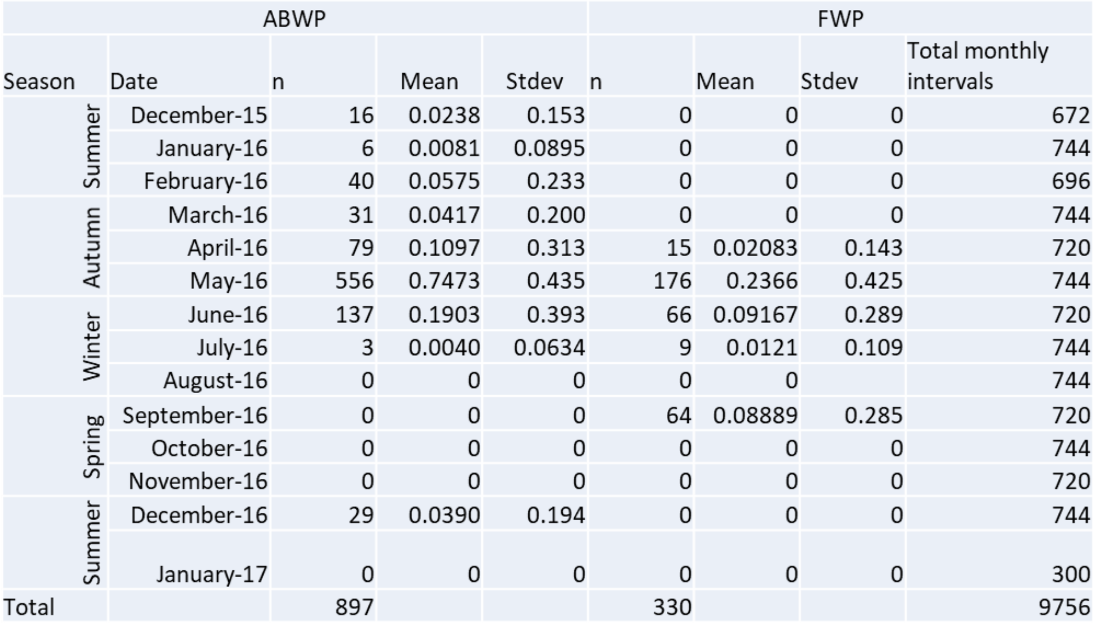
Table 10: Tukey's HSD multiple comparisons for diel seasonal call rates in the shallow (AAR1) and deep station (AAR2) off the South African west coast.

	Shallow		Deep	
Season	Blue	Fin	Blue	Fin
Spring	night - dawn	No calls	No calls	p > 0.05
Winter	night - dawn night - day	p > 0.05	p > 0.05	p > 0.05
Autumn	p > 0.05	p > 0.05	night - day	p > 0.05
Summer	p > 0.05	No calls	p > 0.05	No calls

Table 11: Total monthly occurrence (n), mean and standard deviation of proportion of occurrence per month of blue (ABWP) and fin whales (FWP) in AAR1, the shallow station.

		ABWP			FWP			
Season	Date	n	Mean	Stdev	n	Mean	Stdev	Total monthly intervals
Summer	December-15	12	0.018	0.133	0	0	0	672
	January-16	21	0.028	0.166	0	0	0	744
	February-16	20	0.029	0.167	0	0	0	696
Autumn	March-16	173	0.233	0.423	0	0	0	744
	April-16	180	0.250	0.433	0	0	0	720
	May-16	596	0.801	0.399	5	0.00672	0.0818	744
Winter	June-16	666	0.925	0.264	215	0.2986	0.4580	720
	July-16	706	0.949	0.220	186	0.25	0.433	744
	August-16	581	0.781	0.414	74	0.0995	0.2995	744
Spring	September-16	23	0.032	0.176	0	0	0	720
	October-16	81	0.109	0.312	0	0	0	744
	November-16	47	0.065	0.247	0	0	0	720
Summer	December-16	115	0.155	0.362	0	0	0	744
	January-17	0	0	0	0	0	0	24
Total		3221			480			9480

Table 12: Total monthly occurrence (n), mean and standard deviation of proportion of occurrence per month of blue (ABWP) and fin whales (FWP) in AAR2, the deep station.



		ABWP			FWP			
Season	Date	n	Mean	Stdev	n	Mean	Stdev	Total monthly intervals
Summer	December-15	16	0.0238	0.153	0	0	0	672
	January-16	6	0.0081	0.0895	0	0	0	744
	February-16	40	0.0575	0.233	0	0	0	696
Autumn	March-16	31	0.0417	0.200	0	0	0	744
	April-16	79	0.1097	0.313	15	0.02083	0.143	720
	May-16	556	0.7473	0.435	176	0.2366	0.425	744
Winter	June-16	137	0.1903	0.393	66	0.09167	0.289	720
	July-16	3	0.0040	0.0634	9	0.0121	0.109	744
	August-16	0	0	0	0	0		744
Spring	September-16	0	0	0	64	0.08889	0.285	720
	October-16	0	0	0	0	0	0	744
	November-16	0	0	0	0	0	0	720
Summer	December-16	29	0.0390	0.194	0	0	0	744
	January-17	0	0	0	0	0	0	300
Total		897			330			9756

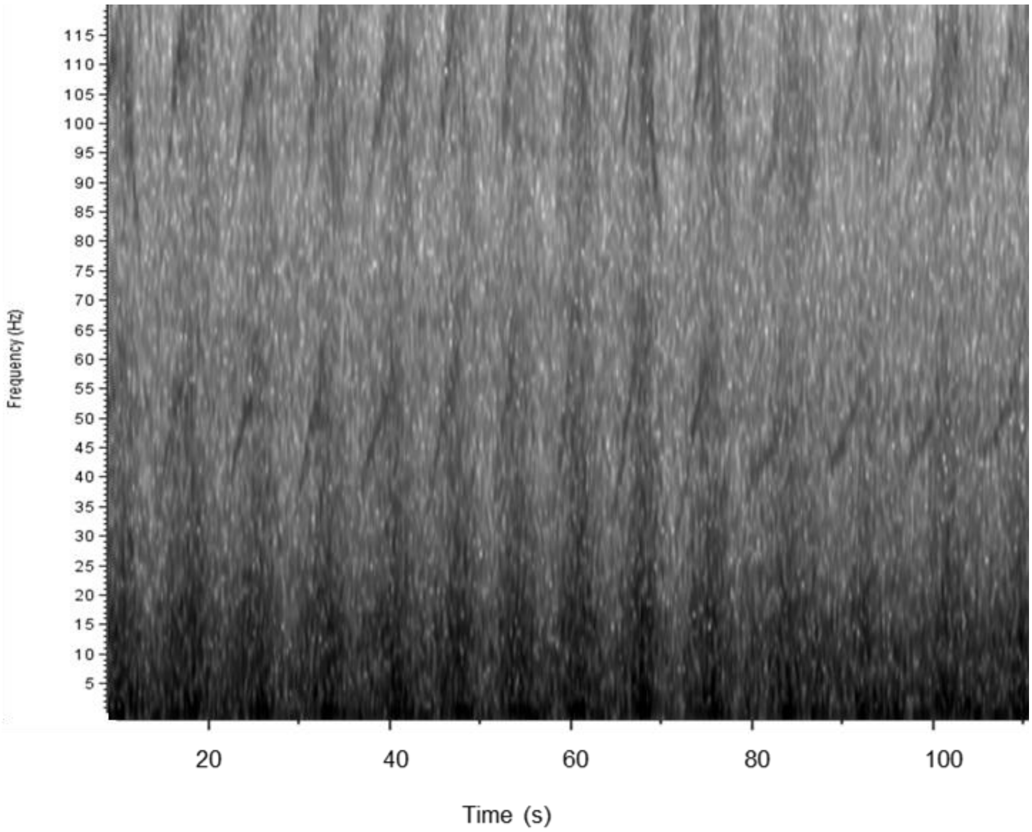


Figure 32: Spectrogram of unidentified sound four recorded from AAR2 (deep station) off the South African west coast; Spectrogram parameters (16,384-point FFT, 50% overlap, 4100 hop size, Hanning window).

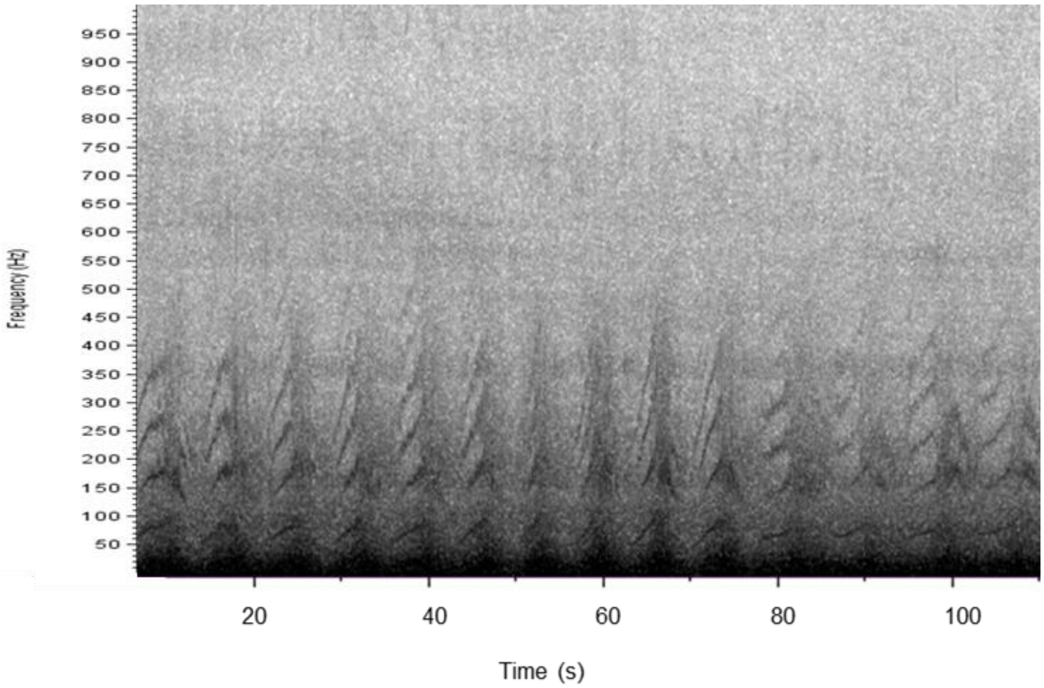


Figure 33: Spectrogram of unidentified sound five recorded from AAR2 (deep station) off the South African west coast; Spectrogram parameters (16,384-point FFT, 50% overlap, 4100 hop size, Hanning window).

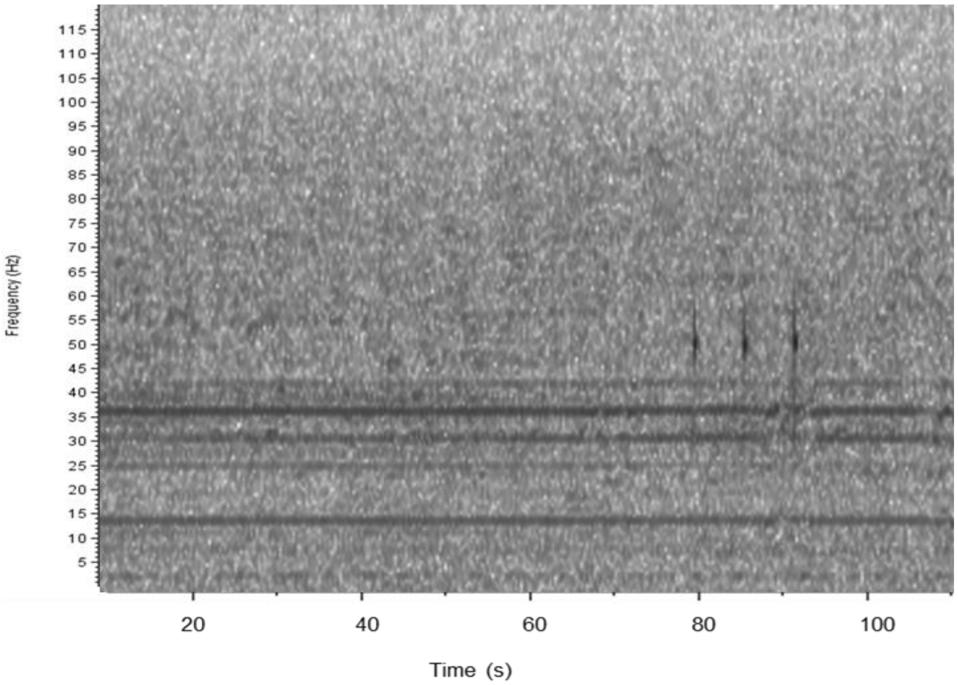


Figure 34: Spectrogram of unidentified sound six recorded from AAR1 (shallow station) off the South African west coast; Spectrogram parameters (16,384-point FFT, 50% overlap, 4400 hop size, Hanning window).

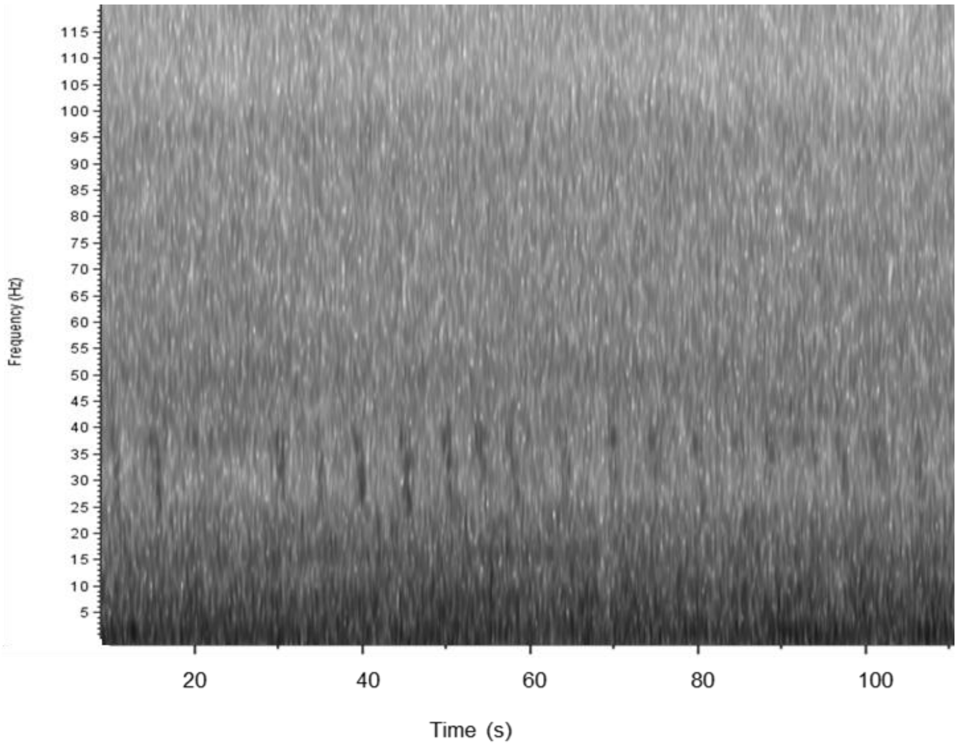


Figure 35: Spectrogram of unidentified sound eight recorded from AAR2 (deep station) off the South African west coast; Spectrogram parameters (16,384-point FFT, 50% overlap, 3800 hop size, Hanning window).

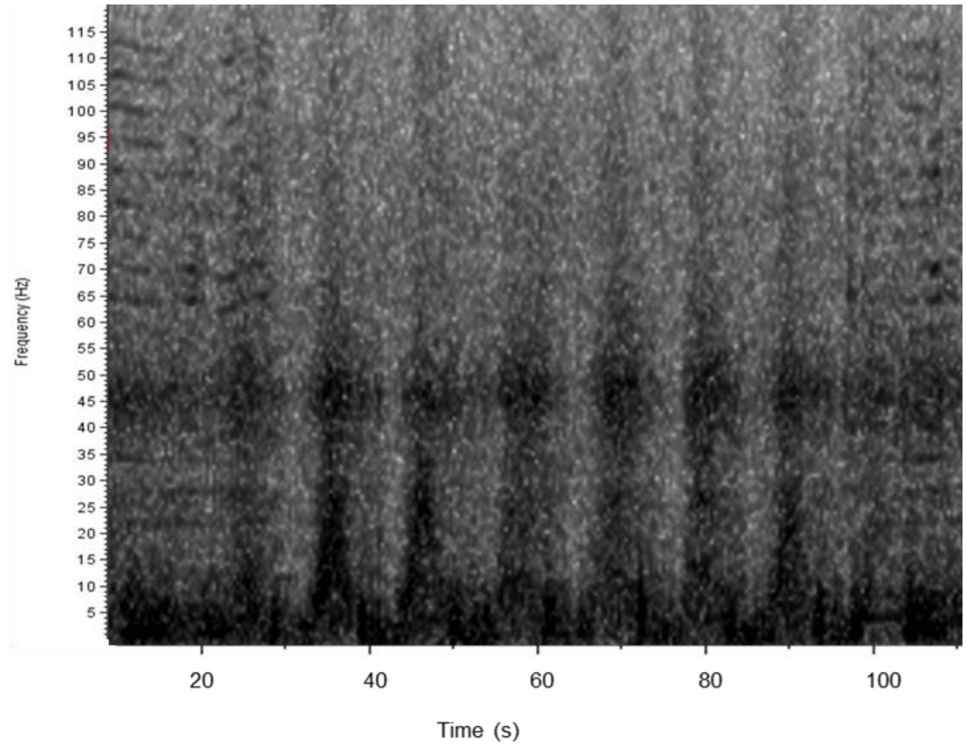


Figure 36: Spectrogram of unidentified sound nine recorded from AAR2 (deep station) off the South African west coast; Spectrogram parameters (16,384-point FFT, 50% overlap, 3800 hop size, Hanning window).