Acoustic occurrence patterns of Prince Edward Islands' killer whales on diel, monthly, and seasonal scales

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Abstract

Killer whales are highly social marine mammals which utilise their vocalisations for communication, feeding and navigation. They are poorly studied within the Southern Hemisphere, particularly in remote regions such as the sub-Antarctic Prince Edward Islands (PEIs) where fieldwork can be logistically challenging. This region is subject to rapid rise in temperatures and subsequent climate variability potentially causing ecosystem changes. This study therefore aims to investigate killer whale presence using two modalities (acoustic as primary and visual as validation), two methods of acoustic detection and a variety of potential influences, both biotic (primary production and killer whale prey) and abiotic (wind, sea surface height (SSH), sea surface temperature (SST)) factors across multiple temporal scales. A hydrophone was deployed at 46° 46.4’S, 37° 54.7’ E and recorded from April 2021 to April 2023. SST, SSH, chlorophyll-a concentration (chl-a) and wind speed data were sourced from satellite and reanalysis data, and prey and sightings data from land-based surveys. Automated call detection was used to investigate these objectives and compared to manual detection. Results indicated that killer whales’ calls were detected intermittently throughout the year with a higher occurrence of calls in the spring and early-summer months and no significant year-to-year variability was observed. Their sightings displayed similar patterns, but the environmental variables and prey abundance did not indicate matching year-to-year variability. This was attributed to fine-scale changes in their social structure, long-term resistance in their call behaviours to larger temporal scale environmental anomalies and substantial short-term variability of SSH and wind speed. Random forest modelling identified wind speed and hour of the day as the primary predictors of the occurrence of calls while SST, SSH, chl-a and prey abundance were moderately important. Strong diel call patterns were observed only in winter and summer, reflecting adaptive foraging and social behaviour. Automated call detection was found to be an effective method but is not to be used in isolation as it produced false positive and negative detections. These results provide important insights into PEIs’ ecosystem functioning by disentangling the effects of climate variability on keystone species such as killer whales using cost-effective methods such as passive acoustic monitoring, automated detection, and satellite and reanalysis data.

Keywords: killer whales, acoustic ecology, environmental variability, bioacoustics, sub-Antarctic ecosystem

Acknowledgements

Killer whale acoustic ecology, a research topic I stumbled across during my honours year at university captured my heart from the get-go. While only scratching the surface during that year, I found myself looking forward to discovering more. During that process, I found that my strengths lie in executing interdisciplinary research or projects. This epiphany has allowed me to not only explore aspects of marine mammalogy, bioacoustics or physical oceanography, but also avenues of applied ocean science to bring about significant change to our society. With that being said, this research would not have been possible without the support and guidance of key people in my life. First and foremost, my supervisors, Dr Tarron Lamont and Dr Fannie Shabangu, who have been with me on this journey for three years, you have my utmost gratitude for all your efforts to expand my knowledge, skillset and overall research abilities. Thank you both for your commitment to helping me achieve my goals as well as providing me with several opportunities to present my research at local and international conferences and for publications. This exposure will always be one of the highlights of my postgraduate studies.

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List of Symbols/Abbreviations

AABW - Antarctic Bottom Water

AAIW - Antarctic Intermediate Water

ABFZ - Andrew Bane Fracture Zone

ACC - Antarctic Circumpolar Current

ACW - Antarctic Circumpolar Wave

ADASYN - ADAptive SYNthetic

APF - Antarctic Polar Front

CDW - Circumpolar Deep Water

Chl-a - Chlorophyll-a concentration

CMEMS - Copernicus Marine Environment Monitoring Service

DFT - Discrete Fourier Transformation

DUACS - Data Unification and Altimeter Combination System

EEZ - Exclusive Economic Zone

ENSO - El Niño Southern Oscillation

ERA5 - Fifth generation of European Centre of Medium-Range Weather Forecasts reanalyses

GEBCO - General Bathymetry Chart of the Oceans

GlobColour - Global Ocean Colour for Carbon Cycle Research

GVIFs - Generalized Variance Inflation Factors

HNLC - High Nutrient Low Chlorophyll

IME - Island Mass Effect

KW - Killer whale

LCDW - Lower Circumpolar Deep Water

M-APF - Middle branch of the Antarctic Polar Front

MARiS - Marine and Antarctic Research centre for Innovation and Sustainability

MIMMP - Marion Island Marine Mammal Programme

MPA - Marine Protected Area

M-SAF - Middle branch of the sub-Antarctic Front

n - Sample size

NADW - North Atlantic Deep Water

N-APF - Northern branch of the Antarctic Polar Front

ns/NS - Non-significance

OSTIA - Operational Sea Surface Temperature and Sea Ice Analysis

PAM - Passive Acoustic Monitoring

PEIs - Prince Edward Islands

RF - Random Forest

SACCF - Southern ACC Front

SAF - sub-Antarctic Front

SAM - Southern Annular Mode

SAMOC -South Atlantic Meridional Overturning Circulation

SAMW - sub-Antarctic Mode Water

SAO - Semi-Annual Oscillation

SASW - sub-Antarctic Surface Water

SES - Southern Elephant Seal

SMOTE - Synthetic Minority Over-sampling Technique

SNRs - signal-to-noise ratios

SO - Southern Oscillation

SOI - Southern Oscillation Index

S-SAF - Southern branch of the sub-Antarctic Front

SSH - Sea Surface Height

SST - Sea Surface Temperature

SSTa - Sea Surface Temperature anomalies

STF - sub-Tropical Front

STSW - sub-Tropical Surface Water

SWIR - South-West Indian Ridge

UCDW - Upper Circumpolar Deep Water

UTC - Coordinated Universal Time

wav - Waveform Audio File Format

Chapter 1. Introduction

1.1. Background

Killer whales (*Ornicus orca*) are the largest dolphins in existence (Ford 2009) and typically rely on their vocalisations to communicate with conspecifics. They are highly social marine mammals and their ability to effectively communicate play essential roles in all aspects of their lives (Holt et al. 2011). Their social calls which include pulsed calls, tonal calls and whistles are used to maintain group cohesion during navigation, hunting and for group recognition (Riesch and Deecke 2011; Filatova et al. 2013). Their echolocation clicks are used during navigation as they allow these dolphins to gauge the direction and distance of objects in the marine environment. Additionally, clicks are produced to locate and target prey through the mechanism of echolocation. Clicks become frequently faster and create a buzzing sound when pinpointing the exact location of prey (Richard et al. 2021). The arrangement and occurrence of their calls can therefore provide information on their social dynamics and their feeding ecology (Shabangu et al. 2024a).

Passive acoustic monitoring (PAM) would therefore be an invaluable tool to study these marine mammals and investigate the drivers of their presence in a particular area (Shabangu et al. 2024a; b). This is especially useful as killer whales are highly mobile (Condy et al. 1978), making them challenging to study in remote regions such as the sub-Antarctic Prince Edward Islands (PEIs) in the Indian Ocean stretch of the Southern Ocean. This archipelago consisted of the larger Marion Island and the smaller Prince Edward Island (*Figure 1.1*). They lie in the direct path of the Antarctic Circumpolar Current (ACC) (Reisinger et al. 2017; Toolsee and Lamont 2022), thus subjecting the marine environment around the islands to varying conditions. The strong eastward flowing ACC has fontal systems and jets with sharp gradients in physical and chemical water properties (Rintoul and da Silva 2019; Chapman et al. 2020). As a result of the unique bottom topography of the region, the frontal system tends to meander forming high mesoscale variability (Toolsee and Lamont 2022) which can promote upwelling and increased primary productivity (Patel et al. 2020). Additionally, the region is subject to the frequent passage of atmospheric low-pressure systems which ultimately contributes to the environmental variability (Rouault et al. 2005).

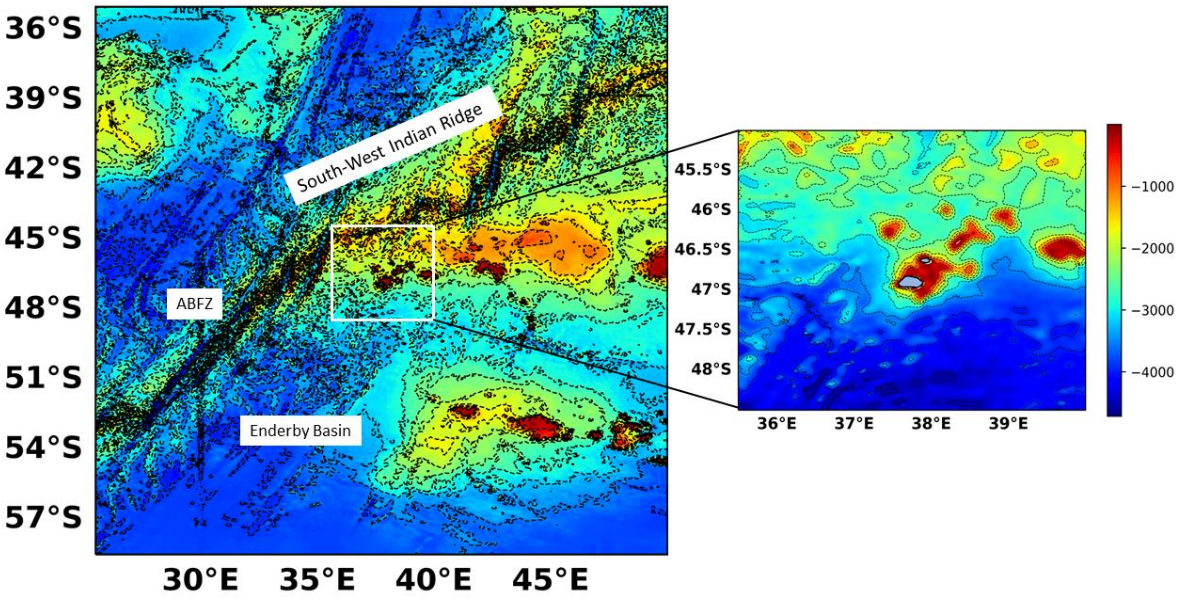

Figure 1.1. Map depicting the bathymetry in the sub-Antarctic Prince Edward Islands region. The largescale map displays the bathymetric features important to the region, namely the Andrew Bain Fracture Zone (ABFZ), the South-West Indian Ridge (SWIR) and the Enderby Basin. The solid-lined white box indicates the magnified area of focus for this study (latitude 45°S - 48.5°S; longitude 35°E - 40°E). Depth contours are in intervals of 500m and ranges from 100m to 6000m. The gridded bathymetric dataset 'GEBCO_2022 Grid' was sourced from the General Bathymetry Chart of the Oceans (GEBCO) and can be accessed from http://www.gebco.net/data_and_products/gridded_bathymetry_data/. GEBCO provides elevation data in meters on a 15 arc-second interval grid. Extracted from Daniels (2022).

Considering this broad range of environmental variability sources at the PEIs, the killer whale population observed to be present year-round at the islands may be influenced by this as well as their prey population on which they so heavily rely. The PEIs population consists of 54 unique dolphins, and they occur more often during seasons of large prey aggregations (Ryan and Bester 2008; Reisinger et al. 2011c; Jordaan et al. 2021; Shabangu et al. 2024a). Their main prey item is the southern elephant seal (*Mirounga leonine*), but they do hunt two other seal species and four penguin species utilising the islands for breeding purposes (Reisinger and de Bruyn 2014). There are four killer whale ecotypes existing within the Southern Ocean - A, B, C and D (Pitman and Ensor 2003, Pitman et al. 2011). These are defined as populations which differ in their morphology, genetics, diet, social structure, habitat preference, foraging behaviour and vocal repertoire (known to a much lesser extent) (de Bruyn et al. 2013). The PEIs' killer whale population is genetically related to the seal hunting specialists of ecotype B (Moura et al. 2015).

1.2. Rationale, Objectives and Key Questions

Killer whale distribution and occurrence is largely driven by the occurrence and abundance of their prey. They have been observed to change their foraging behaviour, movements and social cohesion during periods of prey aggregations (Keith et al. 2001; Ryan and Bester 2008; Ford et al. 2010; Dragon et al. 2010; Reisinger et al. 2011c; Reisinger et al. 2015; Jordaan et al. 2021; Shabangu et al. 2024a). There have been some studies indicating that they are also influenced by suitable environmental conditions and sexual maturity in the PEIs region (Reisinger et al. 2015; Jordaan et al. 2023; Shabangu et al. 2024a), but these studies addressing the direct effects of the environment on their occurrence are far and few in-between. Because the sub-Antarctic region is such a dynamic environment with variability on multiple scales and is also subject to climate change (Ansorge et al. 2014), it is essential to fill in knowledge gaps on their direct and indirect influence on the apex predators of this ecosystem as well as through effects on their prey populations.

Killer whales play an important role in the marine ecosystem. They are apex predators with large body size, high energy requirements and are opportunistic hunters (Reisinger et al. 2011a; Reisinger et al. 2011c; Reisinger and de Bruyn 2014). Their diet includes fish, sharks, reptiles, marine mammals, cephalopods and seabirds. They can therefore affect marine ecosystem structure and function at multiple trophic levels (Reisinger et al. 2011c; Reisinger et al. 2015). There are multiple examples of killer whales causing trophic cascades: in the water of the Aleutian archipelago in Alaska, killer whales started hunting sea otters (*Enhydra lutris*), subsequently resulting in the boom of the sea urchin population that altered the kelp forest ecosystem (Estes et al. 1998). In the Gansbaai waters of South Africa, they have driven the white sharks out of the region as a fear-response to increased killer whale predation, inducing a trophic cascade as bronze whaler shark abundances increased (Towner et al. 2022). There have also been suggestions of killer whale predations causing declines in pinniped numbers at the PEIs and the Crozet archipelago (Reisinger et al. 2011a). Because apex predators, including killer whales, can feed on multiple trophic levels, they sit in a unique position in the food web (Navia et al. 2016), thereby increasing the trophic diversity of an ecosystem and its subsequent buffering capacity to environmental variability (Kuparinen et al. 2019).

Large marine mammals additionally play an essential role in mitigating the effects of climate change through the process of deadfalls. When they die, they sequester organic carbon (which is stored in their large body mass) from the surface ocean to the deep sea and potentially becoming stored in the ocean interior sediments for millions of years (Smith 1992; Smith and Baco 2003). This also transports nutrients to deep-sea ecosystems (Li et al. 2022) and is important for ecological succession, development of life and nutrient cycling in this environment (Wang 2021). In Icelandic waters, killer whales have been estimated to export approximately 103 tonnes of organic carbon per year (with a 95% confidence interval between 38 and 227 tonnes) into the ocean interior (Dyrland 2024).

The PEIs is an important Marine Protected Area (MPA) aimed at informing future management as a scientific reference point, the recovery of the Patagonian toothfish (*Dissostichus eleginoides*) population and the reduction of seabird bycatch of this fishery (Lombard et al. 2007). Because killer whales can potentially have huge impacts on the PEIs' marine ecosystem, it is essential to study their ecology for effective ecosystem management of the region (de Bruyn et al. 2013). Doing so using PAM will also provide insights into differentiating the killer whale ecotypes acoustically and closing the knowledge gaps in this space, which is especially limited in the Southern Hemisphere (Shabangu et al. 2024a). Studying their acoustic behaviour will provide important insights into their foraging behaviour, social structure, reproduction, navigations, and responses to prey availability. The overarching aim of the current study is firstly to add to the knowledge pool of acoustic behaviours of this population and use the presence of their calls to determine how the dynamic environment of the PEIs may be influencing them. Additionally, the study examined new detection methodology and the potential refinement thereof for future studies.

The primary objective of this study was to use satellite-derived oceanographic data for the period of May 2021 to April 2023 to determine the year-to-year variability of the environmental conditions of sub-Antarctic region surrounding the PEIs and compare it to year-to-year variability of killer whale call occurrences between May 2021 to December 2022 across expanding time scales, from diel variations, to comparisons of months and seasons to each and across years, additionally linking this to the abundance of their prey. To achieve these objectives, the following key questions were asked:

1. How does automated call detection, using the *Spectrodetector* (JASCO Applied Science Ltd), compare to manual call detection of killer whales at the PEIs?
2. What are the diel, month-to-month, and seasonal differences in environmental conditions, prey abundance, and killer whale call occurrence between the two recorded periods?
3. What is the relative importance of environmental conditions (sea surface temperature, sea surface height, wind speed and chlorophyll-a concentration), prey availability (southern elephant seal abundances), and temporal categories (hour, month, year) for killer whale call occurrence?

Chapter 2. Literature Review

2.1. Killer whales of the Southern Ocean

There are four ecotypes known to exist within the Southern Ocean – Ecotype A, B, C and D (*Figure 2.1*; Pitman and Ensor 2003, Pitman et al. 2011). These are populations which differ in their morphology, genetics, diet, social structure, habitat preference and foraging behaviour, but additional evidence-based ecological and taxonomic data is needed to substantiate ecotype-related characteristics (de Bruyn et al. 2013).

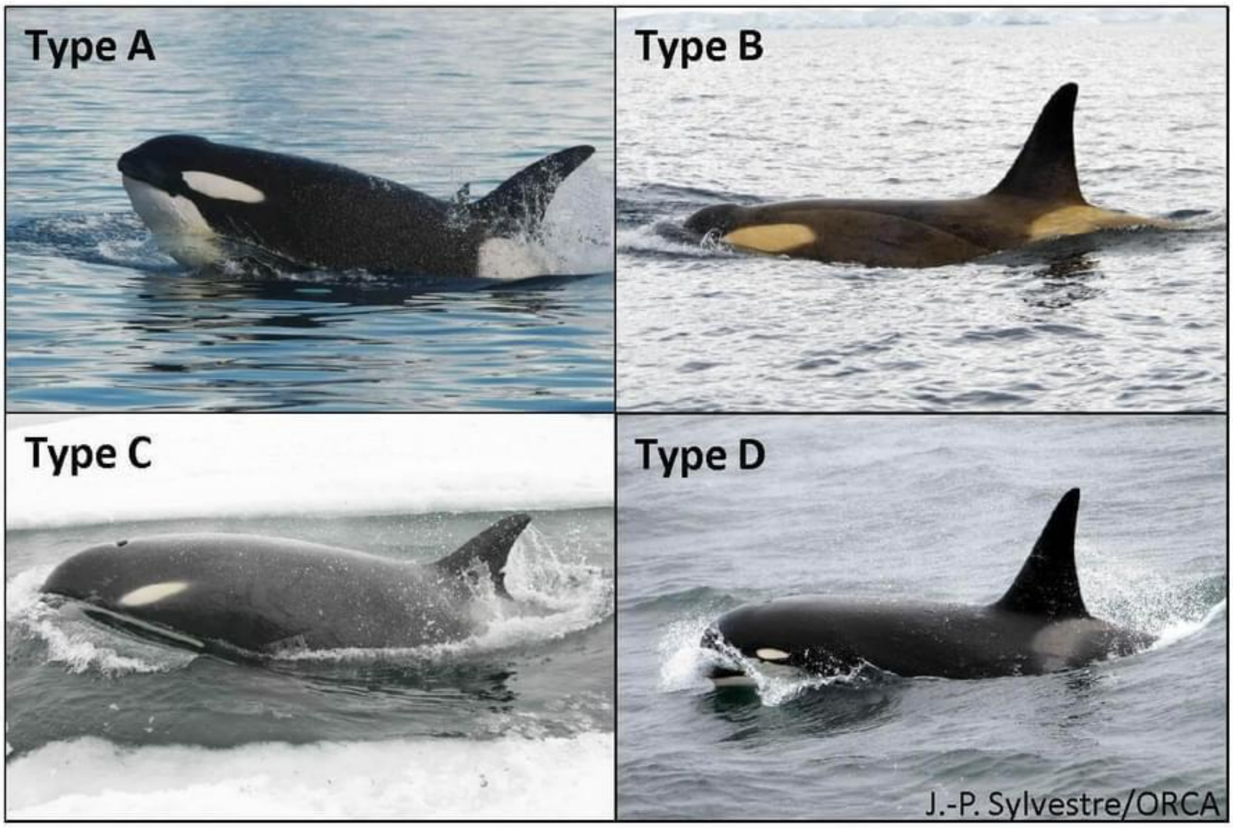

Figure 2.1. Images of the various killer whale ecotypes existing within the Southern Ocean. Extracted from https://orca.org.uk/news-blog/iconic-orcas-a-deep-dive-into-this-enigmatic-species.

Ecotype A has quite a large body size, with a medium-sized eyepatch parallel to the body, the dorsal cape is absent, and they occur in relatively small groups (10-15 dolphins) (Pitman and Ensor 2003; Schall and Van Opzeeland 2017). This population occurs in Antarctic ice-free waters and their migration patterns follow that of their main prey item, the Antarctic minke whale (*Balaenoptera bonaerensis*) as they migrate from Antarctica to the lower latitudes in austral autumn and vice versa in summer (Berzin and Vladimirov 1983). Ecotype B differ in their colours quite starkly from the other ecotypes as they have a yellow cast over their two-toned grey and white bodies as a result of the growth of a diatom biofilm (Pitman and Ensor 2003). They have a large eyepatch parallel to the body and a dorsal cape (Reisinger et al. 2011). They occur year-round in Antarctic water but within the inshore region among loose pack-ice (Pitman and Ensor 2003). They are seal hunting specialists (Pitman and Ensor 2003; Pitman et al. 2011) but also hunt other whales and penguins (Reisinger et al. 2011).

Ecotype C killer whales are the smallest in body size and have a slanted eyepatch. Their dorsal capes are present, and they occur in large pods (10-150 dolphins) in inshore waters off East Antarctica in dense pack-ice and polynyas. Their movements are restricted, and their diet mostly consists of Antarctic fish such as Antarctic toothfish (*Dissostichus mawsoni*) (Pitman and Ensor 2003). Ecotype D's characteristic morphological features are that of its bulbous head, small eyepatch parallel to the body, absent dorsal cape and sharp-tipped backswept dorsal fin (particularly evident in adult males). They occur in the sub-Antarctic with a pod size between 9 and 35 dolphins. This ecotype was only recently discovered and not much is known about their diet and foraging behaviour. Pitman et al. (2011) showed that they have been observed to depredate Patagonian toothfish from longline fishing vessels and Richard et al. (2021) suggested that they could be more specialized hunters as they can dive deeper for fish.

The PEIs' killer whale population is genetically related to the seal hunting specialists of ecotype B (Moura et al. 2015) but are generally understudied within the southern Indian and Atlantic Oceans (Reisinger et al. 2011c). This population consists of 54 unique individuals and their presence and social structure is largely driven by resource abundance (Jordaan et al. 2021; Shabangu et al. 2024a). During periods of high prey abundance, they form closer social bonds and are more frequently sighted during periods of large prey aggregations, for example during breeding and moulting seasons of seals and penguins which utilise the PEIs for these activities (Ryan and Bester 2008; Reisinger et al. 2011c; Jordaan et al. 2021; Shabangu et al. 2024a).

The PEIs' killer whales have a diverse selection of prey to choose from. These include their main prey item the southern elephant seal which has high fat content, Antarctic fur seals (*Arctocephalus gazella*), sub-Antarctic fur seals (*A. tropicalis*), King penguins (*Aptenodytes patagonicus*), gentoo penguins (*Pygoscelis papua*), macaroni penguins (*Eudyptes chrysolophus*) and eastern rockhopper penguins (*E. chrysocome filholi*) (Reisinger and de Bruyn 2014). They also consume cephalopods and cause major economic losses through depredation of Patagonian toothfish from demersal longliners around the Crozet Archipelago (950km east of the PEIs) (Reisinger and de Bruyn 2014; Reisinger et al. 2015; Reisinger et al. 2016). Their survival was found to be positively correlated to the Patagonian toothfish fishing effort offshore from the PEIs (Jordaan et al. 2023). The abundance of prey drives their movements around the islands – they are frequently sighted inshore and around seamounts where prey tend to aggregate (Keith et al. 2001). There is a lack of knowledge on their whereabouts offshore (Ford 2009; Reisinger et al. 2011; Reisinger et al. 2015).

Regarding their long-ranged movements, only one study has provided evidence on ecotype B migration from cold Antarctic waters to warmer sub-tropical waters using satellite telemetry (Durban and Pitman 2012). They were fast, directional movements to repair their outer skin layer while sustaining their thermal integrity in the warmer waters. Findlay and Best (2016) indicated that the abundance of South African killer whales (which are of a different morphotype than PEIs' population (Best 2007)) mirror the migration of minke whales and other baleen whales. Southern Ocean killer whales also depict this behaviour (Berzin and Vladimirov 1983). Shabangu et al. (2024b) recently showed that there is an overlap in acoustic detection of Antarctic minke whale bio-duck calls between the PEIs and South African waters from August to February. This could possibly suggest a spatial overlap or interaction between South African and Southern Ocean killer whales. Especially as they follow similar prey (Findlay and Best 2016; Schall and Van Opzeeland 2017), their offshore movements and distribution are unknown (Reisinger et al. 2015) and there are increased killer whale sightings in South African waters (Towner et al. 2022) possibly related to prey population declines elsewhere (Englebrecht et al. 2019). Only one study so far indicated no matches between killer whale individuals between the two locations (Reisinger et al. 2015), but additional tagging studies are needed to investigate this further.

Killer whales are highly social and rely on their acoustics to communicate with conspecifics (Miller and Bain 2000; Miller 2002). Shabangu et al. (2024a) preliminary discovered 5 social call types within the PEIs population which mostly consisted of stereotypical pulsed calls and tonal whistles. The former are broadband sounds with strong harmonics and high pulse-repetition rates and the latter are narrowband vocal signals with relatively higher frequency (Schall and Van Opzeeland 2017; Wellard et al. 2020). Echolocation clicks were also found which are used for locating prey and navigation (Zimmer 2011; Richard et al. 2021). These are short, broadband signals (10 – 100 kHz) used universally by dolphins (Schall and Van Opzeeland 2017; Wellard et al. 2020).

There is a lack of information on how the ecotypes differ acoustically as only three (B, C and D) have been acoustically described previously and only a total of seven studies have been conducted on their vocalisations within the Southern Ocean (Awbrey et al. 1982; Mossbridge and Thomas 1999; Richlen and Thomas 2008; Schall and Van Opzeeland 2017; Wellard et al. 2020; Richard et al. 2021; Shabangu et al. 2024a). Awbrey et al. (1982), Richlen and Thomas

(2008) and Shabangu et al. (2024a) indicated that Southern Ocean killer whale call structure and characteristics were similar to that of herring-eating residents of the Northern Hemisphere (Deecke et al. 2011). These included temporal acoustic differences, large vocal repertoire, high call rates and higher number of aberrant call types (no repeated distinct temporal and spectral features). Shabangu et al. (2024a) specifically found call rates and diel vocalisation patterns of the PEIs population comparable to that of whistles in the Icelandic population (Richard et al. 2017). This study also indicated similar structured calls to long-finned pilot whales (*Globicephala melas*) (Vester et al. 2017), humpback whale song units (Shabangu and Kowarski 2022) and sperm whale clicks (Shabangu and Andrew 2020).

Ecotype C was described to have 28 discrete call types which were highly complex with multiple frequency-, amplitude-modulated, pulsed and biphonic calls. Biphonic calls are two simultaneous independent modulated calls with overlapping high and low frequently components (Wellard et al. 2020). Ecotype D killer whale vocalisations included high rates of whistles, pulsed calls and clicks recorded at demersal longline vessels at the Crozet Archipelago (Mossbridge and Thomas 1999). These discoveries indicated evidence of adaptations to ambient noise and to gain leverage over other predators by occupying niched acoustic environments by ecotypes C and D respectively.

2.2. The Southern Ocean

2.2.1. The Antarctic Circumpolar Current

The Antarctic Circumpolar Current (ACC) is known to be the largest ocean current on Earth, at an estimated length of 24 000 km occurring in the Southern Ocean (Carter et al. 2008). It has an important feature influencing global climate as its eastward zonal flow connects all major ocean basins (*Figure 2.2*; Donohue et al. 2016) and their mechanisms for transporting water masses, distributing heat and other properties. The ACC's deep vertical and horizontal structure also serves as a link between atmospheric forcing and the ocean interior, thereby causing the Southern Ocean to respond to changes within the atmosphere (Thompson and Naveira Garabato 2014; Gille et al. 2016). The disconnection of Antarctica from Australia, from South America and the opening of the Tasman Gateway, i.e. the absence of continental barriers, resulted in the onset of this dominating current (Lefebvre et al. 2012) which presently occurs between the sub-Tropical Front (STF) northward of Marion Island and the westward current flowing along the continental iceshelf of the Antarctic – the East Wind Drift (Lutjeharms and Ansorge 2008; Chapman et al. 2020).

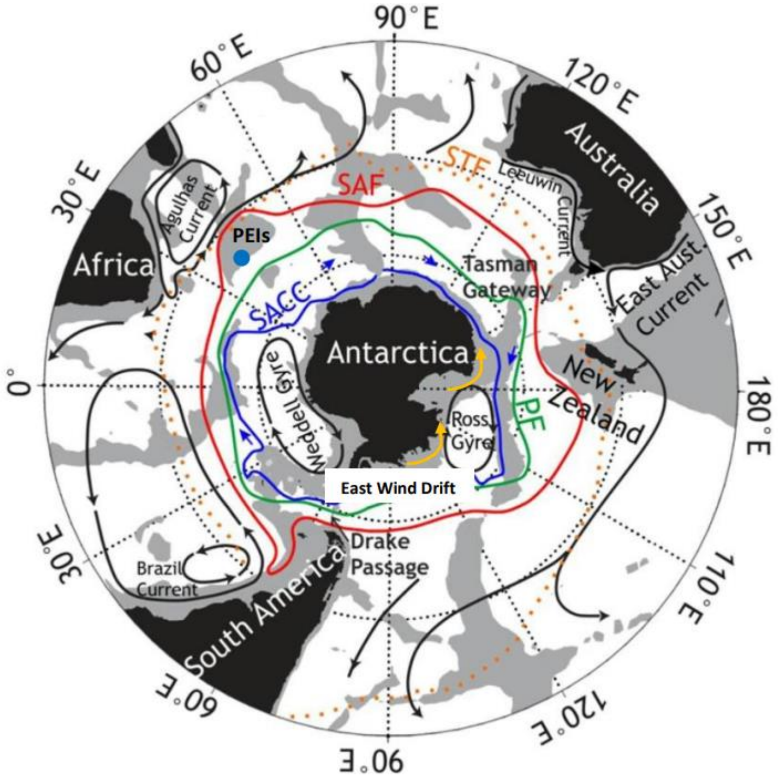

Figure 2.2. Schematic indicating the flow of the Antarctic Circumpolar Current (ACC; blue arrows) and its associated fronts – the sub-Tropical, sub-Antarctic and Antarctic Polar Front (STF (orange dots), SAF (red solid line) and PF (green solid line) respectively) as well as the location of the Prince Edward Islands (PEIs) represented by the blue dot. The East Wind Drift (yellow arrows) is a westward surface flowing-current between the Antarctic continent and the ACC flowing in the opposite direction. Grey areas show elevated bathymetry. Adapted from Sarkar et al. (2019).

The ACC is mainly driven by westerly wind stress between 35 °S and 55 °S in the Southern Ocean and the air-sea buoyancy forcing (Barker et al. 2007; Rintoul et al. 2010; Rintoul and da Silva 2019), with the former creating a direct transfer of momentum to the surface layer of the ocean. This results in convergence to the north of the ACC and divergence to the south of the current, thereby influencing stratification at its northern limits helping to set up the baroclinic current component (Allison et al. 2010). The strong westerly winds in this region cause the surface current to be highly variable, deflecting to the left of the wind direction and initiating upwelling to the south and downwelling to the north of the wind stress maximum (Rintoul et al. 2010). To balance the surface wind forcing, the ACC's pathway is also controlled by bottom form stress caused by its interaction with seabed topography and dynamic instabilities such as eddies (Nowlin and Klinck 1986; Lazarus and Caulet 1993; Rintoul et al. 2010).

The majority of the ACC's geostrophic volume transport is facilitated through the deep-reaching jets associated with the fronts in the region, namely the Polar Front (PF), the sub-Antarctic Front (SAF) and the Southern ACC Front (SACCF). The historic value used within global circulation and climate models for this mean ACC transport was 134 Sverdrups (Sv) (1 Sv = 10^6 m^3 s^{-1}) (Whitworth and Peterson 1985; Barker et al. 2007), but a recent study by Donohue et al. (2016) indicated that the total transport through the Drake Passage was 173.3 Sv which was 30% higher than this historical value. This was attributed to improved measurement systems. At the PEIs specifically, approximately 20 Sv, 40 Sv and 100 Sv of water is transported via the jets of the STF, APF and through the Andrew Bain Fracture Zone (ABFZ) respectively (Lutjeharms and Ansorge 2008).

2.2.2. Fronts of the Southern Ocean

As previously mentioned, most of the ACC's water flow is concentrated at the fronts (*Figure 2.2*). These are defined as rapid transitions of different temperatures, salinity, density profiles, chemical and ecological characteristics which extend from the seafloor to the sea surface. Zones between the fronts have homogenous physical and chemical water properties at depth and indicate similar seasonality (Rintoul and da Silva 2019; Chapman et al. 2020). These fronts are associated with the fast-flowing jets of the ACC as the strength of the current is strongly linked to the change in horizontal density which is prominent across the fronts (Lutjeharms and Ansorge 2008; Rintoul and da Silva 2019). The three fronts most influential to the PEIs are the sub-Tropical Front (STF) at approximately 42 °S (north of the PEIs), the SAF and the APF which both have a high degree of meridional variability (Ansorge and Lutjeharms 2003). At a depth of 200 m, these fronts are recognized by their 10 °C, 6 °C and 2 °C isotherms respectively. The STF is an intense front which becomes enhanced when it joins with the Agulhas Front further north (between 13.5 °E and 25 °E longitude), thus making its exact location quite difficult. The STF has a temperature gradient of 0.047 °C km^{-1} (Lutjeharms and Ansorge 2008) and does not form part of the ACC frontal system, but it is important as it separates the cold sub-Antarctic waters from the warmer sub-tropical waters (Shangheta 2021).

The PEIs are located between the SAF and the APF at approximately 47 °S to the north of the islands and 50 °S to their south respectively, but their interannual meridional variability is not well captured and substantiated (Ansorge and Lutjeharms 2003; Treasure et al. 2015; Lamont et al. 2019; Venkatachalam et al. 2019). Factors which influence the positions of these fronts around the PEIs and the structuring of the marine environment are temperature, prevailing winds and bottom topography (Graham et al. 2012). The SAF and APF both have a temperature gradient of 0.018 °C km^{-1} (Lutjeharms and Ansorge 2008). They also play an important role in nutrient cycling in the Southern Ocean as they are associated with higher primary productivity because of enhanced vertical mixing, advection of micronutrients, upwelling caused by eddies and topographic interactions. Contrastingly, the frontal jets can also prevent the cross-frontal exchange of nutrients to adjacent comparatively nutrient-deplete waters, thus defining the mixing barrier effect (Rintoul and da Silva 2019; Chapman et al. 2020). The relatively close proximity of the SAF and APF to the PEIs during certain conditions would have created localized primary productivity hotspots in the inshore region of the islands (Pakhomov et al. 2000; Chapman et al. 2020), allowing energy to cascade from lower trophic levels to higher trophic levels such as fish, seabirds and marine mammals (Rintoul and da Silva 2019). King penguins (*Aptenodytes forsteri*) and seals forage within the APF Zone and along these fronts (Chapman et al. 2020; Toolsee and Lamont 2022). Animals' feeding patterns are therefore influenced by their proximity to the fronts (Rintoul and da Silva 2019).

2.2.3. Meridional Overturning Circulation and Water Masses of the Southern Ocean

The ACC is connected to the weaker vertical circulation in the region known as the thermohaline or meridional overturning circulation which is density driven (*Figure 2.3*; Carter et al. 2008; Rintoul and da Silva 2019). This has key implications for global overturning circulation as it plays a role in transport and transfer of water masses, heat, salt and climate anomalies (Sallée et al. 2008; Thompson 2008; Rintoul and Naveira Garabato 2013). It is equally as important for biogeochemical cycles as nutrient-rich deep-water masses are upwelled south of the ACC, some transported north by westerly winds developing unique water masses by gaining heat and freshwater through air-sea exchange. This is also important for carrying carbon dioxide into the ocean interior when water masses sink (Rintoul and da Silva 2019), for example when Antarctic Bottom Water (AABW) sinks because of super-cooling and high salinity levels off the Antarctic ice shelf (Lutjeharms and Ansorge 2008; Carter et al. 2008).

The AABW is the coldest and densest water mass originating around Antarctica. The Circumpolar Deep Water (CDW) occurs at depths between 2000 and 3500 m north of the ACC (Rintoul and da Silva 2019), rising to the surface closer to Antarctica with a salinity maximum of 34.8 psu. This water mass originates from the Indian, Atlantic and Pacific Oceans. The waters at ACC's northern limits form the sub-Antarctic Mode Water (SAMW) and the Antarctic Intermediate Water (AAIW) which is distributed northwards at a depth of 1400 m (Carter et al. 2008). These water mass properties at the PEIs are different to other regions of the same latitude in the Southern Ocean – for example, the AAIW has a salinity minimum at 5 °C. This is saltier in comparison to the Atlantic sector of the Southern Ocean as more mixing and entrainment occurs as the ACC flows eastward. The sub-Antarctic Surface Waters (SASW) formed by subducting beneath sub-Tropical Surface Waters (STSW) at the Sub-Tropical Convergence with a salinity measure of less than 34.3 psu (Lutjeharms and Ansorge 2008).

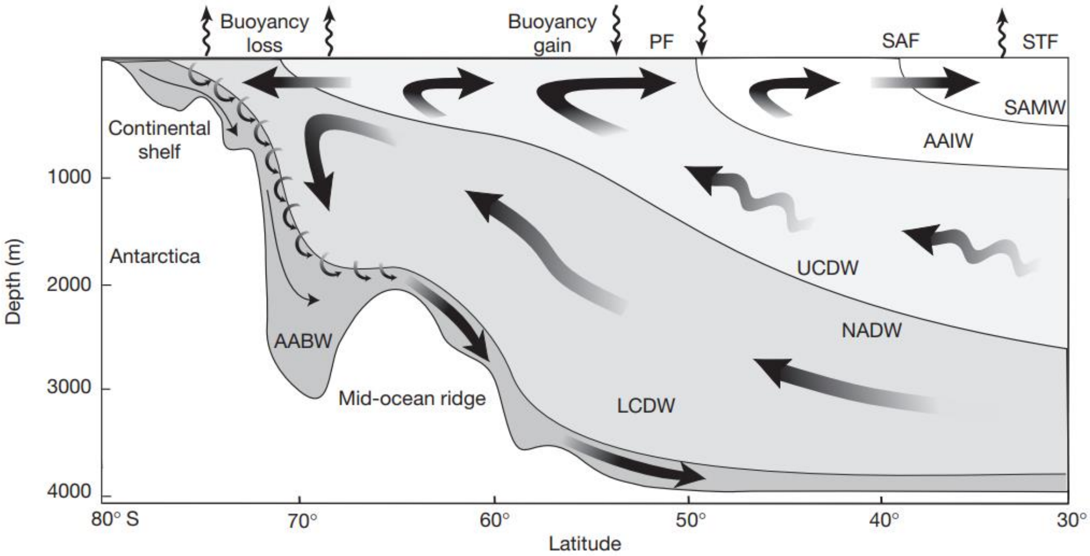

Figure 2.3. Schematic indicating the meridional overturning circulation in the Southern Ocean. The water masses displayed are as follows: the sub-Antarctic Mode Water (SAMW), Antarctic Intermediate Water (AAIW), Upper Circumpolar Deep Water (UCDW), Lower Circumpolar Deep Water (LCDW), North Atlantic Deep Water (NADW) and the Antarctic Bottom Water (AABW). Extracted from Rintoul and da Silva (2019).

2.2.4. Mesoscale eddy activity around the Prince Edward Islands

Dynamic instabilities such as eddies develop when the deep-reaching ACC interact with bottom topography, causing the meandering of its fronts which further releases and transfers energy stored in the ACC's sloping isopycnals into mean flow with different temporal properties (Rintoul and da Silva 2019; Toolsee and Lamont 2022). Mesoscale eddies have a diameter of 30 - 300 km with lifespans of weeks to months (Patel et al. 2020). Their intensity is strongly associated with changes in sea surface height (SSH) and their depths can extend further than 1000 m (Lutjeharms and Ansorge 2008). Eddies are therefore more frequent and have high mean kinetic energy around prominent topographic features and choke points such as the South-West Indian Ridge (SWIR) (Toolsee and Lamont 2022), the Drake passage (Joyce et al. 1981), the region south of Australia (Phillips and Rintoul 2000) and the Crozet and Kerguelen Plateaux (Gille 2003). Mean kinetic energy is much more reduced over deep-ocean basins with minimal topographic constraints (Ansorge et al. 2012).

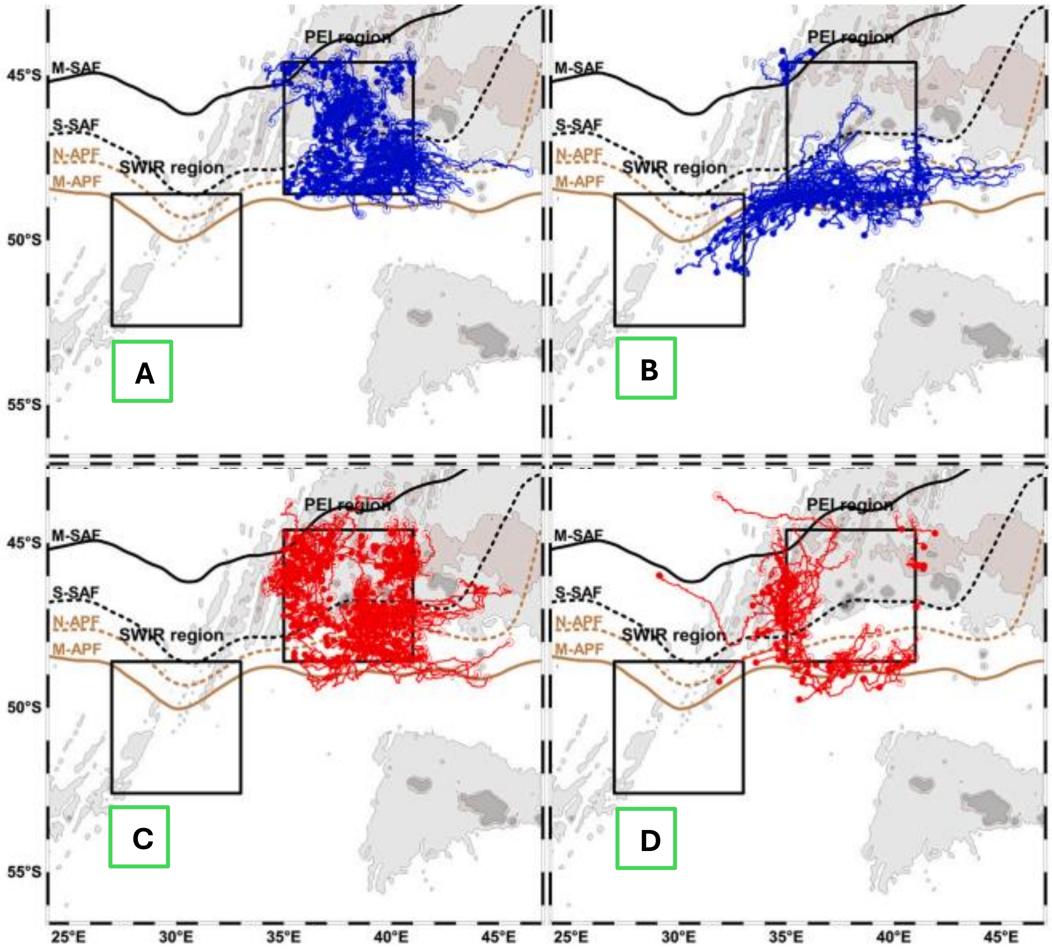

Figure 2.4. Maps indicating the origin of formation and pathways of cyclonic (blue) and anticyclonic (red) eddies between 1993 and 2018. The average positions of the middle and southern branches of the sub-Antarctic Front (M-SAF & S-SAF) are depicted in black. The average positions of the northern and middle branches of the Antarctic Polar Front (N-APF & M-APF) are depicted in brown. The Prince Edward Islands (PEI) region and South-West Indian Ridge (SWIR) region are enclosed by black boxes. Maps A and C show eddies formed locally within the PEI region. Maps B and D show eddies formed outside the PEI region. Adapted from Lamont and van den Berg (2021).

Focusing on the PEIs region, the ACC will respond to the shallow bathymetric features of the SWIR by forcing its fronts to converge through the Andrew Bain Fracture Zone (ABFZ) –

specifically the SAF and APF. This process increases the frontal meandering, current speed and eddy occurrence downstream of the SWIR (Toolsee and Lamont 2022). These eddies will then travel north-east into the Enderby Basin and towards the PEIs (*Figure 2.4*; Lutjeharms and Ansorge 2008). Contrastingly, the eddies which do pass into the PEIs region from the SWIR do not interact with the islands' shelf (Lamont and van den Berg 2021; Toolsee and Lamont 2022). Lamont and van den Berg (2021) indicated less than 10 eddies formed within the SWIR region interacted directly with the PEIs' shelf between 1993 and 2018 and there were no long-term or seasonal patterns in their numbers or characteristics. Most of the eddies that interacted with the shelf were locally formed and remained there until they dissipated (Lamont and van den Berg 2021). These physical changes to the PEIs' oceanic shelf environment could have a substantial impact on the diet, biomass and spatial distribution of top predators inhabiting the islands in the long-term (Crawford et al. 2014; Carpenter-Kling et al. 2019).

The westerly wind stress which drives the ACC has been known to strengthen in the last few years and has been hypothesised to strengthen the eddy energy field in the Southern Ocean and increase poleward heat transport across the ACC (Gille et al. 2016). Eddies also transport colder waters equatorward and towards the PEIs. This transfer of heat in the abyssal ocean is essential for balancing global climate (Nowlin and Klinck 1986; Lutjeharms and Ansorge 2008). Additionally, standing eddies (deviations of east to west flow) and transient eddies (temporally variable) also transfer momentum into the ocean interior, initializing the deeper component of the ACC (Rintoul and da Silva 2019). Eddies also play an important role in biogeochemical cycling and nutrient distribution across the ACC fronts (Ardyna et al. 2017). This concept is understudied and depends heavily on the local environmental context and mechanisms followed (such as eddy pumping, eddy-Ekman pumping, eddy trapping and eddy advection) (Chenillat et al. 2016). A study by Patel et al. (2020) showed that most nutrient re-distribution occurs below the mixed layer within an eddy. Eddies are essential features contributing to the biodiversity of the PEIs' oceanic environment as they enhance mixing and upwelling which increases primary productivity and create microhabitats at their edges. Many of the islands' top predators such as the southern elephant seals and macaroni penguins forage within eddies' spatial ranges (Chapman et al. 2020; Toolsee and Lamont 2022).

2.2.5. Climate Change at the Prince Edward Islands

The PEIs' climate is largely shaped by the surrounding oceanic environment – it is hyper-oceanic. The islands experience decreased thermal variability as the Southern Ocean has a characteristic high thermal inertia which acts as a thermal buffer. As a result of this feature, the daily air temperature at the PEIs fluctuates less than 2 °C and 3 °C in summer and winter respectively. Additionally, this causes air temperatures to reach freezing points randomly during the year and the maxima can be experienced randomly during the day. Eddies in the oceanic environment can also cause changes to air temperatures on the medium temporal scale (le Roux 2008). There is evidence of rapid warming within the sub-Antarctic region of the Southern Ocean, as well as in the inshore region of the PEIs (Mélice et al. 2003; Shangheta 2021). This increase in sea surface temperature (SST) trend was indicated by Mélice et al. (2003) who studied SST records between 1949 and 2003 at Marion Island and by Shangheta (2021) who found a 0.022 °C year^{-1} increase in SST between 1949 and 2018.

An increase in SST and surface air temperatures were partly attributed to changing atmospheric circulation in the region (Smith 2002). The passage of numerous atmospheric low-pressure systems across the region (Rouault et al. 2005) creates substantial short-term variability at the islands which masks the seasonal and long-term changes in the wind patterns (Toolsee and Lamont 2022). Pre-passage of these systems brings strong north-westerly winds, warm sub-tropical air and increased cloud cover. Post-passage brings cold, dry Antarctic air, strong south-westerly winds and decreased cloud cover (Nel 2012). The westerly wind component of the system has weakened as a result of climate change causing more anticyclonic conditions over the PEIs (Nel 2012) and as the westerly wind belt moves southwards, the winds at the islands become weaker (Toolsee and Lamont 2022).

As previously mentioned, the ACC and its fronts have migrated southwards as an indirect result of climate change, and this has many implications for the oceanic environment and biological communities of the PEIs (Ansorge et al. 2012). Climate change therefore may affect the short- and long-term oceanic circulation and atmospheric patterns in the sub-Antarctic and in the general Southern Ocean (Graham et al. 2012; Constable et al. 2014). Sub-Antarctic islands are considered important indicators for climate change and how ecosystems may respond to these changes (le Roux 2008; Venkatachalam et al. 2019). Seabirds and marine mammals which utilise the PEIs for breeding purposes were indicated to be sensitive to climate change (Toolsee and Lamont 2022). Additional evidence of climate change includes melting of perennial snow and ice on the islands (le Roux 2008).

There are other phenomena which affect the climate variability around the PEIs. These include the Southern Oscillation (SO), the Southern Annular Mode (SAM), the Semi-Annual Oscillation (SAO) and the Antarctic Circumpolar Wave (ACW). The SO is used as measurement of the Walker circulation in the South Pacific tropical region, is a metric for the El Niño Southern Oscillation (ENSO) index (Ferster et al. 2018) and is influential to SST, atmospheric temperature and sea-ice in Antarctica (Fogt and Bromwich 2006; Welhouse et al. 2016; Cerrone et al. 2017). Modelling studies have indicated that Southern Ocean warming is also attributed to the change in amplitude of the ENSO (Wang et al. 2022). At the PEIs, ENSO indicated weak and mostly insignificant influence on SST anomalies and spatial correlations of SST, wind and geostrophic currents at 1 – 5 year time lags (Toolsee and Lamont 2022).

SAM describes the meridional shifts of westerly winds around Antarctica through the measurement of the pressure gradient between the polar and subpolar regions around the South Pole (Gallego et al. 2005; Richard et al. 2013) on an interannual time scale (le Roux 2008). In combination with the expanding Antarctic ozone hole (Thompson et al. 2011), SAM has caused the southward shift of the westerly wind belt and intensity (Thompson and Solomon 2002) as well as affecting SST (Sen Gupta and England 2006) and chlorophyll-a concentrations in the sub-Antarctic (Lovenduski and Gruber 2005). Contrastingly, Toolsee and Lamont (2022) recently showed no strong direct impact of SAM on SST at the PEIs, thereby indicating that the effects of SAM are not the same across the Southern Ocean, but longer time series are needed to draw out significant relationships between these variables.

The SAO is a phenomenon related to the prominent biannual cycle in temperature, pressure and wind within the Southern Hemisphere mid-latitudes as a result of the temporal variability of the annual cycle of iced-over high latitudes and oceanic mid-latitudes (Rouault et al. 2005). SAO’s effects are observed on an intra-annual time scale and cause the biannual strengthening and southward movement of the atmospheric Antarctic circumpolar trough and jet stream. The SAO has weakened since the 1980s (le Roux 2008), ultimately causing an increase in eddy heat transport (Carleton 2003) and changes to seasonal wind, temperature and rainfall at the PEIs (Rouault et al. 2005).

The ACW is described as an eastward-moving circumpolar anomaly within the Southern Ocean influencing SST, air temperature, sea-level winds and Antarctic sea ice-extent bimodally. It takes between 8 to 10 years to fully encircle Antarctica and is hypothesized to cause the inter-decadal variation of SST at the PEIs (le Roux 2008; Mélice et al. 2003). Evidence of this effect was found by Toolsee and Lamont (2022) as independent signals of the ACW coincided with interannual periodicity and decadal-scale signals of SST.

2.2.6. The Island Mass Effect

The sub-Antarctic region in general is largely characterized by low phytoplankton growth and high nutrient content, marking it as a High Nutrient, Low Chlorophyll (HNLC) region (Bristow et al. 2017). This is apart from increased chlorophyll-a regions of the ACC fronts and around sub-Antarctic islands (Sokolov and Rintoul 2007). These islands cause localized areas of enhanced primary production (Gove et al. 2016) because of high concentrations of macronutrients from the guano, dung, urine and animal remains of large masses of animals utilising the islands which runoff from the land into the shelf waters (Allanson et al. 1985; Duncombe Rae 1989). A Taylor column also promotes upwelling and retains water on the islands' shelf (Lamont et al. 2019). This phenomenon is known as the Island Mass Effect (IME), and it contributes to biodiversity as enhanced primary production sustains rich benthic communities and populations of top predators (von der Meden et al. 2017). The inshore portion of the PEIs' ecosystem is sustained by this phenomenon (Pakhomov and Froneman 1999). A recent study by Lamont and Toolsee (2022) indicated that surface chlorophyll-a concentrations increase in October-May and the IME is spatially connected to the shelf during December and February seasonally (*Figure 2.5*).

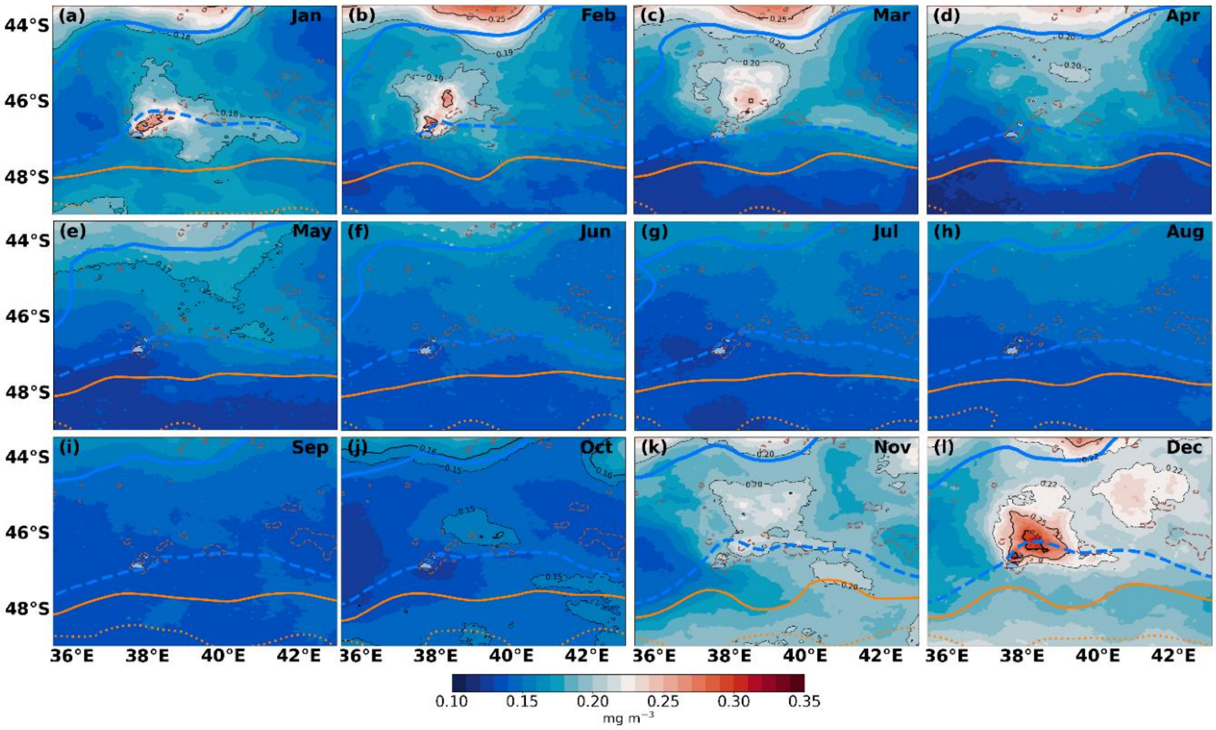

Figure 2.5. Monthly climatology of Copernicus-GlobColour chlorophyll-a concentration (mg m^{-3}) extracted from Lamont and Toolsee (2022) of the Prince Edward Islands. The dashed brown contours indicate the 1000 m isobath. The solid and dashed thick blue lines show the climatological mean positions of the middle and southern branches of the SAF, respectively. The solid and dotted thick orange lines illustrate the climatological mean positions of the northern and middle branches of the Antarctic Polar Front, respectively.

2.3. Environmental Influences on Killer Whales

There is very limited understanding of the direct influence on killer whales' occurrence, distribution and behaviour not only within the Southern Ocean, but in the Southern Hemisphere as a whole. Odontocetes such as killer whales are not as broadly studied as the popular baleen whales (Van Waerebeek et al. 2010). There is therefore an urgent need to fill these knowledge gaps and a few studied have aimed to do so.

Jones et al. (2019) assessed the environmental drivers of killer whale seasonal aggregations in the Bremer Canyon of Australia with the use of spatial ecological modelling with dolphin presence, bathymetry and sea surface conditions as inputs. The results indicated that killer whale aggregations were most influenced by depth and distance from the continental shelf as they prefer habitats deeper than 1000 m and distances of 5000 m from the shelf. This was largely because of increased prey abundance which in turn is due to complex topography enhancing upwelling and primary productivity (Baumgartner 1997; Rennie et al. 2009a). This is comparable to the topographical features driving the marine biogeochemical cycles around the PEIs (Rintoul and da Silva 2019; Chapman et al. 2020). Hodge et al. (2013) also indicated similar results as killer whales were found to vocalise more at depth at Onslow Bay because of increased diversity and occurrence of prey which was again associated with increased primary productivity influenced by frontal activity along the Gulf Stream. A local study of killer whale occurrence in the South African exclusive economic zone (EEZ) showed that they are more likely to occur within 180 km of the inshore region and between depths of 300 and 3000 m (Purdon et al. 2020).

More recent studies within the PEIs region by Jordaan et al. (2023) and Shabangu et al. (2024a) have made progress in this context. The former stipulated that this killer whale population's survival, social structure and reproductive success was not significantly correlated with environmental proxies of prey abundance. These proxies included the Southern Oscillation Index (SOI), SAM and sea surface temperature anomalies (SSTa) and would likely affect killer whales on a longer timescale. Climate variability and ecosystem dynamics are not well understood within the southern Indian Ocean (Pardo et al. 2017; Seyboth et al. 2016). Shabangu et al. (2024a) indicated that wind speed at the islands was the most important factor affecting their acoustic occurrences and moderately important factors included SSH, chl-a and SST on a seasonal scale. A higher probability of vocalisation was evident at SSH below 0.07 m, indicating preferred marine habitat conditions at the islands for both predator and prey and will also therefore be affected by ACC frontal variability. This population also shows adaptability to varying SSTs and prey abundance as they are present year-round at the PEIs. These variables were also of importance to their diving, foraging, social structure and movement found in previous studies (Passadore et al. 2014; Reisinger et al. 2015; Reisinger et al. 2018).

Chapter 3. Data and Methods

The following chapter addresses the datasets and methods used during statistical analyses to answer the previously proposed objectives (*Chapter 1*) of this study.

To answer these questions, satellite data was obtained and analysed using figures produced in R software (R Core Team 2023), version 4.4.1 available at https://www.r-project.org/ as well as in Python software, version 3.9 available at http://www.python.org. The acoustic data was manually processed in Raven Pro, version 1.6.3 available at https://ravensoundsoftware.com (K. Lisa Yang Center for Conservation Bioacoustics 2022) and was scanned in an automated acoustic detector using Matlab Compiler Runtime launcher.

3.1. Environmental Data

Satellite, reanalysis and near real-time environmental data was spatially averaged across a 2° (222 km latitude) × 2° (156 km longitude) area centred over the mooring system location (46° 46.40 S, 37° 54.70 E) deployed between the PEIs (*Figure 3.1*). This was processed in Python software and performed for daily chlorophyll-a concentration (chl-a), sea surface temperature (SST), sea surface height (SSH) and hourly wind speed (averaged to the daily scale). These datasets provide a good representation of the surface ocean conditions of the region and the details of the data sets are provided in *Table 3.1*.

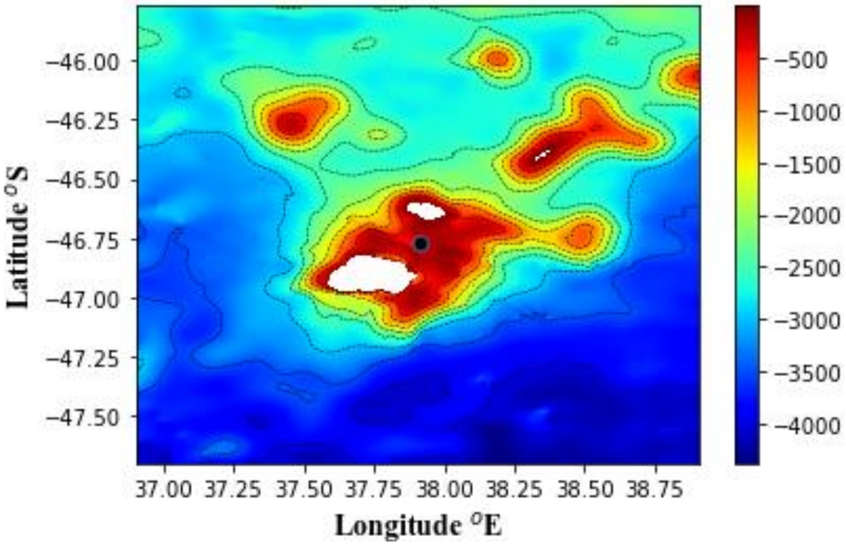

Figure 3.1. Bathymetric map of the 2° x 2° sub-Antarctic Prince Edward Islands region. This is the magnified area used for spatial averaging of environmental data (latitude 45.77 °S - 47.77 °S; longitude 36.91 °E – 38.91 °E). The blue-black dot indicated the location of the mooring system on which the hydrophone was mounted. Depth contours are in intervals of 500 m and range from 500 m to 6000 m. The gridded bathymetric dataset 'GEBCO_2022 Grid' was sourced from GEBCO

(http://www.gebco.net/data_and_products/gridded_bathymetry_data/). GEBCO provides elevation data in meters on a 15 arc-second interval grid.

Table 3.1. List of environmental variables, their proxies and data products used for each. Where the temporal range of a certain level 4 reprocessed product could not span the range of the study period, the remaining time was supplemented with the near real-time dataset listed. CMEMS is defined as the Copernicus Marine Environment Monitoring Service. GlobColour is the Global Ocean Colour for Carbon Cycle Research, OSTIA is the Operational Sea Surface Temperature and Sea Ice Analysis and DUACS is the Data Unification and Altimeter Combination System. ERA5 is defined as the fifth generation of European Centre for Medium-Range Weather Forecasts reanalyses.

Variable & Proxy	Data product	Source	Spatial resolution	Temporal range
Chl-a (mg m^{-3}) Primary productivity	CMEMS: GlobColour	https://data.marine.copernicus.eu/product/OCEANCOLOUR_GLO_BGC_L4_MY_009_104/description	0.04° x 0.04° (4 x 3 km)	May 2021-April 2023
SST (°C) Physical oceanographic environment affecting primary productivity	CMEMS: OSTIA	https://data.marine.copernicus.eu/product/SST_GLO_SST_L4_REP_OBSERVATIONS_010_011/ https://data.marine.copernicus.eu/product/SST_GLO_SST_L4_NRT_OBSERVATIONS_010_001/description	0.05° x 0.05° (6 x 4 km) 0.05° x 0.05° (6 x 4 km)	May 2021–April 2022 June 2022-April 2023
SSH (m) Position of ACC fronts	CMEMS: DUACS	https://data.marine.copernicus.eu/product/SEALEVEL_GLO_PHY_L4_MY_008_047/description	0.25° x 0.25° (28 x 19 km)	May 2021-April 2023
Wind speed (m.s-1) Sea state	CMEMS: ERA5	https://cds.climate.copernicus.eu/cdsapp#!/dataset/ reanalysis-era5-pressure-levels?tab=form	0.25° x 0.25° (28 x 19 km)	May 2021-April 2023

3.2. Passive Acoustic Monitoring Data

A passive acoustic monitoring (PAM) system was established between the islands (46°46.40 S, 37°54.70 E) which consisted of an oceanographic mooring with an SoundTrap ST500 STD autonomous hydrophone (Ocean Instruments NZ, New Zealand) attached to it at 162 m depth. To reduce noise, the linking chains were braided with ropes. A PAM system was chosen to survey the acoustic environment as it is a useful and ideal tool to use in a logistically challenging environment such as the PEIs situated in a harsh, remote location where field workers are limited in their monitoring abilities. It also allows for a greater spatial and temporal data set to be collected with minimal animal disturbance (Zimmer 2011; Shabangu et al. 2024a).

The PAM system was deployed at approximately 10 km from Marion Island and 9 km from the Prince Edward Island and the complete mooring system constitute part of the South

Atlantic Meridional Overturning Circulation (SAMOC) program which aims to link the observation network of global overturning circulation of the South Atlantic Ocean and the Southern Ocean (https://www.aoml.noaa.gov/phod/SAMOC_international/). The hydrophone recorded the acoustic environment (area around the islands as killer whale calls propagate 10 km from the source (Richard et al. 2021)) for 14 minutes of every hour of every day of the sampling period (*Table 3.2*).

Table 3.2. PAM system deployment details and SoundTrap (ST500) autonomous recorder calibration specifics.

Latitude & Longitude	Water depth (m)	Hydrophone depth (m)	Sampling rate (kHz)	Sampling protocol (min.h^{-1})	Duty cycle (%)	Hydrophone sensitivity (dB re 1 V µPa^{-1})	Recording start & stop date
46° 46.4’S 37° 54.7’ E	167	162	96	14	24	-165	26 April 2021 – 6 May 2022 9 May 2022 – 26 April 2023

3.3. Predator-Prey Sightings Data

To corroborate the year-to-year variability of the acoustic occurrence of killer whales, their land-based visual sightings were also investigated during the study period. These killer whale sightings were collected during dedicated (3-10 hours) and opportunistic survey sessions from the coasts of Marion Island by skilled observers using photograph identification and other additional data was collected (behaviour, sex, pod size, age). This killer whale populations’ main diet is that of the southern elephant seal (SES) which has high fat content (Reisinger and de Bruyn 2014) and will therefore be used as a proxy for general prey abundance. SES abundances were obtained through surveys conducted on Marion Island’s eastern beaches every 9 days during their breeding season (August-November) and every 10 days outside of their breeding season. Because SES tend to stay in one area for a long time (Hofmeyr et al. 2012), the SES abundances on days in between the survey days were extrapolated and filled using 5-day groupings and given the nearest survey date. Both datasets were provided by the Marion Island Marine Mammal Programme (MIMMP).

3.4. Data Analysis

3.4.1. Killer Whale Call Detection Methodology Comparison

R software was utilised to plot and compare the two acoustic detection methods for social calls – manual counting of calls through spectrogram interrogation and the automated call detector with 75% accuracy, namely *Spectrodetector* developed for Northern Hemisphere killer whales. Both years' sound files were additionally scanned for social calls at a 50% confidence threshold. The *Spectrodetector* is a customized acoustic data analysis software developed by JASCO Applied Science Ltd, Victoria, British Columbia, Canada. This random forest model detector classifier is used for the detection and classification of killer whale calls but also includes by-products of humpback whale and fish classes (Moloney et al. 2014; Mouy et al. 2013). Matlab Compiler Runtime launcher was used to independently run the detector on a Windows PC even without Matlab installed. Instructions for running the software were provided privately by JASCO. Calls identified using the automated detection method was used for all plotting and analysis after validating its performance against the manual method.

The number of social calls for both methods were plotted in a bar graph side-by-side for the full 2021-2022 data set and the first 10% of the 2022-2023 data set (May – June 2022) separately. Thereafter, the difference in call number was plotted for easier visualisation. To statistically analyse how accurate the automated detector is compared to the manual method, a Pearson correlation test was conducted between the number of calls detected for each method. This was done using the Pearson Product-Moment correlation coefficient (r), also known as the correlation coefficient (Asuero et al. 2006). This is a measurement of linear association strength between two variables, and is calculated by the equation below (Emerson 2015):

$$r = \frac{n(\sum xy) - (\sum x)(\sum y)}{\sqrt{[n\sum x^2 - (\sum x)^2][n\sum y^2 - (\sum y)^2]}}$$

Where n represents the number of ordered pairs in the data set, x and y represent the first and second set of values of the data set respectively. A correlation coefficient of 0 indicates no correlation, with increasing positive correlation as it increases to 1 and decreasing negative correlation as it decreases to –1. In the interest of time, a simpler analysis such as a correlation test was chosen to statistically analyse this comparison instead of other more complex accuracy metrics such as receiver operating characteristics, detection-error-trade-offs, precision-recall and cost curves typically used for checking automated detections against manual detections (Rodofili et al. 2022; Hildebrand et al. 2022). Statistical comparison between manual detections and classification algorithms is uncommon (Fleishman et al. 2023).

3.4.2. Killer Whale Vocalisations

Sound files (.wav format) were manually scanned for calls using audio and visual spectrogram tools in Raven Pro software for the whole year of April 2021-May 2022 and the first 10% of the remaining study period. This software is typically used for the acquisition, visualisation, measurement and analysis of sound in the field of bioacoustics (K. Lisa Yang Center for Conservation Bioacoustics 2022). Spectrograms were analysed between a maximum of 15-20 kHz at 2 minute and 45 second frames. The spectrogram settings used were Hann window, 0.0394 second frame size, 4096 sample discrete Fourier transformation (DFT) size and a 50% overlap. Both years' sound files were additionally scanned for social calls using the automated acoustic detector as previously described.

Previously described killer whale call types were used for this study (Shabangu et al. 2024a). These include social calls (tones, upsweeps, squeaks, downsweeps, whistles) and echolocation clicks (*Figure 3.2*). Acoustic experts in killer whale vocalisations from the University of Iceland were also consulted to confirm the calls found (Shabangu et al. 2024a) and a more detailed call catalogue and naming convention is currently being developed. Because the automated acoustic detector was only able to identify and count the social calls for the study period and not echolocation clicks, a Pearson correlation test was used to determine the relationship between the occurrence of social calls and echolocation clicks for the manually counted 2021 – 2022 PAM data set. The Pearson correlation coefficient of this relationship equated to 0.62, thus indicating a moderate positive association between social calls and echolocation clicks. We can therefore assume that echolocation clicks occur together with social calls. Contrastingly, a two-sample t-test conducted indicated that the mean of the call rates of the two call groups was significantly different from each other (number of social calls per hour = 1.14; number of echolocation clicks per hour = 0.38; $p\text{-value} < 0.005$). This may be attributed to the underestimation of echolocation click counts using manual methods. For the purposes of this study, social calls were used as a proxy for occurrence of echolocation clicks as there was limited time to learn automated detection methods specifically for killer whale clicks.

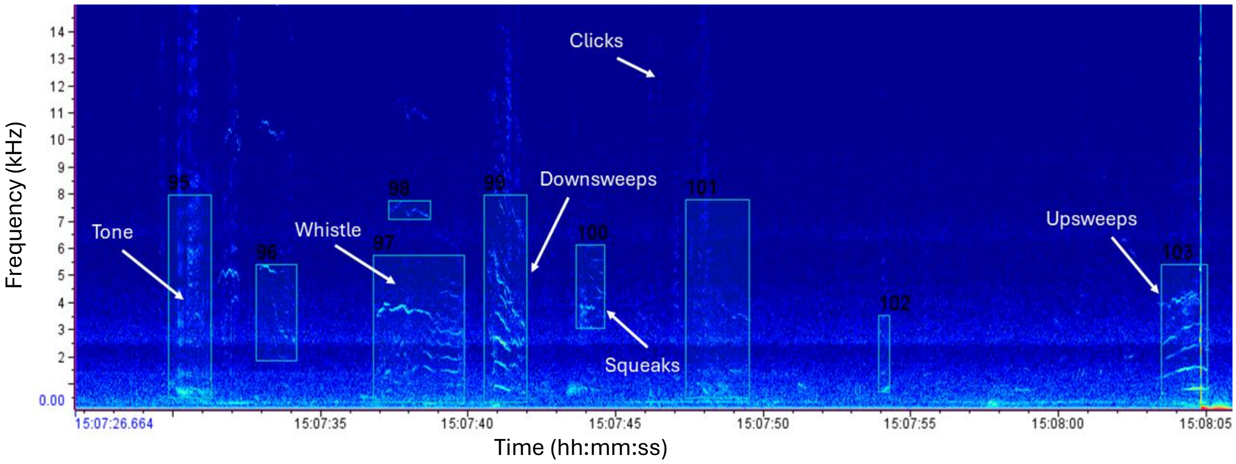

Figure 3.2. Spectrogram indicating the killer whale call types present during the acoustic survey period from April 2021 to May 2023 in the study region. The boxed calls are those recognized and annotated using the automated killer whale social call detector. Frequency (kHz) is represented on the y-axis and time (hh:mm:ss) on the x-axis.

Killer whale acoustic occurrence was represented using hours per day with social calls and was calculated as the total number of 14-minute recordings which has one or more calls for each day of the study period. Each 14-minute recording represented the hour it took place in. Social call rates were calculated as follows:

Call rate = Number of calls within each sampling session / Duration of sampling session, where the duration of the sampling session is 14 minutes.

These outputs were then used to do all the above-mentioned plotting. Killer whale hourly call rates were calculated, separated into bins for easier visualisation and plotted in a Hovmöller plot using R software to determine their diel call patterns. The nautical daylight regime for the PEIs were obtained from the 'suncalc' package (Thieurmel and Elmarhraoui 2019) in R for the specific oceanographic mooring location (*Table 3.2*). Daytime was between sunrise and sunset. Nautical dawn and dusk were defined as the time before sunrise and after sunset respectively when the sun is between 0° and 12° below the horizon geometrically. Nighttime is therefore between dusk and dawn, and the sun is more than 12° below the horizon geometrically (Shabangu et al. 2020). UTC (Coordinated Universal Time) was used as it is a universally understood time zone. The statistical tests to examine differences between daylight regimes between the two years and for each year separately were done through multiple pairwise t-test comparisons using Bonferroni's adjustment for multiple testing through the 'rstatix' R package (Kassambara, A., 2021).

3.4.3. Seasonal Environmental Conditions, Acoustic Parameters and Sightings Climatology

R software was used to compile spatially averaged environmental data into a seasonal climatology over the specified study period. The seasonal climatology plot contains 2-year-long seasonal averages of the daily chl-a, SST, SSH and wind speed, killer whale sightings, SES abundances data for May 2021 – April 2023, and 1 year and 8 months of data for seasonal averages of the acoustic parameters. The austral seasonal cycle was used for this data, namely summer (December to February), autumn (March to May), winter (June to August) and spring (September to November). Interpretation of this climatology provides information about the relationships between these variables on seasonal time scales.

3.4.4. Monthly Environmental Conditions, Acoustic Parameters and Sightings Time Series

The spatially averaged environmental data, acoustic (call occurrences and rates) and predator-prey sightings data was plotted together on the same x-axis for May 2021-April 2022 and May 2022-April 2023 on a monthly scale using the ggplot package (Wickham 2006) in R. These two time periods were referred to as 2021-2022 and 2022-2023 (or 2022 for the acoustic parameters respectively. The dedicated and opportunistic killer whale visual sightings were summed and plotted together on one y-axis and all other variables had separate y-axes. Studying the environmental conditions at the islands will allow for the comparison of the environmental variability against that of the killer whale acoustic occurrences. The environmental data's temporal and spatial range was chosen to match that of the acoustic occurrence. A time series is defined as an ordered sequence of data of a certain variable with specified time intervals. This data was plotted together for easier visualisation and interpretation.

3.4.5. Statistical Analyses

Random Forest (RF) modelling was used to determine the most important predictors and significant partial effects of these predictors for the acoustic call patterns observed for both years of the study period. Predictor variables included SST, SSH, chl-a, wind speed, hour of the day, month, SES abundance, number of unique killer whale sightings and year. A RF model was chosen as it was found to perform better than generalized additive and boosted regression trees models when analysing marine mammal acoustic occurrences (Shabangu et al. 2017; Shabangu et al. 2019). RF models additionally have high prediction accuracy and have non-parametric inferences. P-values were generated using permutations and RF modelling performed in R using the 'randomForest' package (Liaw and Wiener 2002) processed through the 'ranger' package (Wright and Ziegler 2017). Prior to running the RF, a multicollinearity test was conducted between the predictor variables. This was performed using generalized variance inflation factors (GVIFs) through the 'car' R package (Fox and Weisberg 2019). Season was initially included to be fitted into the model, but this predictor variable indicated very strong collinearity to month (GVIF = 10) and was chosen to be excluded from the model. All other predictor variables showed weak to low collinearity (GVIF < 5). For better comparison to previous acoustic studies on this killer whale population (Shabangu et al. 2024a) and future studies, the downsampling sample balancing method was chosen to address potential future differences in class imbalance of acoustic detection between social calls and echolocation clicks. This downsampling method also indicated better probability distributions between observed and predicted data than other sample balancing methods (ADAptive SYNthetic (ADASYN; He et al. 2008), Synthetic Minority Over-sampling Technique (SMOTE; Chawla et al. 2002) and upsampling (Nallamuthu 2020) as shown in *Figure 3.3* where the smoothed line remained close to the ideal diagonal line. The RF model was tuned using 70% of the balanced data for training and 30% for testing. The predictor importance values were represented as a percentage.

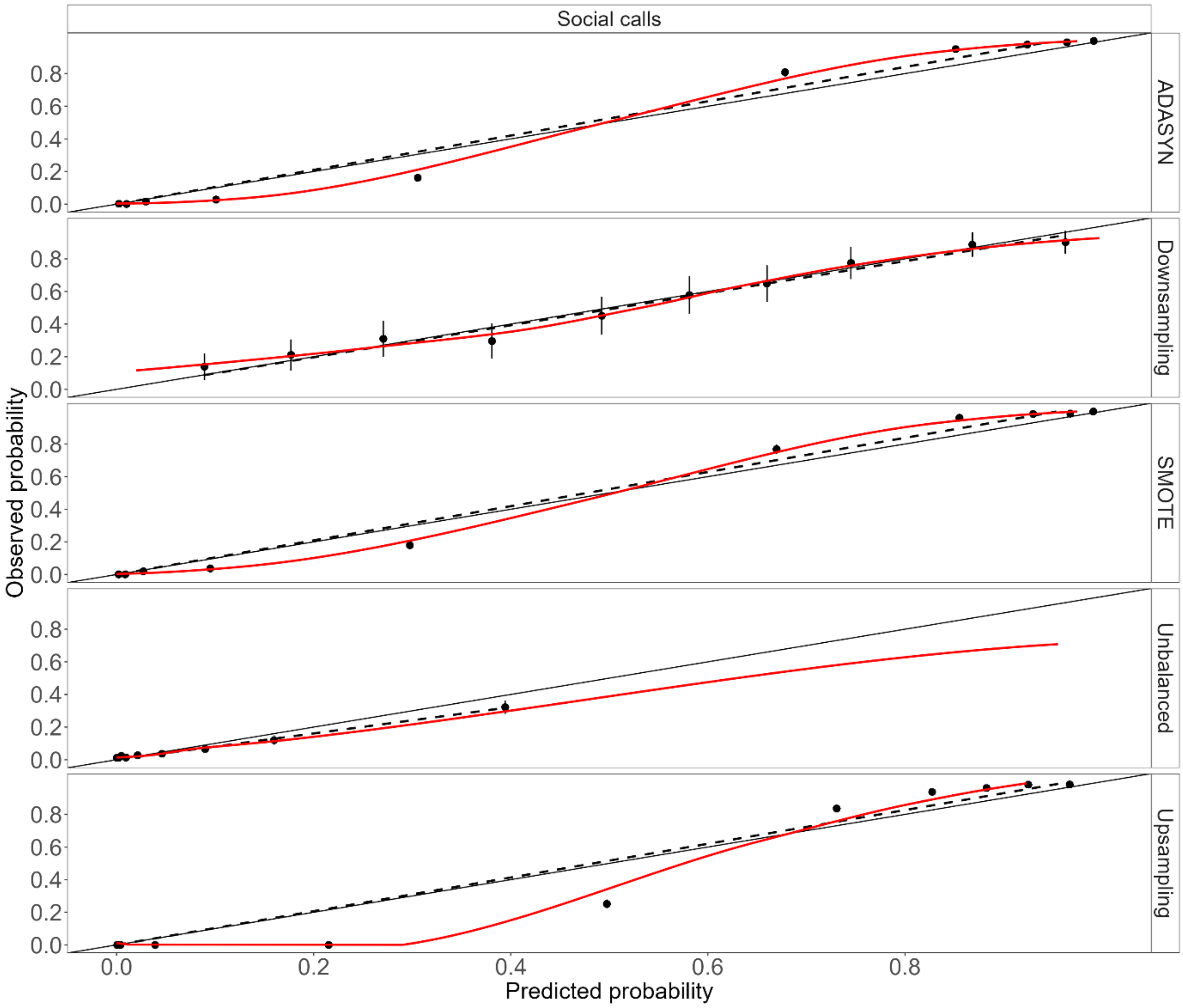

Figure 3.3. Calibration plots indicating the RF model predictive performance for killer whale social calls detected in the acoustic environment of the PEIs using different sample balancing methods.

To assess the significant differences in environmental variables and acoustic occurrences of killer whales around the PEIs between period 2021-2022 and period 2022, two-tailed t-tests were conducted for each month and for each season. The null hypothesis states that both years tested have the same mean values. The alternative hypothesis states that both years tested have unequal mean values. The significance level was set at 5%. P-values below this level will be considered statistically significant and the null hypothesis was rejected. P-values above the significant level of 5% were considered statistically insignificant and there is a lack of sufficient evidence to reject the null hypothesis.

Chapter 4. Results

This chapter presents the results of the proposed objectives (*Chapter 1*) of this study. The environmental variability, killer whale acoustic occurrences on a seasonal and monthly scale as well as statistical analyses were plotted and described.

4.1. Acoustic effort

The total acoustic effort (TAE) over the sampling period between April 2021 to April 2023 equated to 4083,83 hours over the 730 days (*Table 4.1*). The TAE for the months of April 2021 and April 2023 were not at its maximum, recording only for 27,77 and 141,39 hours respectively. This was due to routine deployment and retrieval of the hydrophone that occurred during those months.

Table 4.1. Total acoustic effort per month across the sampling period between 26 April 2021 and 26 April 2023.

Year	Month	Hours recorded	Number of days containing recordings
2021	Apr	27,77	5
2021	May	173,37	31
2021	Jun	167,77	30
2021	Jul	173,37	31
2021	Aug	173,37	31
2021	Sep	167,77	30
2021	Oct	173,37	31
2021	Nov	167,77	30
2021	Dec	173,37	31
2022	Jan	173,39	31
2022	Feb	156,57	28
2022	Mar	173,37	31
2022	Apr	167,77	30
2022	May	173,35	30
2022	Jun	167,77	30
2022	Jul	173,37	31
2022	Aug	173,37	31
2022	Sep	167,77	30
2022	Oct	173,37	31
2022	Nov	167,77	30
2022	Dec	173,37	31
2023	Jan	173,41	31
2023	Feb	156,57	28

2023	Mar	173,37	31
2023	Apr	141,39	26
	Total	**4083,83**	**730**

The automated acoustic detector identified 7247 social calls produced in 2021-2022 and 7315 social calls in 2022-2023. Visual inspection of spectrograms (*Figure 4.1*) revealed that many of the signals detected between January – April 2023 were false positives, i.e. not killer whale calls but electrical noise produced by a malfunctioning hydrophone. This was true even as data was filtered to remove calls with less than 50% confidence. All analyses performed in this study therefore excluded the period containing the faulty acoustic data from January to April 2023.

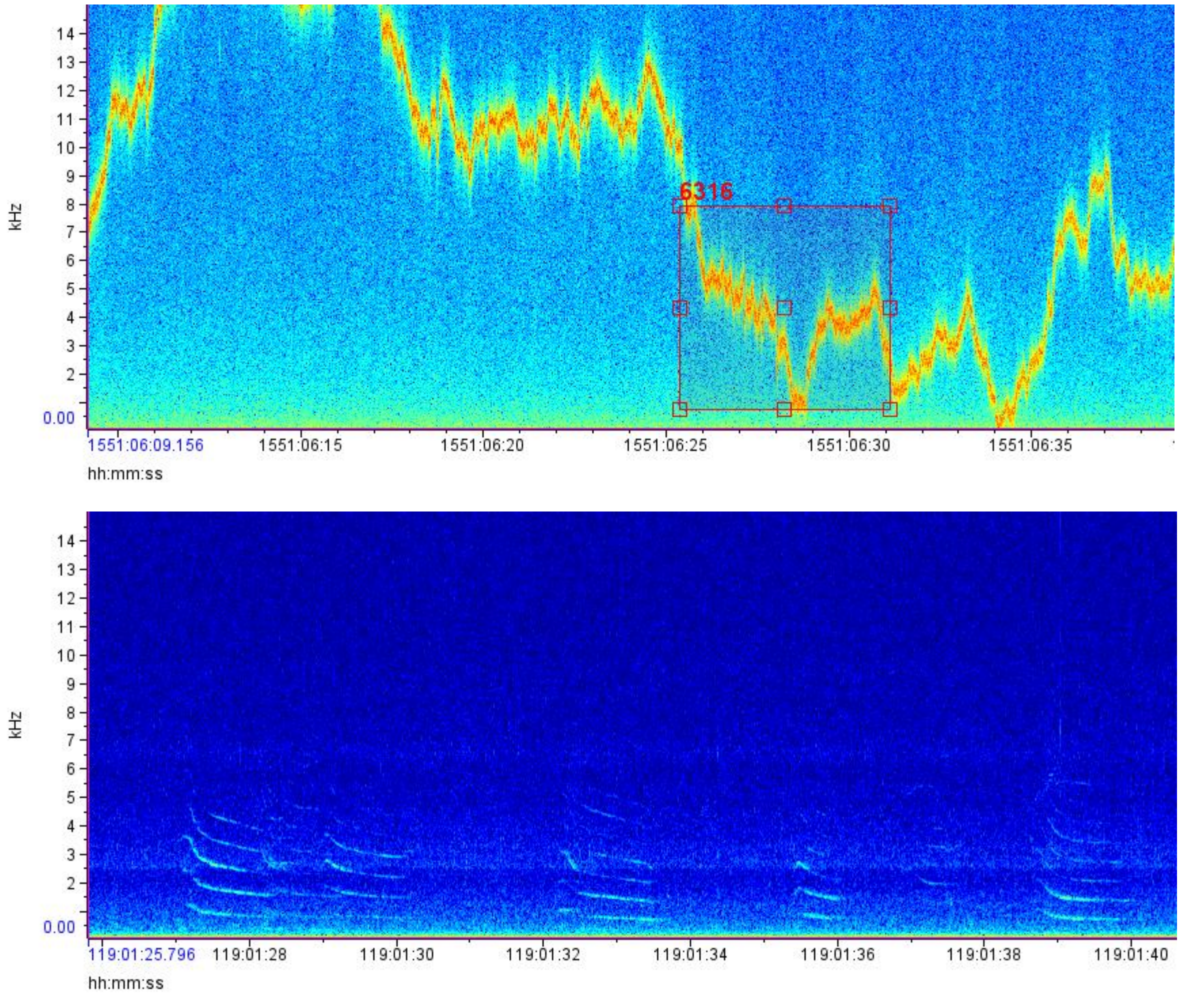

Figure 4.1. The top panel spectrogram indicates the electrical noise being produced by the hydrophone that the automated acoustic detector, namely the *SpectroDetector* run at 50% confidence, identified and annotated (in red) as killer whale vocalisations during the January – April 2023 period. The bottom panel spectrogram indicates an example of a true killer whale call type and visualised using the same colour palette, frequency range and page size configuration (45 seconds). The

spectrogram settings used were Hann window, 0.0394 second frame size, 4096 sample discrete Fourier transformation (DFT) size and a 50% overlap.

4.2. Detection Methodology Comparison

This section describes the performance between the two detection methods used within this study, namely using the automated acoustic detector – *SpectroDetector*, and the manual annotation and counting of social calls using spectrograms in Raven Pro software. This comparison will determine whether the automated detector can be used in place of the time-consuming manual detection method for identifying killer whale calls.

Figure 4.2 indicated the total monthly killer whale call numbers for the period between April 2021 and June 2022 – the longest time period that contains manual detections. This was compared to the total monthly number of calls identified using the automated detection method. Generally, both detection methods highlighted the peaks in calls in August 2021 and May 2022, as well as the increase in call numbers between October to December 2021. Therefore, both methods indicate similar timings of when vocalisations occur. When observing the number of calls detected in more detail, the automated detector underestimated the number of calls at most instances. The total number of manually identified calls found equated to 11 147 and automated identified calls equated to 8 134.

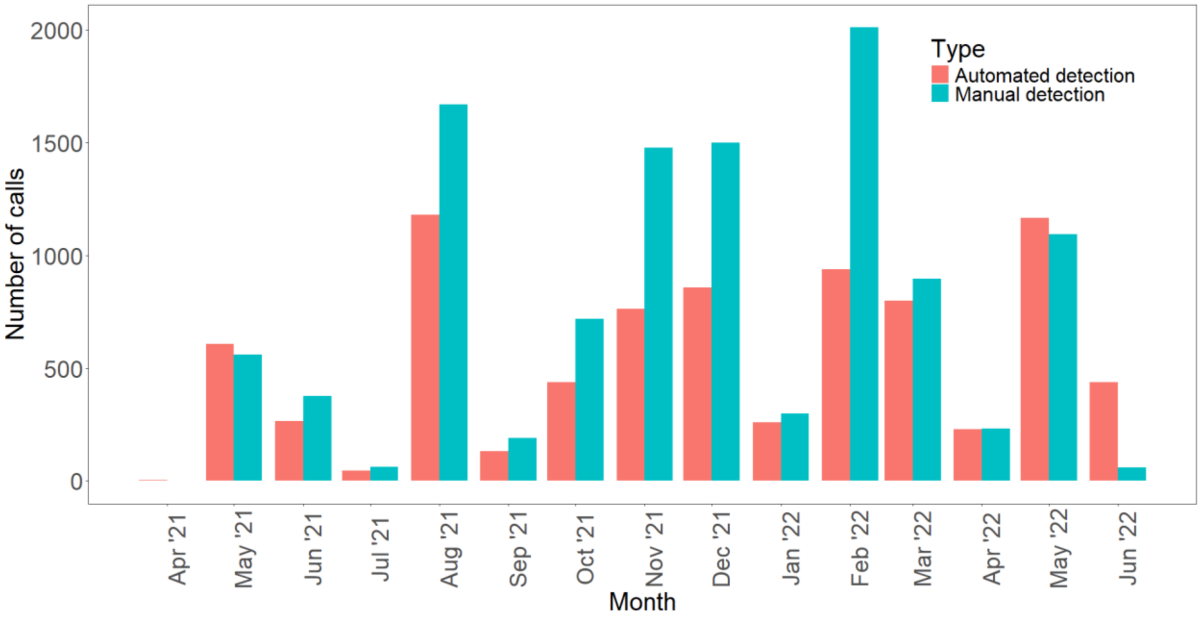

Figure 4.2. Bar graph indicating the total number of killer whale calls identified per month using two different detection methods, namely the automated acoustic detection method (pink) and the manual detection method (blue) through the visual inspection and annotation of spectrograms between 26 April 2021 and 30 June 2022.

According to *Figure 4.3*, a largest difference in monthly calls were observed in November – December 2021 and February 2022 (1074 more manually detected calls than automated ones). May 2021, 2022, and June 2022 were the only months that displayed higher automated call detections – the highest difference of 378 calls was observed in June 2022. These calls were relatively low in frequency and were difficult to detect using manual inspection (*Figure 4.4*). More manual detections than automated detections resulted in a false negative rate of 22%, but there was an accuracy rate of 78.7% between the two methods. A Pearson correlation test produced a correlation coefficient of 0.87, thereby indicating a strong positive association between the total monthly call numbers detected using the two methods. A two-tailed t-test conducted returned a mean value of 743 and 542 for the number of calls found using manual and automated detection respectively and these means were found not to be significantly different (p-value = 0.32).

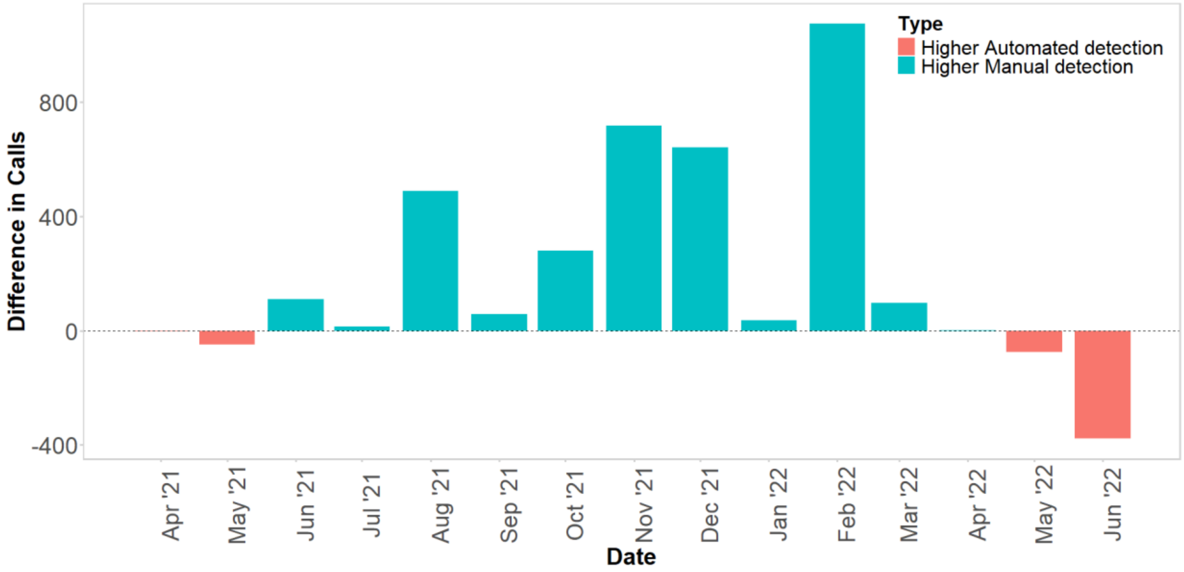

Figure 4.3. Bar graph indicating the difference in total number of killer whale calls identified per month using two different detection methods, namely the automated acoustic detection method (pink) and the manual detection method (blue) through the visual inspection and annotation of spectrograms between 26 April 2021 and 30 June 2022.

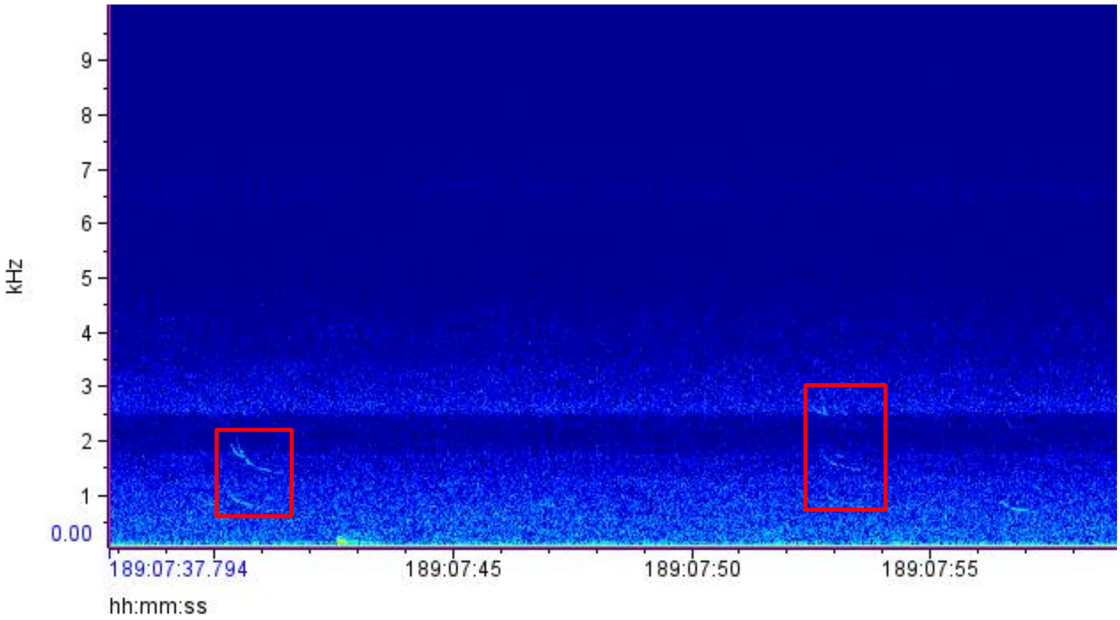

Figure 4.4. Spectrogram indicating killer whale calls (in red) identified by the automated acoustic detector, namely the *SpectroDetector* run at 50% confidence on 12 June 2022 when more automated identification was made than manual. The spectrogram settings used were Hann window, 0.0394 second frame size, 4096 sample discrete Fourier transformation (DFT) size and a 50% overlap.

4.3. Killer Whale Diel Call Patterns

This section describes the seasonal and year-to-year variability of the diel call pattern for killer whale social vocalisations between May 2021 – December 2022. The comparison over the two full year periods (May 2021 to April 2022 versus May 2022 to April 2023) was not possible as the period between January to April 2023 was affected by electrical noise. This was represented using hourly call rates (calls per minute) and the daylight regime extracted from the oceanographic mooring system location between the PEIs.

Figure 4.5 indicated that there were generally more hourly calls in 2021-2022 compared to the following months from April 2022 – December 2022. The winter months of 2021 displayed a strong diel call pattern – call rates were higher at night between 16:00 and 22:00 with a maximum call rate between 8.01 – 9 calls per minute specifically within August 2021. The same diel pattern was observed for the winter months of 2022. August again displayed high call rates between the same hours as well as during dusk. The highest call rates observed for this duration were between 6.01 – 7 calls per minute. Call rates during the daytime of the 2022 winter months were generally higher than that of 2021. Both 2021 and 2022's spring months displayed weak diel call patterns. Spring 2021 had slightly higher day call rates compared to night and, contrastingly, 2022 had higher call rates at night (4.01-5 calls per minute at 01:00 and 6.01 -7 at 22:00 in September) and at dusk (5.01-6 calls per minute in November). Call rates reached a relatively large value of 11.01-12 calls per minute for only one hour at 06:00 in November 2022. Both years' summer months (at least looking at December of 2022) indicated a strong diel call pattern with higher consecutive call rates during the day – up to 6 calls per minute in 2021 and 5 in 2022. Autumn 2021 indicated a very weak diel call pattern with slightly higher call rates during the day and Autumn 2022 barely indicated any difference between day – night call rates.

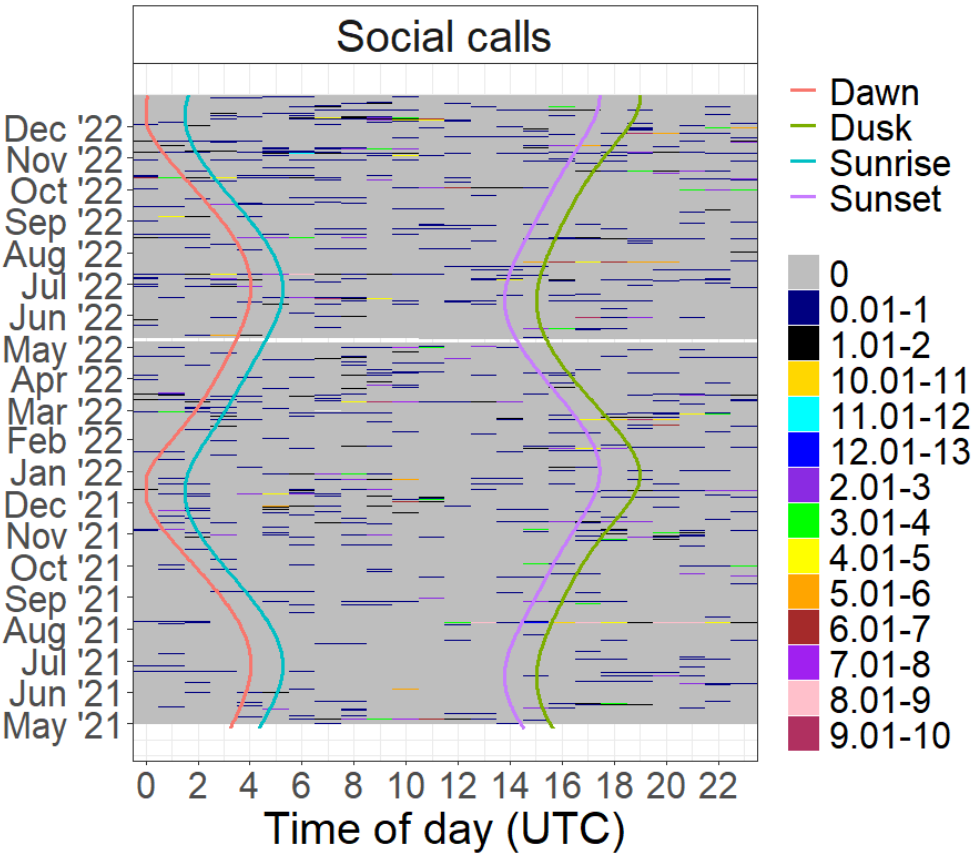

Figure 4.5. Hovmöller plot indicating the diel pattern of hourly social call rates spanning over the months from May 2021 – December 2022. Calls used for these calculations were identified using the automated acoustic detection method. Time is represented in UTC (Coordinated Universal Time). White areas show periods without PAM effort. Daylight regimes are indicated by vertical lines and social call rates are grouped in categories as described in the key.

When statistically comparing the daylight regimes between 2021-2022 and 2022, pairwise t-tests revealed that only the call rates during dawn, day and night were deemed to be significantly different to each other (*Table 4.2*). Call rates were higher at dawn in 2022 (maximum of 2.6 calls per minute) and higher at night in 2021-2022 when compared to the alternative year (maximum of 11 calls per minute; *Figure 4.6*). Daytime call rates were higher in 2022 (maximum of 11.5 calls per minute) and dusk call rates were not significantly different between years (*Table 4.2*).

Table 4.2. Pairwise t-test comparisons of killer whale social call rates of each daylight regime between the period May 2021 – April 2022 and May 2022 – Dec 2022 (represented as 2021-2022 and 2022 respectively). Statistically significant results have their p-values printed in red.

Daylight regime	Pairwise t-test comparison of hourly call rates	Degrees of freedom	P-value adjusted
Dawn	2021-2022 (n = 1828): 2022 (n = 1188)	1713	0.00373
Day	2021-2022 (n = 17812): 2022 (n = 11200)	19836	0.0000146
Dusk	2021-2022 (n = 1828): 2022 (n = 1188)	3050	1
Night	2021-2022 (n = 13992): 2022 (n = 9632)	18678	0.0027

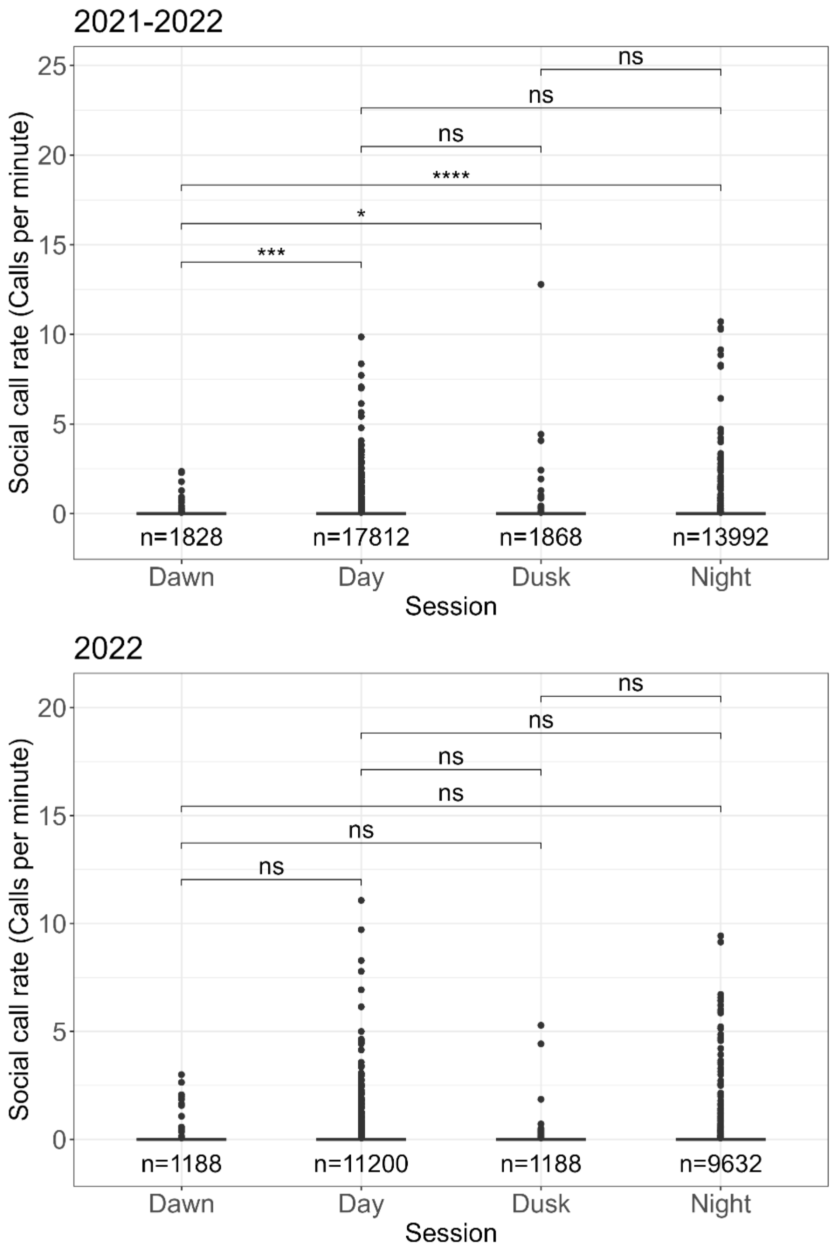

Figure 4.6. Box plots indicating the spread of the killer whale social call rates data for each daylight regime as well as the statistical results for the multiple pairwise comparisons between them. Adjusted p-values were used for comparison of significance and a significance level of $p < 0.05$ was used. Non-significance was represented using "ns", significance with an asterisk and "n" indicates the sample size. The top panel displays the results for 2021-2022 and the bottom panel for 2022.

Overall, for 2021-2022, only call rates during dawn were significantly different to the other daylight regimes as it had the lowest rates observed (maximum value of 2.5 calls per minute; *Figure 4.6*). Day and night consisted of similar maximum call rates at approximately 10 calls per minute. Overall, for 2022, none of the daylight regime call rates were significantly different to each other (*Figure 4.6*). Lower call rates were produced during dawn (maximum of 2.6 calls). Daytime had the highest call rates in total (11.5 calls per minute).

4.4. Seasonal and Year-to-Year Killer Whale Acoustic Occurrences, Sightings and Environmental Conditions

This section describes the seasonal and year-to-year variability of the environmental conditions using a seasonal climatology, monthly averaged time series and seasonal averages specifically focused on SST, SSH, chl-a and wind speed between May 2021-April 2022 and May 2022-April 2023. Additionally, the same will be described for the acoustic occurrences, call rates (between May 2021 – December 2022), unique sightings and SES abundances and compared to that of the environmental variability. This will provide insight into how these variables change seasonally and if the same seasonality is witnessed the following year.

4.4.1. Killer Whale Acoustic Occurrences

The acoustic occurrence of killer whales is represented by hours per day with social calls. Spring and summer had similar seasonal averages (approximately 1.6 hours per day with calls; *Figure 4.7*). Winter had the lowest social call occurrences (1.2 hours per day) on a seasonal scale. Pairwise t-test comparisons found that all seasonal averages were not significantly different to each other (*Table 4.3*). There was a lot of within-season variability as depicted by the large standard deviations of the season averages (*Table 4.3*). This variability is seen when observing seasonality on a monthly scale. Acoustic occurrences were lowest in the winter months, specifically in July 2021 (0.42 hours per day) and were highest in spring to autumn months, peaking in November 2021 (1.83 hours per day; *Figure 4.8*; *Table 4.4*). A similar seasonal cycle was observed for the following year with generally less call occurrences in early winter and early spring months (lowest observed was 1.13 and 0.9 hours per day with calls in June and September 2022 respectively). The peak for the second period occurred in spring months (highest was 3.13 in November 2022). There was substantial within-month variability over most months of both years as indicated by large standard deviations (*Table 4.4*). When comparing the monthly year-to-year variability, calls occurrences were generally higher in the second period compared to the first, more so within July and November, although pairwise t-tests indicated no statistically significant differences between periods. When comparing the seasonal year-to-year variability (which unfortunately only compares spring and winter between the two periods), the same result is evident. Call rates displayed a clear seasonal cycle with the lowest observation in winter (0.054 calls per minute), followed by a steep increase in spring and increasing gradually until peaking in autumn (0.077 calls per minute;

Figure 4.7). Pairwise t-tests indicated no significant differences in call rates between seasons (*Table 4.3*). Autumn and winter depicted relatively higher within-season variability as shown by the slightly higher standard deviations of these months (*Table 4.3*). This variability is seen when observing seasonality on a monthly scale. Call rates alternated between high and low in winter months and in May 2021 (ranging between 0 – 0.11 calls per minute) and was generally higher in Oct – Dec 2021 and Feb – March 2022. The following year indicated similar alternating call rate patterns in winter months and a peak in November 2022 (0.169 calls per minute). The timing of this peak is shared with that of call occurrences, at least for the 2022 period. In contrast, while alternating peaks in call rates were observed in May and July 2022, the number of hours per day with calls did not show similar peaks. The same is true for the August peak (0.113 calls per minute) in the 2021-2022 period. There was substantial within-month variability in months when call rates were at their maximum (*Table 4.4*). Of the months that could be compared, call rates were generally lower in 2021-2022 compared to the following year, except in August. No statistically significant differences were observed in monthly averaged call rates between the two periods (*Table 4.4*). This was also observed on a seasonal scale (*Table 4.4*).

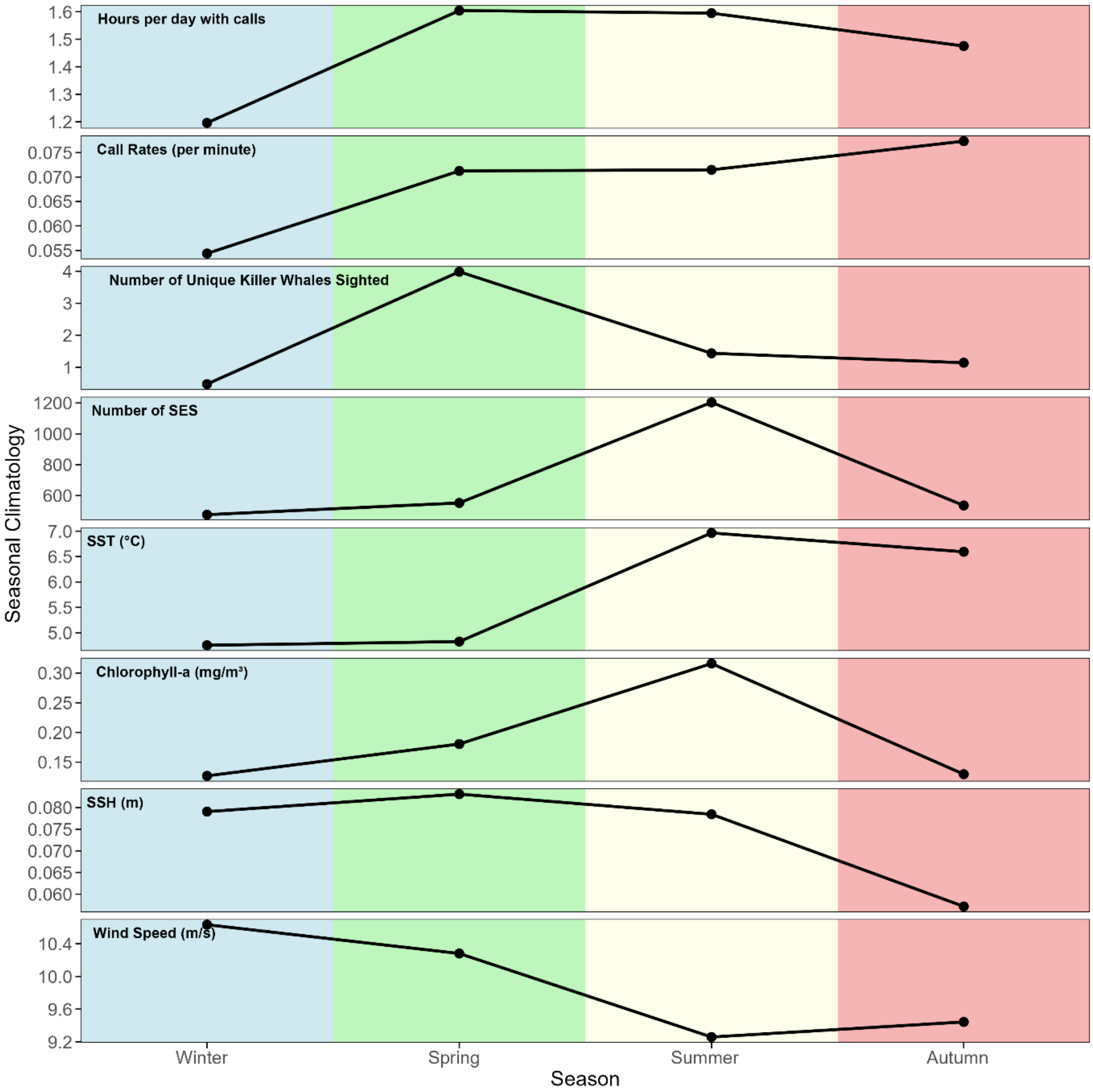

Figure 4.7. Seasonally averaged time series indicating the patterns in the killer whale acoustic occurrences represented as hours per day and call rates per minute, the number of unique killer whales sighted, southern elephant seal abundance (SES), SST (°C), SSH (m), chlorophyll-a concentration (mg m^{-3}) and wind speed (m s^{-1}) calculated across May 2021 – December 2022 for the acoustic parameters and the whole study period for the remaining parameters (May 2021 – April 2023). The shaded colours represent seasons, namely austral winter (blue), spring (green), summer (light yellow) and autumn (red).

Table 4.3. Pairwise t-test comparisons conducted to examine statistical differences between seasonal averages calculated across the entire study period (May 2021 – Dec 2022 for the acoustic parameters; May 2021 – April 2023 for the remaining parameters). Statistically significant results are indicated in red.

Variable & Seasonal Averages	Pairwise t-test comparison	n1	n2	P-value adjusted
Hours per day with calls	Autumn-Spring	4	6	1
Autumn = 1.48 ± 2.29	Autumn-Summer	4	4	1
Spring = 1.60 ± 2.31	Spring-Summer	6	4	1
Summer = 1.60 ± 2.08	Autumn-Winter	4	6	1
Winter = 1.20 ± 2.28	Spring-Winter	6	6	1
	Summer-Winter	4	6	1
Call Rates (calls per minute)	Autumn-Spring	4	6	1
Autumn = 0.077 ± 0.23	Autumn-Summer	4	4	1
Spring = 0.071 ± 0.15	Spring-Summer	6	4	1
Summer = 0.071 ± 0.18	Autumn-Winter	4	6	1
Winter = 0.054 ± 0.26	Spring-Winter	6	6	1
	Summer-Winter	4	6	1
Unique number of killer whales sighted	Autumn-Spring	6	6	0.012
Autumn = 1.1 ± 2.3	Autumn-Summer	6	6	1
Spring = 4 ± 4.8	Spring-Summer	6	6	0.025
Summer = 1.4 ± 3.3	Autumn-Winter	6	6	1
Winter = 0.5 ± 1.3	Spring-Winter	6	6	0.002
	Summer-Winter	6	6	1
Southern Elephant Seal Abundances	Autumn-Spring	6	6	1
Autumn = 536 ± 128	Autumn-Summer	6	6	0.036
Spring = 552 ± 366	Spring-Summer	6	6	0.041
Summer = 1204 ± 631	Autumn-Winter	6	6	1
Winter = 476 ± 115	Spring-Winter	6	6	1
	Summer-Winter	6	6	0.019
SST (°C)	Autumn-Spring	6	6	0.002
Autumn = 6.59 ± 0.86	Autumn-Summer	6	6	1
Spring = 4.83 ± 0.35	Spring-Summer	6	6	< 0.001
Summer = 6.97 ± 1.03	Autumn-Winter	6	6	0.001
Winter = 4.75 ± 0.29	Spring-Winter	6	6	1
	Summer-Winter	6	6	< 0.001
Chlorophyll-a Concentration (mg m^{-3})	Autumn-Spring	6	6	1
Autumn = 0.13 ± 0.02	Autumn-Summer	6	6	0.084
Spring = 0.18 ± 0.09	Spring-Summer	6	6	0.412
Summer = 0.32 ± 0.22	Autumn-Winter	6	6	1
Winter = 0.13 ± 0.02	Spring-Winter	6	6	1
	Summer-Winter	6	6	0.078
SSH (m)	Autumn-Spring	6	6	0.833
Autumn = 0.057 ± 0.02	Autumn-Summer	6	6	1
Spring = 0.083 ± 0.04	Spring-Summer	6	6	1
Summer = 0.078 ± 0.02	Autumn-Winter	6	6	1
Winter = 0.079 ± 0.04	Spring-Winter	6	6	1
	Summer-Winter	6	6	1
Wind Speed (m s^{-1})	Autumn-Spring	6	6	1
Autumn = 9.4 ± 3.63	Autumn-Summer	6	6	1
Spring = 10.3 ± 3.30	Spring-Summer	6	6	0.87
Summer = 9.3 ± 3.26	Autumn-Winter	6	6	0.55
Winter = 10.6 ± 3.63	Spring-Winter	6	6	1
	Summer-Winter	6	6	0.317

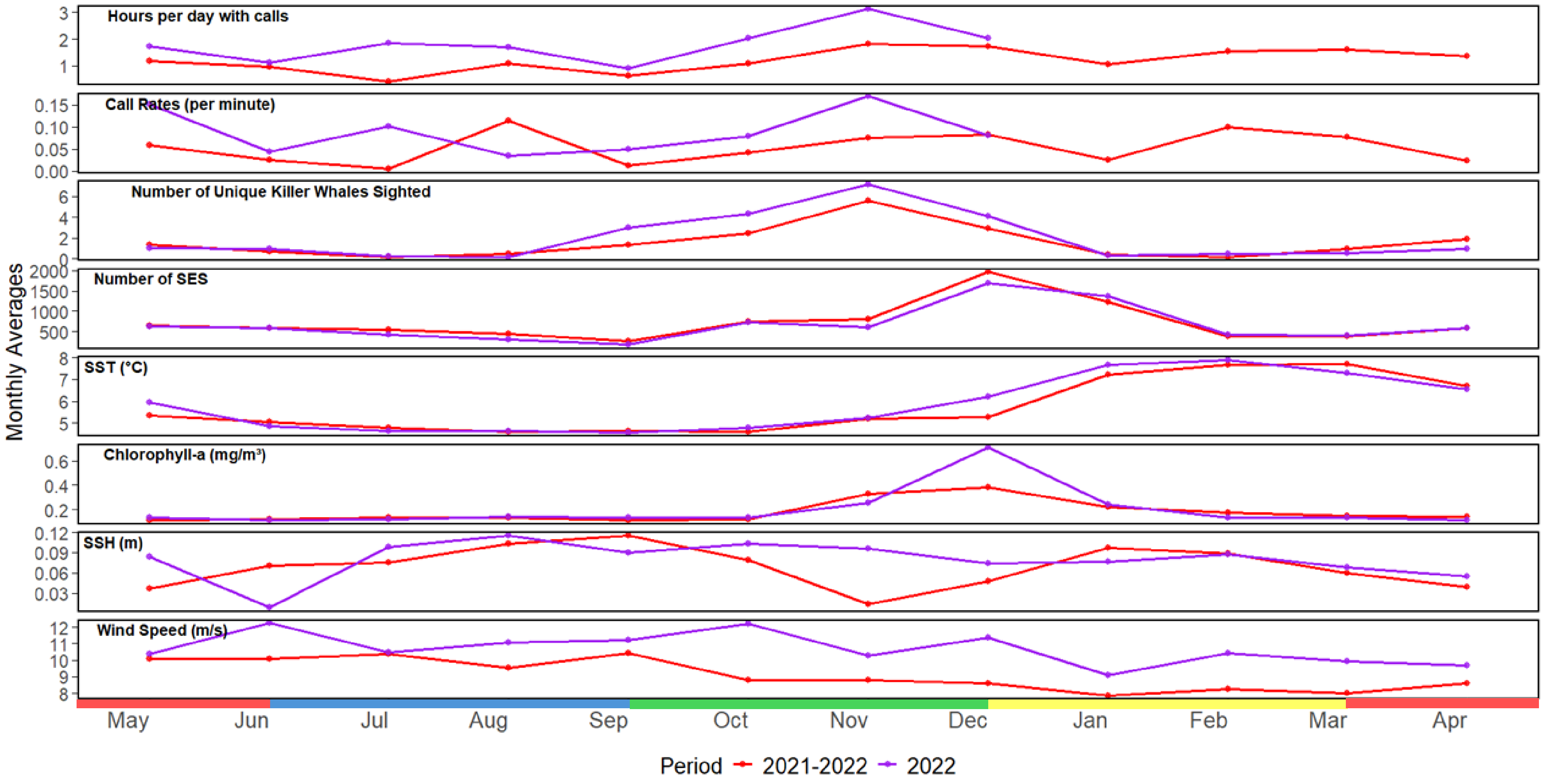

Figure 4.8. Monthly averaged time series indicating the patterns in the killer whale acoustic occurrences represented as hours per day and call rates per minute, the number of unique killer whales sighted, southern elephant seal abundance (SES), SST (°C), SSH (m), chlorophyll-a concentration (mg m^{-3}) and wind speed (m s^{-1}) for two separate time periods for easier comparison of year-to-year differences. The 2021-2022 period indicates months following calendar months from May 2021 to April 2022 (red) and the 2022 period indicates May 2022 to December 2022 (purple). The bar below the plots indicates the different seasons, namely austral autumn (red), winter (blue), spring (green) and summer (yellow).

Table 4.4. Pairwise t-test comparisons conducted to examine statistical differences of monthly averages between the period May 2021 – April 2022 and period May 2022 – December 2022. Additionally, monthly averages' standard deviations are included, and statistically significant results are indicated in red.

Variable	Month	Monthly average ± standard deviation (2021-2022 period)	Monthly average ± standard deviation (2022 period)	n1	n2	Degrees of freedom	P-value adjusted
Hours per day with calls	May	1.19 ± 1.70	1.73 ± 3.31	31	30	43	1
	June	0.97 ± 1.54	1.13 ± 1.91	30	30	55.6	1
	July	0.42 ± 0.96	1.84 ± 3.11	31	31	35.6	0.163
	August	1.10 ± 2.75	1.71 ± 2.55	31	31	59.6	1
	September	0.63 ± 1.16	0.90 ± 1.18	30	30	58	1
	October	1.10 ± 1.51	2.03 ± 2.51	31	31	49.3	0.654
	November	1.83 ± 1.80	3.13 ± 3.75	30	30	41.7	0.754
	December	1.74 ± 2.29	2.03 ± 2.20	31	31	59.9	1
	January	1.06 ± 1.63					
	February	1.54 ± 2.13					
	March	1.61 ± 2.20					
	April	1.37 ± 1.63					
Call Rates (per minute)	May	0.058 ± 0.177	0.152 ± 0.344	31	30	43	1
	June	0.026 ± 0.059	0.043 ± 0.131	30	30	40.4	1
	July	0.005 ± 0.013	0.102 ± 0.296	31	31	30.1	0.614
	August	0.113 ± 0.543	0.035 ± 0.105	31	31	32.3	1
	September	0.013 ± 0.032	0.050 ± 0.117	30	30	33.3	0.84
	October	0.042 ± 0.073	0.079 ± 0.173	31	31	40.5	1
	November	0.076 ± 0.121	0.169 ± 0.250	30	30	41.8	0.582
	December	0.082 ± 0.138	0.081 ± 0.153	31	31	59.4	1
	January	0.025 ± 0.086					
	February	0.100 ± 0.281					
	March	0.077 ± 0.221					
	April	0.023 ± 0.042					
Unique number of killer whales sighted	May	1.4 ± 2.8	1.0 ± 1.9	31	30	52.5	1
	June	0.7 ± 1.6	1.0 ± 2.0	30	30	54.3	1
	July	0.2 ± 0.7	0.3 ± 0.7	31	31	59.6	1
	August	0.5 ± 1.4	0.2 ± 0.6	31	31	43.1	1
	September	1.4 ± 2.0	3.0 ± 3.4	30	30	47.5	0.33
	October	2.5 ± 3.8	4.4 ± 5.5	31	31	53.4	1
	November	5.6 ± 4.9	7.2 ± 5.9	30	30	56.2	1

	December	2.9 ± 5.3	4.1 ± 4.0	31	31	56.1	1
	January	0.4 ± 1.6	0.3 ± 1.0	31	31	51.9	1
	February	0.2 ± 0.8	0.5 ± 1.3	28	28	46.8	1
	March	1.0 ± 2.2	0.6 ± 1.4	31	31	52.1	1
	April	1.9 ± 2.9	1.0 ± 2.1	30	26	52.7	1
Southern Elephant Seal Abundances	May	652 ± 36	629 ± 95	31	30	36.8	1
	June	576 ± 42	580 ± 49	30	30	56.6	1
	July	534 ± 11	431 ± 20	31	31	47.0	< 0.001
	August	435 ± 112	308 ± 82	31	31	55.0	< 0.001
	September	261 ± 132	175 ± 81	30	30	48.3	0.046
	October	741 ± 118	724 ± 134	31	31	59.1	1
	November	804 ± 553	597 ± 320	30	30	46.5	0.994
	December	1971 ± 110	1687 ± 238	31	31	42.2	< 0.001
	January	1231 ± 258	1373 ± 331	31	31	56.6	0.774
	February	378 ± 178	431 ± 182	28	28	54.0	1
	March	383 ± 87	411 ± 70	31	31	57.3	1
	April	577 ± 89	583 ± 52	30	26	47.9	1
SST (°C)	May	5.34 ± 0.43	5.95 ± 0.18	31	30	40.1	< 0.001
	June	5.03 ± 0.25	4.86 ± 0.36	30	30	51.6	0.504
	July	4.77 ± 0.25	4.64 ± 0.19	31	31	55.7	0.343
	August	4.61 ± 0.25	4.64 ± 0.15	31	31	49.4	1
	September	4.62 ± 0.22	4.57 ± 0.18	30	30	56.1	1
	October	4.59 ± 0.16	4.77 ± 0.12	31	31	56.5	< 0.001
	November	5.18 ± 0.21	5.23 ± 0.33	30	30	48.5	1
	December	5.29 ± 0.26	6.20 ± 0.21	31	31	58.2	< 0.001
	January	7.21 ± 0.63	7.68 ± 0.54	31	31	58.4	0.028
	February	7.66 ± 0.10	7.91 ± 0.31	28	28	32.6	0.004
	March	7.70 ± 0.25	7.30 ± 0.30	31	31	57.9	< 0.001
	April	6.70 ± 0.34	6.55 ± 0.32	30	26	53.7	1
Chlorophyll-a Concentration (mg m^{-3})	May	0.11 ± 0.01	0.13 ± 0.01	31	30	57.5	< 0.001
	June	0.12 ± 0.01	0.11 ± 0.01	30	30	58	0.295
	July	0.13 ± 0.02	0.12 ± 0.02	31	31	59.3	0.355
	August	0.14 ± 0.02	0.14 ± 0.02	31	31	59.9	1
	September	0.11 ± 0.01	0.13 ± 0.02	30	30	51.1	< 0.001
	October	0.12 ± 0.03	0.13 ± 0.01	31	31	45.4	0.161
	November	0.33 ± 0.08	0.25 ± 0.08	30	30	57.6	0.003

	December	0.39 ± 0.09	0.71 ± 0.18	31	31	44.6	< 0.001
	January	0.22 ± 0.08	0.24 ± 0.13	31	31	48.7	1
	February	0.17 ± 0.02	0.13 ± 0.02	28	28	52.1	< 0.001
	March	0.14 ± 0.03	0.13 ± 0.02	31	31	52.3	1
	April	0.14 ± 0.02	0.11 ± 0.02	30	26	51.2	< 0.001
SSH (m)	May	0.036 ± 0.010	0.085 ± 0.019	31	30	43.8	< 0.001
	June	0.071 ± 0.018	0.009 ± 0.032	30	30	45.6	< 0.001
	July	0.076 ± 0.009	0.098 ± 0.021	31	31	41.6	< 0.001
	August	0.103 ± 0.011	0.116 ± 0.013	31	31	58.9	0.001
	September	0.116 ± 0.026	0.090 ± 0.014	30	30	45.4	< 0.001
	October	0.079 ± 0.006	0.103 ± 0.008	31	31	56.1	< 0.001
	November	0.014 ± 0.017	0.096 ± 0.016	30	30	58.0	< 0.001
	December	0.048 ± 0.010	0.074 ± 0.004	31	31	40.1	< 0.001
	January	0.097 ± 0.026	0.077 ± 0.013	31	31	43.7	0.005
	February	0.089 ± 0.005	0.088 ± 0.007	28	28	52.1	1
	March	0.060 ± 0.014	0.068 ± 0.008	31	31	45.4	0.137
	April	0.040 ± 0.007	0.055 ± 0.008	30	26	49.8	< 0.001
Wind Speed (m s^{-1})	May	10.1 ± 3.4	10.4 ± 3.1	31	30	58.8	1
	June	10.1 ± 2.8	12.3 ± 4.4	30	30	49.1	0.332
	July	10.4 ± 2.9	10.5 ± 4.0	31	31	55.2	1
	August	9.5 ± 3.1	11.1 ± 3.9	31	31	57.1	1
	September	10.4 ± 3.3	11.2 ± 3.4	30	30	57.9	1
	October	8.8 ± 3.0	12.2 ± 2.7	31	31	59.5	< 0.001
	November	8.8 ± 2.6	10.3 ± 3.5	30	30	53.8	0.830
	December	8.6 ± 3.0	11.3 ± 3.1	31	31	60.0	0.0082
	January	7.9 ± 3.0	9.1 ± 3.6	31	31	58.1	1
	February	8.3 ± 2.4	10.4 ± 3.1	28	28	51.1	0.071
	March	8.0 ± 3.0	9.9 ± 4.2	31	31	54.3	0.505
	April	8.6 ± 3.5	9.7 ± 4.2	30	26	48.7	1

Table 4.5. Pairwise t-test comparisons were conducted to examine statistical differences of seasonal averages between the period May 2021 - April 2022 and May 2022 - April 2023.

Variable	Season	Seasonal average (2021-2022)	Seasonal average (Acoustic parameters – 2022; remaining parameters – 2022-2023)	n1	n2	Degrees of freedom	P-value adjusted
Hours per day with calls	Spring	1.19 ± 1.58	2.02 ± 2.81	3	3	3.08	0.672
	Winter	0.826 ± 1.91	1.57 ± 2.56	3	3	1.56	0.142
Call Rates (per minute)	Spring	0.044	0.099	3	3	2.95	0.524
	Winter	0.048	0.060	3	3	3.38	1
Unique number of killer whales sighted	Autumn	1.4 ± 2.7	0.9 ± 1.8	3	3	3.0	0.636
	Spring	3.1 ± 4.1	4.8 ± 5.3	3	3	4.0	1
	Summer	1.2 ± 3.5	1.7 ± 3.1	3	3	3.6	1
	Winter	0.5 ± 1.3	0.5 ± 1.3	3	3	3.2	1
Southern Elephant Seal Abundances	Autumn	537 ± 136	535 ± 120	3	3	3.8	1
	Spring	604 ± 409	501 ± 311	3	3	4.0	1
	Summer	1221 ± 675	1188 ± 588	3	3	3.9	1
	Winter	515 ± 91	438 ± 124	3	3	3.0	1
SST (°C)	Autumn	6.58 ± 1.04	6.61 ± 0.63	3	3	3.2	1
	Spring	4.80 ± 0.34	4.86 ± 0.36	3	3	4.0	1
	Summer	6.69 ± 1.11	7.27 ± 0.85	3	3	3.7	1
	Winter	4.80 ± 0.30	4.71 ± 0.27	3	3	3.3	1
Chlorophyll-a Concentration (mg m^{-3})	Autumn	0.13 ± 0.03	0.13 ± 0.02	3	3	3.8	1
	Spring	0.19 ± 0.11	0.17 ± 0.07	3	3	3.1	1
	Summer	0.26 ± 0.12	0.36 ± 0.29	3	3	2.5	1
	Winter	0.13 ± 0.02	0.12 ± 0.02	3	3	2.9	1
SSH (m)	Autumn	0.045 ± 0.015	0.070 ± 0.018	3	3	3.9	0.44
	Spring	0.070 ± 0.046	0.097 ± 0.014	3	3	2.1	1
	Summer	0.078 ± 0.028	0.079 ± 0.011	3	3	2.3	1
	Winter	0.083 ± 0.019	0.074 ± 0.052	3	3	2.4	1
Wind Speed (m s^{-1})	Autumn	8.9 ± 3.38	10.0 ± 3.81	3	3	2.4	0.856
	Spring	9.3 ± 3.05	11.2 ± 3.28	3	3	4.0	0.280
	Summer	8.24 ± 2.82	10.3 ± 3.37	3	3	2.4	0.308
	Winter	10 ± 2.94	11.3 ± 4.12	3	3	2.9	0.480

4.4.2. Killer Whale Sightings and Southern Elephant Seal Abundances

Killer whales sighted within the inshore region of Marion Island indicated large significant differences in seasonal averages between spring and all other seasons (*Figure 4.7*; *Table 4.3*). All other pairs of season combinations comparing seasonal averages were not significantly different (*Table 4.3*). A clear seasonal cycle was therefore evident across both time periods, but there were no statistically significant differences in monthly averages of killer whale sightings between 2021-2022 and 2022-2023 (*Figure 4.8; Table 4.4*). Their sightings increased in the spring months, reaching a maximum of 6 dolphins in November 2021 and 7 in November 2022. There was a large degree of within-month variation in spring as indicated by the standard deviation (*Table 4.4*). For the remainder of the year, their numbers decreased to approximately less than 2 dolphins on average per month. Their average monthly sightings were lowest in mid-winter and mid-summer months. On a seasonal scale, there were no significant differences in killer whale sightings between the two years (*Table 4.5*).

Summer indicated the largest change in SES abundances when compared to the other seasons (*Figure 4.7*) and was supported by the pairwise t-test outputs which deemed summer to be significantly different to all other seasons (*Table 4.3*). SES abundances therefore indicated a very clear seasonal cycle (*Figure 4.8*) and low within-month variation year-round as shown by the standard deviation (*Table 4.4*). Abundances gradually increased during the spring months, peaked in December for both periods (1971 seals in 2021 and 1687 seals in 2022) and thereafter gradually decreased until February. The lowest abundances were observed in September (261 seals in 2021 and 175 seals in 2022). There were generally higher SES abundances in 2021-2022 compared to the following year with the months of July, August, September and December flagged as having significantly different monthly averages (*Table 4.4*). On a seasonal scale, there were no significant differences in SES abundances between the two years (*Table 4.5*).

Figure 4.8 showed that the peak in killer whale sightings correspond to one of the peaks in call rates and the acoustic occurrences in the spring months across both years. Contrastingly, there were observed to be high call rates in winter months when concurrent killer whale sightings around the islands were comparatively less. An interesting result to note is that in the month of December during the peak in SES abundance, acoustic occurrences, call rates and their visual sightings were beginning to decline. A similar inverse relationship was also evident on a seasonal scale (*Figure 4.7*). Killer whale sightings decreased from spring to summer while SES abundance increased, although and acoustic parameters remained more or less the same.

4.4.3. Sea Surface Temperature and Chlorophyll-a Concentration

Figure 4.8 indicated that both SST and chl-a displayed a very clear seasonal pattern with low within-month variability across all months of both time periods (*Table 4.4*). SST was lowest in winter and early spring months. The lowest SST values were in October 2021 (4.59 °C) and September 2022 (4.57 °C), and SST gradually increased during spring to eventually peak in summer. This maximum specifically occurred in March 2022 (7.7 °C) and February 2023 (7.91 °C; *Table 4.4*). Thereafter, SST gradually decreased again into the autumn months. The seasonal average of summer was significantly different from spring and winter (*Table 4.3*), thereby corroborating the above-described seasonality. Additionally, the autumn average paired with those of spring and winter also produced significantly different results ($p < 0.05$). Examining year-to-year differences, SST observations were slightly higher in May and the transitions months (December – February) from spring to summer in 2022-2023 compared to the previous year, but only May, October and December-February had significantly higher monthly averages. For 2021-2022, June, July and March were slightly higher than the following year, but only March's monthly average was significantly different. When examining the seasonal averages of SST between these two periods, they were not significantly different (*Table 4.5*).

When examining seasonal averages (*Figure 4.7*), chl-a values spanned a small range (0.13 – 0.32 mg m^{-3}) and pairwise t-test comparisons indicated that these values were not significantly different between seasons (*Table 4.*3). Chl-a was low for majority of the year (approximately 0.1 mg m^{-3}; *Figure 4.8*), only increased in mid-late spring months and had very little within-month variability (*Table 4.4*). The peak in chl-a concentration occurred in December of both years at 0.39 mg m^{-3} in 2021 and 0.71 mg m^{-3} in 2022, almost double the previous year's concentration. The monthly peak in chl-a coincided with the increase in SST, but decreased after December, when SST continued to increase (*Figure 4.8*). Additionally, this also coincides with the increase in SES abundance. Year-to-year differences in monthly averages were not immediately obvious for the remainder of the year as this variable had a very small range in this low concentration period (0.1 - 0.17 mg m^{-3}). A pairwise t-test indicated that there were significant differences in monthly averaged chl-a between 2021-2022 and 2022-2023 for the months of May, September, February and April even though differences were small. There were also significant differences in November and December's monthly averages where a large difference in monthly averages was observed. When examining the seasonal averages of chl-a between these two periods, they are not significantly different on a seasonal scale (*Table 4.5*).

The seasonal cycle of SST and chl-a concentration matches that of the acoustic occurrence of killer whales to a certain extent. On a seasonal scale, the seasonal patterns of SST and chl-a followed that of the acoustic parameters from winter to summer only (increasing gradually; *Figure 4.7*). More detail is observed on a monthly scale: during the late autumn and winter months, these variables were relatively low compared to the rest of the year and a coincidence of increased or peak observations happened during spring, specifically in November for both time periods (*Figure 4.8*). Thereafter, only the increase in SST observations in summer coincided with an elevation in call rates in the 2021-2022 period. This pattern was not observed for chl-a as it declined again mid-summer. Call rates fluctuated a bit during the autumn and winter months, but the corresponding peak to increased SST and chl-a in November of both time periods was still evident. Another noteworthy observation was that SST and chl-a had significant year-to-year differences between months, but none of the acoustic parameters did.

4.4.4. Sea Surface Height and Wind Speed

Figure 4.7 indicated that SSH did not display a clear seasonal cycle. SSH had similar values in winter and spring (0.08 m), decreasing slightly in summer and steeply in autumn. Seasons were not significantly different (*Table 4.3*). On a monthly scale, SSH remained high for majority of both years, except for November 2021 and June 2022 (*Figure 4.8*). Year-to-year examination indicated two large monthly differences. In November 2022, SSH was 0.082 m higher than in November 2021 when SSH was at its minimum (0.014 m). In June 2021, SSH was 0.062 m higher than in June 2022 when SSH was at its minimum (0.009 m). Within-month variability was minimal and pairwise t-test comparisons deemed all month's averages to be significantly different between periods, apart from February and March (*Table 4.4*). These differences were not seen on a seasonal scale (*Table 4.5*).

On a seasonal scale, wind speed displayed clear seasonality (*Figure 4.7*) as values decreased gradually from the maximum in winter (10.6 m s^{-1}) to the minimum in summer (9.3 m s^{-1}) and thereafter slightly increasing in autumn. Pairwise t-test comparisons deemed none of the seasons' averages as significantly different (*Table 4.3*). Monthly-averaged wind speeds displayed seasonality to a lesser degree (*Figure 4.8*). Generally, higher wind speeds were observed for autumn - early spring months with the highest values noted in May – September 2021 (≈ 10 m s^{-1}) and June and October 2022 (≈ 12 m s^{-1}). Wind speed values steadily decreased thereafter, reaching a minimum in summer of both years (7.9 m s^{-1} and 9.1 m s^{-1} in 2022 and 2023 respectively). Year-to-year examination indicated that 2022-2023 had consistently higher wind speeds across all months compared to the previous year and only one similar value noted in July. Even though almost all months showed large differences in wind speeds between periods, only October and December were significantly different (*Table 4.4*). There was also a large within-month variation for each month of each year. No year-to-year differences in wind speeds were observed between periods on a seasonal scale (*Table 4.5*).

On a seasonal scale, SSH was observed to have a completely opposite seasonal pattern to the acoustic occurrences as there were more calls produced during seasons of low SSH and vice versa. A clear pattern between SSH and the acoustic parameters could not be distinguished on a monthly scale. For example, in the spring months when peaks in hours per day with calls occurred for both years, both highest and lowest SSH were observed for separate years. The highest SSH values in winter also occurred when call rates fluctuated monthly for each time period and there were relatively less hours per day with calls. The acoustic parameters appeared to increase or decrease irrespective of SSH on a monthly timescale. Wind speed observations appeared to have some correspondence to acoustic occurrence patterns. There were generally more calls during times of lower wind speeds such as in summer and autumn on a seasonal scale and in mid-spring to late summer months on a monthly scale and less calls when wind speeds were relatively higher (*Figure 4.7*; *Figure 4.8*). The higher wind speeds in 2022 are also reflected in the acoustic occurrence patterns as this period had overall higher monthly acoustic occurrences year-round.

4.5. Predictors of Acoustic Occurrences

This section describes the results of the random forest (RF) modelling and the predictability of the killer whale acoustic occurrences to the varying environmental conditions, prey abundances and killer whale sightings over time.

Figure 4.9 indicated that the probability of detecting killer whale social calls was high at low chl-a (0.1 mg m^{-3}- 0.4 mg m^{-3}), chl-a between 0.5 and 0.7 mg m^{-3} and was consistently high at values more than 1 mg m^{-3}. Social calls were more likely to occur between 03:00 and 10:00 and at 18:00. There was low probability of acoustic occurrence at 13:00. High probability of social call occurrence was evident at different ranges of number of killer whales sighted, namely when sighting numbers were low (2-3 dolphins), medium (6-7 & 10 dolphins) and high (12-18 dolphins). Probability of acoustic occurrence generally increased from January through to December with peaks in May and November. January was the least likely month to have social calls. An interesting result to note is that the probability of acoustic detection decreases with SES abundances. Killer whales were more likely to vocalise when seal abundances were below 500 and between 600 and 1200, and less likely when seal abundances were between 1300 and 2000.

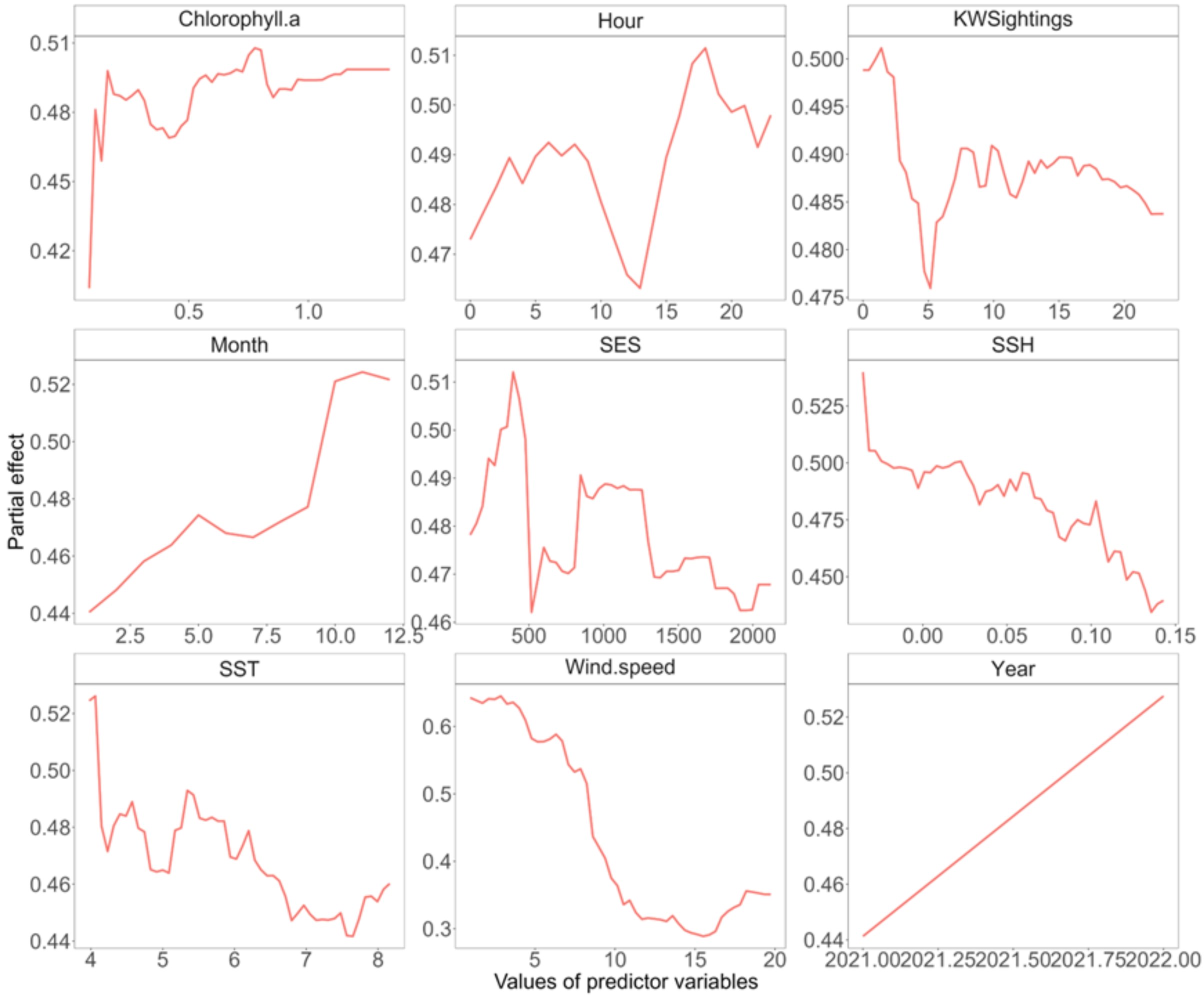

Figure 4.9. Random forest (RF) model results indicating the partial effects of the predictor variables on the probability of acoustic occurrence of killer whales, specifically social calls for April 2021 – Dec 2022 and is based on the downsampling method. Y-axes scales are different for each predictor variable. KW, SES, SSH and SST represents killer whale, southern elephant seal abundances, sea surface height and sea surface temperature respectively.

The probability of acoustic occurrence also increases with a decrease in SSH (*Figure 4.9*). The probability of detecting social calls fluctuated with changes in SST but was generally higher at lower SST. This was more likely at SST less than 4 °C, at 4.5 °C and between 5.4 – 5.9 °C. Probability of detection decreased progressively after 6°C, only increasing slightly at 8°C. An inverse relationship between probability of acoustic occurrence and wind speed is evident. Probability of occurrence decreased with an increase in wind speed only up to approximately 15 m s^{-1}, thereafter, probability increases slightly. When looking at the predictor variable year, probability of detection was highest in 2022 compared to 2021.

The most important predictor of killer whale acoustic occurrence, specifically social calls, was wind speed followed by hour of the day (*Figure 4.10*). Importantly, of the two predictors, only wind speed was a statistically significant predictor and hour of the day was not. SST, chl-a, SSH and SES abundance were moderately important predictors of the occurrence of social calls. Month, year and killer whale sightings were the least important predictors of social call occurrences. Most variables (wind speed, SST, SES abundance, month and year; *Figure 4.10*), except hour of the day, chl-a, SSH and killer whale sightings, were deemed as informative variables for making these predictions as they were identified as significantly important predictor variables.

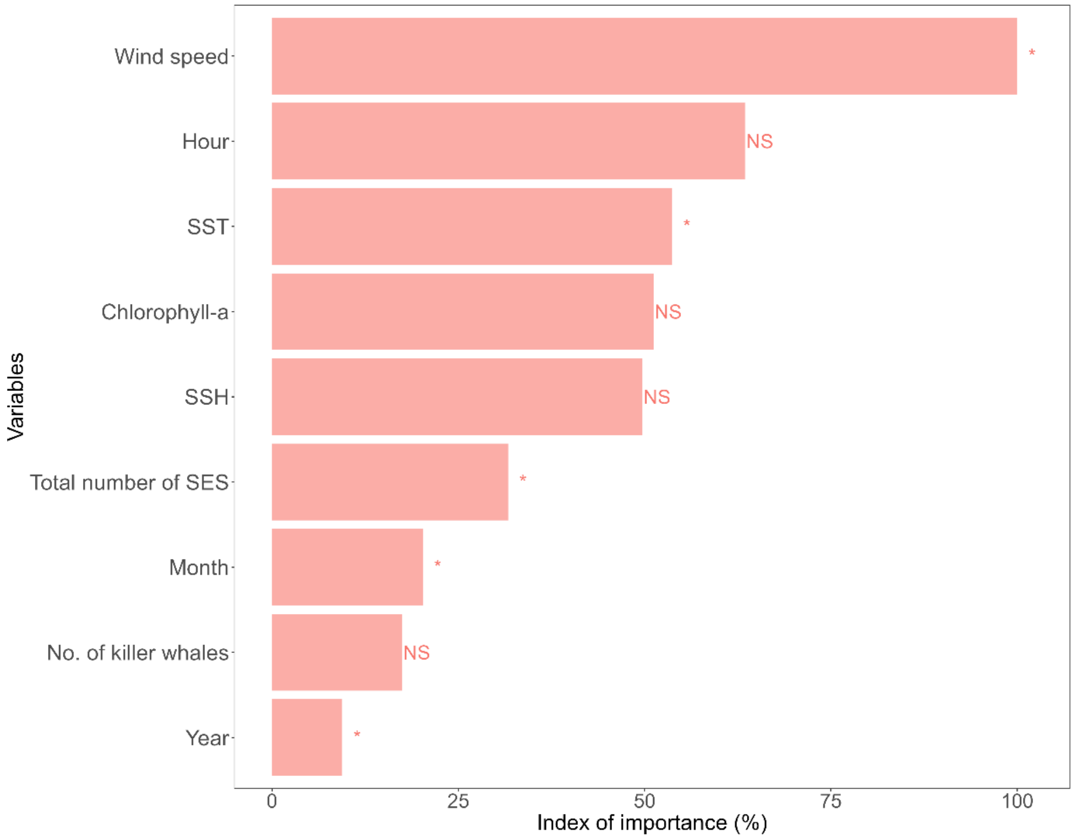

Fig 4.10. Random forest (RF) model results indicating the relative importance of the predictor variables on the probability of acoustic occurrence of killer whales (social calls) based on the downsampling method for April 2021 – Dec 2022. Asterisks (*) indicate variables of significant importance ($p < 0.05$) and “NS” indicates non-significant importance (Altmann et al. 2010).

Chapter 5. Discussion

The primary objective of this study was to use satellite-derived oceanographic data for the period of May 2021 to April 2023 to determine the year-to-year variability of the environmental conditions of sub-Antarctic region surrounding the PEIs and compare it to year-to-year variability of killer whale call occurrences between May 2021 to December 2022 across expanding time scales, from diel variations, to comparisons of months and seasons to each and across years, additionally linking this to the abundance of their prey. To achieve these objectives, the following key questions were asked:

1. How does automated call detection, using the *Spectrodetector* (JASCO Applied Science Ltd), compare to manual call detection of killer whales at the PEIs?
2. What are the diel, month-to-month, and seasonal differences in environmental conditions, prey abundance, and killer whale call occurrence between the two recorded periods?
3. What is the relative importance of environmental conditions (sea surface temperature, sea surface height, wind speed and chlorophyll-a concentration), prey availability (southern elephant seal abundances), and temporal categories (hour, month, year) for killer whale call occurrence?

5.1. Killer Whale Call Detection Methodology

The automated acoustic *SpectroDetector* of 75% accuracy performed well in general to identify killer whale social calls within the 1 year and 8 month-long data set and showed good positive correlation to the calls identified manually in a subset of the data. This therefore may be a good alternative option to solely using time-consuming manual analysis which are often impractical for large data sets (Kanes 2018). The higher number of manual calls compared to automated detection can be attributed to the fact that human analysts typically detect vocalisations at lower signal-to-noise ratios (SNRs) than automated detectors, thereby causing this disparity (Hannay et al. 2013; Kanes 2018). When comparing our true positive rate of 78.7% to that of other literature, it faired quite well as it was only slightly lower than other comparisons between automated detected calls and manual ones (Baumgartner et al. 2019; Hamard et al. 2024; Cheng et al. 2025).

Detector results displayed some substantial issues such as the underestimation of calls (which is not uncommon (Hildebrand et al. 2022)), with a false negative rate of 22% and the inability to correctly distinguish between calls and the electrical sound above a certain noise level (even at a high confidence threshold and with an obvious difference in appearance on spectrograms). The noisy data was not included in the detector performance analysis because of limited time to analyse the full data set in complete manual detail, but through a quick visual perusal of the full data set's spectrograms, these false positive detections were discovered. Sources of potential error using automated detection were identified as incorrectly annotating humpback whale calls as killer whale calls as they are similar in structure (Shabangu et al. 2024a) and detector design. This detector was developed for Northern Hemisphere killer whale populations, and not specifically for the Southern Hemisphere, thereby causing some spurious results. Killer whale populations display distinct dialects with population/pod specific calls (Filatova et al. 2015). The acoustic data used to train this algorithm used different calls characteristics compared to that of the PEIs population, using calls specific to their region (British Columbia and adjacent USA waters) of differing frequency, amplitude, ranges of interquartile time and frequency envelops, region-specific noise levels, and different mooring designs and recorders (Mouy et al. 2015). Another method to improve the indication of killer whale presence around the PEIs would be to include other call types such as echolocation clicks in the acoustic analysis (Rice et al. 2017). This would likely have to be done with another automated detector specifically designed for clicks as they can be severally underestimated during manual analysis (Shabangu et al. 2024a).

Other studies utilising the *SpectroDetector* or other JASCO's customised acoustic analysis software for automated detection displayed successful detection of other marine mammals. Insley et al. (2021) used this software to identify bowhead whales, beluga whales and bearded seals' vocalisations in the Canadian Arctic. Frouin-Mouy et al. (2017) identified clicks from narwhals, beluga whales and sperm whales. These studies as well as the current study highlighted that although the automated method is feasible, it cannot be used in isolation and needs some form of manual validation. Most automated detection methods will yield some percentage of both false positives and false negatives, especially in noisy environments or when closely related species are simultaneously present (Frouin-Mouy et al. 2017). Manual detection and the use of professional expertise can reduce this unreliability by disentangling vocalisations by different species, focusing on species-unique calls, ensuring no calls are missed or removing false positive detections as well as using manually annotated data to further develop automated methods (Frouin-Mouy et al. 2017; Kanes 2018). An automated acoustic detector with 92% preliminary accuracy is currently being developed by a company called *DeepVoice* for killer whale calls from the PEIs which may work better to reduce the high number of false positive and negative detections as detectors are developed for each social call type. This detector uses a similar technique that is used in Ismail et al. (2024).

5.2 Killer Whale Diel Call Patterns

Strong diel call patterns were observed in winter and summer across both years. Winter displayed higher killer whale call rates at night and at dusk in contrast to summer which only had high call rates during the day. In winter, when food is scarcer and killer whale groups are smaller (Jordaan et al. 2021), they may be executing an adaptive vocalising response to this to maintain group contact/foraging strategies to increase hunting success (Jordaan et al. 2023; Shabangu et al. 2024a). These results were also similar to the Icelandic herring-eating killer whales which also vocalised and hunted more at night (Richard et al. 2017). This was also comparable to other studies indicating nocturnal calling behaviour reflecting feeding activity in Bigg's marine mammal hunting killer whales (Deecke 2003; Newman and Springer 2008; Pilkington et al. 2023). These killer whales portrayed adaptive behaviour to use stealth to successfully hunt prey through passive listening to find prey, thereby developing effective nocturnal hunting (Barrett-Lennard et al. 1996; Deecke et al. 2013). There is also substantially high call rates observed after success killings (Deeck 2003; Deeck et al. 2005; Saulitis et al. 2005; Riesch and Deecke 2011). The PEIs' population might be sporting the same hunting strategy.

Summer also indicated a strong diel call pattern across both years with higher daytime call rates. This was directly related to increased foraging behaviour as this season showed the greatest average southern elephant seal abundance and prey availability. This was also discovered in Shabangu et al. (2024a) and for North Atlantic killer whales in Norwegian waters (Dietz et al. 2020). Reisinger et al. (2015) showed that PEIs' killer whales dive deeper during the day, thereby increasing the need to acoustically communicate to conspecifics in darker environments (Shabangu et al. 2024a). If they indeed sport the stealth hunting strategy as suggested previously, their high daytime call production may be occurring directly after silent predation events when the pressure of acoustic detection by their prey may not be relevant in that specific social context (Deeck 2003; Deeck et al. 2005; Saulitis et al. 2005; Riesch and Deecke 2011). This disparity in call rates on an hourly scale is averaged out at larger-temporal scales as seen in the current study.

The weak diel call patterns in autumn and spring were similar to that of Shabangu et al. (2024a) who indicated equally high rates of echolocation clicks during both day and nighttime regimes. The lowest call rates occurred during dawn (maximum of 2.5 calls per minute) and differed significantly between years. The same was true for night and daytime, but call rates were very high (maximum of 11 and 11.5 calls per minute respectively). These diverse adaptive acoustic behaviours again may be reflective of fine-scale context specific foraging and social settings such as resting, diving, group cohesion and structure, period of prey abundance and silent hunting (Condy et al. 1978; Keith et al. 2001; Deecke et al. 2005; Reisinger et al. 2015). More detailed visual studies will need to be conducted to unpack these behaviours. This will provide details on what the killer whales are actually doing during certain times of the day and what their behaviours and interactions are like with conspecifics. This will help link their behaviours to their vocal patterns during the same time that their calls were recorded. These short-term changes in foraging and social contexts could lead to significant year-to-year variability in call rates in various daylight regimes as evident in the current study. When looking at call rates for each year, on average there was no significant difference between day and nighttime call rates, only between some pairings containing dawn. The weaker diel call patterns in spring and autumn therefore averaged out the strong diel call patterns in winter and summer. Lower calls rates at dawn and dusk in general may be attributed to resting or silent hunting (Condy et al. 1978; Barrett-Lennard et al. 1996).

5.3. Killer Whale Acoustic Occurrences, Sightings and Environmental Conditions

5.3.1. Killer Whale Acoustic Occurrence, Sightings, and Southern Elephant Seal Abundances

The killer whale social calls detected during this study were similar to the contour shape of pulsed calls found by Schall and Van Opzeeland (2017) and were comparatively less complex indicating acoustic behaviour typical of marine mammal hunters (Wellard et al. 2020). These calls also resembled tonal and pulsed calls of long-finned pilot whales (*Globicephala melas*) and humpback song units, although the former is rarely sighted in the PEIs region (R.K.J.

unpublished data) and the latter is distinguished from killer whale calls by song unit repetition and low frequency production (<500 Hz (although harmonics can be produced as high as 24 kHz); Shabangu and Kowarski 2022).

When examining the year-to-year differences in acoustic occurrences of killer whales on a monthly scale, none were found. This was expected as acoustic patterns typically changed seasonally as they were previously found to partially driven by the seasonal presence of their prey (Reisinger et al. 2011c, Reisinger et al. 2015; Jordaan et al. 2021; Shabangu et al. 2024a). A similar seasonal cycle of acoustic occurrences was observed between May 2021 – April 2022 and May 2022 – December 2022. Calls were detected intermittently year-round on a monthly scale with less calls observed in winter and more in spring and early summer. The clear seasonal cycle of killer whale sightings within the inshore region of Marion Island provides meaningful validation for their acoustic presence which typically followed the same seasonality. This result was also found by Jordaan et al. (2021). A study by Rice et al. (2017) studied the acoustic occurrences of resident and transient killer whales off Washington, USA for a period of 10 years and after examining a subset of the data which contained consecutively high acoustic encounters, discovered that there were no significant interannual variability of their occurrences at several sites. This study stipulated that resident killer whales' acoustic occurrences' seasonality was shaped by the presence of their preferred prey – Chinook salmon in their re-entry peak season between May and August. The same was observed for transient killer whales which had high acoustic presence during periods of higher elephant seal abundances. Another study by Pilkington et al. (2023) in the Northern Strait of Georgia indicated the same patterns of acoustic residency time, sightings and tagging of killer whales during their wintertime use of the habitat matched that of their historical use across a time span of 50 years (Bigg et al. 1976). This study took place over three-winter periods and showed a potential decrease in southern resident killer whale's detection days per unit effort which was again suggested to be driven by prey availability, but additional studies were needed on the Chinook salmon abundances during winter to make solid conclusions (Pilkington et al. 2023). It is also worthwhile noting that the Northern Hemisphere studies took place over longer time periods than the two-year period of the current study, which may also affect the ability to see significant changes from one year to the next.

The PEIs killer whale population’s acoustic seasonality may be subject to the same driver. SES abundance showed clear seasonal cycles across both periods, which is consistent with previous studies as they exhibit extreme fidelity to their haul-out sites at the PEIs (Hofmeyr et al. 2012). Their acoustic occurrences appear to coincide with the haul-out period between August – November for breeding (Kirkman et al. 2004) and December – March for moulting (Hofmeyr et al. 2012). Killer whales appear to take advantage of this predictable prey resource (Reisinger et al. 2011; Reisinger et al. 2015; Jordaan et al. 2021; Jordaan et al. 2023) and this may be shaping the seasonality of their acoustic occurrences to a certain degree. On the other hand, during peak SES abundance, call numbers began to decrease and there was a lack of corresponding significant year-to-year variability between these parameters. This may be a result of marine mammal hunting killer whales’ stealthy nature (Barrett-Lennard et al. 1996; Deecke et al. 2002) to avoid detection by prey with good underwater hearing abilities (Guinet 1992; Shabangu et al. 2024a). Months leading up to this peak in SES, they may be food calling to attract conspecifics to food sources during times of relatively lower resources (Hauser and Marler 1993), but additional studies on this population’s social groups are needed to confirm this as a viable explanation for the patterns observed. Alternatively, killer whales may be moving away to forage in different locations (Reisinger and de Bruyn 2014; Reisinger et al. 2015) as indicated by their decrease in sightings after the peak seal abundance months. Another alternative is the influence of the environmental conditions on their presence in the region.

Year-to-year variability in acoustic occurrences of killer whales around the PEIs were also not seen on a seasonal scale. This may be a result of fine-scale temporal changes in vocalisations that may be masking any year-to-year variation on both a seasonal and monthly scale. When examining the acoustic parameter hours per day with calls, it ranges between approximately 0 – 3 on a monthly scale and 1.2 – 1.6 on a seasonal scale. This is relatively much lower than the daily acoustic occurrence of 12 hours per day calculated previously for the 2021-2022 dataset (Shabangu et al. 2024a). This result was expected as both periods displayed large daily variability which is averaged out at larger temporal scales. Social calls such as stereotypical pulsed calls and whistles are produced during social activities, which include maintaining killer whale group cohesion, coordination, recognition and role-reversal during play (Jacobsen 1986; Riesch and Deecke 2011; Filatova et al. 2013). These activities typically involve rapid changes in their behaviour (Jacobsen 1986) and thereby, possibly their acoustic behaviour. This increases fine-scale temporal variations in their acoustic patterns. Fine-scale changes in their social structure may also influence their acoustic behaviour. For example, the process of “fission-fusion” where social groups break down into smaller groups or form bigger groups for effective hunting and resource exploitation (Krumer 1971) occur not only over years, but it can also occur in a matter of hours (Whitehead and Kahn 1992; Archie et al. 2006). Other fine-scale changes include strong diel patterns observed on an hourly scale for the PEIs (Shabangu et al. 2024a) as similarly observed for several other killer whale populations in the Northern Hemisphere (Frouin-Mouy et al. 2022). These complex fine-scale changes may therefore inhibit the ability to see year-to-year differences on a monthly and seasonal scale.

Killer whale call rates discovered for this study were relatively small when compared to those on the hourly scale presented by Shabangu et al. (2024a) which indicated call rates up to 47 calls per minute for social calls. On the other hand, the average social call rate for the whole of this study, 0.084 calls per minute, was more comparable to the seasonal and monthly averages of social call rates of the current study which ranged from 0.055 – 0.080 and 0 – 0.20 calls per minute for each respectively. Both studies therefore provide evidence for vocal behaviour similar to that of transient killer whales in the North Pacific (Deecke et al. 2005). Deecke et al. (2005) discovered median pulsed call rates of 0.05 calls per individual per minute across a four-year period and an interquartile range of 0.00 – 0.23. This is very similar to the current study, although we do not account for individual dolphins. The current study had lower call rates than resident killer whales (Deecke et al. 2005) and Shabangu et al. (2024a) indicated that the PEIs population also displays echolocation call rates comparable to transient killer whales in the Northeastern Pacific. Both the PEIs’ resident population and transient killer whale population are marine mammal hunters (Rice et al. 2017; Reisinger et al. 2016) and therefore may exhibit the same acoustic, social and foraging behaviours. Additional studies at the Crozet Archipelago in the sub-Antarctic Southern Indian Ocean also indicate similar vocal behaviour to transients which developed independently as they are only distantly related (Guinet 1992; Guinet et al. 2000; Hoelzel et al. 2002).

Killer whale call rates were generally higher in spring, summer and autumn on a seasonal scale. This indicates elevated social or foraging activity occurring during these seasons as well as information sharing for navigation and group cohesion during hunting (Miller and Bain 2000;

Miller 2002). Killer whale sightings typically follow the seasonality of call rate patterns on a monthly scale (with the exception of winter when the inverse was observed (high call rates and low sighting)), which can still provide meaningful validation for their presence and need for communication. Previous findings on call rates of transient killer whales also indicated elevated vocal rates during social activities such as surface-active behaviour and milling after killing and were generally silent during travelling (Deecke et al. 2005). Deecke et al. (2005) defined the former behaviour as frequent physical contact between pod members and occasional aerial and percussive behaviours (breaches, tail-slaps, pectoral slaps and spyhops). Milling after killing was described as movement less than 3 km/h and no clear direction, including aerial and percussive behaviour and occurrence after a confirmed kill.

No year-to -year differences in call rates were observed on a monthly or seasonal scale. This result was hypothesized to be caused by the same reasons as previously mentioned for acoustic occurrences. Call rates did not follow the same seasonal patterns as the acoustic occurrences as killer whales may be vocally present for one or two hours per day but can vocalise very quickly or very slowly for each minute within that hour depending on social or foraging context (Deecke 2003; Deecke et al. 2005; Saulitis et al. 2005; Riesch and Deecke 2011; Shabangu et al. 2024a). The lack of year-to-year differences in these parameters makes sense as the acoustic parameters follow similar seasonality to killer whale sightings which generally change intra-annually.

5.3.3. Sea Surface Temperature and Chlorophyll-a Concentration

The clear seasonal cycle of SST in 2022-2023 followed that of previous studies as the highest SST values were observed in February 2023 (7.9 °C) and the lowest in September 2022 (4.57 °C). The previous year differed only slightly as the lowest and highest SST values were in October 2021 (4.59 °C) and March 2022 (7.7 °C). The seasonality of 2022-2023 SSTs followed the long-term seasonal variability indicated by Toolsee et al. (2021) and Mélice et al. (2003). These studies utilised SST satellite and *in situ* datasets spanning over 23 and 49 years respectively at the PEIs. Another study by Shangheta (2021) utilising a longer *in situ* SST dataset between 1949 - 2018 also indicated a minimum SST value in September (4.6 °C), but the maximum was instead in March (6.7 °C) which was in agreement with the 2021 – 2022 SST maxima.

The clear seasonal cycle in chl-a generally followed that of previous studies as lower concentrations were observed during winter, increasing in spring and peaking in late-spring early-summer (Lamont and Toolsee 2022; Shabangu et al. 2024). In contrast to the current study, Lamont and Toolsee (2022) indicated relatively larger chl-a in late-summer to early-autumn as well as a much lower peak in December at 0.26 mg m^{-3} compared to the current study's maximum of 0.71 mg m^{-3}. It is important to note that this result by Lamont and Toolsee (2022) was determined over a longer period, from 1997 to 2020. The seasonal cycle of chl-a, as a proxy for primary productivity and reflection of phytoplankton biomass, is strongly driven by the seasonality of incoming solar radiation which controls the water stability, light availability and nutrient supply to phytoplankton within the euphotic zone (Blain et al. 2007; Arrigo et al. 2008; Graham et al. 2015; Swart et al. 2015; Browning et al. 2021). These factors allow the proliferation of phytoplankton reflected by the peak period in chl-a of the current study. SST typically follows the seasonality of chl-a between winter and spring, but this was in contrast to other studies which typically show positive correlation between spring through to autumn as a result of increased phytoplankton growth during elevated temperatures (Toolsee et al. 2021; Lamont et al. 2022; Lamont and Toolsee 2022). Other factors that may be influencing the elevated chl-a during this period include the meridional movement of the middle branches of the sub-Antarctic Front and the Antarctic Polar Front around the PEIs (Moore and Abbott 2002; Sokolov and Rintoul 2007 ;Graham et al. 2015; Pinkerton et al. 2021) as well as the Island Mass Effect which was observed to increase localised chl-a between mid-spring and autumn (Lamont and Toolsee 2022). In combination with the above-mentioned factors, mesoscale eddies formed because of prominent bathymetry (Ansorge et al. 1999; Lamont et al. 2019; Lamont and Toolsee 2022) and meandering of the SAF and APF (Nel et al. 2001) may contribute to the year-to-year variability in chl-a around the islands (Lamont et al. 2019).

Seasonality in SST and chl-a was observed to match that of the SES abundances (only from May to January for SST) and all three variables additionally depicted year-to-year variation on a monthly scale. The same pattern in seasonality between these variables were also observed in Shabangu et al. (2024a), providing evidence that increased primary productivity can sustain large masses of prey such as southern elephant seals (Reisinger et al. 2018; Lamont et al. 2022; Lamont and Toolsee 2022). Killer whale acoustic occurrences therefore generally followed the same seasonality of both SST and chl-a to a certain degree (only until spring) as it matches with their main prey item, the SES. It is therefore expected that the acoustic parameters show similar year-to-year variability, but this was not the case as only SST and chl-a showed significant year-to-year variability on a monthly scale. Interannual variability in SST was previously suggested to be related to large scale processes such as ENSO, SAM and SOA (Toolsee 2021). Toolsee (2021) suggested a minor influence of ENSO on SST anomalies at a lag of 1 - 2 and 4 years as well as the influence of ACW (associated with ENSO) on the interannual variation of SST anomalies as the PEIs. Additional studies are still needed to have a more holistic understanding of this atmospheric-ocean climate mode. Toolsee (2021) and Richard et al. (2013) did not depict strong influence of SAM on the interannual variability of SST at the islands. SOA also did not previously depict any strong relation to interannual SST variability (Hurrell and van Loon 1994; Toolsee 2021).

An explanation for the lack of year-to-year acoustic occurrence matching that of the SST and chl-a may be because of how killer whale call structure and behaviour are resistant to temporal changes on the scale of the environmental anomalies. Killer whales are long-lived species, therefore studying their acoustic temporal variability can be difficult (Deecke 1998). They transmit their calls through social vocal learning through several transmission nodes: parent to offspring, from other individuals from the parental generation and among members of the same generation (Filatova et al. 2015). Their acoustic behaviour, call structure, duration, call usage and dialect were previously found to change over very long timespans (20 – 50 years) through cultural drift that may be directional (in response to extrinsic factors) or nondirectional which is through random processes within a group of killer whales (Ford 1991; Foote et al. 2008; Deecke 1998; Wieland et al. 2010). Filatova et al. (2015) suggested that long-term dialect is generally relatively stable over the timespan of at least one generation. Ford et al. (2019) stipulated that their long-term cultural traditions and foraging specialisations are deep rooted and resistant to change, limiting their adaptability to relatively shorter temporal environmental variability (such as the timespan of the current study). The same may be true for their acoustic behaviour. Jordaan et al. (2023) additionally indicated that the long-term survival of PEIs' killer whales (12 years) did not correlate with the environmental proxies of their prey availability (SOI, SAM and SST anomalies). It was suggested that these environmental indices would affect lower trophic level organisms first and take time before the effect reaches apex predators. The connection between acoustic occurrence and environmental variability on the other hand was observed on much smaller temporal scales (sub-annually) (Shabangu et al. 2024a).

5.3.4. Sea Surface Height and Wind speed

The seasonality of SSH for the current study was largely biased by the short-term variation of the meridional movement of the S-SAF (Lamont et al. 2019; Toolsee et al. 2021; Shabangu et al. 2024a). When the S-SAF is in close proximity of the PEIs, SSH is lower and when further south, SSH is higher (Ansorge et al. 1999). This spatial variation in SSH may be masked when calculating average SSH over the 2° x 2° area around the islands. Transient mesoscale eddies evident in the region also cause short-term SSH variability (Lamont et al. 2019). These eddies do not indicate clear seasonality in their number or characteristics and there is large variability between months and years (Lamont and van den Berg 2021). This agreed with the current study as no seasonality in SSH was observed and there was significant year-to-year variability on a monthly scale.

Higher wind speeds in autumn through to early spring months correspond to other long-term trends (Toolsee and Lamont 2022). Wind speeds were only significantly higher for two months in 2022 – 2023 compared to the previous year. Other studies indicated no significant long-term trends (Toolsee and Lamont 2022). Generally, wind speeds in the sub-Antarctic region and at the PEIs are weaker (Rouault et al. 2005; Perren et al. 2020) and are related to the strengthening and slight southward migration of the westerly wind belt in the Southern Hemisphere. The large sub-annual variability in wind speed is likely to be influenced by the frequent and rapid movement of atmospheric low-pressure systems in the region (Rouault et al. 2005; Toolsee and Lamont 2022).

Both SSH and wind speed were thought to display substantial short-term variability which masks seasonal and year-to-year variability respectively. As a result of this, the relationship between these variables and the acoustic parameters was not clear on large timescales as they could be changing on a daily scale as discovered by Shabangu et al. (2024a). Reisinger et al. (2015) also did not find clear movement behaviour associated with SSH anomalies. Alternatively, the effect of the year-to-year variability in SSH and wind speed on the acoustic parameters may only be seen over a much longer time as killer whales were previously found to be resistant to long-term changes in their cultural traditions in response to changes in environmental conditions (Ford et al. 2019). Some correspondence was observed between acoustic occurrence and wind speed – less calls during periods of higher wind speed in winter may be associated with high underwater noise decreasing the ability of their detection (Shabangu et al. 2024a).

5.4. Predictors of Acoustic Occurrences

Wind was found to be the most important significant predictor of acoustic occurrences, thereby indicating the effect of suitable noise levels for the detection of calls. Significant predictors are more informative for call prediction (Shabangu et al. 2024a). This validates the results seen in the year-to-year variation in calls and wind speeds – higher winds speed in the winter months corresponding to lower number of calls. Wind-induced turbulence in the upper layers of the ocean in winter (Carranza and Gille 2015) create air bubbles at the sea surface which absorbs some the acoustic energy of calls reaching the surface (Shabangu et al. 2014; Dähne et al. 2017). Underwater noise related to wind overshadows noise levels above 500 Hz (Shabangu et al. 2022).

Hour of the day was the second most important predictor of acoustic occurrence of killer whales around the PEIs, and although this was insignificant, it does indicate some effect on call occurrence albeit it being too small to be significant and informative (Shabangu et al. 2024a). As previously described in the diel call pattern section, these social calls are mostly related to social and foraging contexts on a fine scale. Killer whales are more likely to vocalise during the early hours of the morning before sunrise, generally during dawn and in the evening after sunset indicating important social activity or foraging related vocalisations. Shabangu et al. (2024a) indicated a similar result as call rates were observed to be higher after sunset in summer and winter potentially indicating social activity related to movement or hunting strategies. Condy et al. (1978) also observed higher feeding activities at dawn and dusk around the islands. Contrastingly, killer whales were previously found to produce more echolocation clicks during the daytime to aid hunting (Shabangu et al. 2024a). These context-specific behaviours should further be investigated and validated using physical sightings data and behavioural studies in parallel with the acoustic results where possible.

In order of importance for predicting killer whale calls after hour of the day, the remaining environmental variables SST, Chlorophyll-a and SSH were ranked. These were moderately important, but only SST was significantly informative. Irrespective, this still indicates some reflection of their influence on driving killer whale ecology, acoustic and foraging behaviour of the PEIs’ population. This result agreed with similar findings which indicated SST and SSH was included in their best models to investigate their behaviours and habitat preferences (Reisinger et al. 2015; Reisinger et al. 2018; Shabangu et al. 2024a). They appeared to prefer very small and negative SSH conditions. The probability of acoustic occurrence fluctuated with changes in SST. They vocalised during both low and high SST values. This was consistent with previous studies which indicated killer whale’s adaptability to high environment variability on small time scales (Reisinger et al. 2015; Shabangu et al. 2024a). A study by Durban and Pitman (2012) using satellite telemetry to track their long-distance movements showed facultative, fast, and direct travel from colder Antarctic waters to warmer subtropical waters to maintain their skin layer while conserving their thermal integrity. This further indicates their temperature adaptability and use of the environment for physiological purposes.

The random forest (RF) modelling results indicated that killer whale calls are more likely to occur at very low chl-a which is also reflected in the low number of SES during these periods. This could suggest that certain social behaviour may be occurring instead of foraging as social calls such as pulsed calls and tonal signals are produced during social activities and are not used for foraging (Riesch and Deecke 2011; Filatova et al. 2013; Shabangu et al. 2024a). The high probability of acoustic occurrence during periods of high chl-a may reflect acoustic behaviour relating to foraging and echolocation click production (Zimmer 2011; Richard et al. 2021). Chlorophyll-a was not a significant predictor of call occurrences may be related to the fact that peaks in primary production would take time to propagate through the food chain to sustain their prey populations (Lamont and Toolsee 2022; Lamont et al. 2022; Jordaan et al. 2023) and their direct influence on their calls may not be seen immediately.

It is only after the environmental variables that SES prey abundance and month (relating to prey breeding and haul-out seasons) was listed as a significantly important predictor of killer whale acoustic occurrences. While this may appear to contradict previous literature that states that prey abundance drives the presence of killer whales around the islands (Reisinger et al. 2011; Reisinger et al. 2015; Jordaan et al. 2021; Jordaan et al. 2023), the RF model still identifies prey as a moderate informative partial driver of call occurrence, thus not disagreeing with previous findings. In this case, however, the environmental variables, specifically the significant predictor of SST and wind were more important for predicting their calls and indirectly drive prey populations at critical times of the year (Pakhomov et al. 2000; Rintoul and da Silva 2019; Chapman et al. 2020). Jordaan et al. (2023) stipulated that killer whale survival was likely to be affected by lags in the environmental proxies for prey abundance and these responses may not be seen directly. The relatively lower ranking of prey as a predictor and the inverse relationship observed between probability of acoustic occurrence and the direct measure of SES abundance may alternatively be a result of killer whales undertaking a stealth strategy to avoid detection by their acoustically aware prey (Guinet 1992; Barrett-Lennard et al. 1996; Deecke et al. 2002; Shabangu et al. 2024a). Mid- to late spring also depicts the starting date of arrival for several other prey species which breed in large masses at the islands (du Plessis et al.1994; Crawford et al. 2003b; Crawford et al. 2003c), increasing probability of acoustic detection by their prey.

Year and killer whale sightings were the least important predictors, and killer whales vocalised to a lesser effect from these factors. Number of killer whales sighted was not an informative predictor of calls because this is not linearly related to call occurrence. One individual present in the inshore region of the islands may be very vocally active and at the same time, a pod can also be very quiet depending on social and foraging context (Deecke 2003; Deecke et al. 2005; Saulitis et al. 2005; Riesch and Deecke 2011; Shabangu et al. 2024a). Year was found to be a significant predictor of calls, although only 20 months of data could be used to represent years. The higher probability of calls in 2022 may have been an adaptive response to the elevated wind speed during that year and its associated underwater noise (Shabangu et al. 2014; Carranza and Gille 2015; Dähne et al. 2017; Shabangu et al. 2022; Shabangu et al. 2024a). It is important to note that the year 2022 had more months sampled than 2021, thus also influencing this result. A longer time period is needed to fully investigate this as their traditions are very resistant to short-term environmental change (Ford et al. 2019).

Chapter 6. Conclusion and Future Recommendations

When comparing the manual and automated detection methods of killer whale calls of the PEIs' population, the automated *SpectroDetector* fared well considering it was designed for Northern Hemisphere populations, and this study was its first application within the study region. However, a moderate number of false negatives were produced by this method (although not uncommon and can be corrected for) and a substantial number of false positives calls were identified as more concerning as the detector annotated obvious electrical noise as calls. It is therefore necessary to utilise automated methods in conjunction with manual inspection of spectrograms to obtain the most accurate results. Additional improvements on automated detectors and extensive research on their vocal repertoire are also essential to progress call identification. These developments are currently underway and will greatly complement studies using PAM and lengthy acoustic data.

SST and chl-a displayed clear seasonal cycles generally matching that of other long-term studies, with only slight deviations. There was significant year-to-year variability in these parameters which was found to be linked to large-scale oceanic and atmospheric processes. Contrastingly, SSH and wind speed did not display clear seasonal cycles as these parameters were largely influenced by substantial short-term variability caused by meridional movements of the S-SAF and mesoscale eddies, and the frequent movement of low-pressure systems across the region respectively, ultimately contributing to year-to-year variability. RF modelling indicated that wind speed was one of the most important predictors for killer whale social calls, followed by hour and the remaining environmental variables SST, chl-a and SSH. The connection between the year-to-year variability of these environmental variables and the acoustic occurrence and call rates, were not observed in the time span of 1 year and 8 months. It is hypothesized that because killer whales are long-lived, they are resistant to changes on the temporal scale over which these large-scale processes occur. For future research, it would be ideal to collect a much longer acoustic time series across generations to holistically investigate this notion or to continue studying killer whale acoustic ecology on a sub-annual temporal scale.

Killer whales were sighted year-round in the inshore region of the islands and displayed similar seasonality to their acoustic occurrences. This parameter did not display year-to-year variability as fine-scale changes in their group structure typically occur sub-annually. The seasonality of their main prey, the SES, appeared to shape their acoustic occurrences to a certain degree. Surprisingly, RF modelling indicated that SES abundance as an important predictor of their social calls only after the environmental variables but was still a significant partial driver and predictor of their occurrences. This may still be a result of environmental factors driving the seasonal presence of killer whale prey. To determine if this inverse relationship between predator and prey is a hunting strategy or if they are migrating to other foraging sites, satellite tracking studies will need to be conducted to investigate their long-range movements. This can be conducted with satellite tagging or a PAM mooring array can be deployed across a reasonable pathway of the Southern Ocean. Pairing this with spatial analyses of oceanographic features of the same region could provide a more holistic understanding of the drivers of their movements. An important finding was that SST was identified to be a significantly important predictor for social call occurrence, thereby potentially indicating temperature adaptability and habitat preference.

Hour of the day was indicated to be one of the most important predictors for killer whale social call occurrences. They displayed adaptive social and foraging behaviours as stronger diel call patterns were witnessed in winter (more dusk and nighttime calls) and summer (more daytime calls). These behaviours may be related to context-specific events, and further visual surveys would complement this research well. This population also appeared to sport a stealth hunting strategy and have similar call rates and vocal behaviour to that of the transient Northeast Pacific and Icelandic populations.

In conclusion, more studies are needed to disentangle the ecology of these keystone species in the harsh environment of the PEIs which are subject to climate change. This can be achieved through the use of innovative methods and technologies such as PAM, automated call detection methods and the growing use and development of machine learning in this setting. The PEIs uniquely serves as an ideal location to study the effects of global anthropogenic change on remote ecosystem resilience which has minimal local anthropogenic impact. This research is essential as it contributes to understanding of upholding the ecosystem integrity, its future management and provides the basis for future long-term bioacoustics research on the killer whales of the PEIs.

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