Southern right whale (*Eubalaena australis*) migratory and foraging behaviour in a changing climate.

by

Matthew Germishuizen

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SUMMARY

Southern right whale (*Eubalaena australis*) migratory and foraging behaviour in a changing climate.

by

Supervisor: Dr Els Vermeulen

Co-supervisor: Prof. Marcello Vichi

Department: Department of Zoology and Entomology

University: University of Pretoria

Degree: Doctor of Science

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Abstract:

The name "right" whale reflects the violent history of southern right whales (SRW, *Eubalaena australis*) since their sluggish, predictable coastal behaviour and the tendency to float when dead led to the reputation of being the "right" whales to hunt. Now, the characteristics that contributed to their near demise carry a less sinister connotation, that of being the "right" climate sentinel. Their life histories and wide-ranging migratory behaviour make SRWs ideal candidates for monitoring environmental change. SRWs are capital breeders with discrete periods in their life histories dedicated to foraging and reproduction. Therefore, females have a strong impetus to accumulate sufficient energy reserves during their foraging period to sustain them through pregnancy and calf nursing.

Thus, a strong connection exists between foraging efficiency and reproductive success.

Foraging efficiency is largely dictated by the environment's ability to generate productive feeding grounds. Sea ice, for example, has a fundamental role in the life history of Antarctic krill (*Euphausia superba*), a key prey species for SRWs. Changes in reproductive success in SRWs may indicate climate-induced alterations in prey, such as reductions in sea ice, in their offshore feeding grounds. Following a steady period of recovery from commercial whaling, SRW populations recently began displaying signs of reduced population growth rates and reproductive failure. This prompted an in-depth assessment into potential drivers behind these changes, and their contemporary migratory and foraging behaviour.

This thesis is focused on the South African population, which through annual aerial surveys has been extensively monitored since 1969. The resultant time-series of population demographic data has revealed drastic reductions in reproductive success after 2009, together with a northward shift in foraging location as indicated by stable isotopes, and a decline in maternal body condition. To better understand these changes, an assessment into patterns of satellite-derived chlorophyll and sea ice as proxies for foraging habitat quality was performed over the period of observed population-level reductions in reproductive success. This revealed substantial declines in sea ice over historically important foraging grounds for SRWs, which likely contributed to reduced availability of their main prey at high-latitudes; Antarctic krill. The thesis reports on the use of animal-borne Conductivity, Temperature and Depth instruments and dive depth recording tags in better understanding the environmental characteristics of their mid-latitude foraging grounds. Results highlighted the importance of ocean fronts,

temperature and salinity in determining favourable foraging grounds. Finally, through the deployment of 26 location-only satellite tags, a comprehensive investigation into the contemporary offshore migratory and foraging behaviour of South African SRWs was performed. From these, areas of high use were identified, and the presence of foraging whales was predicted from eight environmental covariates using Random forest. This significantly increased our knowledge of SRW contemporary habitat use.

The findings of this thesis highlight the strong connections between SRWs and their environment, and the vulnerability of the species to climate change and variability. This also reaffirms the utility of SRWs as the "right" sentinels for environmental change.

Abstract (Italian):

Il nome balena "franca" riflette la storia violenta della balena franca australe (Eubalena australis) poiche' il loro movimento nelle zone costiere lento e prevedibile insieme alla tendenza a galleggiare dopo la morte ha portato alla reputazione di essere la balena "giusta" da cacciare. Tuttavia, queste caratteristiche, che hanno contribuito alla loro quasi estinzione, portano anche a connotazioni meno negative, rendendole la specie 'giusta' come sentinella dei cambiamenti climaticiInoltre, la loro fenologia e il comportamento migratorio ad ampio raggio rendono la balena franca australe il candidato ideale per il monitoraggio dei cambiamenti ambientali. La fenologia delle balene franche australi è caratterizzata da periodi distinti dedicati al foraggiamento e alla riproduzione, e la disponibilità e l'accesso alle risorse alimentari determinano il successo riproduttivo. L'efficienza del foraggiamento è determinata dalla capacità

dell'ambiente di generare zone di alimentazione produttive. Il ghiaccio marino, per esempio, svolge un ruolo fondamentale nella fenologia del krill antartico (Euphausia superba), una specie di preda chiave per le balene franche australi. Pertanto, i cambiamenti nel successo riproduttivo delle balene franche australi potrebbero indicare un'alterazione nella disponibilità di prede indotta dai cambiamenti climatici, come ad esempio la diminuzione del ghiaccio marino nelle loro zone di foraggiamento in mare aperto. Dopo un costante periodo di ripresa dalla caccia commerciale alle balene, le popolazioni di balene franche australi hanno recentemente iniziato a mostrare segni di riduzione dei tassi di crescita e di fallimento riproduttivo. Queste osservazioni hanno spinto a una valutazione approfondita delle potenziali cause di tali cambiamenti e dei loro comportamenti migratori e di foraggiamento attuali. Questa tesi riguarda la popolazione sudafricana, che è stata ampiamente monitorata tramite rilievi aerei a partire dal 1969. La serie temporale risultante dei dati demografici della popolazione ha rilevato drastiche riduzioni dei tassi riproduttivi dopo il 2009, insieme a uno spostamento verso nord dei luoghi di foraggiamento, come indicato dagli isotopi stabili, e a un declino delle condizioni corporee materne. Per comprendere meglio questi cambiamenti, è stata effettuata una valutazione dei modelli della clorofilla e del ghiaccio marino derivati dai satelliti, utilizzati come indicatori della qualità dell'habitat di foraggiamento nel periodo in cui sono state osservate le riduzioni del successo riproduttivo a livello di popolazione. "Ciò ha rilevato un sostanziale calo del ghiaccio marino nelle zone di foraggiamento storicamente importanti per le balene franche australi, che probabilmente ha contribuito alla ridotta disponibilità delle loro prede principali alle alte latitudini, come il krill antartico. Inoltre, la tesi riporta

l’uso di strumenti di conducibilità, temperatura e profondità, e di tag per la registrazione della profondità di immersione impiantati sulle balene, per comprendere meglio le caratteristiche ambientali delle loro zone di foraggiamento alle medie latitudini. I risultati hanno evidenziato l’importanza dei fronti oceanici, della temperatura e della salinità nel determinare le zone favorevoli per il foraggiamento. Infine, attraverso l’impianto di 26 tag satellitari di sola localizzazione, è stata condotta un’indagine completa sul comportamento migratorio e di foraggiamento attuale in mare aperto delle popolazioni sudafricane della balena franca australe. Da questa analisi sono state identificate aree di elevato utilizzo, e la presenza di balene foraggiatrici è stata prevista in base a otto covariate ambientali utilizzando l’algoritmo Random forests. Ciò ha aumentato significativamente la nostra conoscenza dell’uso attuale dell’habitat delle balene franche australi. I risultati di questa tesi hanno evidenziato le forti connessioni tra le balene franche australi e il loro ambiente, e la vulnerabilità di questa specie ai cambiamenti e alla variabilità climatica. Questo ribadisce l’importanza delle balene franche australi come sentinelle 'giuste' per i cambiamenti ambientali.

RESEARCH OUTPUTS

Technical reports

- Chapter 2 was submitted and presented as a scientific committee for-info paper to the International Whaling Commission.

Journal articles

Germishuizen, M., Vermeulen, E., & Vichi, M. (2024). Population changes in a Southern Ocean krill predator point towards regional Antarctic sea ice declines. Scientific Reports.

Co-authored articles

Vermeulen, E., Germishuizen, M., Kennedy, A., Wilkinson, C., Weir, C.R. and Zerbini, A. 2024. Swimming across the pond: First documented transatlantic crossing of a southern right whale. Marine Mammal Science, 1-8. https://doi.org/10.1111/mms.13071

Conference presentations

Germishuizen, M., Vichi, M., Vermeulen, E. 2024. Population changes in a Southern Ocean capital breeder point towards regional Antarctic sea ice declines. Paper SC/69B/ForInfo40 presented to the 69B IWC scientific committee (Southern Hemisphere Subcommittee), Bled, Slovenia

Vermeulen, E., Tixier, P., Cerchio, S., Collins, T., Gasco, N., Germishuizen, M., Guinet, C., Harcourt, R., Houegnigan, L., Kennedy, A. and Samaran, F., 2024. Multi-method observations suggest recolonization of the Crozet Islands by southern right whales with links to different coastal calving grounds.

Paper SC/69B/SH/12 presented to the 69B IWC Scientific Committee Southern Hemisphere Subcommittee), Bled, Slovenia.

Oral presentations

- 6th SANAP South African National Antarctic Programme symposium

- International Whaling Commission Scientific Committee, SC69B, April 2024, Bled, Slovenia.

Poster presentations

- Natural & Agricultural Sciences Research Symposium 2024
- SAMSS 2022: Southern African Marine Science Symposium

LIST OF ABBREVIATIONS

ACC	Antarctic Circumpolar Current
ARS	Area Restricted Search
CCAMLR	The Convention on the Conservation of Antarctic Marine Living Resources
CTD	Conductivity, temperature and depth instrument
ENSO	El Niño-Southern Oscillation
MCMC	Markov chain Monte Carlo
MIZ	Marginal ice zone
MLD	Mixed layer depth
SAM	Southern Annular Mode
SD	Standard deviation (Chapter 2)
SD	Standard deviation of the density gradient (Chapter 3)
SIC	Sea ice concentration
SO	Southern Ocean

SRW	Southern right whale
SSH	Sea surface height
SSS	Sea surface salinity
SSSM	Switching space state model
SST	Sea surface temperature

DECLARATION

I declare that the dissertation/thesis, which I hereby submit for the degree Doctor of Philosophy at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

ETHICS STATEMENT

The author, whose name appears on the title page of this dissertation/thesis, has obtained, for the research described in this work, the applicable research ethics approval.

The author declares that s/he has observed the ethical standards required in terms of the University of Pretoria's Code of Ethics for Researchers and the Policy guidelines for responsible research.

Matthew Germishuizen
October 2024

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1. Connecting climate and marine predators in the Southern Ocean

CHAPTER 1

1.1 Introduction

All ecosystems are sensitive to climate change and variability (Hoegh-Guldberg & Bruno, 2010; Seddon et al., 2016). Furthermore, ever-increasing rates of habitat destruction are significantly affecting the ability of ecosystems to adapt to both natural and anthropogenic changes in the earth's climate (Thuiller, 2007). At the heart of the earth's climate system is the Ocean, which not only drives the global atmospheric circulation, but also acts as a buffer to rapid rates of change through the absorption of vast amounts of heat and greenhouse gases (Levin & Bris, 2015; Reid et al., 2010). This process, however, has effects throughout marine food webs through warming, ocean acidification and changes in the distribution of prey(du Pontavice et al., 2020; Kortsch et al., 2015).

The effects of climate change on marine systems are not uniform, with significant regional variability in the rates of change and onset of climate change effects (Henson et al., 2017). The Arctic, for example, displayed the earliest onset of regional anthropogenic warming and some of the fastest rates of sea ice loss and environmental change (Henson et al., 2017; Huang et al., 2017). The tropics are also experiencing amplified effects of climate-induced warming and habitat degradation, particularly through coral bleaching and ocean acidification (Henson et al., 2017; Manzello, 2010; Sully et al., 2019).

Climate change and variability in the Southern Ocean (SO) is slightly more ambiguous (Cai et al., 2023; Henson et al., 2017; Purich et al., 2016; Zhang et al., 2019). The SO is a continuous ocean region that connects the Atlantic, Pacific and Indian ocean basins via the broad fast-flowing Antarctic Circumpolar Current (ACC). This current system has largely insulated the

Southern Hemisphere from fast rates of climate change and has delayed warming (Armour et al., 2016; Henson et al., 2017). However, certain regions in the SO are displaying some of the fastest rates of natural and anthropogenic environmental change on earth, such as the western Antarctic Peninsula (Clarke et al., 2007; Zhang et al., 2019).

An important aspect of understanding the relationship between climate and ecosystems is through monitoring marine predators (Hazen et al., 2019; Trathan et al., 2007). Climate has been found to have strong effects on ocean productivity, which alters food web dynamics with implications for the abundance and distribution of prey and its predators (Pinkerton et al., 2021; Thomalla et al., 2023). These changes in food availability are reflected in demographic and physiological parameters such as reproductive success, distribution shifts, body condition and mortality rates (Bastille-Rousseau et al., 2018; Hazen et al., 2013, 2019). This sensitivity to environmental change has highlighted the potential of marine predators as ecosystem "sentinels" to monitor environmental changes and to identify important areas for conservation (Bestley et al., 2020; Hazen et al., 2019; Hindell et al., 2020; Reisinger et al., 2018). Fundamental to this task is understanding the connections between climate and marine predators and disentangling the impacts of various drivers in very complex systems. In this chapter I describe the rationale for this body of work, and the theory behind connecting marine predators and their environment with a focus on the SO.

1.2 Southern Ocean (SO)

The SO hosts a vast array of iconic marine predators (Figure 1). However, the distribution of productive foraging grounds shows a great deal of spatiotemporal heterogeneity resulting in predators often having to travel vast distances in search of food (Hindell et al., 2020), and exerts adaptive pressures on morphology and physiology so animals can take advantage of patchy high density prey. This patchiness in the distribution of productive regions is largely due to the nature of SO physical oceanography and bio-geochemistry. Characteristically, the SO is nutrient rich, but iron and light limited, which impedes primary production in large parts of the region (Bazzani et al., 2023; Quéguiner, 2013). Primary production can be high in the vicinity of sources of iron such as sea ice, glacial melt water, sediments and land masses (Wadley et al., 2014). Regions with such inputs are often hotspots of biological activity (Henley et al., 2020).

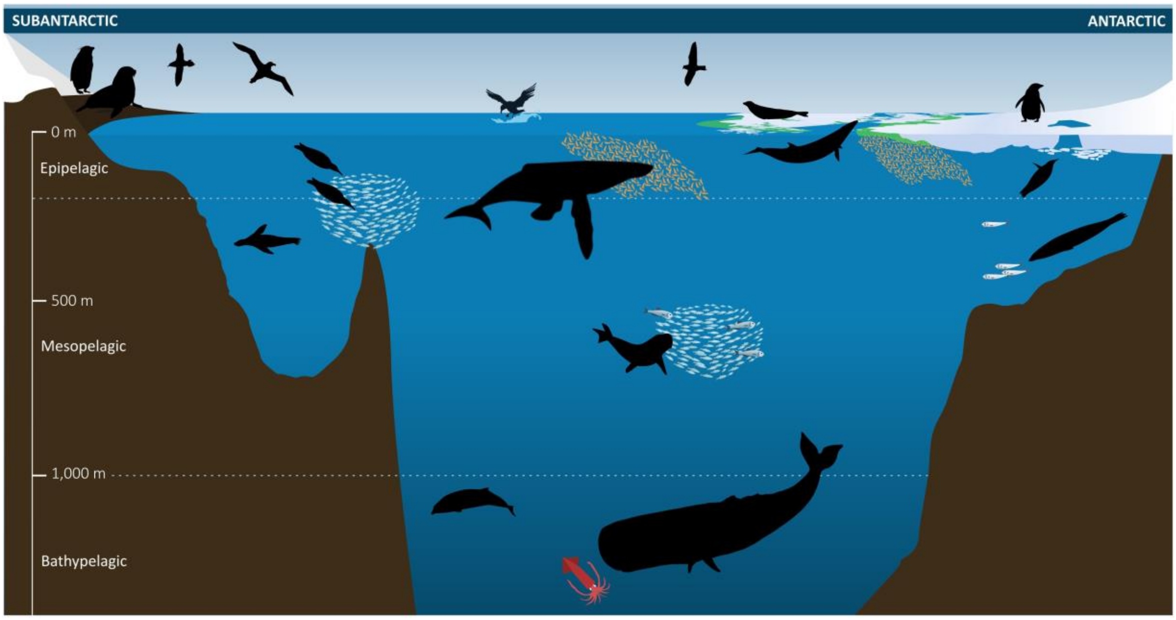


Figure 1. The SO has an iconic suite of top predators, occupying different niches and targeting different species. Image from Bestley et al. (2023).

1.2.1 SO Ocean fronts

A significant portion of SO variability is driven by the fast-flowing westerly wind belt and associated Antarctic Circumpolar Current (ACC), which is unobstructed by landmasses and is one of the fastest current systems on earth (Gordon, 1988). It is also the largest current system, transporting approximately 130 sv of water eastwards around the SO (Meredith et al., 2011). The ACC is generated through a combination of strong westerly surface winds and buoyancy forcing arising from density gradients as waters transition from warmer saltier waters to the north, to colder denser waters to the south (Nowlin & Klinck, 1986).

This transition is however not steady and is punctuated by ocean fronts defined by steepened density gradients, which via thermal wind result in the formation of strong oceanic jets (Chapman et al., 2020; Nowlin & Klinck, 1986). These frontal systems have been found to be the focus for foraging predators due to enhanced productivity from increased vertical mixing of nutrient rich waters from depth with the surface (Bost et al., 2009; Chapman et al., 2020; Sokolov & Rintoul, 2007).

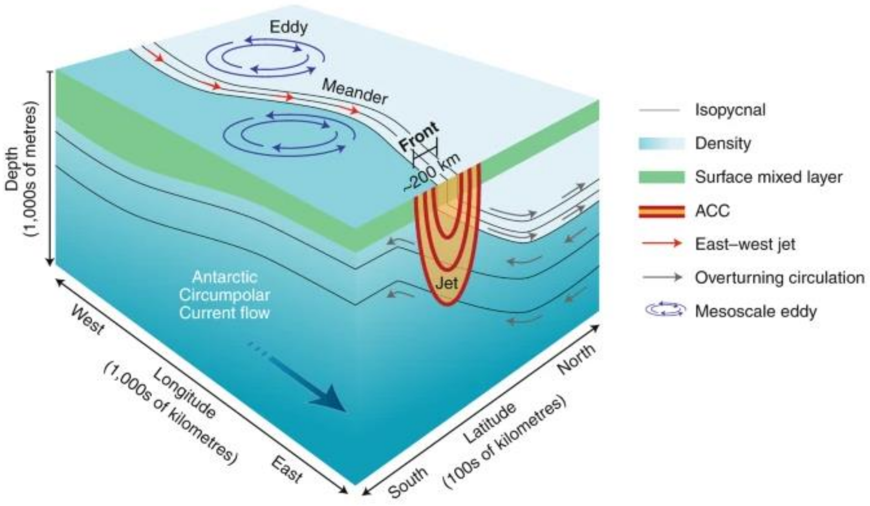


Figure 2. A schematic of the features associated with a typical ACC front. Adapted from Chapman et al. (2020).

There is concern over the implications of climate change on the functioning, position, and variability of these frontal systems, and how these changes will affect the ecology of the SO. Increasing wind stress and warming are expected to result in a southward shift in SO fronts. The extent of this shift is debated; however it appears that since the development of satellite altimetry in 1993, fronts have only shifted by about 50 – 70 km south (Kim & Orsi, 2014; Sallée et al., 2008; Sokolov & Rintoul, 2009). However, further shifts may significantly impact predators, particularly those with shorter foraging ranges. Furthermore, the productivity of some geographical regions is strongly linked with interactions between these frontal features and the underlying bathymetry. For example, interactions between the subtropical front and Agulhas return current have been found to assist in developing and constraining intense phytoplankton blooms north of Crozet Islands (Pollard et al., 2007). Additionally, declines in predators which forage near the shores of the Prince Edward Islands are thought to have been driven by changes in the position of fronts, reducing the productivity of the region (Louise Allan et al., 2013). Therefore, even relatively small shifts in ocean features can have profound implications for such ecosystems.

1.2.2 Sea Ice

A characteristic component of the SO is sea ice, which oscillates in extent between 20 million km^2 in winter, to 2 million km^2 in summer. This immense seasonal change largely modulates the biology and oceanography of the region, as well as playing a fundamental role in the global thermohaline circulation through the formation of cold dense water masses (Johnson, 2008; Solodoch et al., 2022). In addition to the large seasonal change, Antarctic sea ice is highly variable even at daily time scales. Sea ice can change from almost 100% cover to open water in a matter of days (Vichi et al., 2019). This variability is associated with transitional zones from consolidated ice to open water, termed the marginal ice zone (MIZ, Figure 4). In autumn and winter this zone forms a continuous, relatively narrow circumpolar band that moves north with sea ice expansion. After reaching the winter maximum in sea ice extent in September, the ice begins to melt and break apart, resulting in almost the entire region of winter sea ice extent to inherit MIZ characteristics. As the ice melts, relatively fresh water, nutrients and minerals are released, and the water column is primed for the development of summer phytoplankton blooms (Pinkerton et al., 2021; W. O. Smith & Comiso, 2008; Vernet et al., 2008).

Figure 4. The Antarctic marginal ice zone (MIZ); photo taken during the Southern Ocean Seasonal Experiment (SCALE) cruise 2022 (M. Germishuizen).

Furthermore, the ice itself harbours a diverse assemblage of ice-dwelling organisms, both within the ice itself (Caron et al., 2016; Tedesco et al., 2010), and organisms which feed on prey and algae on its surface (Schmidt et al., 2014). The role sea ice has on establishing highly productive foraging grounds, and the strong seasonality, means predators time their foraging behaviour with the seasonal cycle of sea ice (Cherry et al., 2013). Furthermore, fluctuations in sea ice can have implications for the foraging success of many predators. For example, sea ice has an important role in the life history of Antarctic krill (*Euphausia superba*), a keystone species supporting many different species of predators (Flores, van Franeker, et al., 2012; Melbourne-Thomas, 2020; Trathan & Hill, 2016). Therefore, fluctuations in sea ice can significantly affect the abundance of Antarctic krill, which, in turn, impacts the predators that depend on them for food (See section 1.3.2; Bengtson Nash et al., 2018; Nicol et al., 2008; Wege et al., 2021).

1.2.3 Primary production

Phytoplankton primary production forms the basis of most oceanic food webs and is a strong driver of the biological carbon pump. Therefore, ecosystem effects of climate variability are believed to be largely driven by changes to phytoplankton production and its ramifications on the biological carbon pump. The biological carbon pump regulates the supply of remineralized nutrients to surface waters by transporting organic material into the ocean's interior. This process, in turn, affects primary productivity and carbon export in lower latitudes (Sarmiento et al., 2004). Primary production is largely regulated through ocean-atmosphere interactions such as upwelling, ocean mixing and sea ice processes (Deppeler & Davidson, 2017). In the SO, primary productivity is enhanced by the SO frontal systems of the ACC and strength and orientation of westerly winds and associated currents with the complex underlying bathymetry and islands in the region. Sea ice exerts a strong control on the seasonal cycle of phytoplankton and plays a fundamental role in generating the preconditions for spring and summer blooms (Behera et al., 2020; Castagno et al., 2023; Meredith & Brandon, 2016; Vernet et al., 2008). Regions experiencing sea ice loss in both the Arctic and Antarctic have a strong signal of enhanced primary productivity (Brown & Arrigo, 2012; Castagno et al., 2023; Del Castillo et al., 2019; Henley et al., 2020; Pinkerton et al., 2021; Thomalla et al., 2023). Reductions in sea ice are hypothesized to increase primary production by enhancing light exposure and lengthening the growth season for pelagic phytoplankton (Flores et al., 2023; Noh et al., 2021; Thomalla et al., 2023).

Responses to modes of climate variability (such as the Southern Annular Mode; SAM) display high levels of zonal asymmetry (Lovenduski & Gruber, 2005; Noh et al., 2021). These patterns are attributed to an increase and southward shift in westerly winds, enhancing upwelling south of the Antarctic Polar Front during positive SAM, and a relaxation and northward shift of the westerly wind belt during negative SAM. A positive SAM has been linked to regional changes in sea ice conditions, with contractions in the Amundsen Sea and South Atlantic sector and increases in the Pacific and Indian Ocean sectors (Doddridge & Marshall, 2017).

1.2.4 Climate modes

Despite the SO’s noisy background state, modes of variability with distinct implications on the physical environment have been identified. SAM, also known as the Antarctic Oscillation, is the dominant mode of atmospheric variability in the Southern Hemisphere and describes the latitudinal shift in zonally symmetric atmospheric anomalies driven by pressure relationships between the mid-latitudes and high-latitudes (Marshall, 2003). Complex interactions occur with the co-variability between El Niño-Southern Oscillation (ENSO) and SAM (Lachlan-Cope & Connolley, 2006). The ACC plays an important role in establishing teleconnections with the tropics and transmitting tropical climate anomalies such as ENSO to the Antarctic (Li et al., 2021). El Niñozevents, for example, have been linked to fluctuations in prey and predator populations in the Southern Ocean (Agrelo et al., 2021; Murphy et al., 2007; Yuan, 2004).

Over the last few decades, SAM index has been increasing, with the dominance of positive anomalies. During positive SAM phases, the westerly wind belt strengthens and contractspoleward, while under negative SAM anomalies the westerlies drift north and relax. However, the responses in sea surface temperature, sea ice and biology show high degrees of regional variability and asymmetry. Under positive SAM, strengthening wind results in increased upwelling and sea surface cooling and northward sea ice expansion (Kwok & Comiso, 2002; Lefebvre et al., 2004). A notable exception is along the Antarctic Peninsula and Weddell Sea which experiences sea ice contraction and warming (Kwok & Comiso, 2002; Lefebvre et al., 2004). These regional differences have largely been linked to the Amundsen Sea low, a semi-permanent feature whose intensity and position dictate regional sea ice expansion and contraction and is strongly linked to climate variability (Lachlan-Cope & Connolley, 2006; Turner et al., 2016).

1.3 Using marine predators to study the SO

Marine top predators have been extensively studied in the SO, and the knowledge gained has been applied to a variety of fields including conservation, oceanography, ecology, biology and climate sciences (Bestley et al., 2020). Therefore, marine predators act as an important catalyst of interdisciplinary science, connecting various fields and revealing novel insights. As such, many methods are now being employed to gather information about marine predators.

1.3.1 Methods for monitoring marine predators

Time-series data of population counts and indices exist from various survey methods including aerial, ship-based and point counts on foot. For some species, these datasets cover several decades (e.g., Brandão et al., 2023; Forcada et al., 2023; Jordaan et al., 2020). These data sets have been incredibly valuable in revealing population-level changes in numerous species (Brandão et al., 2023; Forcada et al., 2023; Lynch & Larue, 2014; Strycker et al., 2020), and connecting these changes to environmental variability, behavioural ecology and genetics (Cole et al., 2019; Germishuizen et al., 2024; Jenouvrier et al., 2006; Krause et al., 2022). Furthermore, novel technologies such as the use of satellites and drones together with machine learning techniques are assisting with increasing the coverage and reliability of surveys, especially in remote locations (Cubaynes et al., 2019; Fretwell et al., 2023; Guirado et al., 2019; LaRue et al., 2011; McMahon et al., 2014). For cetaceans, an important aspect of monitoring presence and behaviour is through bioacoustics (e.g. Shabangu, Daniels, et al., 2024; Shabangu, Munoz, et al., 2024). These techniques have helped reveal effects of environmental change and variability on the presence and behaviour of several species (Menze et al., 2017; Schall et al., 2021; Shabangu, Daniels, et al., 2024; Shabangu et al., 2017).

Another technology that is rapidly expanding is the use of animal-borne instrumentation. A variety of different instruments including location only tags, depth measuring devices, conductivity, temperature and depth (CTD) instruments, video cameras and acoustic recording devices have been deployed on several species (Bestley et al., 2020). Through these, a wealth of information has been gathered with important applications across multiple disciplines. Relationships between animal behaviour and the environment can reveal important insights into ecosystem functioning. Southern elephant seals (*Mirounga leonina*), for example, have been widely used to carry CTD instruments to collect oceanographic data, and have contributed valuable information about the functioning of the SO (J. B. Charrassin et al., 2008; J.-B. Charrassin et al., 2010; Gordine et al., 2019).

Location only satellite tracks of predators also provide valuable information about animal movements and foraging behaviour (e.g. Dalla Rosa et al., 2008; Lee et al., 2017). Furthermore, combining tracks across multiple species over large areas can help identify important areas for biodiversity with implications for conservation and resource management (Hindell et al., 2020; Reisinger et al., 2018). These approaches can also be used to improve our knowledge of ecosystem functioning at large spatial scales and investigate ecological concepts such as niche partitioning and multi-species biodiversity hotspots (Block et al., 2011).

1.3.2 Connecting marine predators with Antarctic krill abundance

One of the most important and abundant prey species in the SO is Antarctic krill. Antarctic krill have been classified as a foundation species due to their role in modulating the SO ecosystem and the widespread consequences that would hypothetically ensue should the species vanish (Quetin B & Ross M, 2009). Antarctic krill are polar specialists and are generally found in waters <3.5 °C with a thermal limit of -1.8 °C to 5°C (Ross et al., 2000; Schmidt et al., 2014). This sensitivity to temperature, and in particular to warmer waters, limits the northward extent of their distribution as well as making them susceptible to ocean warming (Flores, Atkinson, et al., 2012). Furthermore, the life cycle of Antarctic krill is dependent on sea ice, especially during the early life stages which develop during the winter months feeding on ice-growing algae (McBride et al., 2021). In particular, the formation of large dense swarms, as opposed to more sparsely and homogenously distributed krill, is largely determined by the presence of ice, whereby densities of furciliae under sea ice have been found to be orders of magnitude higher than in open water (Hamner W et al., 1989). As krill progress through their life history stages and increase in size, this reliance on sea ice decreases and their distribution shifts northward during late spring and summer away from the ice edge (Sprong & Schalk, 1992). Due to this dependence, reductions in sea ice and ocean warming are likely to have profound effects on the abundance and distribution of Antarctic krill. Antarctic krill distribution is patchy in nature, shows high degrees of seasonality and spatial heterogeneity and covers an immense part of the Southern Hemisphere (Fielding et al., 2014). This makes direct monitoring of krill biomass and distribution incredibly difficult. These factors have contributed towards high levels of uncertainty in determining absolute or indices of abundance and, therefore, a good understanding of the state of the Antarctic krill-based ecosystem.

Numerous studies have pointed towards an immense decline (70%) and southward contraction of the krill stock, primarily driven by sea ice loss and ocean warming (Flores, Atkinson, et al., 2012; S. L. Hill et al., 2013, 2019a). However, using the same data set (Atkinson et al., 2017), other studies have found no clear indication of a significant decline in biomass or distribution shift in Antarctic krill (Cox et al., 2018, 2019; S. L. Hill et al., 2019b). Given these uncertainties, valuable insights into the state of the Antarctic krill-based ecosystem can be obtained using a combination of proxies of Antarctic krill habitat quality such as satellite derived measurements of sea ice (Ichii et al., 2023), and monitoring predator populations. Table 1 presents a collation of such studies on trends of Antarctic krill predators from the Antarctic peninsula and South Atlantic (Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) management Area 48). This sector is estimated to contain more than 70% of the global Antarctic krill stock (Atkinson et al., 2004), and a wealth of data on top predators.

Table 1. Population trends of Antarctic krill predators in management area 48 of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR).

Species	**Location/ population**	**Parameter**	**Trend (period)**	**Magnitude (p/a = per annum)**	**Drivers of changes**	**References**
Humpback whale (*Megaptera novaeangliae*)	Stock A (Brazil breeding ground)	Growth rate	increasing (2002 - 2011)	6 - 12% p/a	Recovery from whaling	Bortolotto et al., 2016; Wedekin et al., 2017; A. N. Zerbini et al., 2019
	Stock B (West Africa breeding ground)	Growth rate	increasing (2010 - 2015)	2 - 4% p/a	Recovery from whaling	(Jackson et al., 2015)
	Stock G (Central America breeding ground)	Growth rate	increasing (1991 - 2018)	5% p/a	Recovery from whaling	(Félix, 2021)
Southern right whale (*Eubalaena australis*)	South Africa	Reproductive rates	decreasing (2010 - 2020)	From 3 year to 4/5 year calving cycle	Antarctic krill availability	(Brandão et al., 2023)
		Growth rate	increasing (1979 - 2020)	6.5% p/a	Recovery from whaling	(Brandão et al., 2023)
	Argentina	Growth rate	increasing (1970 - 2012)	6.5% p/a	Recovery from whaling	(J. G. Cooke, 2013)

		Rate of increase	declining (2008 - 2016)	-0.7% p/a	Density dependent processes, Antarctic krill availability.	(Crespo et al., 2019)
	South Georgia/Elephant Island	Number of sightings	Increasing (1991 - 2005); declining (2006 - 2010)	>55% , >60%	Antarctic krill availability, observer bias	(Richardson et al., 2012)
Antarctic blue whale (*Balaenoptera musculus intermedia*)	Circumpolar South of 60°S	Growth rate	increasing (1979 - 2004)	7.3 - 8.2% p/a	Recovery from whaling	(Branch, 2007; Branch et al., 2004)
	South Georgia	Number of sightings	increasing (1997 - 2020)	>90%	Recovery from whaling	(Calderan et al., 2020; Richardson et al., 2012)
Fin whale (*Balaenoptera physalus*)	Antarctic Peninsula	Population estimate	increasing (2000 - 2019)	>40%	Recovery from whaling	(Herr et al., 2022; Reilly et al., 2004)
Antarctic minke whale (*Balaenoptera bonaerensis*)	-	-	-	-		
Leopard seal (*Hydrurga leptonyx*)	Antarctic Peninsula	Number of sightings	increasing (1996 - 2014)		Decrease in sea ice habitat	(Forcada et al., 2012; Krause et al., 2015)
Antarctic fur seal (*Arctocephalus gazella*)	South Georgia	Longevity and recruitment	Declined (2015 - 2022)	>50%	Antarctic krill availability, Krill fishery	(Forcada et al., 2023; Forcada & Hoffman, 2014)
		Abundance	declining (2010 - 2022)	-7.2% p/a	Antarctic krill availability	
	Bouvet Island	Pup production	increasing (1964 - 1997); stable (1997 - 2002)	>800%; ~0%	Recovery from harvesting	(Hofmeyr et al., 2005)
		Abundance	declining (2002 - 2008)	-	-	(Hofmeyr, 2016)

	Antarctic Peninsula	Abundance	declining (2007 - 2020)	86%	Increased predation by leopard seals, Antarctic krill availability, Krill fishery	(Krause et al., 2022)
Crabeater seal* (***Lobodon carcinophaga***)	-	-	-	-		
Adelie penguin (*Pygoscelis adeliae*)	South Shetland Islands	Number of nests	declining (1990 - 2010)	>60%	Warming, sea ice loss, Antarctic krill availability	(Hinke et al., 2017)
		Breeding pairs	declining (1998 - 2010)	>60%	Antarctic krill availability	(Trivelpiece et al., 2011)
	South Sandwich Islands	Breeding pairs	increasing (1997 - 2011)	>50%	-	(Convey et al., 1999; Lynch et al., 2016)
Chinstrap penguin (*Pygoscelis antarcticus*)	South Shetland Islands	breeding pairs	declining (1970 - 2020)	30 - 80%	Antarctic krill availability, Sea ice loss, tourism	(Naveen et al., 2012; Sander et al., 2007; Strycker et al., 2020)
	South Orkney Islands	breeding pairs	declining (1980 - 2020)	30 - 80%	Antarctic krill availability, sea ice loss	(Dunn et al., 2016; Lynch et al., 2012; Strycker et al., 2020)
	Bouvet Island	Abundance	declining (1996 - 2008)	80%	Increased Antarctic fur seal predation, landslides and Antarctic krill availability	(Niemandt et al., 2015)
	South Sandwich Islands	breeding pairs	stable (1997 - 2011)		-	(Convey et al., 1999; Lynch et al., 2016)
Gentoo penguin (*Pygoscelis papua*)	Antarctic peninsula	Growth rate	increasing (1979 - 2010)	2.4% p/a	Sea ice loss, warming	(Lynch et al., 2012)

		Abundance	increasing (2003 - 2008)	27%	Sea ice loss, warming	(Lynch et al., 2010)
		Distribution shift	southward expansion	-	Sea ice loss, warming	(Clucas et al., 2014; McClintock et al., 2010)
	South Orkney Islands	Abundance	increasing (1978 - 2004)	>50%	Sea ice loss, warming	(Forcada et al., 2006)
Macaroni penguin (*Eudyptes chrysolophus*)	South Shetland islands	Abundance	stable (1970 - 2020)	-	-	(Strycker et al., 2020)
	South Georgia	Breeding pairs	declining (1985 - 2011)	>70%	Climate, increased predation, Antarctic krill availability	(Horswill et al., 2016; Trathan et al., 2012)
	South Sandwich Islands	Abundance	stable	-	-	(Convey et al., 1999; Lynch et al., 2016)
Emperor penguin (*Aptenodytes forsteri*)	Antarctic Peninsula	Breeding failure	Abandonment of colonies, decline in breeding success (2009 - 2022)	>50% of colonies abandoned	Sea ice loss	(Fretwell et al., 2023)
		Colony status	Colony disappeared (2009)	-	Sea ice loss, warming	(Trathan et al., 2011)

* Current literature lacks data on population trends of crabeater seals.

Regionally, most pinniped and bird species have witnessed declines in abundance and population growth rates. Some groups have experienced drastic reductions (>50%), such as Antarctic fur seals and chinstrap, macaroni and Adelie penguins. These species are well monitored at numerous colonies and have regular surveys where a large proportion of the population can be assessed. For other species, very little is known, particularly for those which don't have accessible, geographically reliable aggregation sites for comprehensive surveys. For example, blue whale (*Balaenoptera musculus intermedia*) abundance trends all stem from three sets of circumpolar surveys (Branch, 2007; Branch et al., 2004), but only include a small fraction of the estimated population size. These provide estimates of abundance at three points in time with high levels of uncertainty. Even less is known about fin whales (*Balaenoptera physalus*), Antarctic minke whales (*Balaenoptera bonaerensis*) and pack ice seals such as leopard (*Hydrurga leptonyx*) and crabeater (*Lobodon carcinophagus*) seals. More is known about trends in humpback whales (*Megaptera novaeangliae*), since they aggregate annually at breeding grounds, and have been more comprehensively studied at their foraging grounds (Meynecke et al., 2020). However, humpback whale behaviour is still not sufficiently predictable to develop reliable time-series demographic data of populations (Meynecke et al., 2020). Despite these uncertainties, estimates suggest that populations are increasing steadily in these more elusive baleen whale species (e.g., Bortolotto et al., 2016; Branch, 2007; Felix, 2021; Zerbini et al., 2019), while even broad trends in pack ice seals remain unknown. Southern right whales (SRW) are a notable exception within baleen whales due to their reliable nearshore calving behaviour, which has resulted in extensive and robust time-series data on population dynamics (e.g., Brandão et al., 2023; J. Cooke et al., 2015; J. G. Cooke et al., 2001; Stamation et al., 2020; Watson et al., 2021); most have revealed steady population increases (with exception of the Chile-Peru and southeast Australia population which remain critically endangered; (Stamation et al., 2020; Vernazzani et al., 2014). Despite population increases, these long-term datasets have also revealed more recent changes in demographic parameters such as declining reproductive rates and consequently population growth rates (e.g., Charlton et al., 2019; Brandão et al., 2023; Crespo et al., 2019; Watson et al., 2021). This indicates that even though most baleen whales are still recovering steadily from commercial whaling, changes in growth rates and reproductive success may not easily be observed, highlighting the value of long time-series data (i.e., annual) at fine temporal scales in studying the impacts of climate change and variability on predators.

To date, all well monitored species have revealed notable changes in population demographics which are temporally aligned with suggested changes in Antarctic krill (S. L. Hill et al., 2013, 2019a; Kawaguchi et al., 2024), and regional changes in sea ice ((Fogt et al., 2022; Ichii et al., 2023; Noh et al., 2021; Schroeter et al., 2023). It is clear that trends in top predator populations suggest significant decreases in the availability of Antarctic krill have occurred. However, all these studies suggest a combination of drivers, and discuss the complexities underpinning the disentanglement of the effects of other impacts such as human disturbance, density-dependent interactions, intra-specific competition and loss of breeding habitat. Therefore, more research should focus on disentangling these drivers, and assess changes in population demographic time-series data across multiple species.

1.4 Project rationale

SRWs are capital breeders, with distinct portions of females' life histories dedicated towards pregnancy, birthing, nursing young and foraging. This puts a strong impetus on mothers to accumulate enough energy reserves to sustain pregnancy and nurse their young, leading to enhanced sensitivity to climate variability in their offshore foraging grounds (Agrelo et al., 2021; Germishuizen et al., 2024; Leaper et al., 2006; Seyboth et al., 2016). SRWs are among the most comprehensively studied marine mammal in the world, with most populations being extensively monitored over the past 20 – 50 years (J. Bannister, 2001; Best et al., 2020; Payne, 1986). This is due to their predictable nearshore presence, making them easy to monitor and identify using distinct configurations in callosity and dorsal pigmentation patterns (Best, 1990a). This combination of accessibility and sensitivity to climate variability makes SRW excellent candidates as climate sentinels (Hazen et al., 2019).

After an extended period of recovery from near extinction due to commercial whaling (T. D. Smith et al., 2012; Tormosov et al., 1998), most populations have seen unprecedented changes in reproductive rates and foraging behaviour over the last 15 years. These include fluctuations in SRW counts (e.g. Vermeulen et al., 2018, Brandão et al., 2023), lengthening of calving intervals (Marón et al., 2015, Charlton 2022, Vermeulen et al., 2018, Brandão et al., 2023) and increased calf mortality (Rowntree et al., 2013, Marón et al., 2015, Sironi et al., 2018) have been observed, with (at least) short-term effects on the population growth rate (e.g., Brandão et al. 2023). Furthermore, northward shifts in foraging location (Derville et al., 2023; van den Berg et al., 2021), together with declines in maternal body condition (Vermeulen, et al., 2023) provide additional support that these changes are related to climate induced changes to the availability of prey. Moreover, SRW reproductive success has been found to display high levels of synchronicity with sea ice and Antarctic krill abundance (Agrelo et al., 2021; Germishuizen et al., 2024; Seyboth et al., 2016). Therefore, I hypothesize that the population level changes observed are strongly linked to declines in Antarctic krill availability driven by reductions in sea ice in offshore foraging grounds.

To better understand these changes, this study aims to conduct an in-depth investigation into the relationship between foraging and migratory behaviour of South African SRWs and environmental variability. Chapter 2 of this thesis describes a drastic decline in the sea ice habitat of Antarctic krill during the period of declining SRW reproductive success; Chapter 3 investigates environmental drivers behind mid-latitude foraging behaviour using animal-borne CTD instruments; and Chapter 4 describes the contemporary migratory behaviour of South African SRWs. Chapter 5 provides a discussion on the significance of these findings and the focus on future work. Through this, the use of SRWs as climate sentinels, as well as the vulnerability of the species to future more drastic changes under increasing rates of global warming are assessed.

1.5 Aims and research questions

At the core of this thesis are three data chapters: Chapters 2, 3 and 4. The specific objectives for each chapter are:

Chapter 2 investigated environmental drivers behind a precipitous decline in reproductive success in the South African population of SRWs after 2009.

Specific research questions:

- Are there any changes in foraging habitat quality over SRW offshore foraging grounds during the period of declining reproductive success?
- Do these patterns in environmental change provide evidence that declining reproductive success, northward shift in foraging behaviour and declines in maternal body condition are related to changes in the seasonal sea ice zone that reduce Antarctic krill availability?

Chapter 3 investigated the oceanographic characteristics of South African SRW mid-latitude foraging grounds using animal borne CTD instruments and movement patterns using depth recording telemetry tags.

Specific research questions:

- Are different behavioural states, as predicted by movement models applied to satellite telemetry tracks, associated with different ocean characteristics?
- What oceanographic features do SRWs target in the SO mid-latitudes?
- Does diving behaviour change with behaviour and over time as animals move into offshore foraging grounds?

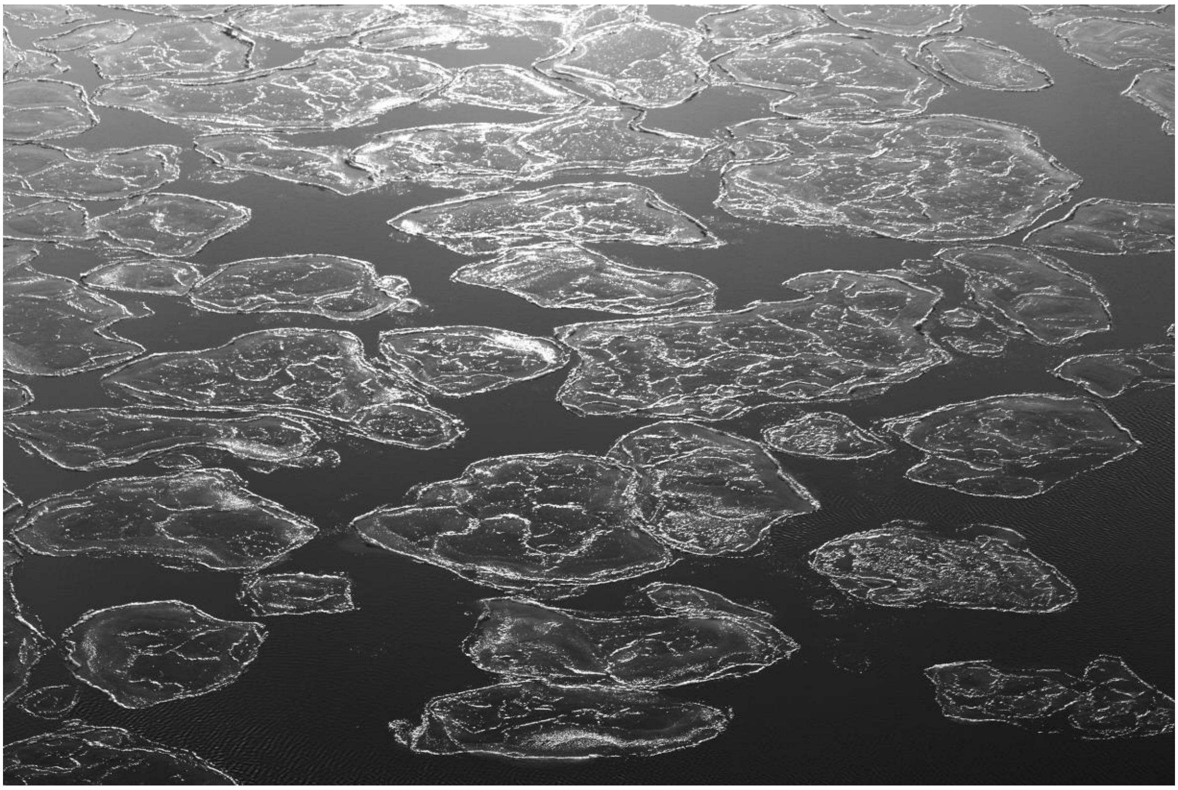
Chapter 4 provides a comprehensive assessment into the contemporary offshore migratory and foraging behaviour using 26 satellite tags deployed on SRWs in 2021, 2022 and 2023.

Specific research questions:

- Which areas are important contemporary foraging grounds for the South African SRW population?

- Are there any changes in foraging behaviour when compared to historical telemetry and whaling data that support a northward shift as indicated by stable isotope studies?

2. Population changes in a Southern Ocean krill predator point towards regional Antarctic sea ice declines



***This data chapter is published:**

Germishuizen, M., Vermeulen, E., & Vichi, M. (2024). Population changes in a Southern Ocean krill predator point towards regional Antarctic sea ice declines. Scientific Reports.

***This chapter is accompanied by Appendix A.**

2.3 Abstract

While foraging, marine predators integrate information about the environment often across wide-ranging oceanic foraging grounds and reflect these in population parameters. One such species, the SRW has shown alterations to foraging behaviour, declines in body condition, and reduced reproductive rates after 2009 in the South African population. As capital breeders, these changes suggest decreased availability of their main prey at high-latitudes, Antarctic krill (*Euphausia superba*). This study analysed environmental factors affecting prey availability for this population over the past 40 years, finding a notable southward contraction in sea ice, a 15 - 30% decline in sea ice concentration, and a more than two-fold increase in primary production metrics after 2008. These environmental conditions are less supportive of Antarctic krill recruitment in known SRW foraging grounds. Additionally, marginal ice zone, sea ice concentration and two primary production metrics were determined to be either regionally significant or marginally significant predictors of calving interval length when analysed using a linear model. Findings highlight the vulnerability of recovering baleen whale populations to climate change and show how capital breeders serve as sentinels of ecosystem changes in regions that are difficult or costly to study.

2.4 Introduction

Climate change has strong effects on marine ecosystems and its impacts have ramifications throughout the food web (Hastings et al., 2020; Hodapp et al., 2023). In the SO, responses to climate change vary regionally and are often masked due to high levels of natural variability(Shokr & Ye, 2023; Trathan et al., 2007; Zhang et al., 2019). The use of sentinel species in improving our understanding of environmental change is quickly gaining recognition, particularly in data-sparse and highly variable regions such as the SO (Hazen et al., 2019; Hindell et al., 2020). Baleen whales are especially useful in this regard due to their life histories as migratory capital breeders, which entails a period of intensive feeding that must fulfill the immense energetic requirements associated with reproduction (Christiansen et al., 2022, 2023; Williamson et al., 2021).

One such baleen whale, the southern right whale (*Eubalaena australis*; hereafter SRW), has been monitored extensively since 1979 in the South African calving ground to assess its continued recovery from extensive whaling (Best, 1981, 1990b; Best et al., 2020). Although the population is still growing steadily, results of this long time-series reveal a decline in reproductive rates after 2009, with an increased probability of a female needing two consecutive resting years between calving (Brandão et al., 2023) . Over the same period a decline in maternal body condition (Vermeulen, et al., 2023), and a northward shift in foraging distribution were also observed (Derville et al., 2023; van den Berg et al., 2021). Due to the temporal scale, these databases provide an opportunity to explore potential environmental drivers behind the observed changes.

Based on historical whaling and telemetry data, South African SRWs are known to make use of high-latitude foraging grounds (Mate et al., 2011; Tormosov et al., 1998) , with Antarctic krill (*Euphausia superba*) playing a significant role in meeting the energy requirements essential for reproduction (Leaper et al., 2006; Seyboth et al., 2016) . This dependence on krill stems from analyses of the stomach contents of 249 SRWs caught during the illegal soviet whaling activities, with 99% of the stomachs of whales caught south of 50°S containing Euphausiids (although it is not specified whether all were Antarctic krill) (Tormosov et al., 1998). Additionally, there are anecdotal reports of SRW feeding on Antarctic krill(Calderan et al., 2023; Hamner et al., 1988) .

The observed reduction in reproductive rates and maternal body condition in South African SRW are therefore believed to be strongly linked to reduced availability of Antarctic krill (Agrelo et al., 2021; Leaper et al., 2006; Seyboth et al., 2016; Vermeulen, Thavar, et al., 2023). In turn, Antarctic krill have an intimate relationship with sea ice, using it primarily as a foraging habitat that offers protection from predation, particularly during early developmental stages (Meyer et al., 2017; Veytia et al., 2021). This association with sea ice and the role of environmental parameters in modulating the primary production necessary to support high densities of Antarctic krill results in vulnerability to environmental change (Kawaguchi et al., 2024; A. Ryabov et al., 2023). In fact, it has been proposed that large-scale recruitment failure of Antarctic krill due to unfavourable environmental conditions in a given year can lead to a 3-to 4-fold variation in Antarctic krill biomass and take several years of good conditions to regain initial densities (Priddle et al., 1988).

A wealth of krill data has been collected over the last century, particularly along the Antarctic Peninsula and south-west Atlantic (Atkinson et al., 2017). However, due to a shortage of repeat surveys, the patchy nature of Antarctic krill swarms and inconsistencies in sampling methods in the region of interest, assessing changes in prey distribution and biomass over the period of observed population level changes is not possible (Kawaguchi et al., 2024). Therefore, proxies for foraging habitat quality are necessary in evaluating changes in environmental conditions which are known to alter prey availability.

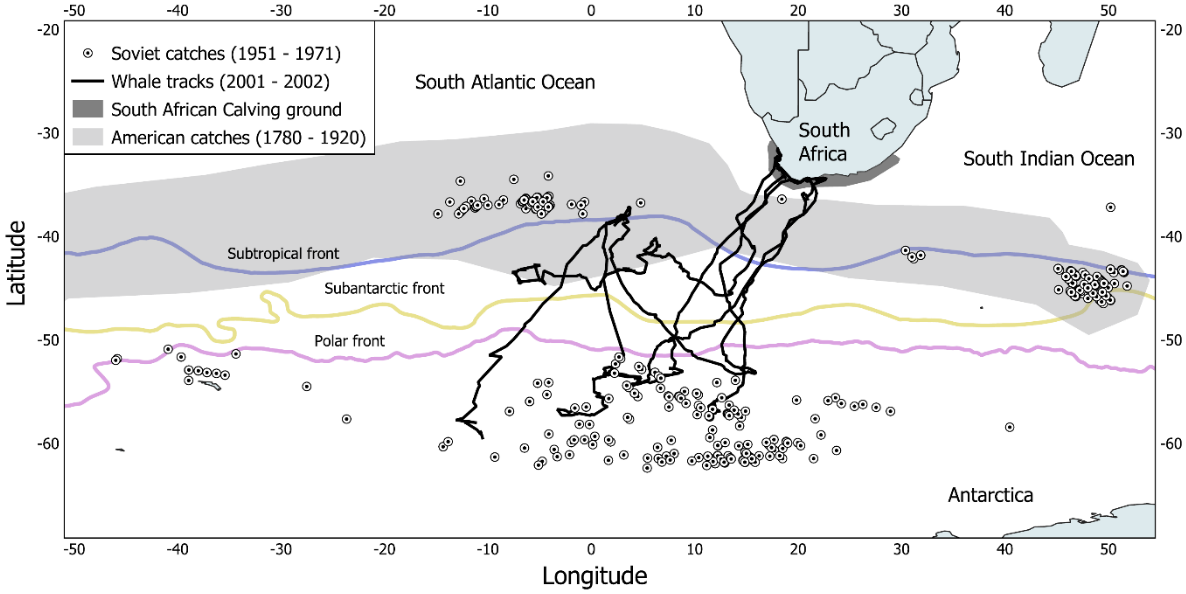


Figure 1. Southern right whale offshore foraging habitat. American and Soviet southern right whale (*Eubalaena australis*) catches and satellite tracks of five individual southern right whales tagged in 2001 (Mate et al., 2011; T. D. Smith et al., 2012; Tormosov et al., 1998), to summarize knowledge of offshore foraging habitat.

Here, we use an approach guided by our knowledge of South African SRW population demographics, as well as migratory and foraging behaviour to asses environmental changes that may have rendered high-latitude foraging grounds less favourable for Antarctic krill recruitment. We investigate temporal patterns in sea ice and primary production which characterize Antarctic krill availability across the known foraging domain of South African SRWs. In doing this, we evaluate the threat that future climate change imposes on krill-predators including still-recovering baleen whales, as well as the utility of baleen whale populations in monitoring the impacts of climate change on ecosystem functioning in the SO.

2.5 Methods

We performed all computations in the R statistical software (R Core Team, 2023) , with the exception of the spatial plots in Fig 6 which were created with QGIS version 3.26.1.

2.1.1 Calving interval

Annual aerial surveys of the South African SRW calving ground have been conducted since 1979 between Nature’s Valley and Muizenberg, providing an extensive time-series of population demographic data. During these surveys, photographs of individuals, with a focus on mothers with calves, are taken to allow for individual identification through distinct callosity patterns and variations in dorsal pigmentation (Best, 1990a) . This process allows for matches between years to be made, and from this, to calculate the calving interval as described in Best et al. (2001). Three-year calving intervals are considered normal for SRWs, including one year of gestation, one year of lactation and one year of recovery (Best et al., 2020; Knowlton et al., 1994). Four-year intervals are regarded as either coming from a failure to conceive (and thus an extra year of recovery) or an early abortion, whereas 5-year intervals are regarded as stemming from late-term abortions (Knowlton et al., 1994). Both 4- and 5-year intervals are thus regarded as reproductive failure. In this study, only details of 3-, 4- and 5-year intervals are provided, because longer calving intervals are difficult to interpret as they may include missed observations.

2.1.2 Study area: Feeding grounds and Antarctic krill data

The core feeding regions for South African SRWs were inferred from American (1780 – 1920) and Soviet whaling (1951 – 1971) data as well as from a telemetry study conducted in 2001 (Mate et al., 2011; T. D. Smith et al., 2012; Tormosov et al., 1998). Due to the potential spatial bias of whaling data, the study area was not limited to those areas with catches alone. Instead, a grid (divided by 5° latitude x 25° longitude cells) was used to connect areas of whaling catches and regions frequented by individuals tagged by Mate et al. (2011), creating a total of 16 regions (Figure 2).

Antarctic krill density and distribution data were obtained from KRILLBASE (Atkinson et al., 2017). Densities from individual net hauls collected during surveys between 1926 - 2016 were averaged over a 2° x 2° grid.

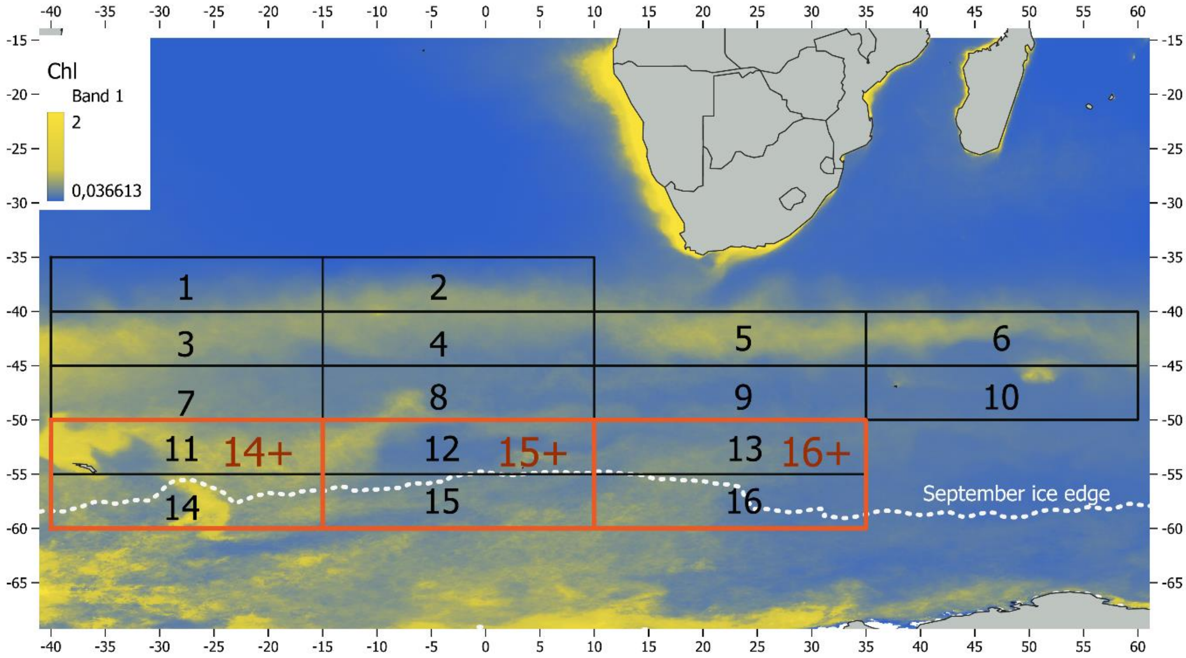


Figure 2. Selected regions (Regions 1 - 16) representing South African southern right whale (*Eubalaena australis*) foraging grounds. Orange boxes combine regions where sea ice was analysed and referred to as 14+ (combination of Regions 11 and 14), 15+ (combination of Regions 12 and 15), and 16+ (combination of Regions 13 and 16) in the text. Colours represent the mean summer (January, February, and March) chlorophyll concentrations (2000 - 2020) from https://oceancolor.gsfc.nasa.gov using Terra-MODIS data, and the dashed line represents the mean position of the September 60% sea ice concentration contour (1988 - 2020) from Climate Data Records (CDR) from NOAA/NSIDC.

2.1.3 Measures of foraging habitat quality

Four measures of potential foraging habitat quality were analysed over the period. Satellite-derived chlorophyll was used to develop two indicators of general foraging conditions for SRW's, and two variables of sea ice were used as measures of Antarctic krill habitat suitability.

Chlorophyll

Daily 4 km resolution Terra-MODIS chlorophyll (mg/m^3) ocean colour data were obtained from https://oceancolor.gsfc.nasa.gov as a proxy for potential food availability through primary production. From these data, a Monthly Chlorophyll Index was calculated for each of the 16 regions by computing the pixel-wise monthly cumulative sum from daily chlorophyll data and calculating the spatial average for each region in every month (2000 - 2020). Only months with more than 90% of measurement days were included. The monthly standard deviation of mean monthly chlorophyll was calculated and averaged for each region as a measure of food variability over the same period (2000 - 2020). The anomalies were calculated by subtracting the monthly means from the mean climatology of the seasonal cycle over the whole period (2000 – 2020). Three-year moving means were calculated for the Monthly Chlorophyll Index and chlorophyll standard deviation using the Zoo package in R (Zeileis et al., 2012).

Sea Ice

All sea ice data was derived from 25 km resolution sea ice concentration data from the sea ice Climate Data Records (CDR) from NOAA/NSIDC to make sea ice metrics comparable (Meier et al., 2017; Peng et al., 2013). Regions influenced by sea ice

(Regions 11 - 16) were pooled into longitudinal bands and were named based on the three most southerly regions (Region 14+ combines Regions 11 and 14; Region 15+ combines Region 12 and 15; Region 16+ combines Region 13 and 16; see Figure 2). The mean monthly sea ice concentration (SIC) was calculated for each region. The MIZ variability indicator proposed by Vichi (2022) was used (Vichi, 2022), which is defined as the standard deviation of daily SIC anomalies from the monthly mean. The mean monthly MIZ extent (for the period 1988 - 2020) was calculated by filtering out pixels with low chances of encountering MIZ conditions (Vichi, 2022), and calculating the area by summing the number of pixels and multiplying by the pixel area. Monthly MIZ extent and SIC anomalies were calculated by subtracting the climatological monthly cycle computed over the 1988 - 2020 period. 5-year moving means were calculated for SIC and MIZ extents using the Zoo package in R (Zeileis et al., 2012) . Additionally, spatial anomaly plots of the MIZ variability indicator and SIC for October and November are also presented to highlight changes over selected periods before and after 2009, being the onset of the observed changes in SRW reproductive rates. These diagnostics were created by computing 5-year means and subtracting them from the 1988 - 2020 mean.

2.1.4 Linear models

Linear models were developed to quantitatively assess the temporal relationship between MIZ, SIC, Monthly Chlorophyll Index, chlorophyll standard deviation and calving interval. To test this, a linear model was fitted to the annual rolling mean of each predictor, with the calving interval as the response variable. Only the years 2000 – 2020 were assessed since this is the time range with data from all four variables. The predictor variables were MIZ extent, SIC, Chlorophyll Index, and chlorophyll standard deviation at 1- and 2-year lags. This is under the hypothesis that, at the individual level, and assuming a 3-year calving interval, foraging conditions within the 2 years leading up to a mother giving birth are the most influential determinant of reproductive success (Christiansen et al., 2023). All predictor variables were normally distributed. However, the calving interval was lognormally distributed, so the natural logarithm of the calving interval was used in the model. Collinearity between continuous predictors was assessed using a cross-correlation matrix._A high threshold of collinearity ($r > 0.9$) was chosen since the focus of this exercise was to assess the role of all variables investigated and collinearity between highly related variables is inevitable. Predictors were considered significant at the $p < 0.05$ level, and marginally significant between $0.05 < p < 0.10$. Three linear models were developed for each of the three sea ice regions (Regions 14+, 15+, and 16+).

2.6 Results

2.1.5 Calving interval

The period between 1983 – 2009 was characterized by a high proportion of 3-year calving intervals, with a mean proportion ± standard deviation of 0.86 ± 0.05 (Figure 3). Between 2010 - 2015, the proportion of 3-year calving intervals declined rapidly, and 4- and 5-year calving intervals became more prevalent. The mean proportion ± standard deviation of 3-year calving intervals between 2010 - 2020 was 0.46 ± 0.15. Following this period, 2016 - 2020 saw a cessation to this rapid decline in 3-year calving intervals, with variable proportions in 3-, 4- and 5-year intervals (Figure 3).

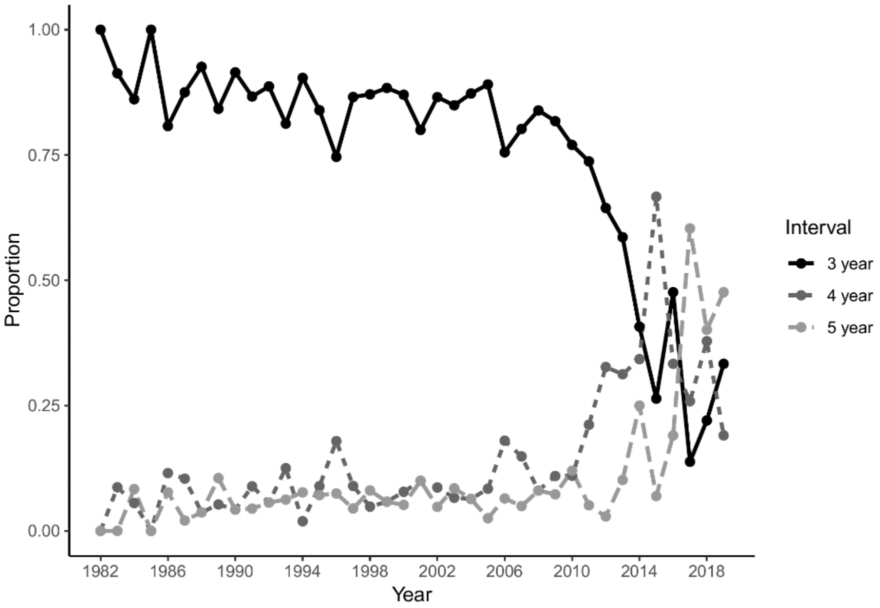


Figure 3. Annual proportion of 3-, 4- and 5-year calving intervals for the South African population of southern right whales (*Eubalaena australis*).

2.1.6 Regional changes in Monthly Chlorophyll Index

Monthly Chlorophyll Index displayed considerable regional and temporal variability. Generally, regions north of 45°S revealed no noteworthy changes over the period (Figure 4 a,b). An exception to this was Region 6 which experienced an increase in chlorophyll production biomass after 2015 (Supplementary Figure S1 d). More southerly regions, particularly south of 50°S exhibited substantial increases in Monthly Chlorophyll Index after 2009 in December – March (Figure 4 c,d, Supplementary Figure S2 d, S3). This signal was strongest in

Regions 11 and 12 (Supplementary Figure S2 and Figure 3 d respectively).

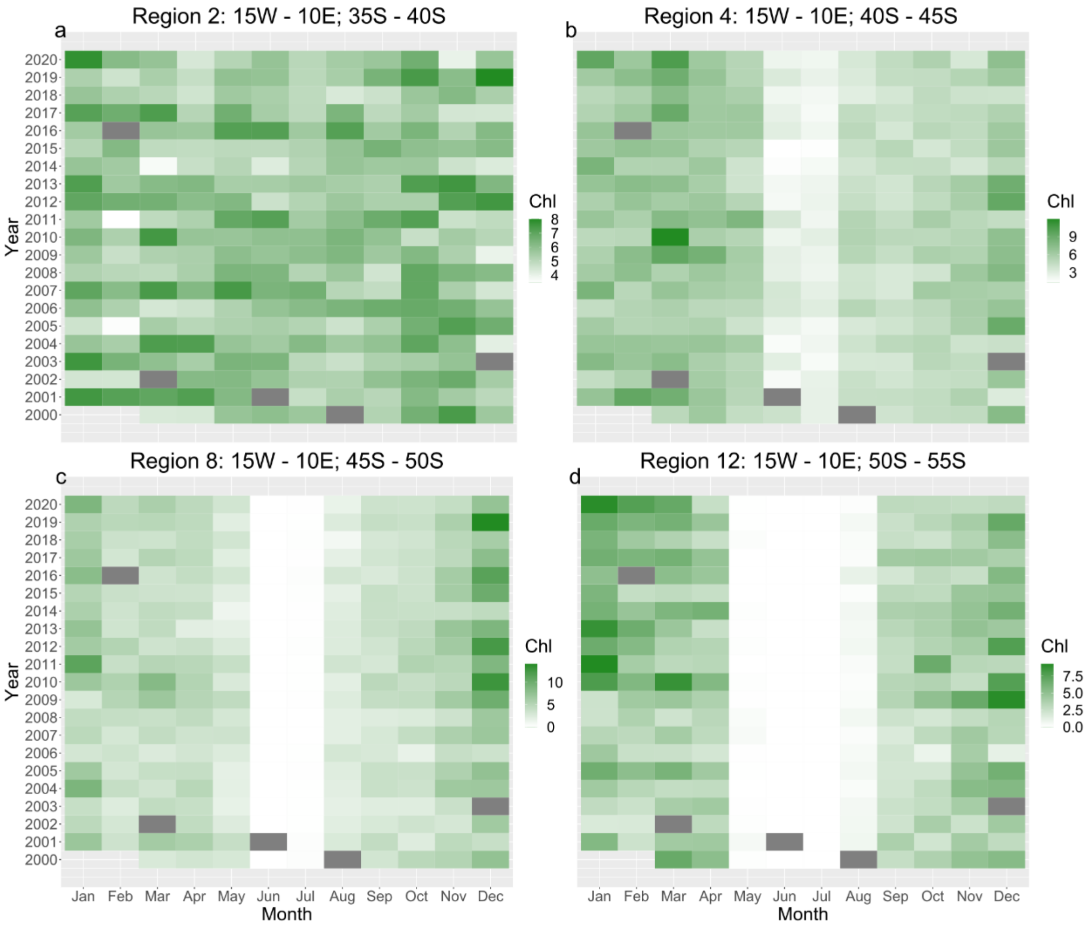


Figure 4. Heat maps of Monthly Chlorophyll Index for selected regions (2000 – 2020). Monthly mean Chlorophyll Index heat maps for (a) Region 2, (b) Region 4, (c) Region 8 and (d) Region 12 over the time-series (2000 – 2020). Grey blocks indicate months which had insufficient observations to compute the Monthly Chlorophyll Index (see Methods). Refer to Supplementary for regions not depicted here.

2.1.7 Environmental changes to the seasonal sea ice zone

The three sea ice regions displayed high - levels of month-to-month variability. Two distinct periods of reduced sea ice were observed over the time-series. The first period occurred between 1996 – 2002 and was centred over Region 16+, with declines in both SIC and MIZ extent in this region, but only in SIC in Regions 14+ and 15+ (Figure 5 a,b and Supplementary Figure S4 and S5). The second period occurred between 2008 – 2014 and was most intense in Regions 14+ and 15+ with substantial declines in both MIZ extent and SIC (Figure 5 a,b and Supplementary Figure S4 and S5). Patterns in primary production metrics mirrored these observed changes in sea ice, with elevated Monthly Chlorophyll Index and chlorophyll standard deviation during periods of reduced SIC and MIZ extent, and increased MIZ variability (Figure 5 c,d and Supplementary Figure S4 and S5). A notable and abrupt increase in both Monthly Chlorophyll Index and chlorophyll standard deviation was observed after 2009 in Regions 14+ and 15+ (Figure 5 c,d and Supplementary Figure S4). Region 16+ also experienced an increase in primary production metrics after 2009, however, highest positive anomalies occurred between 2011 – 2016.

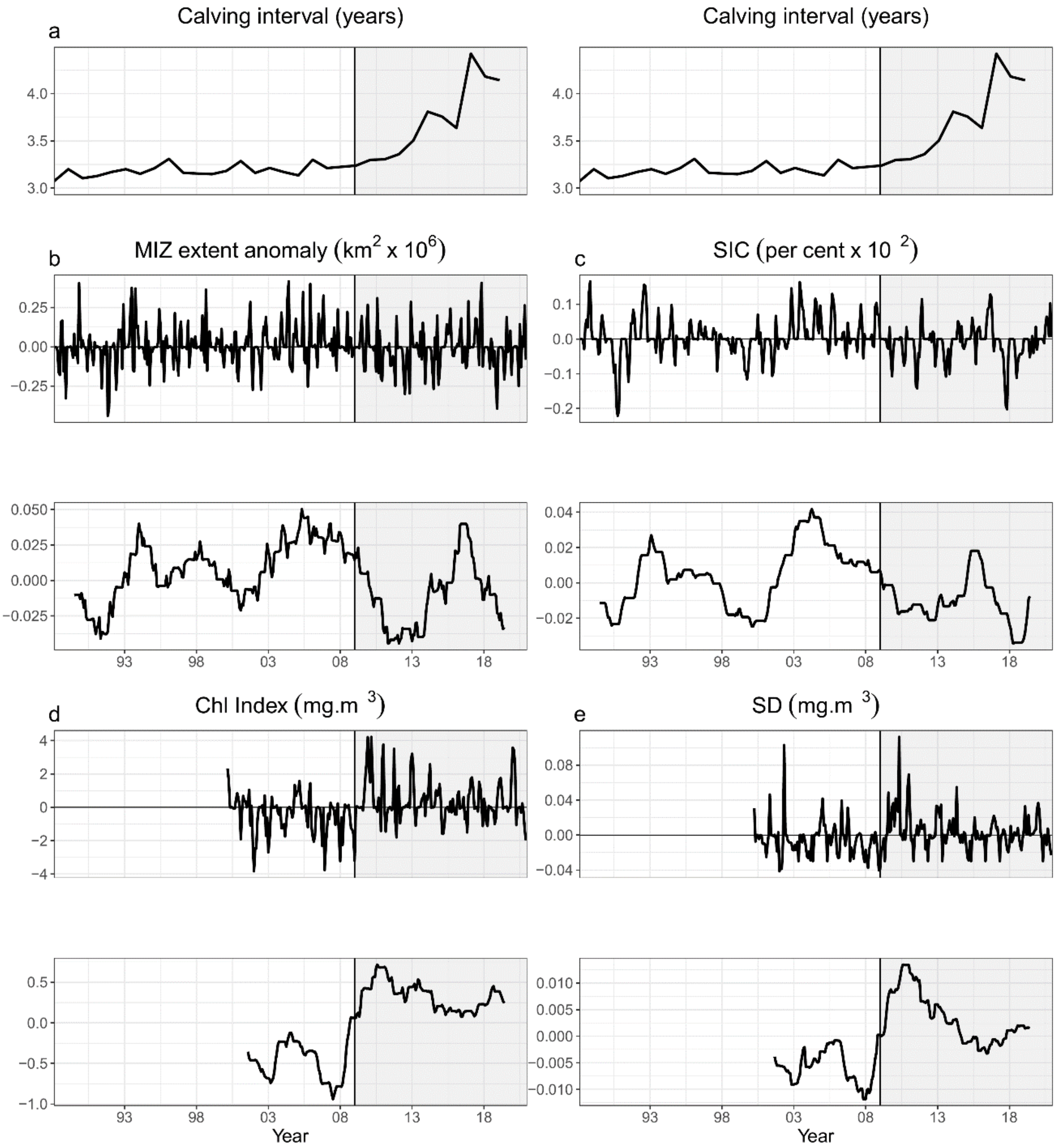


Figure 5. Indicators for Region 15+. Monthly anomalies (top panel) and rolling mean of the anomaly (bottom panel) for (b) Mean monthly marginal ice zone (MIZ) extent anomaly compared to the 1988 – 2020 mean, (c) mean monthly sea ice concentration anomaly (SIC) compared to the 1988 – 2020 mean, (d) Monthly Chlorophyll Index anomaly compared to the 2000 – 2020 mean and (e) Monthly chlorophyll standard deviation anomaly compared to the 2000 – 2020. The top panel (a) shows the mean calving interval. The grey-shaded region highlights the period of reduced southern right whale reproductive success after 2009. Refer to Supplementary for regions not depicted here.

Spatial data shown in Figure 6 provides some context to the regional and temporal variability in sea ice signals shown in Figure 5. Sea ice anomalies of 5-year periods help to elucidate large-scale changes to the sea ice environment, focussing on the two distinct periods of negative SIC anomalies observed over the time-series (Figure 6). The period between 2008 – 2012 reveals an expansive area of negative SIC anomalies, and southward contraction in the MIZ along the Antarctic Peninsula and South Atlantic, encompassing the region where most of the global Antarctic krill stock resides (Figure 6). This configuration of anomalies was unique to the timeframe examined (see Supplementary Figure S6 and S7). On the contrary, the period of reduced sea ice between 1998 – 2002 revealed no clear pattern in the spatial distribution of anomalies, particularly over important regions for Antarctic krill (Figure 6).

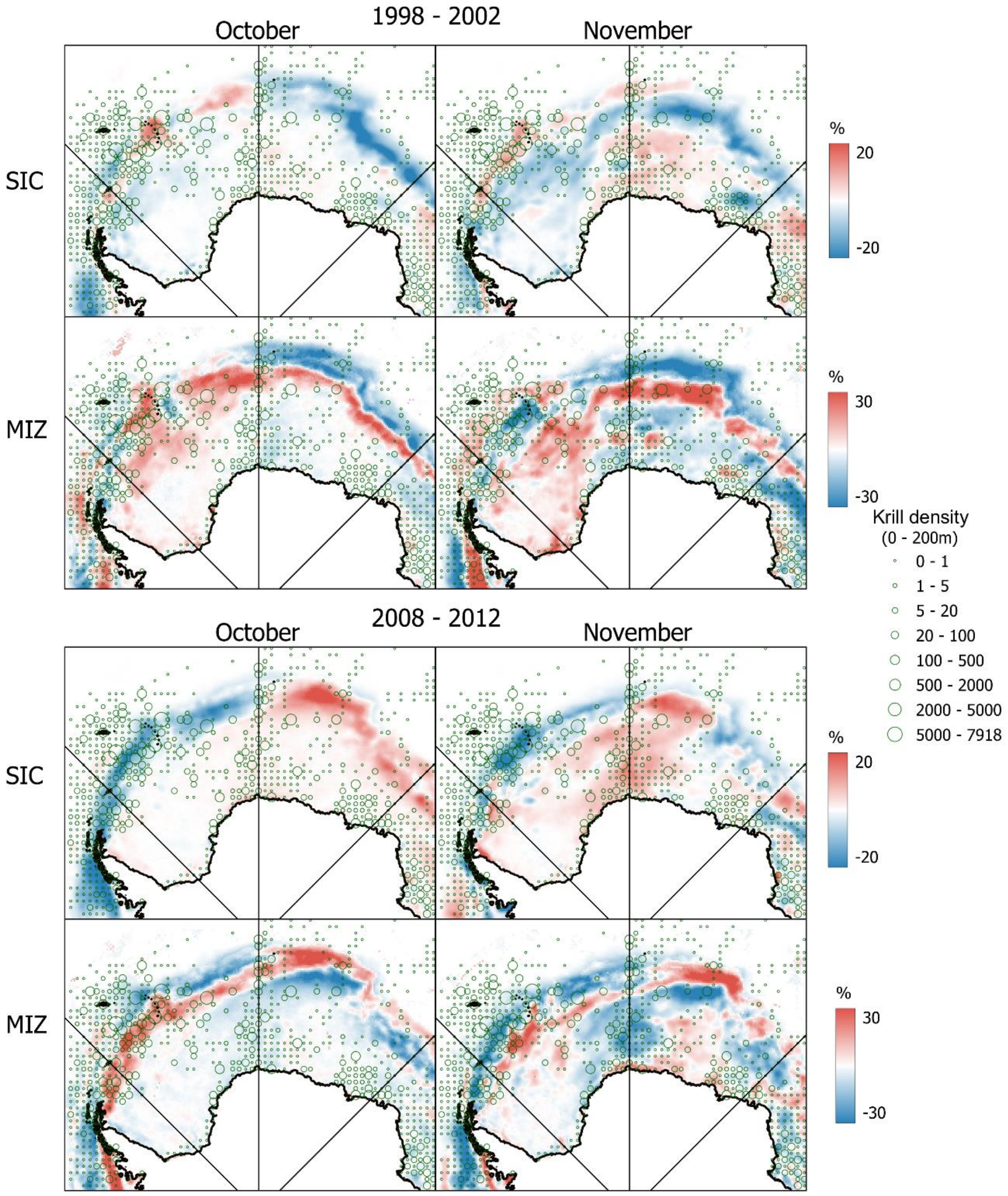


Figure 6. Sea ice concentration (SIC) and marginal ice zone (MIZ) indicator anomalies. The two periods of reduced sea ice (1998 – 2002 and 2008 – 2012) are presented here to compare the spatial configuration in anomalies. The anomalies represent 5-year means compared to the 1988 – 2020 mean. Antarctic krill densities from surveys between 1926 – 2016 are also presented (Atkinson et al., 2017) . Refer to Supplementary figures for regions not depicted here.

2.1.8 Effect of environmental variables on calving interval

All variables analysed were found to influence calving intervals but in different regions and with variable significance (see Table 1). In Region 14+, Monthly Chlorophyll Index and chlorophyll standard deviation at 1-year lags were the only variables significantly impacting calving intervals (p = 0.035 and 0.029 respectively). In Region 15+, MIZ extent at a 2-year lag (p = 0.003) and SIC at a 2-year lag (p = 0.023 and 0.04 respectively) were found to impact calving intervals significantly. Additionally, MIZ extent (p = 0.056), Chlorophyll index (p = 0.058) and chlorophyll standard deviation (p = 0.09) were found to be marginally significant predictors. No environmental predictors in Region 16+ were found to significantly influence calving intervals.

Table 1. Linear model results of the effects of 1- and 2-year lagged variables in Region 14+, 15+ and 16+ on the calving interval. MIZ = Marginal Ice Zone, SIC = Sea Ice Concentration, Chl = Monthly Chlorophyll Index, Chl SD = Chlorophyll standard deviation.

Predictors	**Region 14+**			
	Estimate	*SE*	*t*	*P*
MIZ (1 year lag)	0.125	0.100	1.196	0.266
MIZ (2-year lag)	0.000	0.090	0.001	0.999
SIC (1 year lag)	-0.683	0.590	-1.157	0.281
SIC (2-year lag)	-0.609	0.516	-1.181	0.272
Chl (1 year lag)	0.007	0.003	2.539	**0.035***
Chl (2-year lag)	0.002	0.003	0.456	0.661
Chl SD (1 year lag)	-0.383	0.145	-2.650	**0.029***
Chl SD (2-year lag)	0.203	0.283	0.718	0.493
Model	*SE*	*DF*	*Adj* − R^2	*P*
	0.005	8.000	0.635	**0.024***
Predictors	**Region 15+**			
	Estimate	*SE*	*t*	*P*
MIZ (1-year lag)	0.110	0.052	2.23	0.056.
MIZ (2-year lag)	-0.190	0.044	-4.29	**0.003****
SIC (1-year lag)	-0.550	0.200	-2.80	**0.023 ***
SIC (2-year lag)	0.570	0.230	2.45	**0.040***
Chl (1-year lag)	0.010	0.004	2.21	0.058.
Chl (2-year lag)	0.001	0.005	0.21	0.840
Chl SD (1-year lag)	-0.550	0.290	-1.92	0.090.
Chl SD (2-year lag)	0.200	0.280	0.72	0.490
Model	*SE*	*DF*	*Adj* − R^2	*P*
	0.004	8.000	0.779	**0.004****
Predictors	**Region 16+**			
	Estimate	*SE*	*t*	*P*
MIZ (1-year lag)	0.090	0.198	0.456	0.661
MIZ (2-year lag)	0.021	0.102	0.203	0.844
SIC (1-year lag)	-0.541	0.620	-0.871	0.409
SIC (2-year lag)	-0.390	1.300	-0.300	0.770
Chl (1 year lag)	0.011	0.012	0.969	0.361
Chl (2-year lag)	-0.001	0.009	-0.060	0.950
Chl SD (1 year lag)	-0.690	0.790	-0.870	0.410
Chl SD (2-year lag)	0.240	0.510	0.480	0.650
Model	*SE*	*DF*	*Adj* − R^2	*P*
	0.007	8.000	0.302	0.199

2.7 Discussion

This study reveals large-scale enivoronmental changes in the seasonal sea ice zone in important foraging grounds for South African SRWs, which likely drove a decline in the population's reproductive success (Brandão et al., 2023; van den Berg et al., 2021; Vermeulen, Thavar, et al., 2023). A southward contraction in sea ice marked by a decrease in MIZ extent and a decline in SIC of up to 15 – 30% over 5 years affected the region where most of the Antarctic krill stock is known to reside between 2008 – 2012. These reductions occurred in conjunction with a more than two-fold increase in primary producers' biomass in regions that experienced the greatest declines in sea ice. Furthermore, all variables assessed were either found to be significant or marginally significant predictors of calving interval length when fitted with a linear model. Due to the intimate relationship between sea ice and Antarctic krill, these changes are likely to be an indication of reduced prey availability for SRWs at high-latitudes. On the other hand, mid-latitude foraging grounds (regions north of 50°S) experienced regional increases in chlorophyll metrics but no indication of changes that would have ramifications for prey abundance at large spatial scales.

The influence of food availability on calving success is well documented in baleen whales due to the elevated energetic costs associated with reproduction (Greene et al., 2003; Miller et al., 2011; Williams et al., 2013). Specifically in SRW, sea ice has been shown to influence population demographics due to its crucial role in the recruitment success of Antarctic krill (Agrelo et al., 2021; Flores, van Franeker, et al., 2012; Kawaguchi et al., 2024; Leaper et al., 2006; Meyer et al., 2017; Seyboth et al., 2016; Veytia et al., 2021). Considerable uncertainty exists about the true nature of the relationship between sea ice and Antarctic krill abundance and biomass. Despite these uncertainties, the role of sea ice in providing sheltered foraging habitat is well established (Kawaguchi et al., 2024). Antarctic krill have relatively long and complex life histories and may be dependent on repeated years of favourable ice conditions (V. J. Loeb & Santora, 2015; Quetin B & Ross M, 2009). Additionally, the presence of sea ice is a strong mediator of ecosystem state and plays a pivotal role in shaping community assemblages. Low ice years, for example, have been found to result in the dominance of gelatinous zooplankton such as salps (*Salpa thompsoni)* (Atkinson et al., 2004; V. J. Loeb & Santora, 2015). Sea ice has been impacted by climate change through ocean and atmospheric warming (Cai et al., 2023), and increased poleward wind stress associated with a more positive Southern Annular Mode which prevents sea ice expansion (Sallée et al., 2021; Swart et al., 2014). Therefore, there is considerable concern within the scientific community on the fate of Antarctic krill in the face of rapid climate change (Kawaguchi et al., 2024).

The global Antarctic krill population is predominantly concentrated along the Antarctic Peninsula and the South Atlantic Ocean, with the former considered a vital source region for the latter (Atkinson et al., 2004; Green et al., 2021; Hofmann & Murphy, 2004; Veytia et al., 2021). Based on sea ice conditions described here, the years between 1988 and 2003 appeared to be highly favourable for Antarctic krill recruitment, with extensive sea ice cover over the Antarctic Peninsula and South Atlantic region of the SO. Changes began occurring in the 2000s along the Antarctic Peninsula, with declines in SIC and reduced stability of the MIZ. The analysis performed by Ichii et al. (2023) also revealed a regime shift after the 2000s, characterised by significantly reduced probabilities of Antarctic krill transport from the Antarctic Peninsula to the South Atlantic region due to reduced sea ice cover (Ichii et al., 2023). Therefore, changes to transport processes because of declines in sea ice likely began to negatively impact prey abundance in regions reliant on source regions such as South Georgia and Bouvet Island after 2000 (Fevolden, 1980; Green et al., 2021).

Linear models only indicated a significant effect of sea ice, particularly MIZ extent, in region 15+. Region 14+ displayed high levels of month-to-month variability in MIZ extent and SIC, which likely prevented a significant effect of sea ice on calving intervals from emerging. Region 16+ also didn't reveal any sea ice effects, however this is likely due to the atmospheric circulation patterns that drive regional changes in sea ice extent. The sea ice contraction that occurred in the late 2000s and early 2010s was driven by the presence of the Amundsen Sea Low, which acts to reduce ice along the Antarctic Peninsula, and expand ice over the South Indian Ocean (Turner et al., 2016).

In conjunction with changes in the sea ice environment post-2009, primary production substantially increased in almost all high-latitude feeding grounds. Additionally, primary production metrics were significant, and marginally significant predictors of calving interval in Regions 14+ and 15+ respectively. Towards the end of the time-series (2016 – 2020), primary production and sea ice metrics return to conditions similar to those seen prior to the increase in calving cycles. At the same time, some recovery is evident in the calving interval, however 4- and 5-year intervals were still more prevalent than 3-year intervals.

The increasing trends in chlorophyll concentration are in line with other analyses of chlorophyll trends in the seasonal sea ice zone and are likely a reflection of changes in sea ice dynamics which drive changes in primary production and phytoplankton community structure (Behera et al., 2020; Del Castillo et al., 2019; Ryan-Keogh et al., 2023; Thomalla et al., 2023) . Reduced sea ice extends the growth season for pelagic phytoplankton due to increased periods of open-water conditions from an earlier retreat and later onset of sea ice growth, which allows for more solar radiation to penetrate the water column (Thomalla et al., 2023). At the same time, ice-dependent zooplankton experience a shorter duration of protection under the sea ice habitat, potentially affecting their life histories and rendering them more susceptible to predation(David et al., 2021; Flores et al., 2023). Furthermore, salps have been found to outcompete Antarctic krill under low ice regimes due to faster reproductive and clearance rates, with studies along the Antarctic Peninsula reporting increases in the ratio of salps to krill in recent years (V. Loeb et al., 1997; Pietzsch et al., 2023; Plum et al., 2020). Reduced grazing rates on phytoplankton during periods of low Antarctic krill stocks may have also contributed to the elevated primary production observed in the open ocean (A. B. Ryabov et al., 2017). For example, Ryabov et al., (2017) reported the occurrence of stronger seasonal blooms and increased phytoplankton biomass during periods of reduced Antarctic krill biomass [28]. Additional pressure on Antarctic krill stocks is likely being added by recovering baleen whale populations, particularly humpback (*Megaptera novaeangliae)* and fin (*Balaenoptera physalus*) whales, as well as the growing Antarctic krill fishery (Herr et al., 2022; Ryan et al., 2023; Seyboth et al., 2023; Trathan, 2023). Indeed, intraspecific competition for Antarctic krill is likely increasing as most species recover from commercial whaling(Branch, 2011; Branch et al., 2004). This will inevitably result in the emergence of density-dependent changes in foraging behaviour with implications for reproductive success. Unlike what is observed here, such changes would likely be gradual as species steadily recover, and would act as an additional pressure determining the carrying capacity of the system under different regimes of climate variability. How other krill-dependent species are impacted by the observed environmental changes is difficult to ascertain as time-series data on demographic parameters of marine predators, particularly SO baleen whales, are scarce. Additional data indicative of a South African SRWs response to changing climate conditions in their high latitude foraging grounds relates to changes in their foraging behaviour. This was inferred from shifts in stable isotope values over the same period as the observed declines in reproductive rates (van den Berg et al., 2021), with a suggested reduction in the use of historically important high-latitude foraging grounds (Derville et al., 2023). However, it is evident that these adaptive strategies through altering migratory behaviour are associated with energetic costs as revealed by Vermeulen et al. (2023). These energetic costs may arise due to reduced foraging efficiency in the high-latitudes, individuals having to undertake longer migrations, and/or ecological traps arising from site fidelity to foraging grounds (Valenzuela et al., 2009b; van den Berg et al., 2021; Vermeulen, et al., 2023). Ecological traps arise due to the continued usage of learned migratory routes despite environmental changes which have rendered regions unfavourable for foraging. Therefore, females may be taking longer to achieve the energy requirements necessary to produce a calf, thereby decreasing in body condition (Vermeulen , et al., 2023), and lengthening their calving interval (Brandão et al., 2023).

The presented results highlight the sensitivity of SRWs to environmental variability in their foraging grounds and the risk that climate change poses to continued population recovery post-whaling. This sensitivity also reveals the potential of the species as climate change sentinels in a system of ever-increasing rates of change and the potential baleen whales hold in improving our knowledge of future impacts of climate change in the SO and other krill-dependent predators.

3. The oceanographic characteristics of southern right whale (*Eubalaena australis)* mid-latitude foraging grounds.

*This chapter is accompanied by Appendix B.

3.1 Abstract

Ocean conditions exert a strong control on the distribution and abundance of food for migratory species. We can therefore expect that migratory behaviours vary with changes in environmental conditions. Satellite telemetry has significantly advanced our ability to investigate animal movement patterns in relation to environmental variability, and to characterize foraging grounds of ocean predators. In this study animal-borne CTD instruments and archival satellite tags that record diving behaviour were deployed on southern right whales (*Eubalaena australis*) in South Africa. Changes in behavioural states (transiting and foraging) in relation to oceanographic properties and features as the whales moved offshore to mid-latitude foraging grounds are explored. Results showed that foraging behaviours were associated with distinct water properties associated with theAntarctic Circumpolar Current (ACC). More specifically, foraging behaviour occurred in cool fresher waters, whereas transiting behaviour was documented in a wide range of environmental conditions. Additionally, foraging only occurred in regions of low chlorophyll concentration, and along ocean fronts. There was little effect of behavioural modes on diving behaviour, however, an increase in the proportion of U-shaped dives, associated with foraging, was found over time. By analysing the oceanographic characteristics of whale foraging grounds, insight is gained into the connection between the oceanography and biology. Through this knowledge, a better understanding of how marine mammals respond to climate change and variability can be developed.

3.2 Introduction

Different biological and physical mechanisms probably influence the various stages of animal migrations to and from their foraging grounds. These different mechanisms likely operate at varying spatial scales. For example, a conceptual model of a whale migration may be; first locate the most favourable foraging regions (1000s of km), then locate prey hotspots (100s of km), then locate the densest pray patches (10s of km) and finally feed (<1km) (Hazen et al., 2009; Kenney et al., 2020; Owen et al., 2019). The biological and environmental cues used to progress through these various stages likely change with spatial extent. The location of broadly favourable regions, essentially knowing when to start searching, is probably guided by the detection of oceanographic properties signalling potentially favourable foraging grounds (e.g., temperature, salinity, density) (Baumgartner & Mate, 2003; Owen et al., 2019; Torres, 2017). As spatial scales decrease, sensory perception (visual, olfactory and auditory) likely becomes progressively more important (Bouchard et al., 2019; Cronin et al., 2017; Torres, 2017). Alternatively, whales may communicate over long distances to help each other find prey patches, as suggested for Bowhead whales (*Balaena mysticetus)* synchronizing their dives to potentially advertise on prey abundance up to 100 km apart (Podolsky et al. 2024). However, exactly how whales can find dense patches of food across massive areas, and which oceanographic features affect whale foraging behaviour is still largely a mystery.

Investigating the oceanographic features and properties that whales rely on to forage is an important aspect to unravelling this mystery, with important implications for understanding the impacts of climate change and variability. Numerous baleen whale populations are affected by climate-driven changes in prey distribution (Askin et al., 2017; Meyer-Gutbrod et al., 2015), which ultimately result in nutritional stress with repercussions for population growth rates and continued recovery from historical whaling (Tulloch et al., 2019). One such species that has seen recent changes indicative of nutritional stress including declines in maternal body condition, shifts in foraging distribution and decreased reproductive success, is the South African population of SRW (Brandão et al., 2023; Derville et al., 2023; van den Berg et al., 2021; Vermeulen, et al., 2023).

SRWs overwinter at coastal calving and socialising grounds between June and November (Best, 2000). During spring, they migrate into the SO where they predominantly feed on copepods (north of 50°S) and krill (south of 50°S) (Tormosov et al., 1998). The SO is unique in that it is uninterrupted by land, which has resulted in the broad, fast-flowing ACC. Overall, it is a vast region with significant temporal and spatial variability in primary productivity. Population-level studies have investigated the oceanographic characteristics of regions of high offshore catches of SRWs. In doing so, both Carman et al., (2019) and Torres et al., (2013) broadly identified fronts, chlorophyll, water temperature and mixed layer depth as important predictors of the offshore presence of SRWs.

SRW migratory and foraging behaviour is becoming better understood through a combination of satellite telemetry, stable isotope and historical whaling data(Derville et al., 2023; Kennedy et al., 2023; Mackay et al., 2020; Mate et al., 2011; Smith et al., 2012; Tormosov et al., 1998; van den Berg et al., 2021; Vermeulen et al., 2023; A. Zerbini et al., 2015; Zerbini et al., 2018). For the South African population, it is becoming increasingly evident that they are reliant on three broad regions: the mid-latitude system of fronts associated with the ACC, the seasonal sea ice zone, and highly productive island regions such as Crozet Islands, and islands in the South Atlantic (González Carman et al., 2019; Mate et al., 2011; Tormosov et al., 1998; Vermeulen et al., 2024; Vermeulen et al., 2023).

Satellite telemetry allows for investigations into how environmental conditions vary along individual tracks in relation to changes in behavioural state at finer spatial scales (Lee et al., 2017; Mackay et al., 2020; Owen et al., 2019). For example, some telemetry studies have highlighted the importance of mesoscale features such as eddies and fronts as foraging areas for SRWs (Mackay et al., 2020; Zerbini et al., 2015). The deployment of animal-borne Conductivity, Temperature and Depth (CTD) devicesallows for the concurrent collection of location data and vertical profiles of ocean variables as whales move. This =technology offers valuable insights into environmental changes in both surface and interior ocean waters, which are closely tied to changes in whale behaviour .

This study uses telemetry data to investigate different oceanographic properties encountered during different behavioural states to identify potential oceanographic features related to foraging. Such information is deemed critical in light of recent demographic and behavioural changes observed in the species, suggesting changes in the distribution and abundance of food (Brandão et al., 2023; Crespo et al., 2019; Derville et al., 2023; van den Berg et al., 2021; Vermeulen, et al., 2023).

3.3 Methods

We performed all computations in the R statistical software (R Core Team, 2023) and maps were produced using QGIS version 3.26.1.

3.3.1 Satellite tag deployment and telemetry data processing

Boat-based satellite tagging operations were conducted in Walker Bay (34.4063° S, 19.2687° E) on the south-western coast of South Africa in October and November 2023. Over this period, four CTD Argos satellite-linked and two location and depth recording SPLASH10-373 Wildlife Computers tags were deployed on adult female SRWs (Fig. 1, associated by a calf at the time of tagging; Wildlife Computers Redmond, WA; https://www.wildlifecomputers.com.)

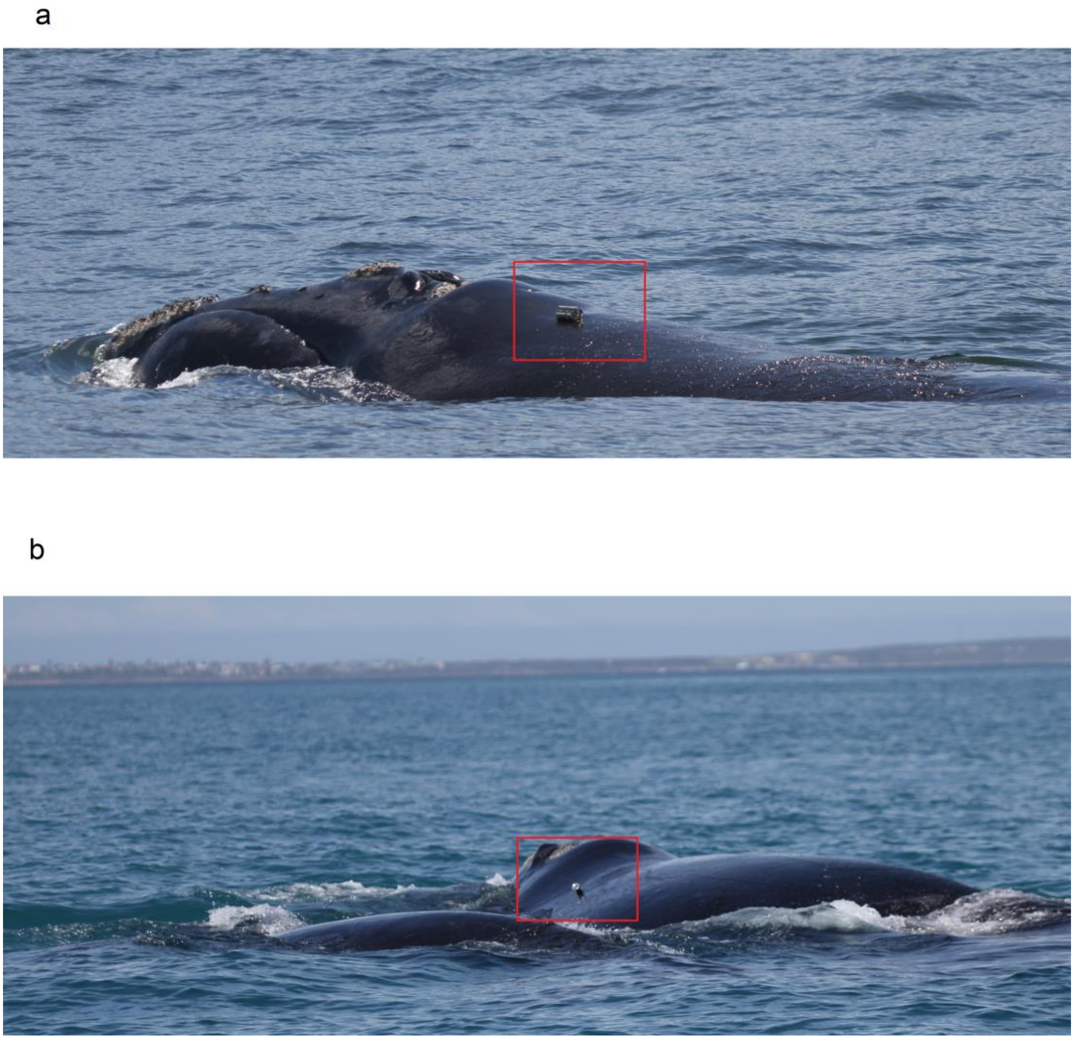


Figure 1. Photographs of a) Conductivity, Temperature and Depth (CTD) instrument and b) SPLASH10 - 372 dive depth and location recording tag deployed on southern right whales (SRW, *Eubalaena australis*) in Walker Bay, South Africa. MRI Whale Unit (2023).

All tags were deployed from a platform mounted to a 6 m rigid-inflatable boat. Specifications of the CTD tags, together with deployment methods are outlined in Teilmann et al., (2020). The CTD tags were attached to a platform secured to an 8-meter carbon fiber pole, which detaches from the tag after implantation (Citta et al., 2021; Teilmann et al., 2020). The SPLASH10-373 tags were deployed with a modified pneumatic rifle(Heide-

Jørgensen et al., 2001), at distances of 3–5 m from the whales by a qualified and experienced tagger. Photographs and video footage were captured during the tagging process with a Canon 7DI and a GoPro, respectively, for the purposes of photo-identification and evaluating tag placement. Following tag deployment and biopsy sampling, the target animal was monitored from a distance of > 500 meters for up to 30 minutes to assess any reactions to the tagging procedure and to capture post-deployment photos of the tag site. All tagging work was conducted under permit conditions of the South African government (RES 2023-18) and animal ethic clearance of the University of Pretoria (NAS040/2020). The instruments and methods for tag deployment and biopsy sampling adhered to the protocols approved by NOAA's Marine Mammal Laboratory Institutional Animal Care and Use Committee.

Argos-derived locations were filtered using the "argosfilter" R package (Freitas & Freitas M. C, 2022) and modelled with a Bayesian switching state-space model (SSSM) (Jonsen, 2016; Jonsen et al., 2005). SSSM models estimate locations by accounting for measurement errors in Argos data and the movement dynamics, utilizing the joint estimate approach described by Jonsen (2016). The model was fit to filter Argos data using the "bsam" package in R (Jonsen, 2016; Jonsen et al., 2005), and Markov Chain Monte Carlo (MCMC) simulations were run using JAGS software). A time step of 4 hours was used to calculate predicted locations. A total of 80,000 MCMC simulations were run, with the first 20,000 discarded and every 10th sample of the remaining 60,000 retained to reduce autocorrelation. From the SSSM models, two behavioural states were inferred from two parameters (θ and γ), which provide a range of 'b-mode' state values between 1 and 2. Values tending to 1 (<1.5) describe a state which is highly directional and consistent and more likely to be associated with 'transiting' behaviour. Values tending towards 2 (>1.5) describe highly variable and localized movements and are more likely to indicate "Area Restricted Search" (ARS) associated with foraging, searching, or lingering and social behaviour at foraging grounds. For the purpose of this study, any ARS behaviour outside of their coastal calving grounds was assumed to be foraging.

3.3.2 Conductivity, Temperature and Depth (CTD) data

The four CTD tags were programmed to store temperature and salinity data at set depth intervals (0, 10, 20, 30, 50, 75, 100, 125, 150, 200, 250, 300, 400, 500, down to 2000 m) of the deepest dive during the preceding 6 hours. To compare the physical environments between the two behavioural states (transiting and ARS), boxplots of temperature and salinity at different depths were presented. Two-sampled unpaired t-tests were conducted to compare the environments of the two behavioural states. P-values were adjusted for multiple comparisons using Bonferroni correction and differences deemed significant at $p<0.05$.

3.3.3 Diving behaviour

Two SPLASH10-373 tags recording depth data were deployed. From these data, three metrics were calculated to describe diving behaviour. Diving rate was calculated by dividing the total number of daily dives by the length of time depth data was recorded on a given day. Additionally, dive shape has been found to indicate different behavioural states (transiting and foraging); U-shaped dives are associated with foraging behaviours whereas V-shaped dives indicate transiting behaviour. For this study, V-shaped dives are defined as dives where the period spent at the deepest depth is <20% of the time between submerging and surfacing. If the time spent at the deepest depth was >20%, these are classified as U-shaped dives. The proportion of U-shaped dives was calculated by dividing the number of U-shaped dives on a day, by the total number of dives on a given day. Linear regressions were used to assess changes in these behavioural metrics as the whales migrated into the SO. The overall distribution of daily dives is presented as violin plots.

3.3.4 Satellite-derived environmental data

Sea surface salinity (SSS) data were obtained from the Multi Observation Global Ocean Sea Surface Salinity and Sea Surface Density product developed by the Consiglio Nazionale delle Ricerche (CNR) (Buongiorno Nardelli et al., 2016; Droghei et al., 2016, 2018; Sammartino et al., 2022). This product provides gap-free 0.125° resolution sea surface salinity data through a combination of satellite-derived estimates and *in-situ* measurements. Sea surface temperature (SST) data were obtained from the Global Ocean OSTIA SST and Sea Ice Analysis product which also provides gap-free 0.05° resolution SST data from a combination of satellite-derived and in-situ measurements (Donlon et al., 2012; Good et al., 2020; Stark et al., 2007). Both salinity and SST data were obtained using E.U. Copernicus Marine Service. Terra-MODIS chlorophyll data at 8-day intervals were obtained from https://oceancolor.gsfc.nasa.gov. All satellite-derived variables are presented as Hovmöller diagrams that capture the physical environment at the time and position of the whale (Persson, 2017). This allows one to visualize the seasonal evolution of the physical environment encountered by the whales as they migrate into the SO.

3.3.5 Comparison of satellite-derived and CTD measurements

Linear regressions were applied to the difference between satellite-derived SST and salinity at the location of the whale, and measurements from the animal-borne CTD instruments.

3.3.6 Front definition

The contemporary definition of SO fronts is becoming increasingly complex, as it is clear that these frontal features are an intricate system of jets and steep gradients of various properties of the ocean that are filamentous and transient in nature rather than large-scale permanent features (Chapman et al., 2020). Therefore, SO fronts can essentially be conceptualized as dynamic zones of high variability, with this variability augmenting productivity and becoming the focus for foraging in many species (Bost et al., 2009). Major SO fronts are often based on the choice of hydrographic thresholds (Orsi et al., 1995), which may not capture the environmental conditions experienced by the transiting whales in space and time. In this study, the front is defined as the standard deviation (SD) of the latitudinal surface water density gradient from the SSS and SST data, which is a proxy for the variability of these dynamic frontal regions. To exemplify this, the derivation of this metric is depicted in Figure 2, which demonstrates how the variability in density gradient (Fig. 2C) is derived from the latitudinal gradient (Fig. 2B), which in turn is derived from the surface density data (Fig. 2A). In this example, extracted from one longitudinal position of the whales' trajectories, the frontal feature appears as an extended density slope (Fig. 2A); the density gradient is a noisy signal, which is, however, normally distributed (Fig. 2B). The calculation of the SD (Fig. 2C) allows us to distinguish a region of higher variability, observed between 42 and 50 degrees south.

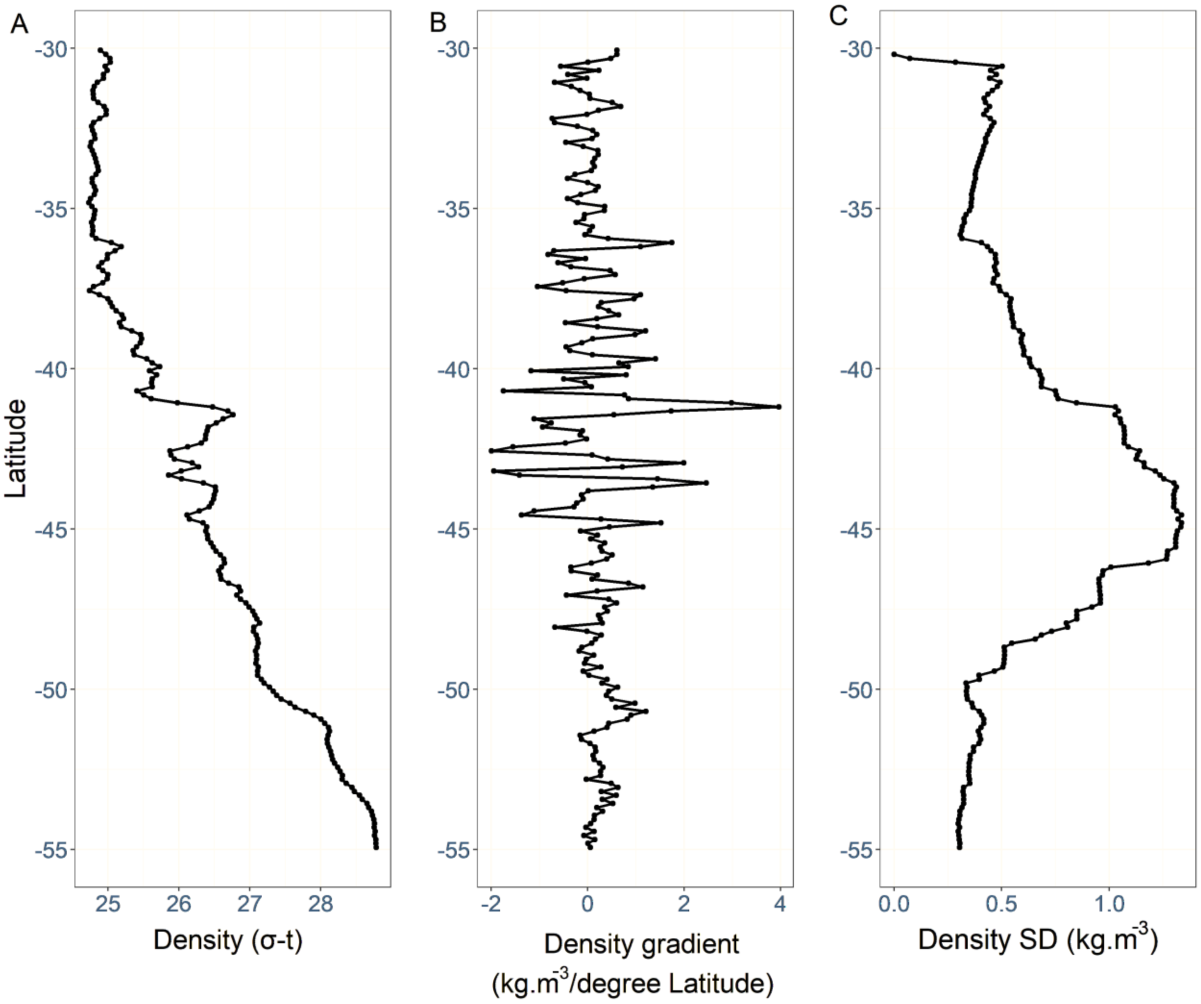


Figure 2. Latitudinal profiles of A) density (σ − t), B) latitudinal density gradient (kg m^3 /deg latitude) and C) density gradient standard deviation (kg.m^{-3}) on the 11/11/2023.

at 7° longitude. This example displays the derivation of the front. The nominal distance from the front was computed by extracting the coordinates of the point of maximum variability for each day. These positions were plotted as a time-series, and a Locally Weighted Scatterplot Smoothing (LOWESS) function was applied to these data. The distance (km) was computed by calculating the perpendicular distance of the whale on each day from this curve. A negative distance indicates the whale is on the poleward side of the front.

3.3.7 Relationship between behavioural states and satellite-derived variables

The relationship between satellite-derived variables (SST, SSS, chlorophyll and distance from front) and behavioural mode was investigated using linear regressions for each tagged whale, and with all whales pooled. Ocean data were extracted for each daily position of the tagged whales. Linear regressions were only applied to ARS due to the high levels of variability in environmental variables associated with transiting behaviours.

3.4 Results

3.4.1 General movements

Of the six adult females with either CTD or a SPLASH tag, five moved offshore whereas one remained inshore until the tag stopped transmitting (Fig. 3). Tag duration ranged from 5 – 116 days with a mean of 41 and 79 days for CTD and SPLASH tags respectively (Table 1). Only tags which transmitted for more than 40 days were included in this analysis (Table 1; whale number 1, 2, 3 and 4). Whales 1 and 2 were tagged with CTD instruments, and SPLASH10 - 373 tags were deployed on whales 3 and 4. Of these whales, three moved in a south-westerly direction and stopped transmitting between -6°W and 9 °E and -40°S and -45°S, and one moved south and stopped transmitting at 18.62°E; -43.48°S (Fig. 3). All whales showed similar behavioural patterns, with a brief period of transiting behaviour until passing 40°S, after which ARS occurred in the same general area and latitudinal band for all whales, until tags stopped transmitting (Fig. 3).

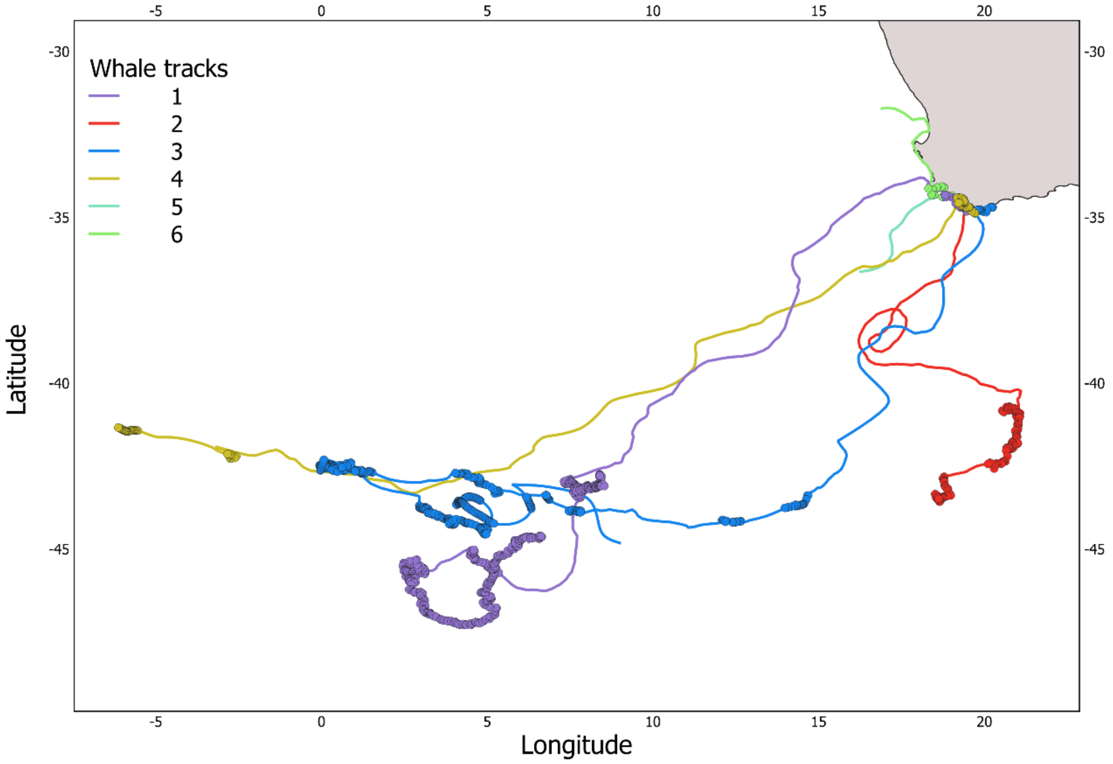


Figure 3. Map of the location tracks of the six adult female southern right whales (*Eubalaena australis*) tagged on the South African coast in October/November 2023. Points indicate ARS which is assumed to be foraging when occurring outside of their coastal calving grounds. Tags

5 and 6 only transmitted for 5 and 11 days, respectively, and were not used in the analyses.

Table 1. Details on the satellite transmitters deployed on six adult SRWs.

Whale Nr	Tag ID	Deployment date	Last position date	Duration (days)	Tagging location	Last known location	Tag type
1	210733	03/11/2023	18/02/2023	107	19.33; -34.44	18.62, -43.48	CTD
2	210739	03/11/2023	14/12/2023	41	19.35, -34.45	6.25, -44.79	CTD
3	87780	12/10/2023	05/02/2024	116	19.36, -34.50	8.99, -44.82	SPLASH
4	87762	12/10/2023	23/11/2023	42	19.23, -34.42	-6.13, -41.33	SPLASH
5	210737	05/11/2023	10/11/2023	5	19.23, -34.42	16.26, -36.64	CTD
6	210734	06/11/2023	17/11/2023	11	19.33, -34.47	16.91, -31.72	CTD

3.4.2 Conductivity, Temperature and Depth measurements

Values of SSS and SST obtained through both the CTD tags and remote satellite-derived measurements were compared to assess the reliability of these measurement techniques over time, and to evaluate the extent to which these measurements can be integrated (Fig. 4). Satellite-derived and CTD measurements of SST and salinity were generally in good agreement (Fig. 4). Weak declining trends in the differences between temperature measurement techniques are observed in whale 2 (Fig. 4A, $R^2 = 0.15$, $p < 0.05$). Differences in salinity measurements in whale 2 were greater and generally increased over time (Figure 5d, $R^2 = 0.29$, $p < 0.001$), with satellite-derived measurements consistently above those captured by CTDs. Differences in salinity measurements in whale 1 were much smaller, and showed weaker declining trends (Fig. 5d, $R^2 = 0.12$, $p = <0.05$). Differences in measurements were consistent across data gaps, which suggests that measurements were reliable once the sensor started working again (Fig. 4c and 4d).

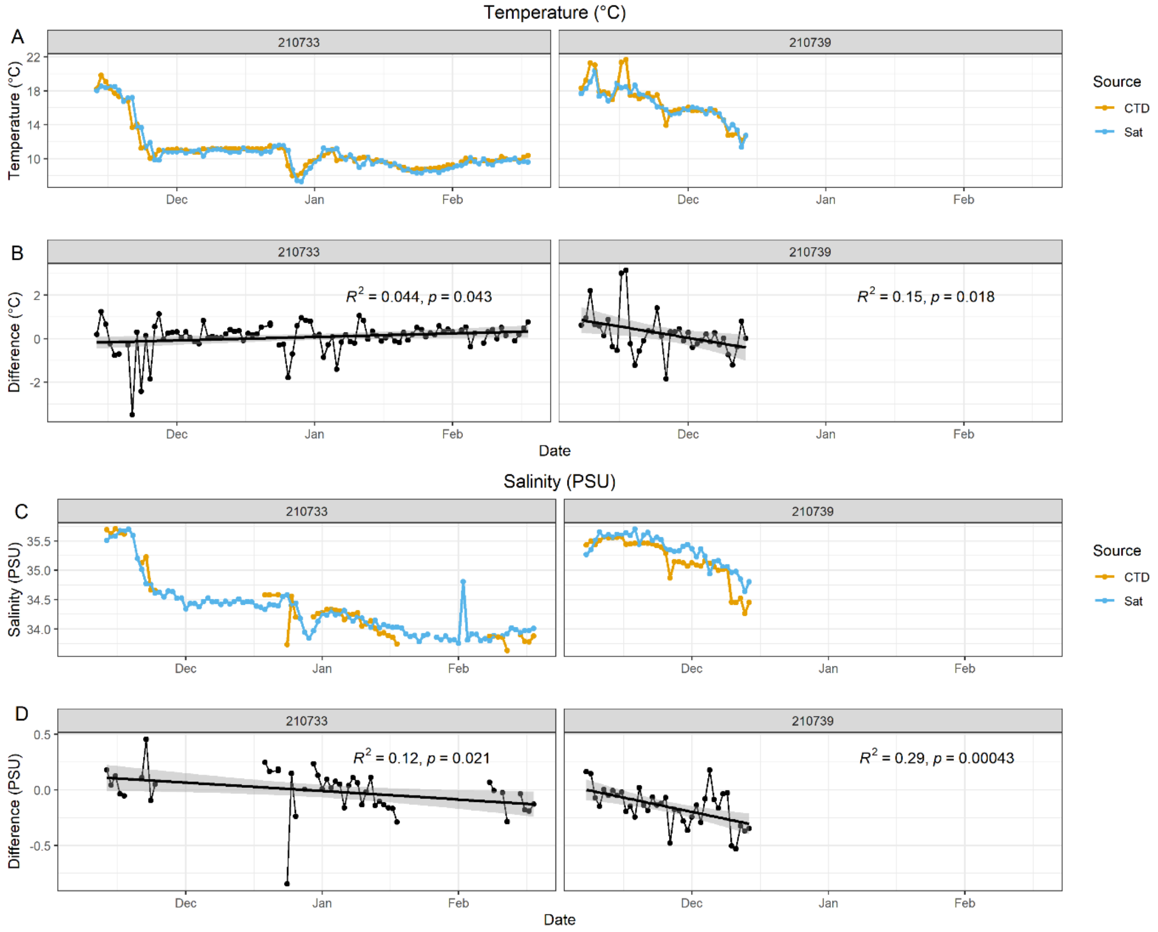


Figure 4. Comparisons between satellite-derived and animal-borne Conductivity, Temperature and Depth (CTD) measurements for whales 1 (PTT 210733) and 2 (PTT 210739) of A) sea surface temperature (SST); B) linear regression of the difference in SST measurements over time, C) sea surface salinity (SSS); D) linear regression of the difference in SSS measurements over time. B and D are aimed to visualise any trends in the discrepancies between the two measurement techniques.

Of the whales instrumented with CTD tags, only two provided sufficient data (> 40 days) for analysis of the offshore environment (Whales 1 and 2). Profiles of conductivity, temperature and depth could be collected from 1,150 and 458 locations for whales 1 and 2 respectively. For whale 1, temperature readings were recorded for > 99% of the profiles, while reliable salinity measurements were only recorded for 68%. This was due to data gaps between the 25/11/2023 - 18/12/2023 and 18/01/2024 - 07/02/2024. For whale 2, temperature was recorded on all profiles, and salinity for > 99%. Mean (+- sd) dive depths over the entire period were 39.52 m ± 41.49 and 29.33 m ± 24.49 for whales 1 and 2 respectively. Hovmöller diagrams following the position and time of the whales are presented alongside the CTD profiles to contextualize the interior features along the whale track, with larger-scale regional surface features. During November 2023, whale 1 initially transited through relatively warm (15 - 20°C) and salty (35 - 36 PSU) water associated with the narrow, and deep Agulhas current (Fig. 5). During this period, dives were noticeably deeper (consistently > 150m). By late November, this whale had entered the cooler (9 - 11°C) fresher (34 - 34.8 PSU) waters of the SO south of 40°S where she began her first bout of ARS (Fig. 5). The whale remained in this area until mid-December after which she transited south for a week, passing through an area of cool, fresher water (Fig. 5). Following this, she remained in an ARS state in this region until the tag stopped transmitting, meandering between 45°S and 47°S.

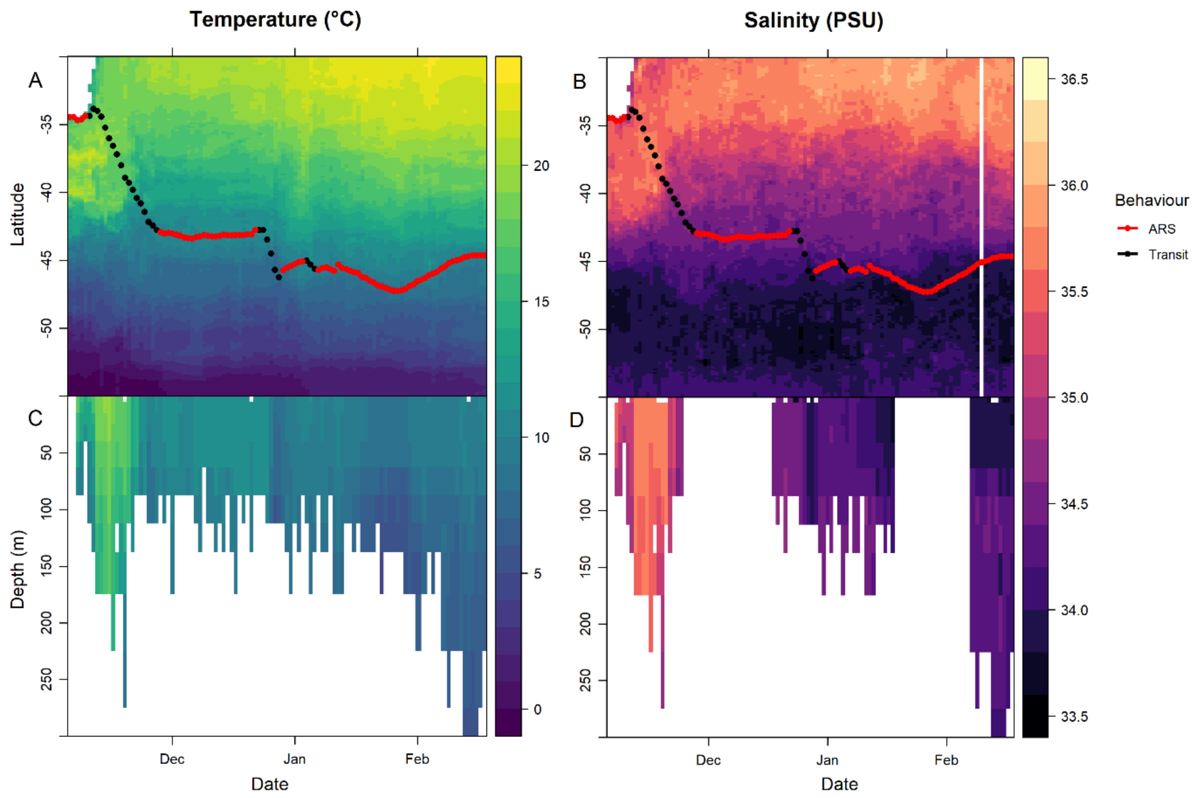


Figure 5. Hovmöller plots of a) temperature and b) salinity and deepest daily dive profile for the date and position of whale 1.

Whale 2 transited through the warm (15 - 22°C), salty waters (35.5 – 35.8 PSU) of the Agulhas current during November (Fig. 6). Towards late November, she began ARS and deeper dives with the onset of cooler (10 - 15°C), yet still relatively salty (34.8 – 35.5 PSU) waters. In early December she moved into fresher water (34.2 – 34.6 PSU).

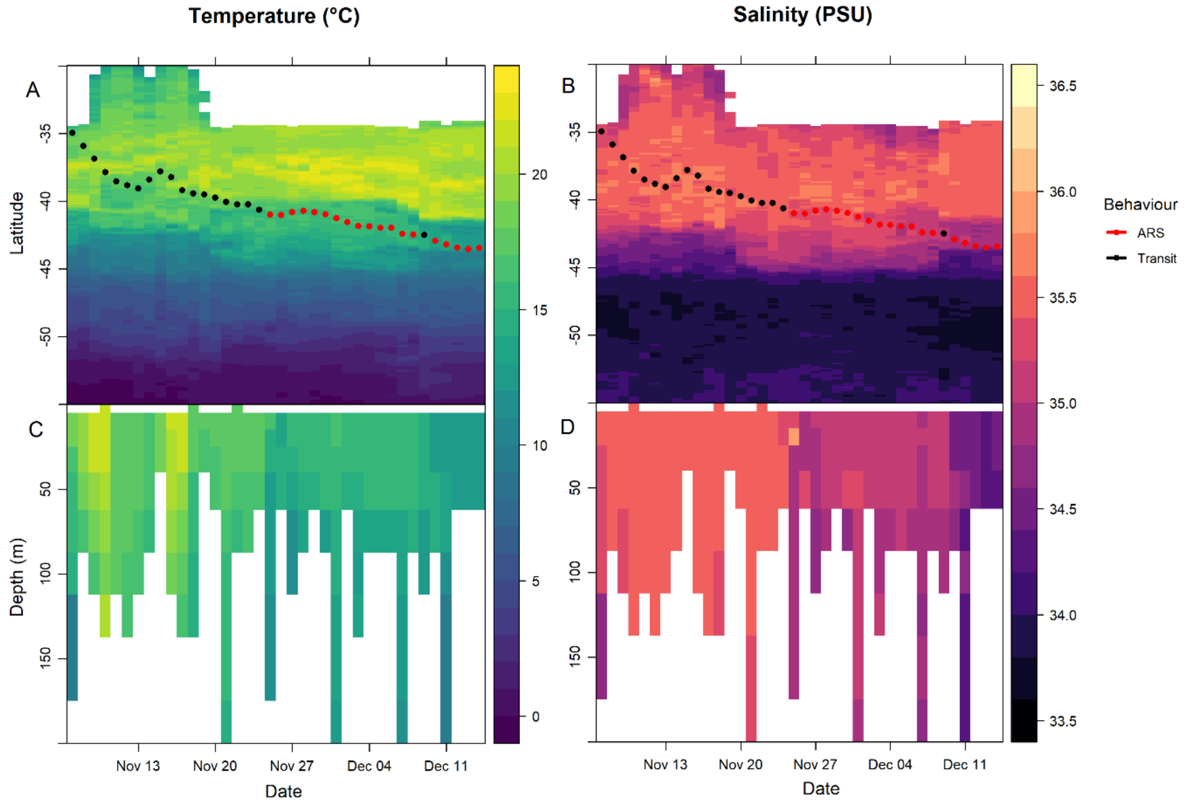


Figure 6. Hovmöller presentations of a) temperature and b) salinity and deepest daily dive profile for the date and position of whale 2.

Water temperature and salinity differed significantly between the two behavioural states at all depths sampled ($p < 0.001$, Fig. 7 and 8). Both in temperature and salinity, these differences increased with depth. Temperature and salinity displayed a larger interquartile range at all depths in profiles sampled during transit vs. ARS. Salinity in ARS profiles increased with depth after 50 m. In transiting profiles, both median temperatures and salinities increased with depth because most dives > 75 m were in the warm deep Agulhas current. Both whales displayed a period of consistently deeper dives when transiting through the Agulhas current (Fig. 7 and 8).

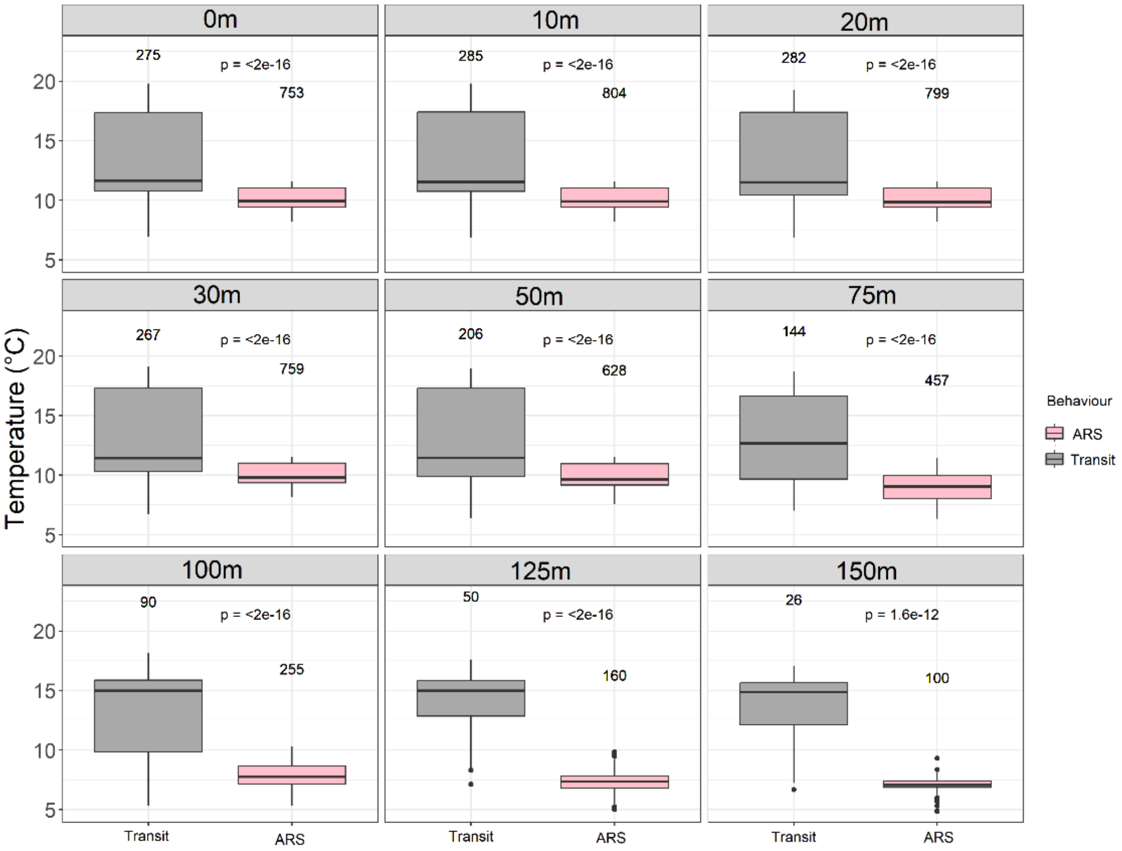


Figure 7. Boxplots comparing temperatures sampled during the two behavioural states (Area Restricted Search (ARS) and Transit) at different depths for Whales 1 and 2 combined. *P*-values from t-tests are shown on each panel, and the number of measurements at each depth is indicated above each box.

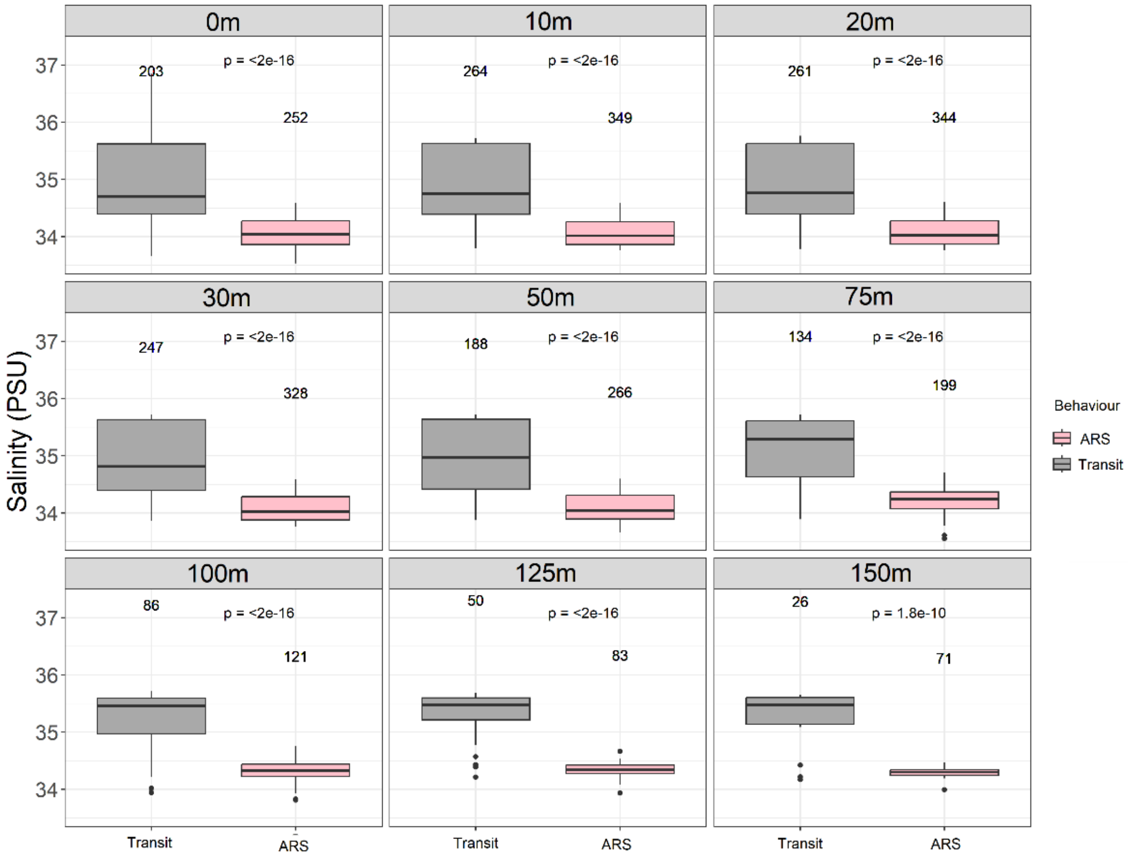


Figure 8. Boxplots comparing salinities sampled during the two behavioural states (Area Restricted Search (ARS) and Transit) at different depths on Whales 1 and 2. *P*-values from t-tests are shown on each panel.

3.4.3 Diving behaviour

Examples of dive profiles with different dive shapes derived from the SPLASH tag of whale 3 are shown in Figure 9. Table 2 summarises the diving behaviour of whales 3 and 4.

Table 2. Summary of diving behaviour for whales 3 and 4 (PTT 87780 and 87762 respectively, instrumented with SPLASH10 – 372 dive depth and location tags.

Whale	Number of dives	Total time (decimal hours)	Max dive depth (m)	Mean ± SD dive depth (m)	Dive rate (dives/hour)
3	225	24.62	176.5	22.86m ± 30.79	9.52
4	136	21.10	465	45.30m ± 53.21	6.54

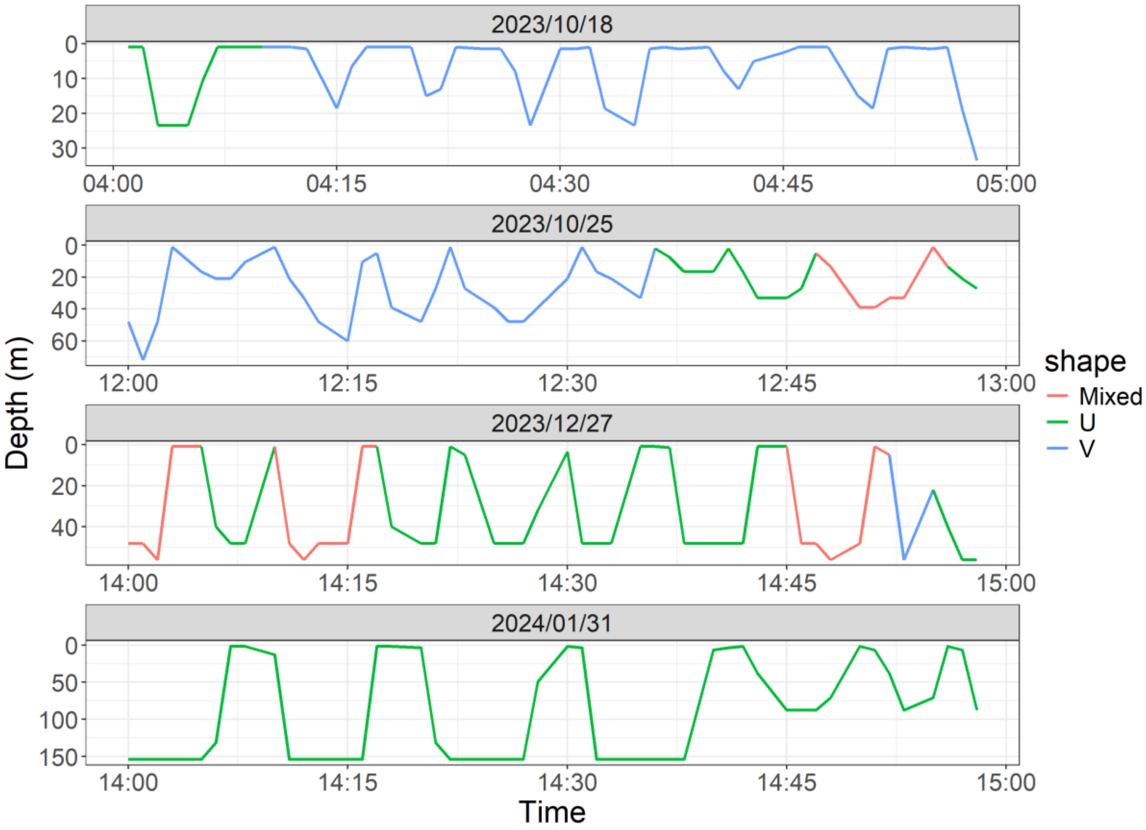


Figure 9. Dive profiles from four days for Whale 3. Dive shapes are colour-coded: pink: mixed shapes (U and V characteristics); green: U-shaped and blue: V-shaped dives.

No clear differences in diving rates and dive shape were apparent between transiting and ARS behavioural modes (Fig. 10). For both whales, an increase in the proportion of U-shaped dives is evident with time, although only whale 3 showed statistically significant increase (R^2 = 0.46, $p < 0.05$, Fig. 10B and C). Diving rates remained consistent in both whales, although the highest and lowest diving rates in whale 3 were recorded during ARS and transiting respectively. In whale 4, ARS was only recorded while the whale was still located at its calving ground.

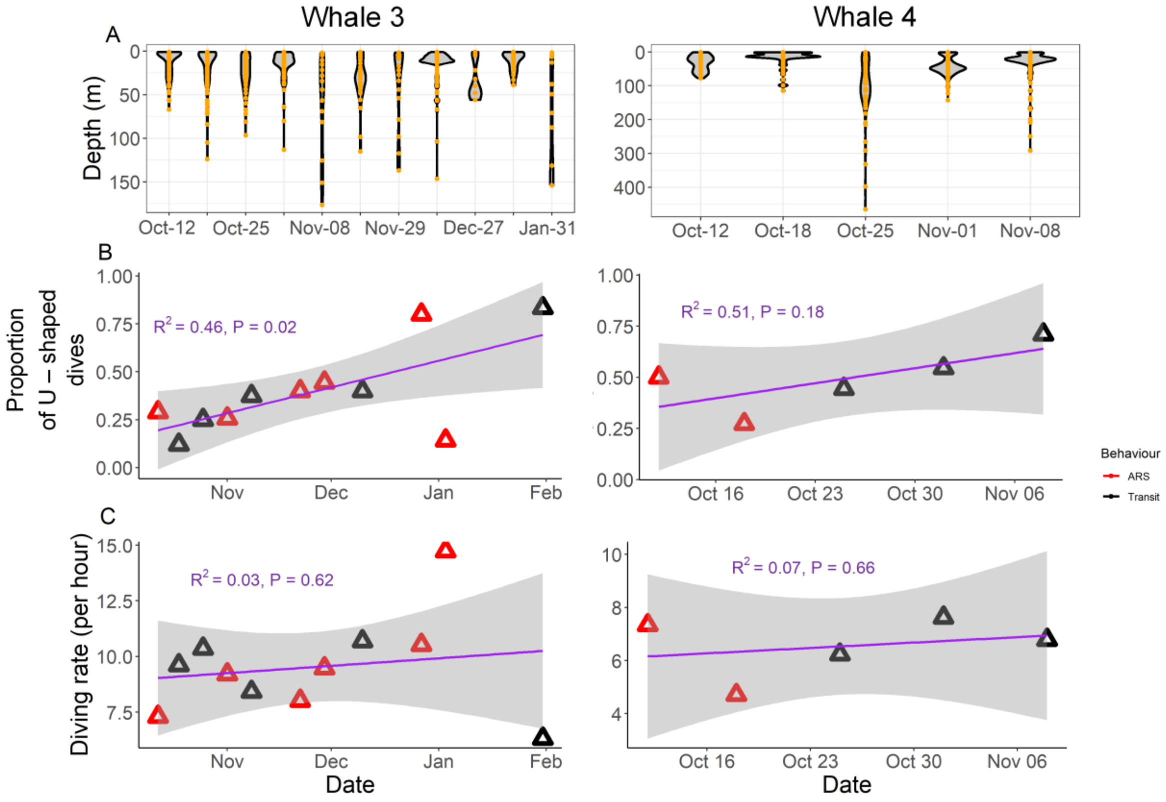


Figure 10. Dive metrics for whale 3 (PTT 87780, left) and whale 4 (PTT 87762, right); A) Violin plots of daily dive depths, B) daily proportion of U-shaped dives and c) daily dive rate for whales 3 and 4.

3.4.4 Whale movements in relation to primary production

To evaluate the movement and behaviour of the whales in relation to phytoplankton blooms, Hovmöller diagrams of satellite-derived chlorophyll at the longitudinal position and time of the whales are presented. Only the two whales with the longest tracks (whales 1 and 3) were analysed, since chlorophyll at eight-day intervals was used. Whales generally seemed to display little affinity for regions of high primary production, and appeared to actively forage in regions of low chlorophyll concentration (<0.6 mg m^3, Fig. 11).

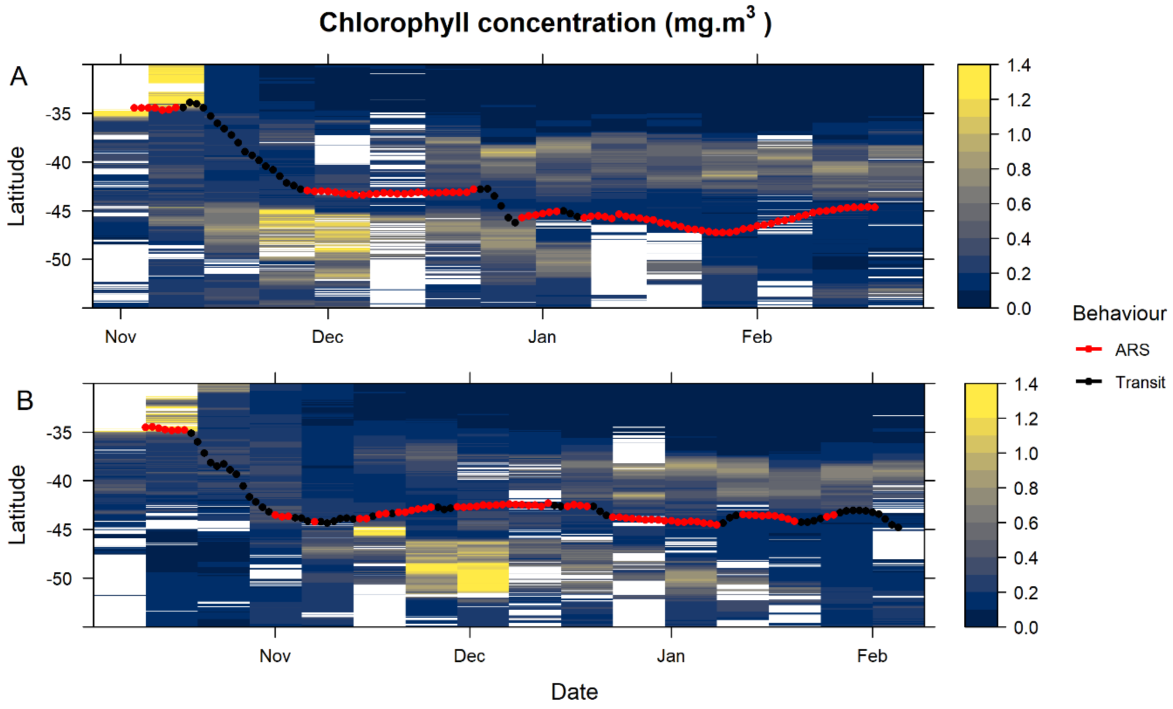


Figure 11. Hovmöller presentations of chlorophyll concentration (mg m^3) for the date and position of A) whale 1 and B) whale 3.

3.4.5 Whale movements in relation to ocean fronts

Whales 1, 2, 3 and 4 seemed to halt their southward transit upon encountering a frontal region (for definition, see methods), and whales 1, 2 and 3 showed high affinity for this region during ARS (Fig. 11). The whales remained in close proximity to the region of maximum variability, and whale movement patterns displayed synchronicity with the latitudinal position of the front.

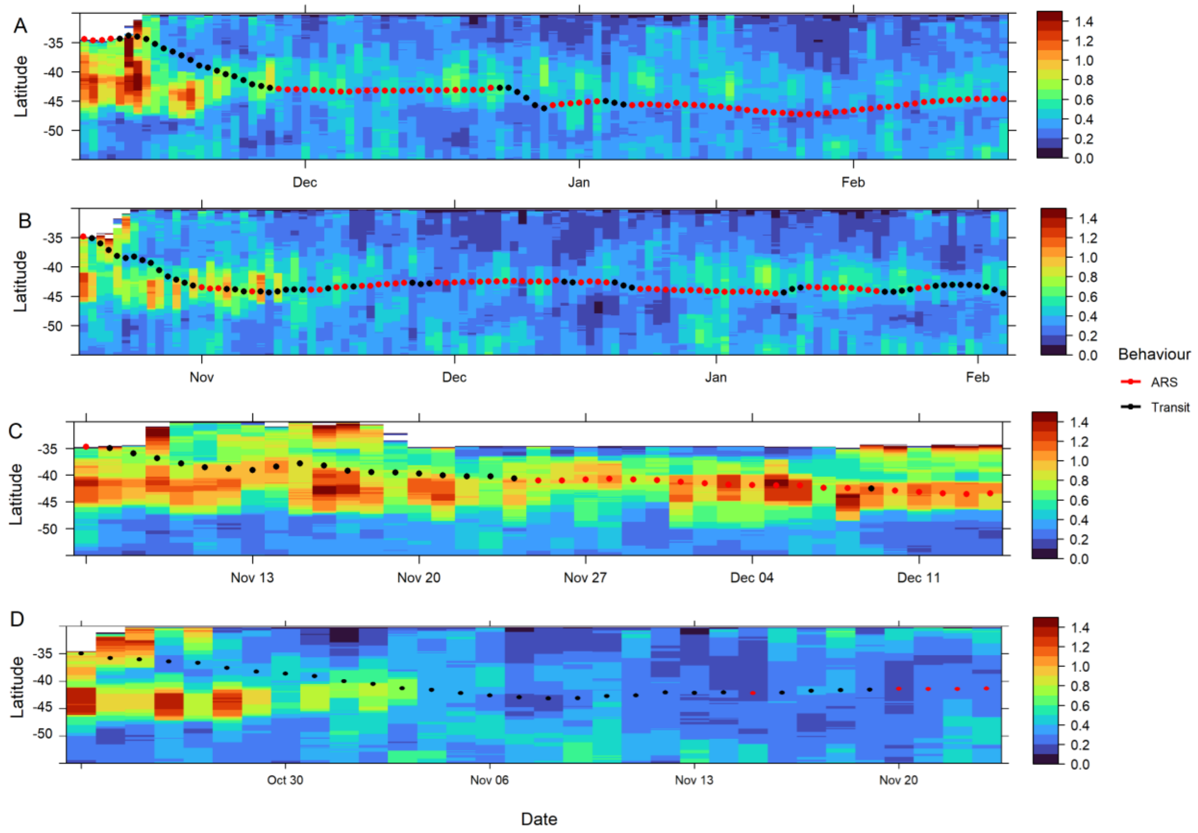


Figure 11. Hovmöller presentations of the density gradient standard deviation (kg.m^{-3}/deg latitude) as a descriptor of ocean fronts for the date and position of A) whale 1; B) whale 3 and C) whale 2.

3.4.6 Relationship between satellite-derived variables and behavioural mode

Due to the high levels of variability in ocean properties encountered during transiting behavioural modes (see earlier Fig. 7 and 8), linear relationships were only assessed in behavioural states associated with ARS ($b > 1.5$). Only weak linear relationships were observed between behavioural mode and the oceanographic variables assessed, indicating consistency in the environmental conditions in which whales forage. Most ARS behaviour occurred within 200 km of the nominal location of the front (see methods) and only weak declining trends were observed in Whale 3 (R^2 = 0.086; p = 0.021) and all whales pooled (R^2 = 0.059; p = 0.002), indicating a strong affinity for this feature (Fig. 12A). Similar patterns were observed with chlorophyll concentration, with all ARS behaviour observed in chlorophyll concentrations < 1 mg m^3, and mostly below 0.5 mg m^3 (Fig. 12B). Only weak negative linear relationships were observed between behavioural mode and chlorophyll concentration in whale 2 (R^2 = 0.34; p = 0.078) and all whales combined (R^2 = 0.044; p = 0.041). No significant relationships were observed in temperature and salinity besides the reduced dispersion for values of b > 1.5 (Fig. 12C and 12D).

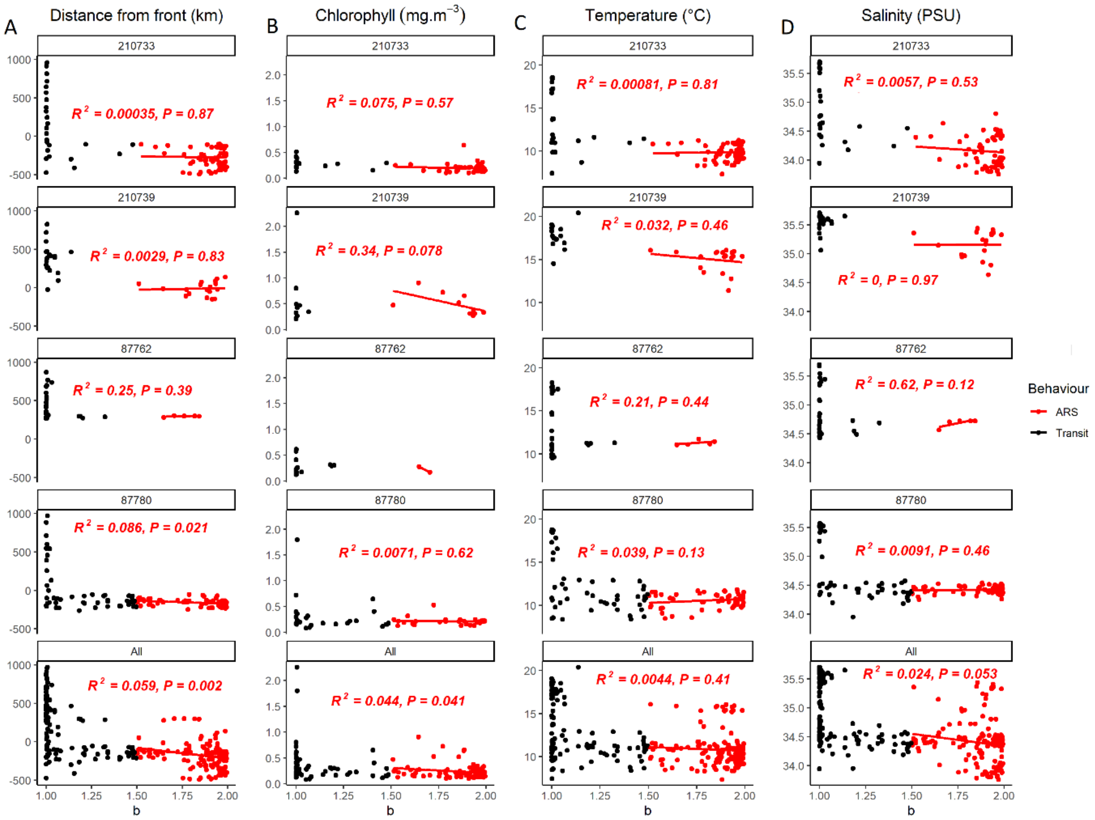


Figure 12. Relationship between behavioural mode and A) distance from front, B) chlorophyll concentration, C) temperature and D) salinity, for all whales analysed (along the rows). Linear regressions are presented for behavioural modes associated with ARS, with adjusted R^2 and *P* values describing the fit and strength of the linear relationships.

3.5 Discussion

Even though our study only used data from 4 whales, our results revealed that ARS, presumably feeding behaviour, was strongly associated with ocean fronts with high variability in meridional gradients of surface density, and characterised by low chlorophyll concentrations. Additionally, ARS only occurred in the cool fresher waters of the ACC. Dive depth recording tags revealed a noticeable increase in the proportion of U-shaped dives, which are generally associated with feeding behaviour. However, there did not appear to be a higher proportion of U-shaped dives during ARS.

When comparing SSS and SST between ARS and transiting behaviours at all depths sampled by the CTDs, ARS was found to occur within fairly constrained environmental conditions, indicating that foraging occurs in water masses with distinct characteristics. At the same time, a large amount of variability in the environmental variables analysed is evident during transit. This was expected since whales often intermittently alternate between transit and ARS states within water with similar properties. When also considering the relationships between satellite-derived variables and behavioural states, it became apparent that the environmental conditions were indistinguishable after b values > 1.25. To further characterise the foraging environment, higher temporal and spatial resolution data are likely required. Furthermore, it is possible that after reaching broadly favourable foraging conditions, other stimuli drive foraging behaviour such as visual, olfactory and communication. In bowhead whales, synchronicity in diving behaviour between individuals was found at distances < 100 km, suggesting an ability to communicate and perhaps collaborate when searching for food(Podolskiy et al., 2024).Also in bowhead whales, studies on the olfactory anatomy have revealed sophisticated structures suggesting that smell may be an important sensory system for locating prey (Thewissen et al., 2011). Using the techniques employed in this study, foraging and transiting environments become indiscernible once whales reach broadly favourable conditions. It is therefore argued that previous thresholds used in distinguishing SRW behavioural states (e.g. b < 1.25 - b > 1.75 for ARS and b < 1.5 - b > 1.5 for transit), be re-evaluated, and perhaps be determined by defining case-specific b parameter value thresholds depending on changes on the environment.

Behavioural responses to temperature and salinity have been reported in numerous species and are likely a strong indicator of foraging habitat suitability for baleen whales (Chambault et al., 2018; Citta et al., 2021; Costa et al., 2006; Owen et al., 2019). However, since most whales are known to forage over wide temperature ranges, perturbations and gradients in temperature and salinity fields are likely to be what elicit a change in behaviour (Agrelo et al., 2021; Barlow et al., 2023; Doniol-Valcroze et al., 2007; Etnoyer et al., 2006; Owen et al., 2019). While population-level effects of water temperature and, to a lesser extent, salinity have been studied over longer temporal and spatial scales, few studies have examined their impact on individual behavioural responses at smaller scales (Owen et al., 2019).

Ocean fronts have been found to be important areas for zooplankton. In particular copepods, SRW’s main prey in the mid-latitudes (Tormosov et al., 1998) are strongly associated with frontal features (Venkataramana et al., 2024). Associations with fronts have also been found in copepods preyed on by North Pacific and Atlantic right whales (*Eubalaena glacialis* and *Eubalaena japonica* respectively) (Davies et al., 2014; Tynan et al., 2001). The physical processes occurring at ocean fronts enhance prey densities by increased primary production through mixed-layer nutrient entrainment, and through retention of zooplankton in eddies (Chapman et al., 2020; Levyet al., 2018). In this chapter a new metric defining ocean fronts is proposed to further investigate the foraging potential of frontal features for SRWs; the standard deviation of the latitudinal density gradient This metric allows for the identification ofbroad regions where density variations and mesoscale features are more likely to be found. In our study the tagged SRWs displayed a strong affinity for this band of high variability in the density gradient, and almost all ARS were documented within this region. The definition of SO fronts is evolving rapidly from a simplistic model of distinct transitional zones to a complex system of transient frontal filaments, jets, and eddies. The standard deviation of the meridional density gradient integrates this inherent variability and may be important in highlighting important biological regions in the SO. Associations with similar features have been described in foraging southern elephant seals (*Mirounga leonina*), where feeding was found to be related to sub-mesoscale turbulence distributed on the edges of coherent mesoscale structures (Siegelman et al., 2019). Further investigations should assess the use of this feature over longer time spans, and with different species in different regions.

In the present study, the frontal region appeared to be associated with regions of low surface chlorophyll concentration when considering 8-day composites. This characteristic is affected by the different time scales in the persistence and evolution of mesoscale features driving chlorophyll enhancement or entrapment (Little et al., 2018). Thus, in this study the presence of foraging whales is not concurrent with high levels of primary productivity. Similar observations have been made on foraging humpback whales (*Megaptera novaeangliae*), with high chlorophyll observed during transiting states, and low during lingering and foraging states (Owen et al., 2019). In a study by Laidre et al. (2010), chlorophyll concentrations in the upper 50 m had little impact on the foraging behaviour of bowhead whales (*Balaena mysticetus*). It appears that high chlorophyll concentrations are not necessarily a good predictor of the simultaneous presence of dense prey aggregations and foraging whales due to the complex interactions of physical and biogeochemical scales in the ocean. Firstly, there is a variable mismatch in the timing of maximum primary and secondary production, since very dense aggregations of zooplankton have high feeding rates, and quickly consume phytoplankton. Therefore, the highest biomass of zooplankton may occur only in the wake of seasonal phytoplankton blooms. Secondly, mesoscale eddies have been found to have an increased probability of zooplankton retention, and therefore anticyclonic eddies, which have low chlorophyll concentrations in the SO, may yield high prey densities in the absence of high chlorophyll concentrations (Condie & Condie, 2016; Dawson et al., 2018; Frenger et al., 2018; Samuelsen et al., 2012). Another contributing factor is the presence of deep chlorophyll maxima. Although water columns in the SO are assumed to be well mixed, deep maxima have been described, and found to persist for > 3 months (Baldry et al., 2020; Boyd et al., 2024; Carranza et al., 2018). However, most of the time spent by the tagged whales was within the range of optical penetration by satellites (10 – 40 m), and therefore deep chlorophyll maxima were unlikely to be a dominant feature in this study.

Although diving behaviour in relation to environmental variables was not directly assessed, diving metrics showed no clear patterns with the two behavioural modes. A general increase in the proportion of U-shaped dives was found over time. These dive shapes are typically associated with feeding, suggesting an increase in the occurrence of foraging behaviour as the whales migrated south. This trend was driven by dives in both transiting and ARS states, indicating that feeding may occur during states modelled as transiting. Therefore, once whales are in favourable foraging habitat, the distinction between foraging and transiting states becomes uncertain. This phenomenon likely contributed to the high levels of variability in environmental conditions observed during transit.

The present study is only based on the tracks of four whales in a restricted part of the SO. Nevertheless, their patterns revealed distinct oceanographic characteristics associated with different behavioural modes. Continued research is recommended with the increased tagging effort of SRWs along the South African coast. Climate change is expected to have significant impacts on the SO, affecting the position of fronts and phytoplankton blooms' phenology, with repercussions for food availability for predators (Ryan-Keogh et al., 2023; Thomalla et al., 2023). Therefore, continued research is needed to better understand how climate variability directly impacts whale foraging success at the individual level and the ramifications of these impacts for population

4. Offshore migratory behaviour and foraging habitat use of South African southern right whales (*Eubalaena australis*).

*This chapter is accompanied by Appendix C.

4.3 Abstract

After a long period of steady population recovery from commercial whaling, South African southern right whales (SRWs) have shown signs of demographic changes related to alterations in prey availability in their offshore foraging grounds. Stable isotopes indicate a northward shift in foraging location, mothers are getting thinner, and calving intervals have lengthened over the last 15 years. To date, knowledge of their migratory and foraging behaviour has been based on historical whaling records, telemetry data from five whales tagged in 2001/2002, and opportunistic surveys and sightings. To better understand recent population-level changes, current migratory behaviour and foraging habitats were assessed. Between 2021 and 2023, 26 satellite transmitters were deployed on 25 adult female and one male SRW. Using the associated telemetry data, contemporary migratory routes were mapped in relation to environmental variables, and random forests models were employed to predict the presence of foraging whales across their known foraging domain. Results showed a continued use of three foraging regions previously defined based on whaling data: the subtropical and subantarctic fronts, the Bouvet Island area and surrounding waters, and the Crozet Islands area. Additionally, there was a clear northward shift in foraging behaviour compared to historical patterns. Furthermore, five whales made trans-Atlantic crossings to the southwest Atlantic and Patagonian shelf not previously recorded. Random forest models predicted the presence of foraging whales with high accuracy based on eight covariates; SST, SSS, sea surface height (SSH), standard deviation of the density gradient (SD), cumulative chlorophyll

of the preceding month, distance from September ice edge, ocean depth, and mixed layer depth (MLD). Results of this study provide the first comprehensive assessment of the contemporary migratory behaviour of South African SRW's. As ecosystems face increasing pressure from climate change, understanding the current migratory behaviour of marine predators is essential for conservation and for interpreting ecosystem changes.

4.4 Introduction

Southern right whales (SRWs) usually migrate between coastal calving grounds and offshore foraging grounds (Mate et al., 2011; Tormosov et al., 1998). During austral winter (June – October), SRWs aggregate along coastlines which provide the ideal conditions to give birth and nurse young, and display a high degree of site fidelity to specific calving grounds (Best, 2000; Burnell, 2001; ;; Carroll et al., 2016; Payne et al., 1990; Rayment et al., 2012; Seyboth et al., 2015;; Watson et al., 2021; Zeh, Dombroski and Parks, 2022). This predictable nearshore presence has resulted in some of the most extensive and robust monitoring programmes for any whale in the world (J. Bannister, 2001; Best et al., 2020; Payne, 1986). Through this intensive long-term monitoring, a wealth of information on population parameters, including population size and calving intervals as well as trends in abundance have been collected (Bannister, 2001; Brandão et al., 2023; Burnell, 2001; Carroll et al., 2011; Christiansen et al., 2018; Cooke, Rowntree and Payne, 2001;;;; Stamation et al., 2020; Watson et al., 2021;). Although these long-term studies have reported the continued steady recovery of SRWs from near extinction due to commercial whaling, the last 15 or so years have revealed some changes in many of the world's SRW populations; Most notably, coastal prevalence has become more erratic, and reproductive rates have decreased in populations that use the shores of Argentina, South Africa and Australia as calving grounds (Brandão et al., 2023; Charlton et al., 2022; Crespo et al., 2019). Furthermore, in the South African population, maternal body condition declined and a notable northward shift in foraging distribution has been reported over the same period (van den Berg et al., 2021; Derville et al., 2023; Vermeulen et al., 2023). Due to the vast energetic requirements needed for reproduction (Christiansen et al., 2014, 2018, 2022), these changes have been hypothesized to be driven by climate variability and change has on the abundance and distribution of prey in their offshore foraging grounds (Leaper et al., 2006; Seyboth et al., 2016; Agrelo et al., 2021; Germishuizen et al., 2024, chapter 2). Ultimately, knowledge of SRW selection of foraging habitat and migratory behaviour is crucial to try to unravel the drivers behind the observed population-level changes.

Previous knowledge of offshore foraging behaviour of SRWs stemmed from historical whaling data, a limited number of satellite telemetry studies and opportunistic and survey sightings data (J. L. Bannister et al., 1999; Branch & Butterworth, 2001; Mate et al., 2011; Richardson et al., 2012; Savenko & Friedlaender, 2022; T. D. Smith et al., 2012; Tormosov et al., 1998). These data have provided a good understanding of the general offshore foraging distribution, as well as information on broad scale foraging habitat selection through ensemble species distribution modelling (González Carman et al., 2019). Furthermore, from analyses of diet and spatial distribution of catch locations, there appears to be two modes of feeding; a mid-latitude mode focussed on the system of fronts associated with the Antarctic Circumpolar Current (ACC), and a high-latitude mode which focussed on Antarctic krill (*Euphausia superba*). That region is influenced by the seasonal cycle of sea ice. Tormosov et al. (1998) found from 249 SRW stomachs that catches north of 50°S contained copepods, and south of 50°S almost entirely euphausiids (presumably Antarctic krill). Specifically for the South African SRW population, historical whaling data and a single satellite tagging study revealed three regions of high usage; the waters surrounding Bouvet Island, the mid-latitude region associated with the sub-tropical and subantarctic fronts, and the shelf waters around Crozet Islands (Tormosov et al., 1998; Best, 2007; Mate et al., 2011; Smith et al., 2012).

In an effort to better understand the contemporary migratory movements of SRWs, and the recent demographic changes seen in most of the populations, satellite tagging studies have been initiated at all major calving grounds (Carroll et al., 2011; Zerbini et al., 2015; Mackay et al., 2020; Watson et al., 2021; Vermeulen, et al., 2023). These have provided a wealth of contemporary information on the migratory routes and fine-scale habitat selection of SRWs, including the discovery of novel behaviours and connectivity between populations (Mackay et al., 2020; Kennedy et al., 2023; Vermeulen et al., 2023; Vermeulen et al., 2024). Additionally, satellite telemetry provides the opportunity to quantify fine-scale habitat selection associated with different behaviours as predicted by movement models (I. Jonsen, 2016; I. D. Jonsen et al., 2005; Panigada et al., 2017; Reisinger et al., 2021; Sahri et al., 2022). Furthermore, machine learning techniques are being used to better understand habitat selection in a variety of different species (Maglietta et al., 2023; Raman et al., 2023; Reisinger et al., 2021; Sittaro et al., 2023). Satellite telemetry data provides an interesting opportunity to explore the environmental drivers behind different behavioural tendencies using machine learning (Reisinger et al., 2018, 2021).

Here the telemetry movements of 26 SRWs from the South African population tagged over three seasons between 2021 – 2023 is reported. Firstly, the general movements and migratory corridors used by the population are described and compared to historical telemetry and whaling data; secondly the environment and seasonal cycle of their migratory behaviour and the environmental conditions encountered is characterised; and thirdly random forest models are used to predict the presence of foraging whales over the foraging domain of South African SRWs based on environmental variables widely used in the literature as well ones determined to be important in chapters 2 and 3.

4.5 Methods

4.5.1 Satellite tag deployment and telemetry data processing

Boat-based satellite tagging operations were carried out in Walker Bay (34.4063° S, 19.2687° E) on the southwestern coast of South Africa during October 2021, 2022 and 2023. During this period, 23 SPOT-372 and two SPLASH10-373 CTD Argos satellite-linked tags from Wildlife Computers were deployed on adult female SRWs accompanied by calves at the time of tagging (Wildlife Computers, Redmond, WA; https://www.wildlifecomputers.com). One SPOT-372 tag was deployed on an unaccompanied adult which was later determined to be male by genetic sexing (methods and results not shown here). Tagging was performed from a platform mounted on a 6m rigid-inflatable boat. All tags were deployed by a skilled and experienced tagger using a modified pneumatic rifle (Heide-Jørgensen et al., 2001), at a distance of 3 – 5 m from the whales. These tags were attached to a delivery carrier, which detached upon successful implantation and was subsequently retrieved for reuse in future deployments. A biopsy sample was collected at the time of tagging using a Panzer V (150 lb draw) crossbow, and samples were kept on ice and frozen immediately after processing. Photographs were taken with a Canon 7D I, and video footage was captured with a GoPro during the tagging process for photo-identification purposes and to assess tag placement. After deploying the tags and collecting biopsy samples, the tagged whale was monitored from a distance greater than 500 meters for up to 30 minutes to observe any reactions to the tagging and to capture post-deployment images of the tag site. All tagging activities were conducted under the permit conditions of the South African government (RES 2021-18, RES 2022-05, RES 2023-18) and the animal ethics clearance from the University of Pretoria (NAS040/2020). The methods and instruments used for tag deployment and biopsy sampling adhered to the protocols approved by NOAA's Marine Mammal Laboratory Institutional Animal Care and Use Committee.

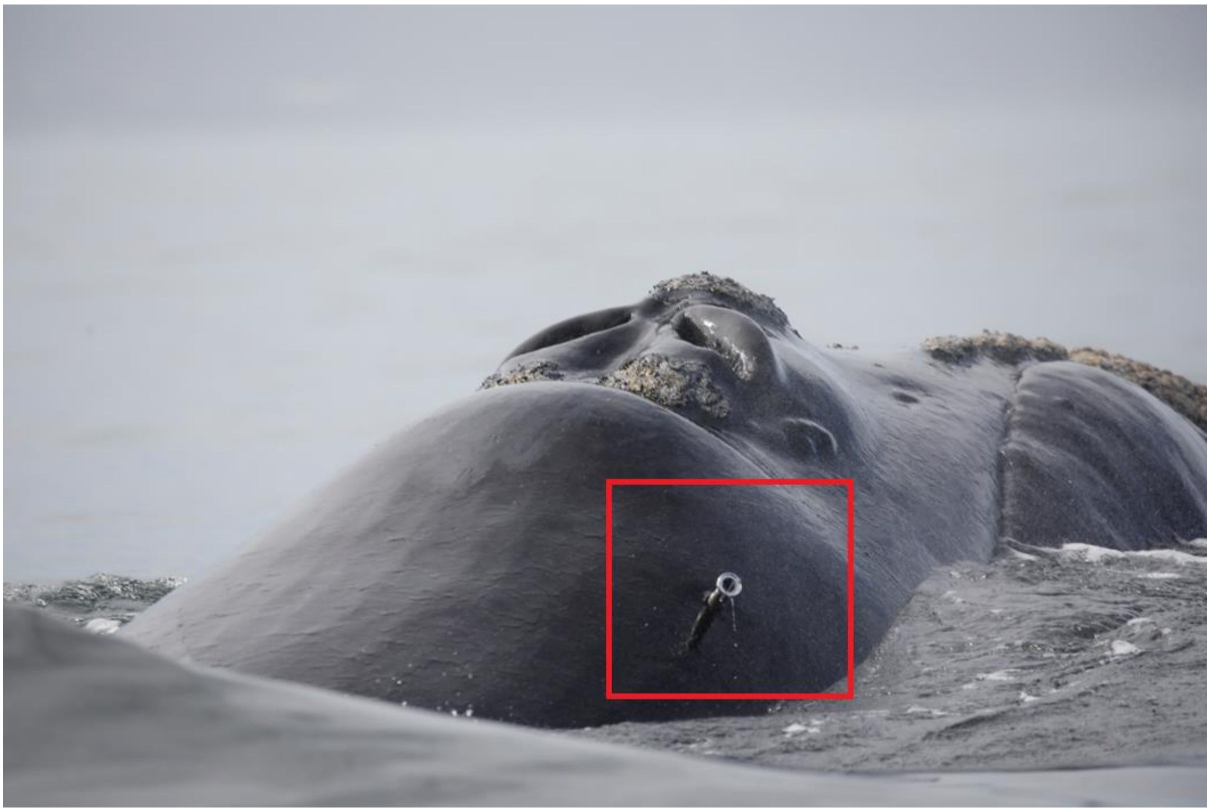


Figure 1. Tagged SRW individual displaying the tag placement.

To process the Argos-derived whale locations, the "argosfilter" R package was used (Freitas & Freitas M. C, 2022), and the data were further analysed with a Bayesian switching state-space model (SSSM) (I. Jonsen, 2016; I. D. Jonsen et al., 2005). The SSSM models estimate locations by accounting for both measurement errors in Argos data and the movement dynamics of the whales, utilizing a joint estimation approach as described by Jonsen (2016). The "bsam" package in R was used to fit the model to the filtered Argos data (I. Jonsen, 2016; I. D. Jonsen et al., 2005), and Markov Chain Monte Carlo (MCMC) simulations were performed using JAGS software. A total of 60,000 MCMC simulations were run, with the first 20,000 discarded and every 10th sample from the remaining 40,000 retained to minimize autocorrelation. A time step of 6 hours was applied to calculate predicted locations. Total path distances were calculated using QGIS version 3.26.1 and represent minimum estimates based on straight lines between consecutive points after filtering and modelling with an SSSM. From the SSSM models, two behavioural states were inferred based on two parameters (θ and γ). These parameters provide a range of 'b-mode' state values between 1 and 2. Values closer to 1 (< 1.5) indicate a highly directional and consistent movement pattern, typically associated with 'transiting' behaviour. In contrast, values closer to 2 (> 1.5) suggest highly variable and localized movements, likely indicative of "Area Restricted Search" (ARS) behaviour associated with foraging, searching, or lingering and social activities at foraging grounds. In this study, any ARS behaviour observed outside of the whales' coastal calving grounds was assumed to be related to foraging.

Comparison with Historical migratory behaviour

To compare contemporary movements with past movements, we obtained data from a previous tagging study and locations from historical commercial whaling catches. In September 2001, satellite tags were deployed on 21 Southern Right Whales (SRWs) (see Mate et al., 2011 for details on the methods; raw data and intellectual property are held by the MRI Whale Unit). Out of these tagged whales, five individuals moved offshore into the Southern Ocean (SO). The raw data from these movements were re-plotted and compared with the movements of the whales tagged in the current study. To ensure a fair comparison of migratory behavior over the same temporal timeframe, only data from the tag deployment date to April 30th of the following year were considered, with any locations recorded after April 30th removed to align with historical tags, which transmitted only from September to March of the following year. To further examine potential changes in migratory behaviour, the movements of the whales tagged in this study are also described in relation to historical whaling catches from the Soviet era (see Tormosov et al., 1998).

4.5.2 Environmental covariates

To describe the offshore environment utilized by SRWs, seven dynamic covariates – sea surface temperature (SST), sea surface salinity (SSS), sea surface height (SSH), standard deviation of the density gradient (SD, refer to Chapter 2), mixed layer depth (MLD), monthly cumulative chlorophyll of the preceding month (Chl), distance from the mean September ice edge of the preceding austral winter (ICE), and one static covariate – depth (Bath), were used (Figure 2 and Table 1). This lag time was chosen for the sea ice variable under the assumption that sea ice conditions in the preceding winter are most likely to affect foraging conditions in the following summer.These variables represent a combination of factors deemed important for generating suitable foraging conditions in the SO both in the literature (e.g., Reisinger et al., 2018, 2021; González Carman et al., 2019; Purdon et al., 2020) as well as in previous chapters of this thesis (chapter 2 and 3). To describe the environmental conditions encountered by each whale, values of each variable were extracted at all locations using daily and weekly data (Table 1).

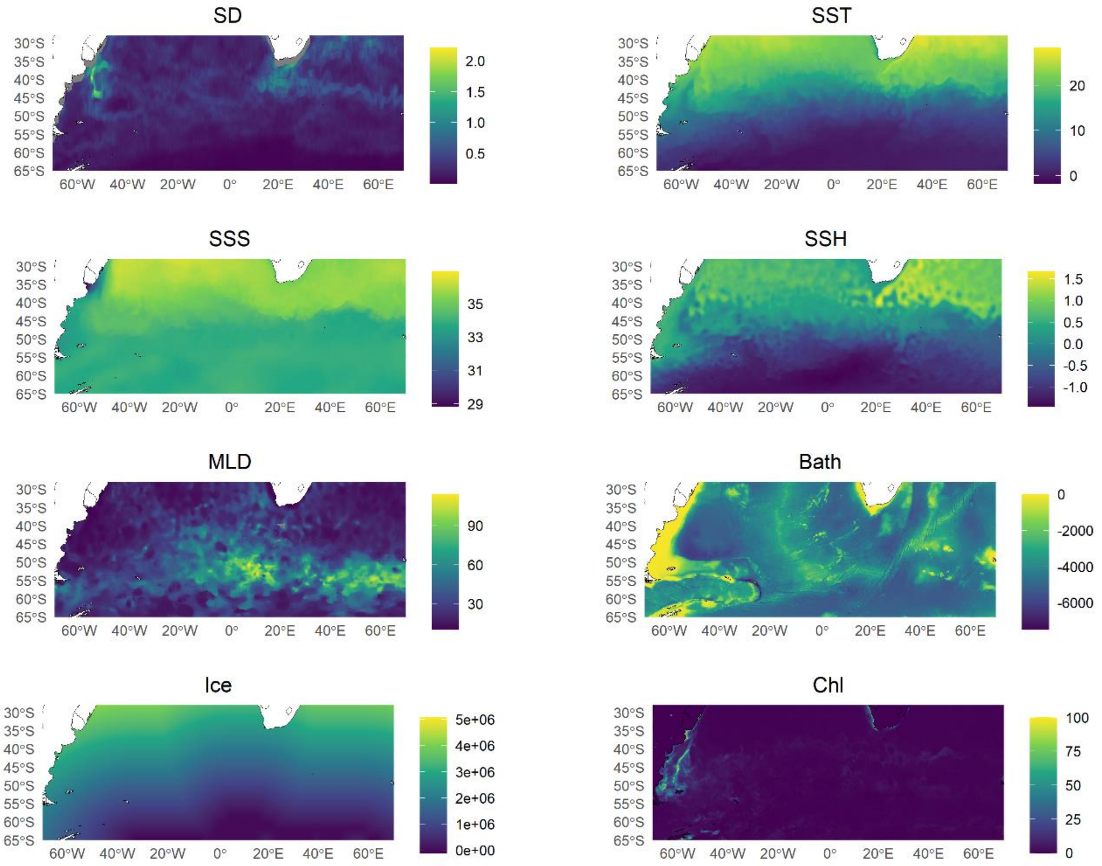


Figure 2. Maps of the 8 environmental covariates used in this study to characterise the environment of southern right whale foraging grounds, and to predict the presence of foraging whales using random forests. For the 7 dynamic variables, the mean of January 2023 is shown in this figure only for visualisation purposes. For details of each of the variables used refer to Table 1.

Table 1. Details of covariates used to characterise southern right whale (*Eubalaena australis*) offshore foraging habitat.

Name	Full name	Units	Notes	Spatial resolution	Temporal resolution	Source	Reference
SST	Sea surface temperature	°C		0.05°	Daily	https://data.marine.copernicus.eu/viewer/	Stark et al., 2007; Donlon et al., 2012; Good et al., 2020
SSS	Sea surface salinity	PSU		0.125°	Daily	https://data.marine.copernicus.eu/viewer/	Buongiorno Nardelli, Droghei and Santoleri, 2016; Droghei, Buongiorno Nardelli and Santoleri, 2016; Droghei, Nardelli and Santoleri, 2018; Sammartino et al., 2022
SSH	Sea surface height	m		0.25°	Weekly	https://data.marine.copernicus.eu/viewer/	Guinehut et al., 2012; Mulet et al., 2012
SD	Standard deviation of the density gradient	kg. m^{-3}	Calculated by computing the standard deviation of the latitudinal density gradient as a measure of ocean fronts	0.125°	Daily	https://data.marine.copernicus.eu/viewer/	Buongiorno Nardelli, Droghei and Santoleri, 2016; Droghei, Buongiorno Nardelli and Santoleri, 2016; Droghei, Nardelli and Santoleri, 2018; Sammartino et al., 2022
MLD	Mixed layer depth	m		0.25°	Weekly	https://data.marine.copernicus.eu/viewer/	(Guinehut et al., 2012; Mulet et al., 2012)

Chl	Monthly cumulative chlorophyll	mg. m^{-3}	The cumulative chlorophyll of the preceeding month was used in the Random forest model.	4 km	Daily	https://oceancolor.gsfc.nasa.gov/l3/	(NASA, 2014)
Bath	Bathymetry	m	GEBCO_2019 grid.	15 arc s (0.004°)		https://www.gebco.net/data_and_products/gridded_bathymetry_data/	GEBCO Compilation Group, 2020
Ice	Distance from ice edge	Fraction /km	Geodetic distance from mean September ice edge (15 - 85% concentration area) calculated using the geosphere package in R.	0.05°	Monthly	https://data.marine.copernicus.eu/viewer/	Stark et al., 2007; Donlon et al., 2012; Good et al., 2020

4.5.3 Random Forest Model

Random forests were used to predict the presence of foraging whales based on the eight environmental covariates. Random forest is a powerful ensemble classification approach which is accurate, fast, and robust and requires minimal parameter tuning (Breiman, 2001; Fawagreh et al., 2014). It has been extensively used in ecological studies to predict species distributions and habitat suitability (Evans et al., 2011; L. Hill et al., 2017; Oppel & Huettmann, 2010; Reisinger et al., 2021). A random forest constructs a large number of decision trees (often hundreds or thousands) to form an ensemble mean. Each tree is developed using a process called recursive binary splitting, which divides the predictor space into regions based on the input covariates. The "impurity" of each split is measured by the Gini Index, and the splits are chosen to maximize the reduction in the mean Gini index. Only one random subset of all available covariates is considered at each split, which helps prevent overfitting. To increase the model's robustness, random forests use a technique called bootstrapping, which involves the creation of multiple random samples of the training data (with replacement) which are used to build each tree. This process decorrelates the trees and provides an internal estimate of model performance through an out-of-bag error estimate, which is derived from the data not included in each bootstrap sample. The final prediction is made by aggregating the outputs of all the trees.

Random forests were fit using the caret and randomForest packages in R to predict the presence of two behavioural modes (ARS and transiting) modelled from the movement patterns of the satellite tracks as described in section 4.5.1(Liaw & Wiener, 2002; Kuhn, 2008; R Core Team, 2023). For each location, values of each covariate were extracted for the day/week of each whale location for all the years of tracking data (2021 – 2024) and used to train the model. The presence of foraging whales was then predicted using this model over the whole foraging domain for each month over the two complete years of satellite tracking data (2022, 2023) to produce monthly maps of foraging habitat suitability. In building the random forests, 70% of the rows were selected for training the model, and 30% were retained for testing during cross-validation. The optimal number of trees (“ntree” parameter) was determined through a grid search which also optimises the number of covariates to possibly split at each node (the “mtry” parameter). Through this process the number of trees used to train the random forest model was determined to be 2,500 and the number of covariates split at each node was 4. Additionally, cross-validation was used on the training data set, which is a more robust approach, but typically yields poore model performance. During this process, the training data set is further divided into 10 folds, and the model is trained across each fold and validated on the remaining folds. To test the model performance, the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curve, depicting the True Positive Rate versus the False Positive Rate at various thresholds was calculated based on the predictive performance of the random forest model on the test data set (remaining 30%). The mean decrease in Gini index was used to rank the covariates according to level of importance. Maps over the known foraging domain of South African SRW predicting the presence of ARS behaviour were created for each month of the two complete years of telemetry data. For this, the probability of ARS was predicted using the trained random forest model for each month using mean monthly data of each of the covariates. The mean annual ARS habitat suitability was then calculated from the monthly data for the two complete years of telemetry data (2022 and 2023).

4.6 Results

4.6.1 General movements

Mean tag duration and path length for all tags was 221.3 ± 120 days and 9,232.6 ± 5,309 km respectively, with 3 tags still transmitting as of the 15th of July 2024 (Table 2). The longest track length was 20,509 km.

Table 2. Details of the satellite transmitters deployed on 25 adult female and one adult male southern right whales (*Eubalaena australis*) during October 2021, 2022 and 2023.

ID	First position date	Last position date	Duration (days)	First known location (lon/lat)		Last known location (lon/lat)		Track length (km)
221420	2021/10/12	2022/06/28	260	19.26	-34.43	-32.6	-59.43	8,833
221422	2021/10/12	2022/05/14	214	19.26	-34.43	4.87	-54.11	6,345
221423	2021/10/12	2022/10/17	371	19.19	-34.42	-38.02	-54.34	15,245
222172	2021/10/12	2022/03/27	166	19.26	-34.44	50.4	-46.02	7,272
222173	2022/10/16	2023/11/13	393	19.19	-34.42	13.24	-41.18	17,563
225991	2022/10/16	2023/02/13	120	19.19	-34.42	18.39	-33.78	3,372
225992	2022/10/16	2023/05/21	217	19.15	-34.41	50.33	-45.79	9,766
236904	2022/10/16	2023/04/22	188	19.16	-34.41	5.95	-49.93	6,488
236905	2022/10/16	2022/12/18	63	19.19	-34.41	39.87	-42.46	3,446
236906	2022/10/16	2023/10/17	366	19.15	-34.42	-50.63	-38.5	20,590
225990	2022/10/17	2024/02/19	491	19.2	-34.42	11.77	-43.58	13,392
225994	2022/10/17	2023/01/17	92	19.2	-34.42	-21.64	-45.34	4,860
225993	2022/10/20	2023/07/01	254	18.94	-34.34	28.75	-42.13	13,237
236907	2022/10/29	2023/09/07	313	19.28	-34.43	31.58	-40.82	8,708
236908	2022/10/29	2023/10/23	359	19.33	-34.46	51.28	-44.66	14,102
84498	2023/10/12	2024/05/23	225	19.31	-34.63	-34.44	-55.42	10,279
87636	2023/10/12	2024/07/14	276	19.2	-34.42	50.08	-45.94	5,812
87762	2023/10/12	2023/11/23	42	19.19	-34.41	-6.13	-41.34	3,088
87780	2023/10/12	2024/02/05	116	19.36	-34.5	8.99	-44.82	5,160
171990	2023/10/12	2023/10/17	6	19.3	-34.63	19.13	-34.4	334
174063	2023/10/12	2024/05/01	203	19.36	-34.56	50.22	-46.13	8,221
174316	2023/10/12	2024/07/15	277	19.19	-34.42	-32.11	-41.56	15,692
221425	2023/10/12	2024/07/14	276	19.18	-34.42	-34.92	-55.08	14,877
171993	2023/10/17	2023/11/10	24	19.35	-34.57	7.59	-40.32	1,471
174061	2023/10/17	2024/07/15	272	19.23	-34.44	5.95	-57.76	15,782
174064	2023/10/17	2024/04/04	170	19.3	-34.43	11.28	-52.37	6,115

Most whales departed the southwestern coast of South Africa in a south – south-westerly direction before dispersing widely across the South Atlantic and Southwest Indian Oceans (Figure 3). The most southerly latitude reached was -63.38°S and the most northerly location was -27.45°S close to the Namibian border. Most ARS locations were concentrated in a band between -8° and 20°E and -40° and -48°S (Figure 3). Other areas of high use were the waters surrounding South Georgia and the South Sandwich Islands, the waters around Bouvet Island as well as Crozet Islands and surrounding area.

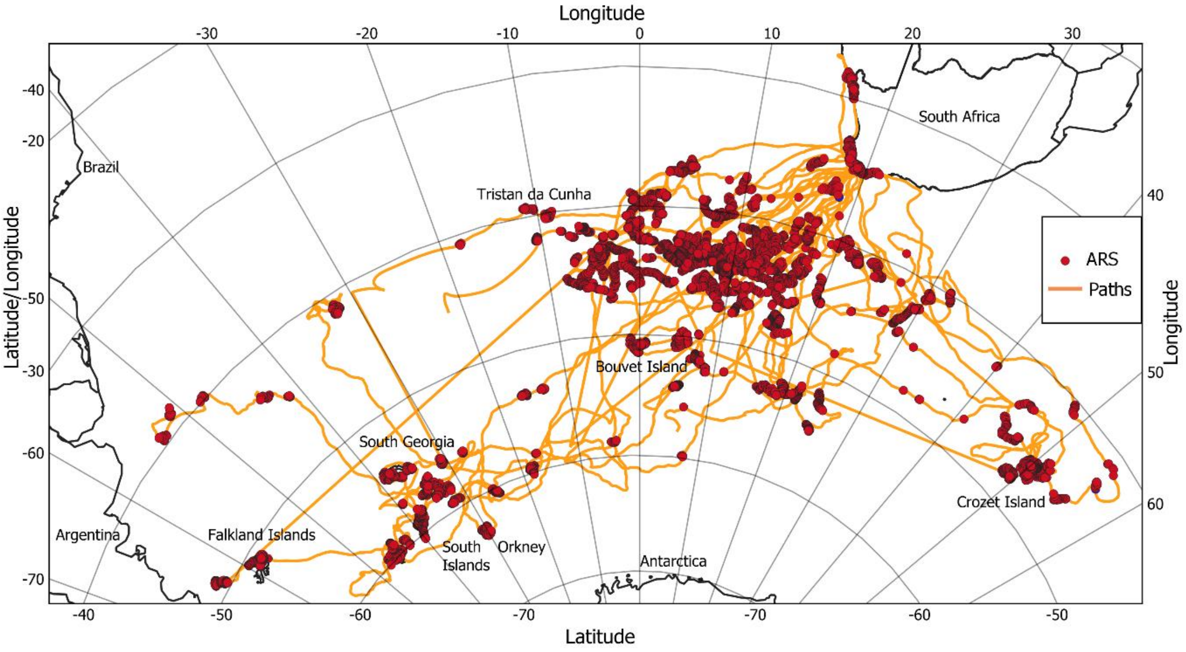


Figure 3. Map of the location tracks of the 25 adult female and one adult male southern right whales (*Eubalaena australis*) deployed during October 2021, 2022 and 2023. Red dots indicate positions where whales performed "Area Restricted Search" (ARS).

Six females conducted transatlantic crossings, with two making it as far west as the continental shelf off the coast of Argentina, and three others foraging in the South Georgia/South Orkney/South Sandwich Islands area (Figure 4a). Five females and a male utilized Crozet Islands and surrounding area as a foraging ground, and none left before the tag stopped transmitting (Figure 4b). Only two individuals spent a considerable amount of time along the African south-western coast (Figure 4c). One migrated north to the South African/Namibian border and spent a couple of months in the region before moving south into the SO on 11th of January 2023. Another animal showed extensive use of the south-western coast of South Africa between the 16th of October 2022 and the 13th of February 2023 after which the tag stopped transmitting.

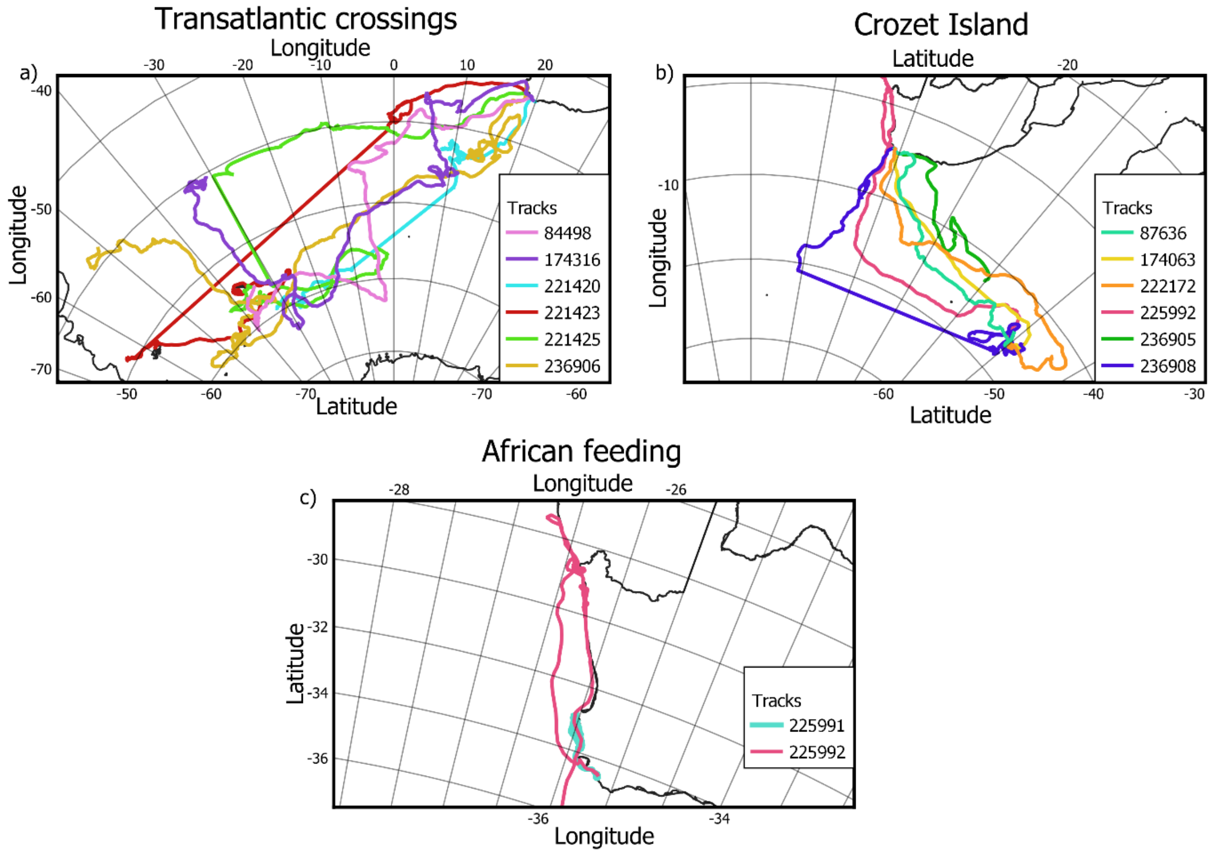


Figure 4. Examples of different migratory corridors used by South African southern right whales (*Eubalaena australis*). a) Satellite tracks of individuals which conducted transatlantic crossings; b) Satellite tracks of individuals that used the Crozet Islands region and surrounding area; c) Individual tracks of whales which remained on the South African coast during the austral summer (December – February).

Seasonality

Telemetry data showed a clear seasonal cycle in the migratory behaviour and environmental conditions experienced by the tagged whales (Figure 5). A consistent southward progression (declining latitude), and related declines in SST, SSS and SSH is evident between October and March, with a mean latitude south of 50°S between March and June. Following this, a gradual increase is observed until June/July after which these variables stabilize. However, between May and October, there is an increased standard deviation in several variables, particularly in the SSTs and SSSs (Figure 5). For SD, MLD and Chl, the seasonality is more subtle. In the SD's, slightly higher values and increased variability is evident during October – March and May – October indicating increased use of mid-latitude frontal systems during this period (Figure 5, SD). Mixed layer depth is fairly stable throughout, with gradual declines between October and March and increasing between March and October (Figure 5, MLD). Higher variability is evident between May and October. Chl peaked in March/April, but otherwise appeared fairly consistent.

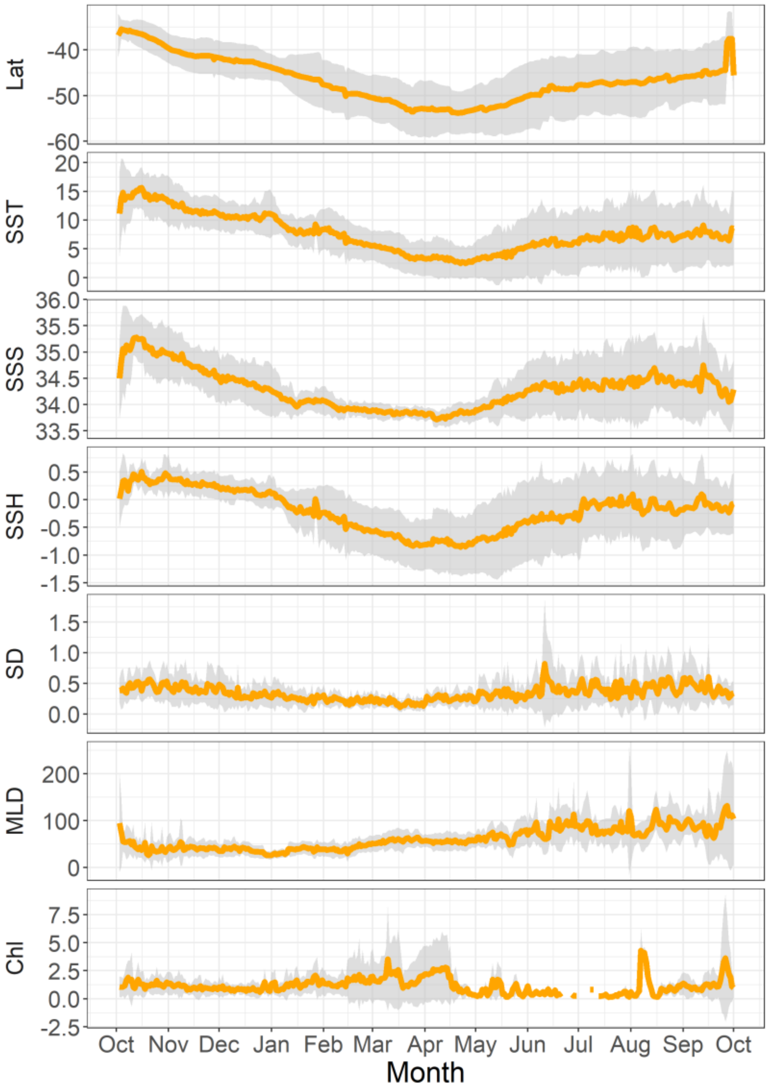


Figure 5. Mean (orange) and standard deviations (grey ribbons) of latitude (Lat, °), sea surface temperature (SST, °C), sea surface salinity (SSS, PSU), standard deviation of the density gradient (SD, kg. m^{-3} , mixed layer depth (MLD, m) and chlorophyll (Chl, $mg.m^{-3}$) per month of the year. The months are arranged from the mean start tag deployment and transmission (16th of October). Refer to methods for details about these variables.

Comparison with historical data on foraging locations

Although only five offshore satellite tracks are available from 2001/2002, there are notable differences in the migratory behaviour of whales compared to those from this study (Figure

6a). By November, four of the five whales tagged in 2001 had crossed south of 50°S. In contrast, among the 26 contemporary tags, the earliest recorded crossing of 50°S occurred on 23 December. The historical tracks suggest that most whales migrated directly in a south-southwest direction towards the Bouvet Island region, an area associated with high SRW catches during the Soviet whaling era. In contrast, contemporary tracks indicate a more gradual southward movement and increased residency time in the mid-latitudes (Figure 6b). After a rapid southward migration between September and October 2001/2002, the mean latitude of the whales became comparable to contemporary tags. Two whales then moved northwards, while the other two, which had reached the Bouvet Island region, ceased transmitting. Between January and March, the whales tagged in 2001/2002 started to move further south than those with contemporary tracks; however, by this point, only two of the 2001/2002 tags were still transmitting.

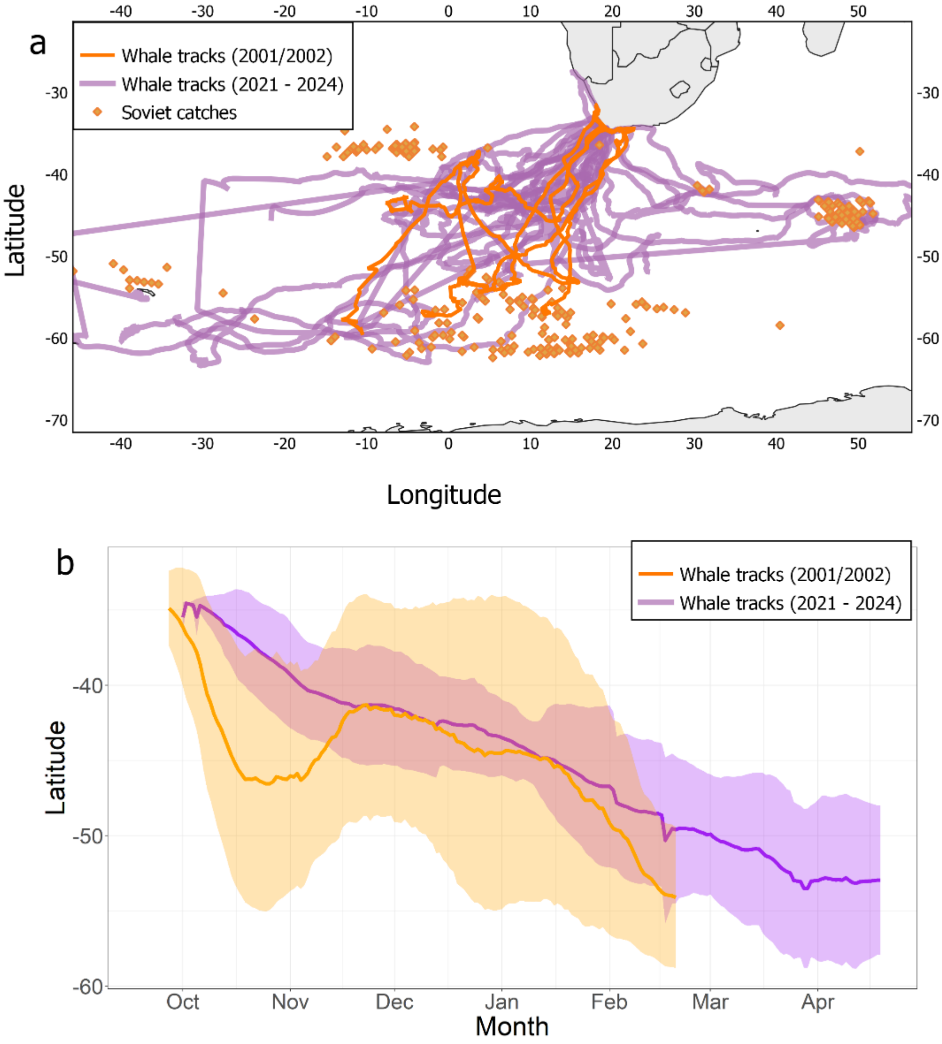


Figure 6. Comparison between southern right whales (*Eubalaena australis*) tagged in 2001/2002 (from Mate et al., 2011), and those tagged in this study. a) Map of the tracks of historical and contemporary telemetry data, as well as historical catches from the Soviet whaling period (Tormosov et al., 1998); b) mean and standard deviations of latitude for historical and contemporary tags.

4.6.2 Random Forest

Model diagnostics and performance

Results from the random forest model demonstrated a strong predictive performance for both cross-validation across multiple folds (AUC: 0.86 – 0.87) and when tested against the test data set (AUC: 0.89). Model classification accuracy was 81.3% (95% CI: 78.6–83.9%), with a Kappa statistic of 0.56, indicating moderate agreement. Sensitivity (true positive rate) for detecting the 'ARS' class was high at 90.8%, while specificity (true negative rate) for the 'transit' class was lower at 62.6%. Positive predictive value was 82.8%, and negative predictive value was 77.4%. The McNemar's test p-value (2.08e-05) suggests a statistically significant difference between the misclassification rates of the two classes. Overall, the balanced accuracy was 76.7%, showing reasonable performance in distinguishing between the 'ARS' and 'transit' classes.

Covariates and habitat selection

Bathymetry, SSS, and SST all had similar variable importances, with mean decreases in Gini index > 125 (Figure 7). This was followed by distance from the ice edge, SSH and MLD, with the two least important variables being cumulative chlorophyll and standard deviation of the density gradient (Figure 7).

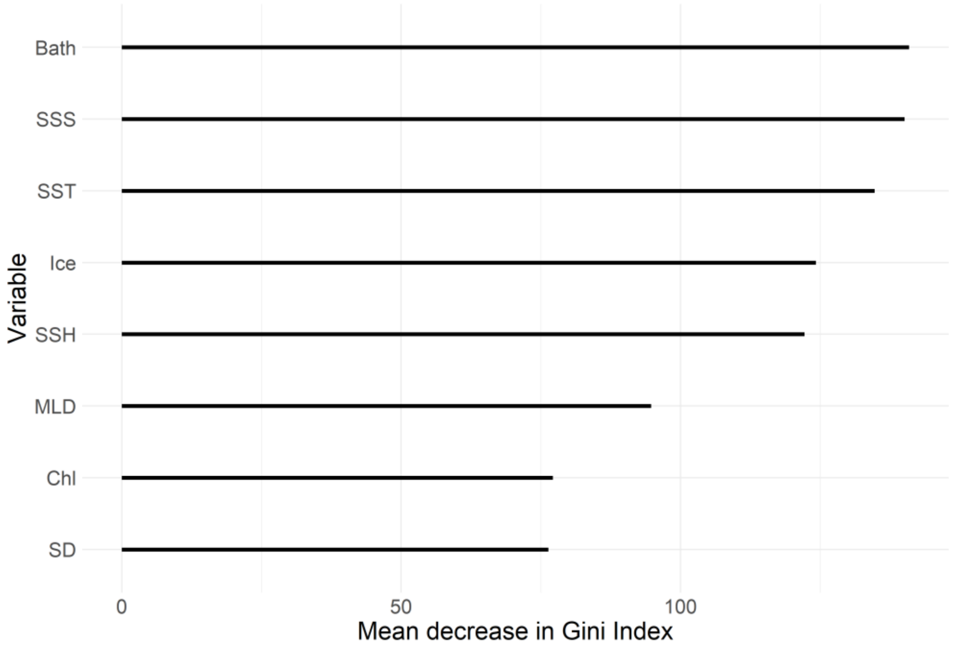


Figure 7. Model covariate importance as indicated by the mean decrease in Gini Index for each covariate. This depicts the relative importance of each covariate in predicting the presence of foraging whales.

Partial dependency plots illustrate how foraging whales select habitats based on various environmental covariates, revealing important ecological preferences and thresholds (Figure 8). SST and SSS show broad ranges of marginal suitability (SST: -1.5 – 16°C, SSS: 33.1 – 34.8 PSU) with narrow peaks (SST: 6 – 10°C, SSS: 33.5 – 34.2 PSU). SSH indicates increasing habitat suitability beyond -1.2 m, stabilizing between -1.1 m and -0.3 m, followed by a peak and decline. Mixed Layer Depth (MLD) and SD of the density gradient show high suitability in narrow ranges (MLD: 10 – 70 m, SD: 0.2 – 0.7 kg. m^{-3}) of enhanced habitat suitability. Distance from the mean September ice edge reveals a gradual increase in suitability beyond 1,000 km, with peaks at 1,700 km and 2,000 km. Ocean depth shows a minor peak between

-5,000 and -3,600 m, with suitability sharply increasing in shallower waters (> -1,000 m), pointing to a preference for continental shelves and slopes. Cumulative chlorophyll concentrations from the preceding month display increasing suitability from 0 to 3 mg. m^{-3}, followed by a slight decline and a plateau until 13 mg. m^{-3}, after which probabilities of habitat selection decline.

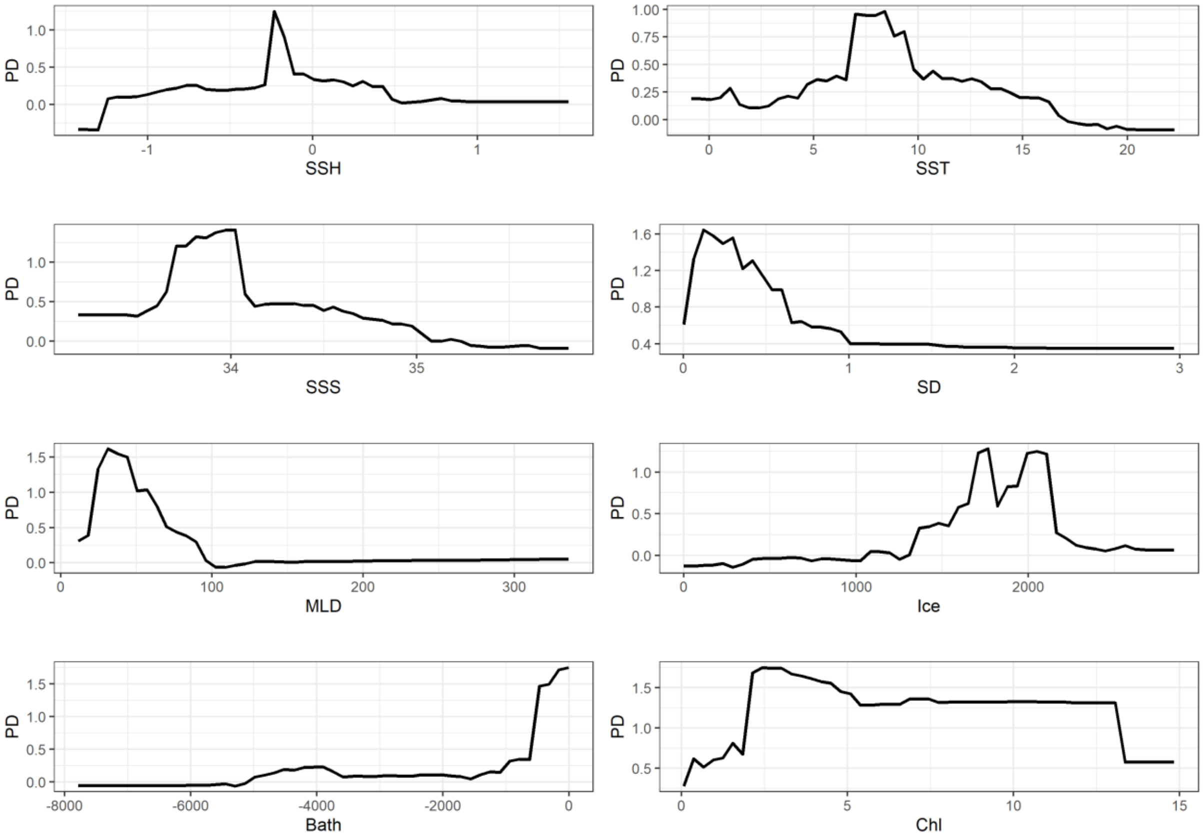
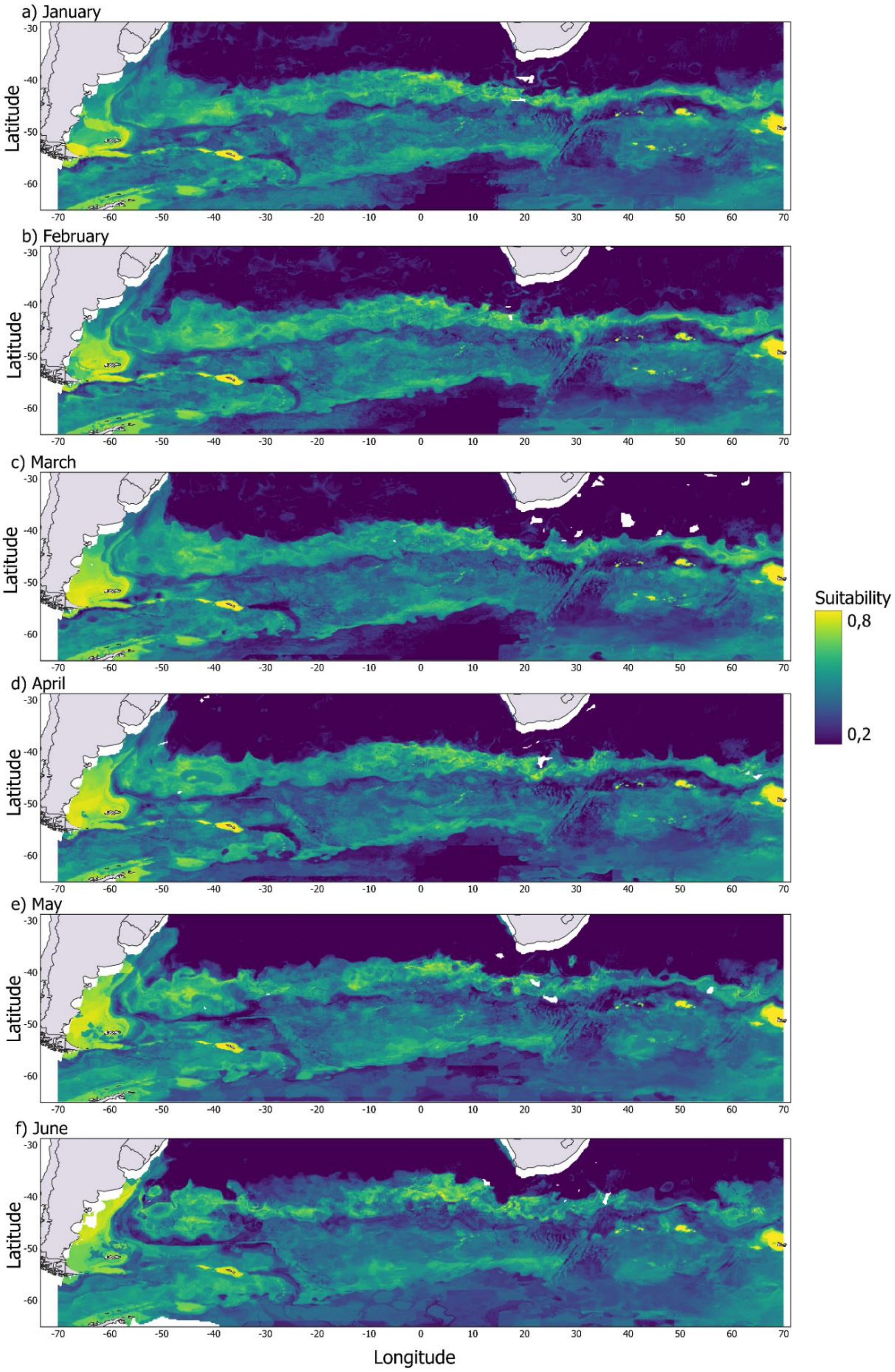


Figure 8. Results of the Random Forest models showing the predicted response probability of Partial dependencies (PD) over values of sea surface height (SSH, m), sea surface temperature (SST, °C), sea surface salinity (SSS, PSU), standard deviation of the density gradient (SD, kg. m^{-3}), mixed layer depth (MLD, m), distance from mean September ice edge (Ice, km), ocean depth (Bath, m), cumulative chlorophyll of the preceding month (mg.m^{-3}).

Monthly maps predicting the presence of foraging SRWs show the seasonal variation in habitat suitability (Figures 9). Generally, shallower continental shelf regions showed high suitability during all months, with subtle increases towards austral summer. Aside from continental shelf areas, two regions of higher use are apparent: 1) A band of high suitability situated between 38°S - 45°S, reaching its maximum northward position in July – September (Figure 9g – i), and its minimum southward position in December – February (Figure 8a, b and Figure 9i), and 2) a region south of 50°S, which appears moderately favourable throughout the year, with slightly more favourable conditions evident in the austral summer and autumn months.


a) January
b) February
c) March
d) April
e) May
f) June
Latitude
-30
-40
-50
-60
-70
-60
-50
-40
-30
-20
-10
0
10
20
30
40
50
60
70
Longitude
Suitability
0,8
0,2

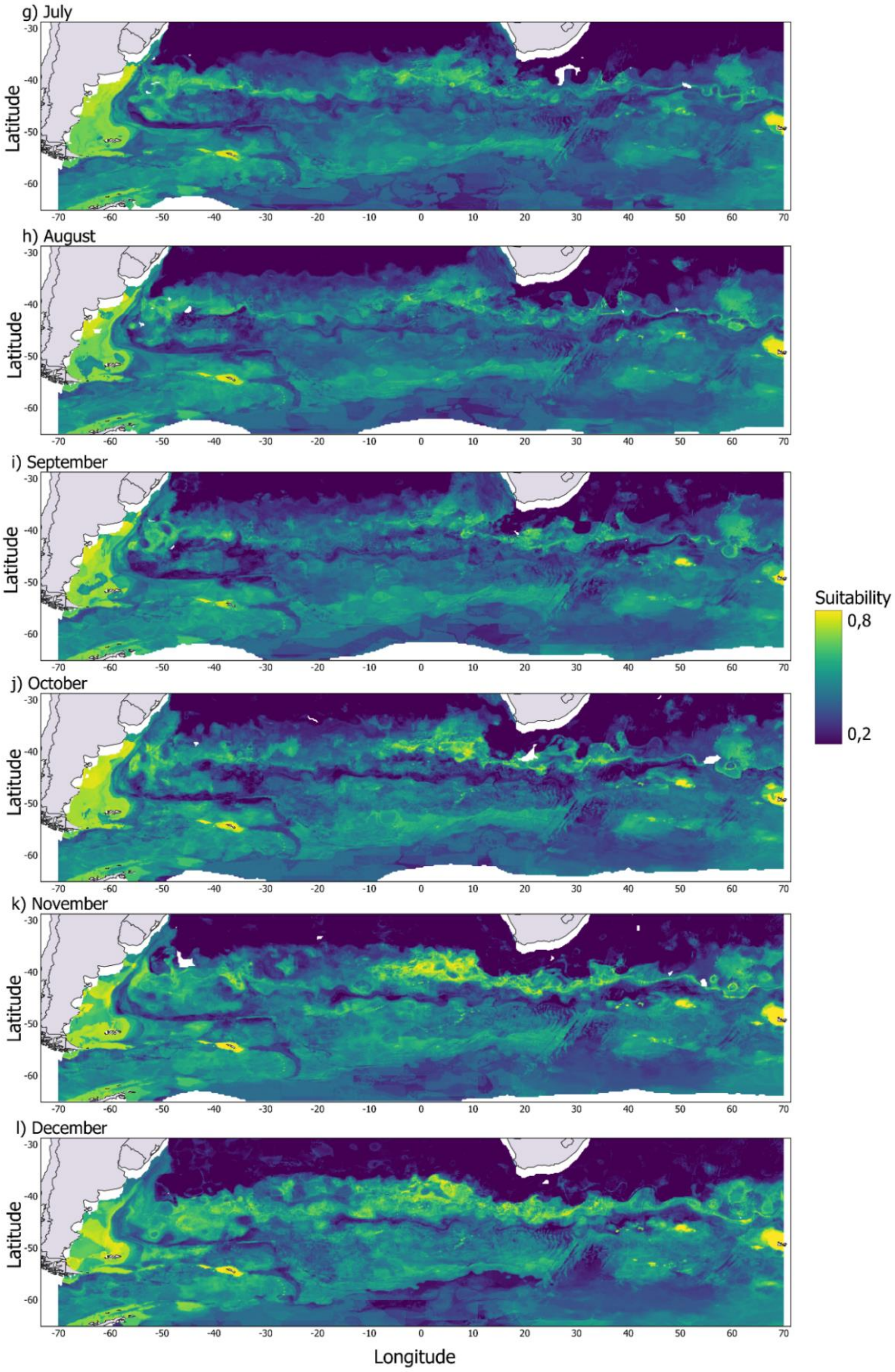


Figure 9. Monthly maps for January – December (a to l) habitat suitability as predicted by random forests for 2023. These were created from the mean of each month of the two complete years of satellite telemetry data (2022 and 2023). Refer to the Appendix for 2022.

The presence of the aforementioned mid-latitude and high-latitude modes of feeding becomes more apparent in the annual mean habitat suitability (Figure 10). Good agreement can be seen with positions where whales performed ARS during the two years analysed (2022 and 2023).

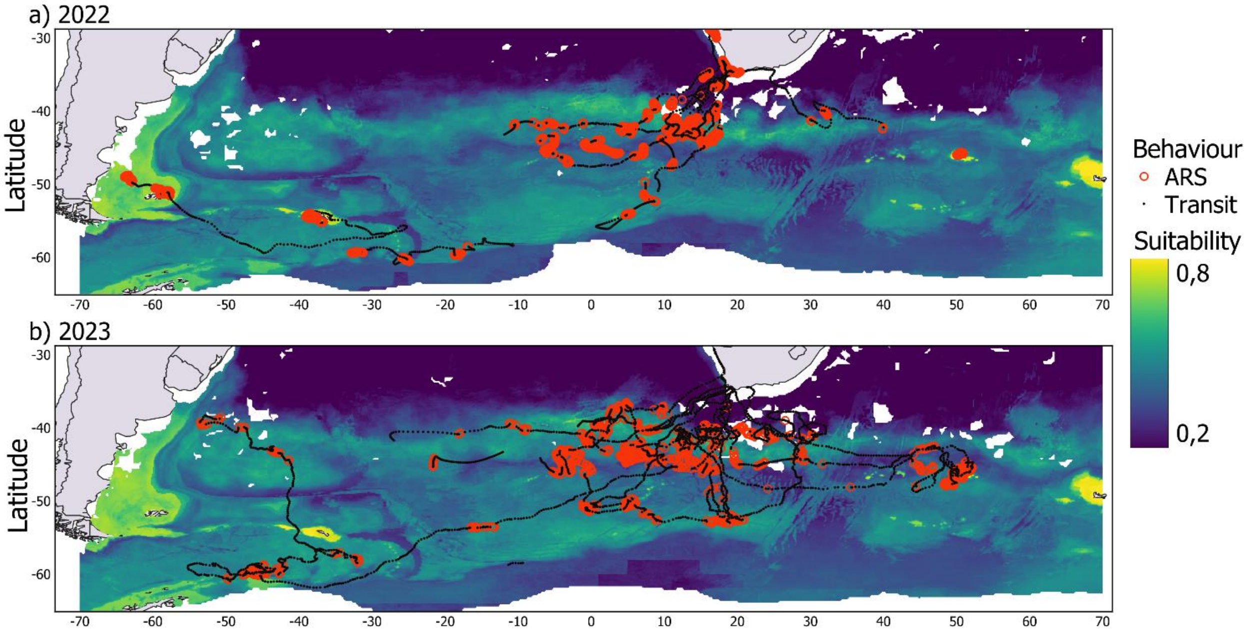


Figure 10. Maps for southern right whales tagged in a) 2022 and b) 2023 depicting tracks (black lines), Area Restricted Search behaviour (red dots) as well as foraging habitat suitability as predicted by random forests. The latter were created by calculating the annual means in habitat suitability from the monthly means of each year.

4.7 Discussion

This study shows, for the first time, the contemporary offshore migratory routes and foraging habitat for the South African population of SRWs. Results indicate the use of several broad regions; the mid-latitude band associated with the subtropical and subantarctic fronts, the waters surrounding Bouvet Island, and the Crozet Islands area. Additionally, the high use of the southwest Atlantic is indicated, including the Patagonian shelf, which was previously unknown for the population. The presence of foraging whales across their known foraging domain is accurately predicted using random forests based on eight environmental covariates, providing insights in the oceanographic characteristics of SRW foraging ground.

Despite a general consistency with the foraging grounds described by historical whaling and telemetry data, novel foraging behaviours were observed. This includes the first documented transatlantic crossings for the population (Vermeulen, et al., 2023), and provides support in addition to genetic evidence for connectivity with the Argentinian and Brazilian populations which share foraging grounds (E. L. Carroll et al., 2015, 2018; Patenaude et al., 2007; Valenzuela et al., 2009a; A. Zerbini et al., 2015). Although the two populations on either side of the Atlantic Ocean are genetically different, they are more similar than those in the Pacific, and the observed use of the same foraging grounds confirms that they interact on a more intimate level than previously thought (E. L. Carroll et al., 2015, 2020; Neveceralova et al., 2022; Patenaude et al., 2007). Carroll et al. (2020) hypothesised that as populations grow, such interactions between populations using different calving grounds will increase, potentially driving enhanced gene flow between populations, and re-establishing historical connections. Additionally, the frequency of these migrations may increase as climate change alters the availability of prey (Carroll et al., 2020; Vermeulen, et al., 2023). Furthermore, the first evidence of shared foraging grounds between the South African and Australian populations was documented at the Crozet Islands, suggesting that even between the two genetically distinct clades of the Atlantic and Pacific (Patenaude et al., 2007), some level of connectivity does exist (Vermeulen et al., 2024).

The ability for SRWs to adapt their migratory behaviour to changing environmental conditions depends on the level of fidelity to foraging grounds, and which mechanisms control behaviour at different stages of their migration. For example, low levels of migratory plasticity (high site fidelity to foraging grounds) would result in ecological traps, rendering the species more vulnerable to climate change (Hale & Swearer, 2016; Schlaepfer et al., 2002). Some degree of culturally inherited site fidelity to foraging grounds is suspected in the species (Valenzuela, et al., 2009), but the high levels of spatial variability evident in the tracks presented here likely indicates SRWs show relatively high levels of migratory plasticity once whales reach broadly favourable regions. Furthermore, additional support for the ability to adapt their migratory behaviour to altered conditions is the northward shift in foraging distribution revealed by isotope analysis (Derville et al., 2023; van den Berg et al., 2021). This shift is hypothesised to be driven by increased variability of the seasonal sea ice zone, with a consequent reduction in Antarctic krill availability, and as such indicates some adaptability to changes in environmental conditions (Agrelo et al., 2021; Germishuizen et al., 2024; Seyboth et al., 2016; van den Berg et al., 2021). The satellite tracking data presented here also shows evidence of this northward shift compared to historical data, confirming a high use of mid-latitudes and a decreased use of high latitude feeding grounds where krill is the primary food source (Mate et al., 2011; Tormosov et al., 1998). Based on the data presented here, high-latitude foraging may only be more prevalent when conditions are favourable in supporting high Antarctic krill biomass. Regardless, the observed changes in migratory behaviour appears to be associated with an energetic cost as suggested by observed declines in body condition and reproductive rates (Brandão et al., 2023; Vermeulen, et al., 2023). An exception to the adaptability described may lie in whales that target specific regions such as Crozet Island, as individuals using this region displayed high levels of residency, and didn't leave the area beforetags stopped transmitting. This may suggest that at least part of the population is reliant on specific geographical regions and related site fidelity, possibly displaying less migratory plasticity. Consequently, certain behavioural cohorts of the population may be more vulnerable to ecological traps arising from an inability to adapt to environmental changes to their offshore foraging grounds. However, data could also simply imply that the Crozet Islands region has sufficient prey biomass to meet the demands of foraging whales. Further investigations into site fidelity to foraging grounds in the South African population is required to provide further insights into the ability of SRWs to adapt their migratory strategies to changing environmental conditions (Valenzuela et al., 2009a).

The random forest performance when validated against a subset of the original data was good, especially considering the huge spatial extent and wide range of environmental conditions over this region. Despite comparing different years, good agreement can also be seen when comparing the habitat suitability maps with telemetry data from other populations that use the Atlantic as a foraging ground (e.g., Zerbini et al., 2015, 2018). Bathymetry, SSS, SST, distance from the September ice edge and SSH broadly had similar importance in predicting whale presence. This was expected since these variables exert a strong control on SO oceanography and the availability of food, and have been widely used in SO marine predator habitat modelling (Praca et al., 2009; Reisinger et al., 2018, 2021; Torres et al., 2015). Interestingly, cumulative chlorophyll of the preceding month and standard deviation of the density gradient were the least important variables predicting foraging whales. Chlorophyll concentration is a widely used variable in habitat modelling as it quantifies the amount of primary production in the system. Once Chl exceeded 2 mg.m^{-3} differences in behavioural mode were indiscernible. Therefore, it appears to be a poor predictor of whale foraging at short time scales (refer to Chapter 2).

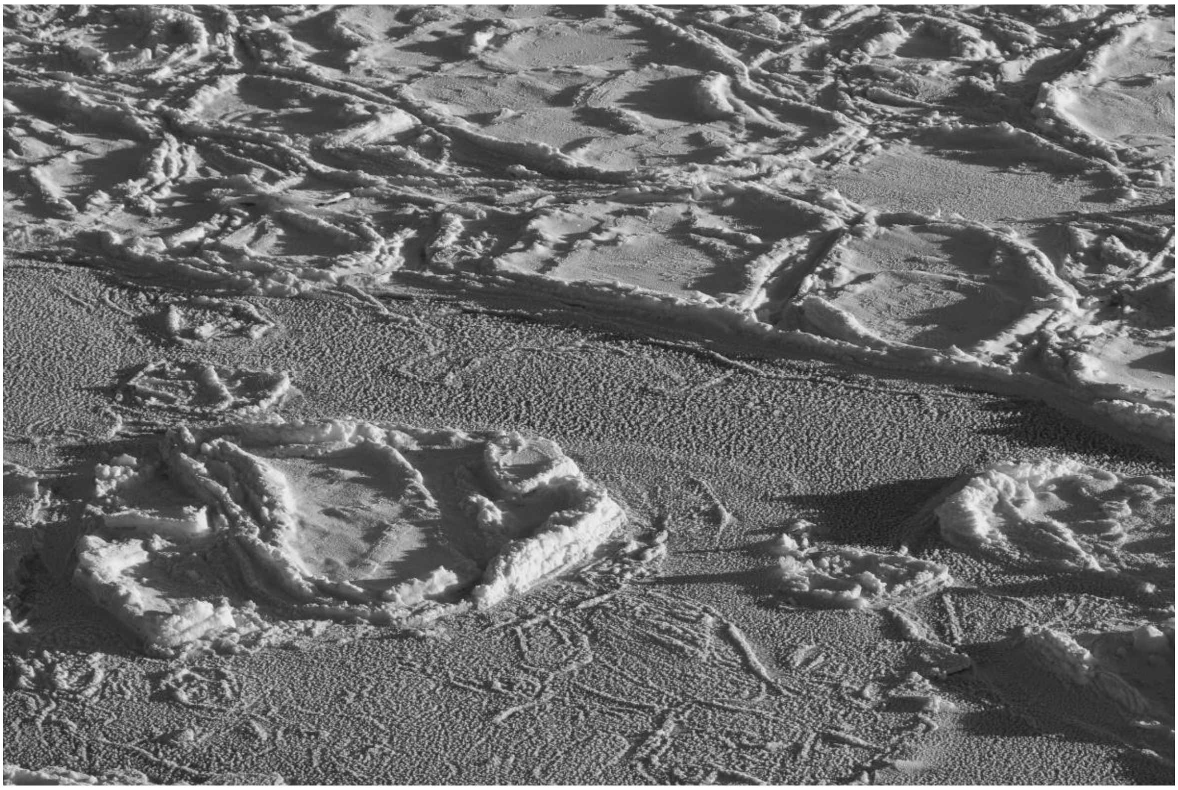
The spatial distribution of suitable foraging habitat for SRW confirms the importance of subtropical and subantarctic fronts (Carman et al., 2019). The seasonal position of this band of high habitat suitability is broadly like that described by Carman et al. (2019) through monthly Ensemble Distribution Models applied to historical SRW whaling data. Despite using different approaches, differences in the relative importance of the high latitudes surrounding Bouvet Island are evident between Carman et al. (2019) and the present study, further highlighting the reduced contemporary use of this region. Despite these differences, the Bouvet Island and surround area is still distinguishable from other regions as an important ecosystem due to its bathymetry, position in the seasonal sea ice zone and ACC (Jacob et al., 2006). The importance of continental shelf regions and other subantarctic islands such as Crozet Islands and South Georgia can be seen, which provide suitable habitat year-round.

Notwithstanding the high predictive performance of random forests in resolving SRW foraging habitat, there are a few aspects to consider. Random forest models are known to be highly sensitive to the training data. For example, models trained on telemetry data from two populations of grey petrels on different SO archipelagos, predicted poorly when validated between archipelagos (Torres et al., 2015). Hence, a more robust methodology is to develop regional models for different populations and validate them against each other, and to calculate the ensemble mean (Reisinger et al., 2021). This is particularly true for telemetry data, which are prone to high levels of autocorrelation (Roberts et al., 2017; Schratz et al., 2019). Future work with the aim of projecting habitat suitability over the whole SO should include comparisons across populations and incorporate a combination of data types (whaling and telemetry) to increase the predictive power of the model.

The findings of this study provide valuable information on the contemporary migratory and foraging behaviour of South African SRW. Given large scale environmental changes already documented in the SO, particularly in the seasonal sea ice zone (Flores, et al., 2012; Hobbs et al., 2016; Kawaguchi et al., 2024;

Melbourne-Thomas, 2020), understanding the relationship between animal behaviour and the environment is crucial to investigating future ecosystem changes

5. General discussion and conclusions



CHAPTER 5

5.1 General discussion

This work provides a comprehensive example of how SRWs can be used to better understand the natural world, and the role of multidisciplinary work in understanding climate change and variability. This thesis demonstrates a strong connection between SRWs and their physical environment, and significantly extends our knowledge of their foraging and migratory behaviour. This not only highlights the threat this species faces under anticipated rates of global climate change, but also its potential as a sentinel of SO climate variability.

This thesis provides a holistic framework for understanding the environment through a variety of different top predator monitoring techniques. Chapter 2 examined the connection between a reduction in reproductive success in the South African SRW population and environmental changes to their offshore foraging grounds. This utilized a long time-series of population demographic data which displayed a steep decline in three-year calving cycles, and an increase in 4- and 5-year cycles after 2009. This period coincided with extensive sea ice declines in key SRW foraging grounds. That Chapter therefore provided further support for the hypothesis that the demographic changes being observed across SRW populations are likely being driven by changes to the sea ice environment (Agrelo et al., 2021; Leaper et al., 2006; Seyboth et al., 2016; van den Berg et al., 2021). The reduced stability of the seasonal ice zone likely negatively impacts Antarctic krill recruitment and dispersal, thus altering high latitude prey availability. This drives distribution shifts in the foraging behaviour of SRWs and reduces foraging efficiency, meaning females must feed for longer to achieve the necessary energy reserves to sustain pregnancy.

Chapter 3 on the other hand investigated the use of animal borne CTD instruments and depth measuring tags to describe changes in migratory behaviour in relation to environmental variables. Although the sample size was small, the findings of that work highlight the importance of ocean fronts as foci for foraging predators (Bost et al., 2009; Carman et al., 2019). Furthermore, the CTD instruments characterised the environment of their offshore foraging grounds. Whales increased the prevalence of foraging behaviour (ARS) when encountering cooler fresher waters. However, once whales reach generally favourable foraging conditions, finer scale changes in foraging behaviour did not accompany changes in environmental variables and likely indicates that other mechanisms of detecting food such as communication, visual and olfactory are used (Bouchard et al., 2019; Cronin et al., 2017; Podolskiy et al., 2024). Furthermore, whales targeted regions of low chlorophyll concentration, highting a mismatch between the presence of high algal concentrations and dense prey aggregations. Work of this nature is crucial for the identification of important features for ocean productivity. Additionally, trends and shifts in these properties can be projected under different climate scenarios to better understand how the population may respond to future changes in the earth’s climate.

Chapter 4 addressed an important knowledge gap of the contemporary migratory behaviour of South African SRW’s. Previous knowledge stemmed from historical whaling locations and telemetry data from only a few animals, and provided a limited understanding of the migratory routes used in the population (Mate et al., 2011; T. D. Smith et al., 2012; Tormosov et al., 1998). A comprehensive analysis of their offshore foraging habitat distribution is fundamental to expanding the use of sentinel species in monitoring the environment. This identifies the specific regions being monitored, providing spatial context to the observed changes. Without this information, only the occurrence of change would be known, without insight into where it has taken place. Results of this chapter significantly extended our understanding of South African SRW foraging distribution by reporting on the movements of 26 whales instrumented with satellite transmitters in 2021, 2022 and 2023. This provides three years of tracking data, and a robust assessment of their contemporary movement. The probability of foraging behaviour was predicted over the whole South Atlantic and south-west Indian ocean sectors using random forest. Through these tags, the importance of the mid-latitude subantarctic and subtropical fronts, the high-latitude Antarctic krill grounds, and continental shelf and island regions such as Crozet Islands are described. Furthermore, additional support is provided for a northward shift in foraging behaviour when compared to historical tagging and whaling data. This shift was previously described by stable isotopes, which suggest reduced use of high-latitude foraging grounds in populations which use the South Atlantic (Derville et al., 2023; van den Berg et al., 2021).

Overall, this thesis provides valuable insights into the relationship between SRWs and their environment, and the threat climate change poses to the recovery of species. Understanding the relationship between animals and the environment has far reaching applications. For example, identifying important oceanographic regions for biodiversity can assist in the development of protected areas (Hindell et al., 2020; Sergio et al., 2008). Top predator diversity and presence is a strong predictor of overall biodiversity and ecosystem function (Natsukawa & Sergio, 2022; Sergio et al., 2005). Therefore, oceanographic features and regions of high use by top predators represent areas with diverse assemblages at all trophic levels.

This is a powerful concept, since by monitoring even at the single species level, a wealth of information can be inferred about the state of the ecosystem.
Furthermore, work focussing on the relationship between predators and their environment is an important proponent of multidisciplinary solutions to climate science. This is because it connects physical processes with biology and provides mutually beneficial information to several fields. This is aside from the more direct examples such as the use of predators as carriers of instrument probes. Behavioural and physiological responses to the environment essentially provide oceanographers with evidence for the implications of physical processes. Amplified phytoplankton growth at frontal zones, for example, provides additional support for increased interactions between nutrients from the deep water and the euphotic zone (Franks, 1992). In the same way, the affinity SRWs portrayed for this new characterization of ocean fronts in Chapter 3, confirms this feature has distinct oceanographic properties that result in increased prey availability. Identifying this relationship can thus lead to further investigations into the mechanisms that distinguish this feature from the rest of the ACC.

Top predators often exude tremendous charisma and connect people across multiple disciplines. Common ground can always be established between people through the appreciation of these majestic creatures. This is not a trivial aspect of the value of these iconic predators, since it creates with it an avenue through which to conserve more ambiguous ecological entities (Sergio et al., 2006). Through using a combination of SRWs reproductive success, migratory behaviour, and foraging strategies, this work highlights the species' sensitivity to its environment. It also provides a solid foundation on which to further our understanding of the SO ecology through SRs, and to predict future alterations to SRW foraging grounds and implications for the conservation of the species. Investigations of this nature highlight the value of multidisciplinary work, and of top predator species as sentinels.

5.2 Future work

The global SRW population has grown steadily since being declared commercially extinct in 1936 and enduring an additional period of Soviet era whaling between 1951-1971 (T. D. Smith et al., 2012; Tormosov et al., 1998). Despite the extent to which the population has recovered, the work of this thesis indicates another brooding pressure which SRWs face, that of climate change. Therefore, future work should focus on quantifying and projecting future population trajectories under increasing rates of environmental change. This may include the development of a predictive model using the relationship between high-latitude variability to the seasonal ice zone and SRW reproductive success described in Chapter 2. It will also involve a better understanding of these effects, and the mechanistic pathways through which reproductive rates are impacted. This can be addressed through continued monitoring of reproductive success in relation to environmental variability and assimilating more recent years of demographic data. Furthermore, the on-going satellite tagging effort should continue to increase sample size, and so that investigations into interannual variability in migratory behaviour can be conducted in relation to changing environmental conditions. This can provide an understanding into the adaptability of the species to changing conditions, as well as better insights into how changes in foraging behaviour can impact reproductive success. For example, insight into migratory behaviour changes in relation to different sea ice conditions may provide further support for the relationship between sea ice and SRW reproductive success. Underscoring this body of work is the value of time-series data, and it thus imperative that annual surveys are continued as the potential of such data sets continue to increase with time. This also applies to satellite telemetry to provide an understanding of changes in migratory behaviour over time. Furthermore, most tagged individualswere biopsy sampled. Therefore, satellite tagging data can be used in combination with isotope data, and the relationship between isotope signatures and migratory behaviour can be investigated. This can be used to improve predictions of foraging locations based on stable isotopes alone. Moreover, population health monitoring is a crucial piece of the puzzle, and variables such as maternal body condition should continue to be assessed. The combination of these two data sets will significantly increase our understanding of the relationship between population dynamics and environmental change.

The tremendous potential of CTD tags is highlighted in Chapter 3. This is especially valuable considering the amount of information gathered from only two tags that provided enough locations to be able to perform a robust analysis. Therefore, increasing the sample size will significantly strengthen the analysis and findings of this work. The South African population of SRW hold huge potential for the use of CTD tags due to the geography of the South African coastline, which has a narrow continental shelf thus resulting in whales quickly moving into oceanic regions where they can gather deeper profiles. Their fairly predictable movement south provides transects of the upper ocean with high spatial resolution and have the potential to provide important oceanographic information in data sparse regions. Therefore, the use of SRWs in filling data gaps should be investigated.

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7. Appendices

7.1 Appendix A: POPULATION CHANGES IN A SOUTHERN OCEAN KRILL PREDATOR POINT TOWARDS REGIONAL ANTARCTIC SEA ICE DECLINES

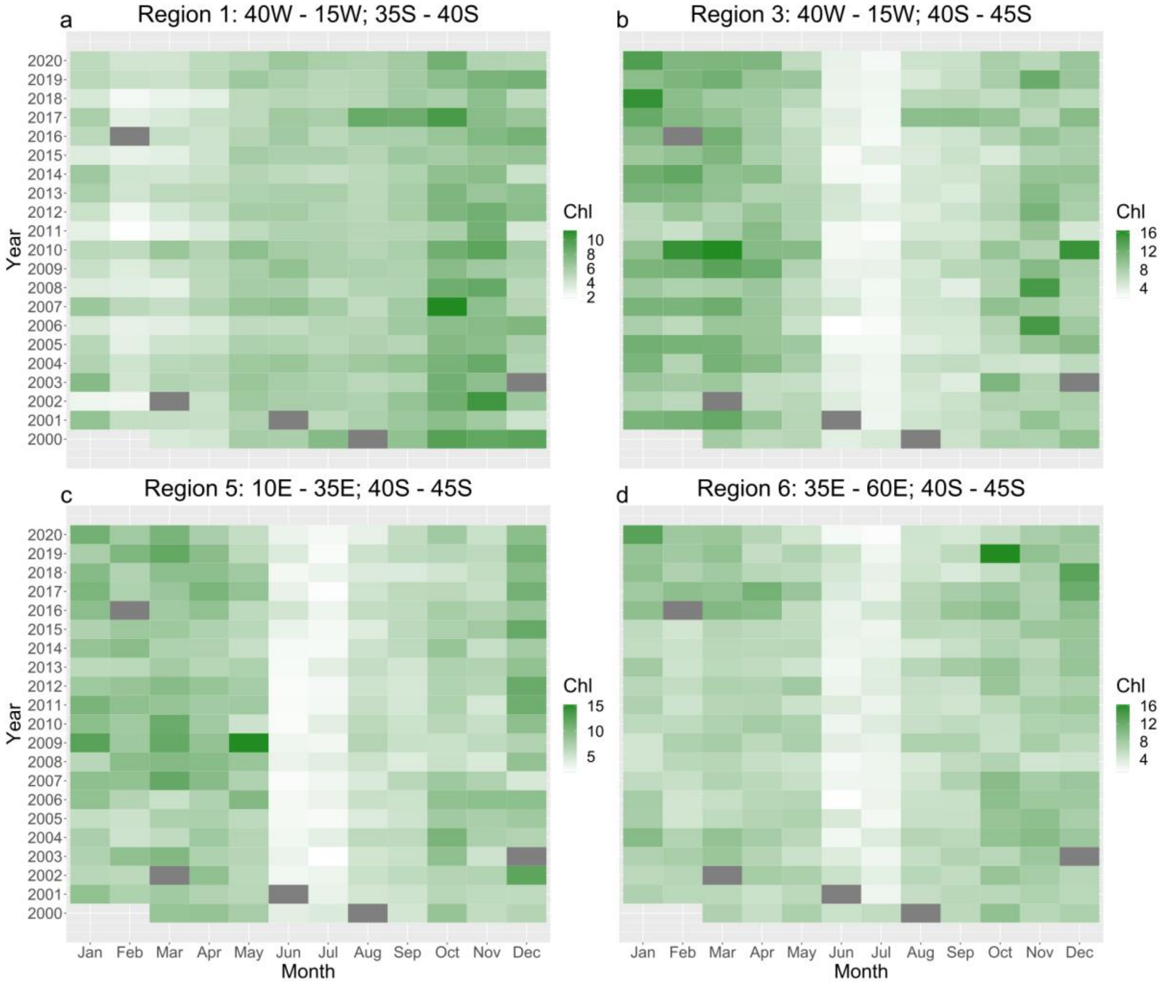


Figure A1: Heat maps of Monthly Chlorophyll Index for selected regions (2000 – 2020). Monthly mean Chlorophyll Index heat maps for (a) Region 1, (b) Region 3, (c) Region 5 and (d) Region 6 over the time-series (2000 – 2020). Grey blocks indicate months which had insufficient observations to compute the Monthly Chlorophyll Index (see Methods)

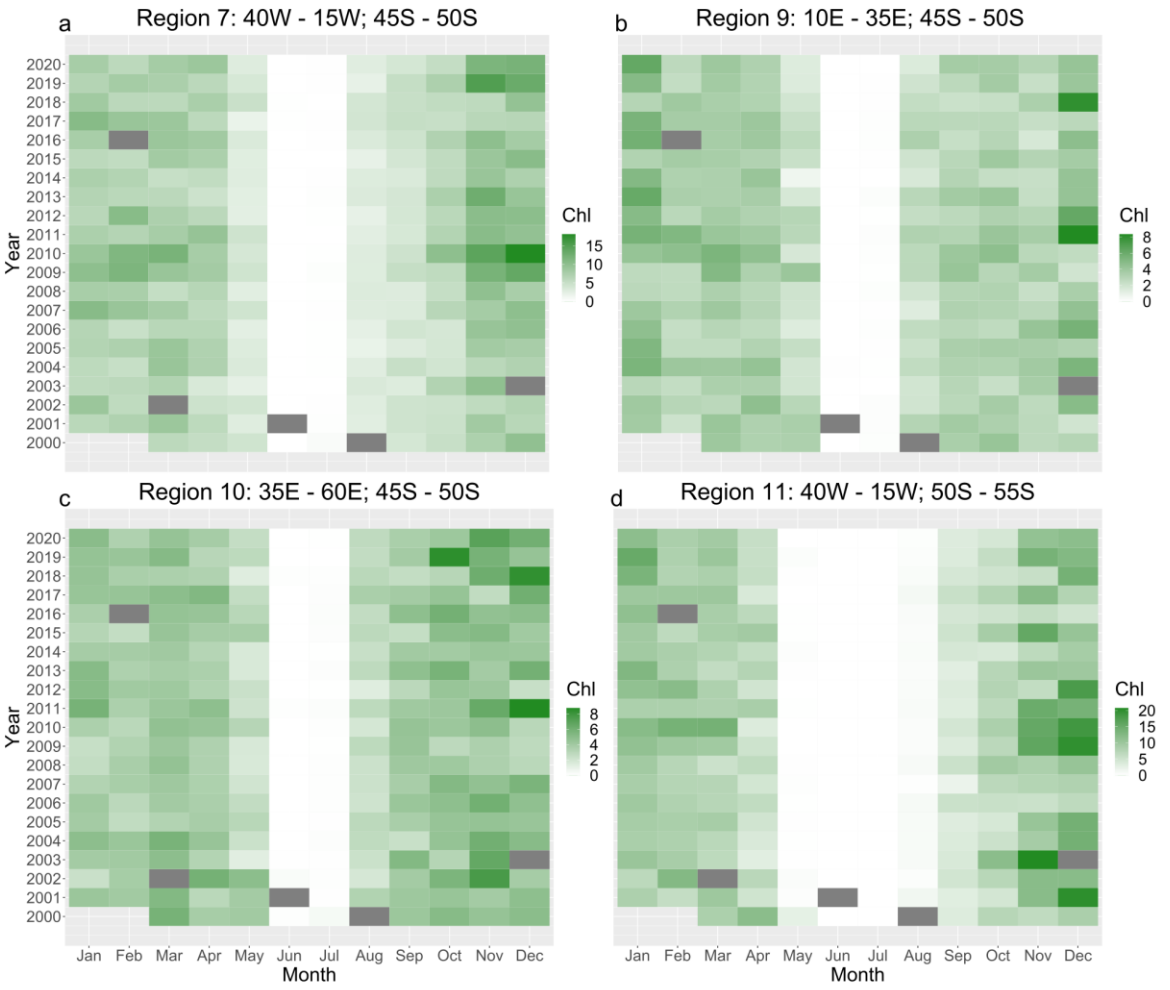


Figure A2: Heat maps of Monthly Chlorophyll Index for selected regions (2000 – 2020). Monthly mean Chlorophyll Index heat maps for (a) Region 7, (b) Region 9, (c) Region 10 and (d) Region 11 over the time-series (2000 – 2020). Grey blocks indicate months which had insufficient observations to compute the Monthly Chlorophyll Index (see Methods).

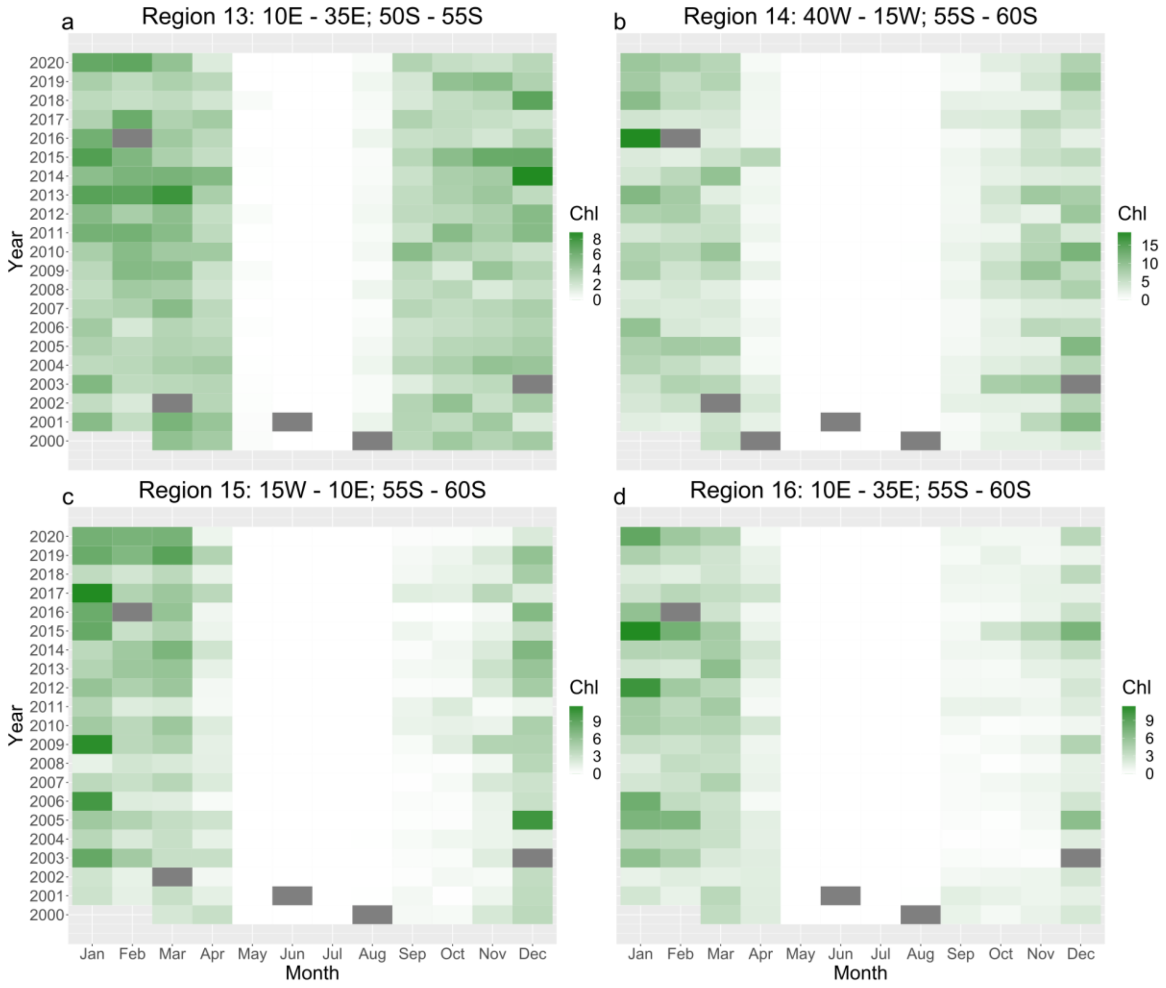


Figure A3: Heat maps of Monthly Chlorophyll Index for selected regions (2000 – 2020). Monthly mean Chlorophyll Index heat maps for (a) Region 13, (b) Region 14, (c) Region 15 and (d) Region 16 over the time-series (2000 – 2020). Grey blocks indicate months which had insufficient observations to compute the Monthly Chlorophyll Index (see Methods).

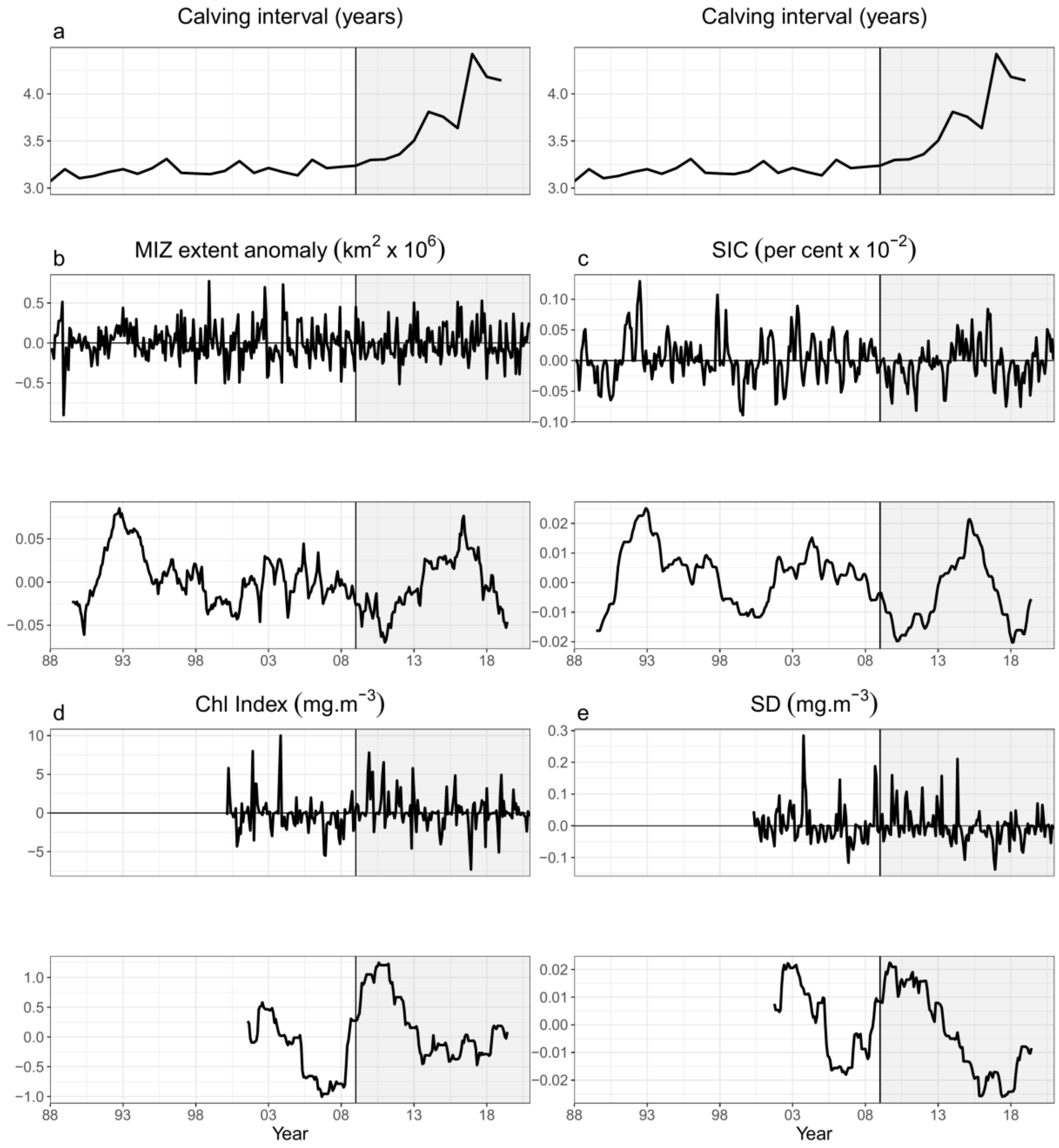


Figure A4: Indicators for Region 14+. Monthly anomalies (top panel) and rolling mean of the anomaly (bottom panel) for (b) Mean monthly marginal ice zone (MIZ) extent anomaly compared to the 1988 – 2020 mean, (c) mean monthly sea ice concentration anomaly (SIC) compared to the 1988 – 2020 mean, (d) Monthly Chlorophyll Index anomaly compared to the 2000 – 2020 mean and (e) Monthly chlorophyll standard deviation anomaly compared to the 2000 – 2020. The top panel (a) shows the mean calving interval. The grey-shaded region highlights the period of reduced southern right whale reproductive success after 2009.

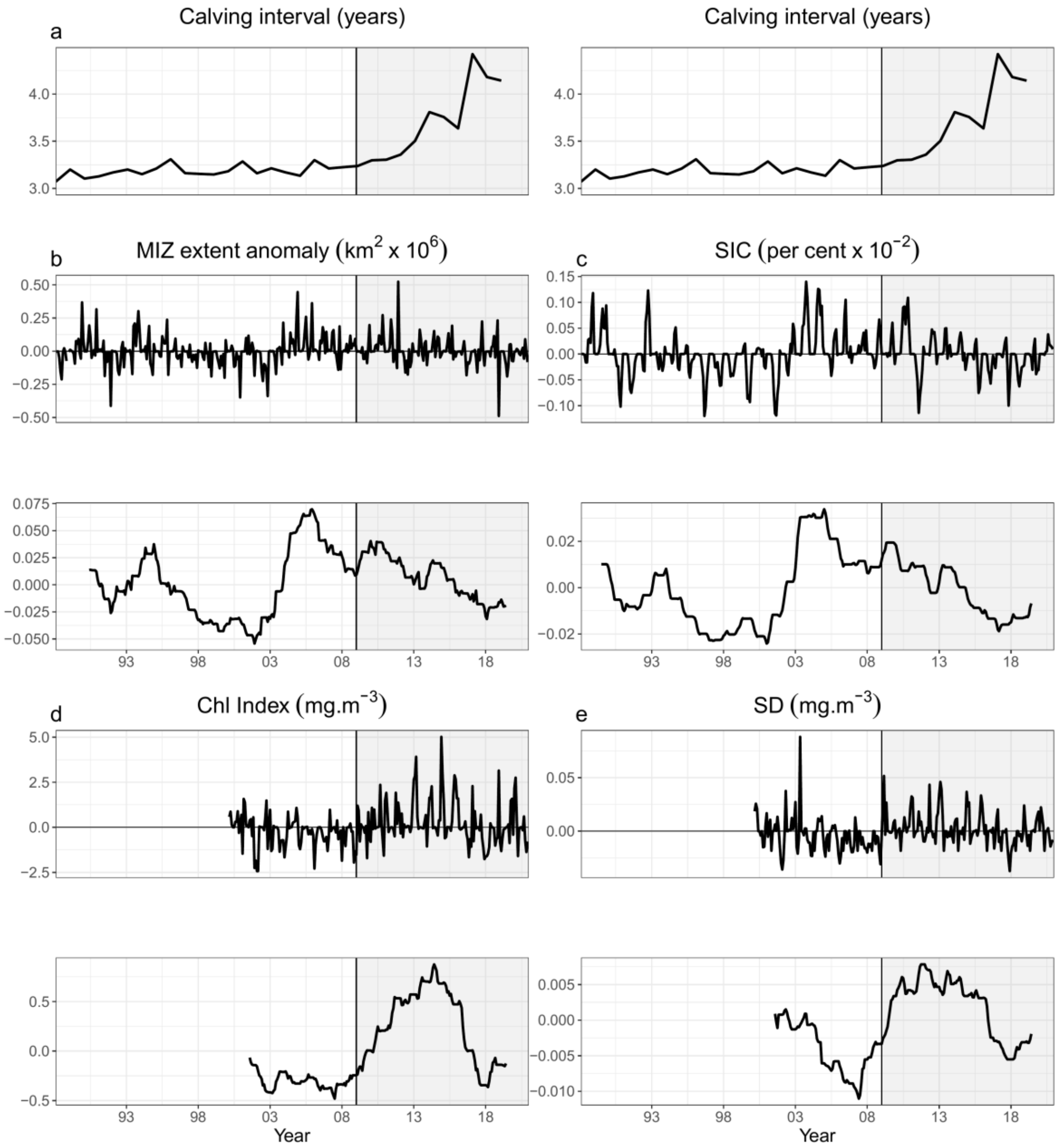


Figure A5: Indicators for Region 16+. Monthly anomalies (top panel) and rolling mean of the anomaly (bottom panel) for (b) Mean monthly marginal ice zone (MIZ) extent anomaly compared to the 1988 – 2020 mean, (c) mean monthly sea ice concentration anomaly (SIC) compared to the 1988 – 2020 mean, (d) Monthly Chlorophyll Index anomaly compared to the 2000 – 2020 mean and (e) Monthly chlorophyll standard deviation anomaly compared to the 2000 – 2020. The top panel (a) shows the mean calving interval. The grey-shaded region highlights the period of reduced southern right whale reproductive success after 2009. Refer to Supplementary for regions not depicted here.

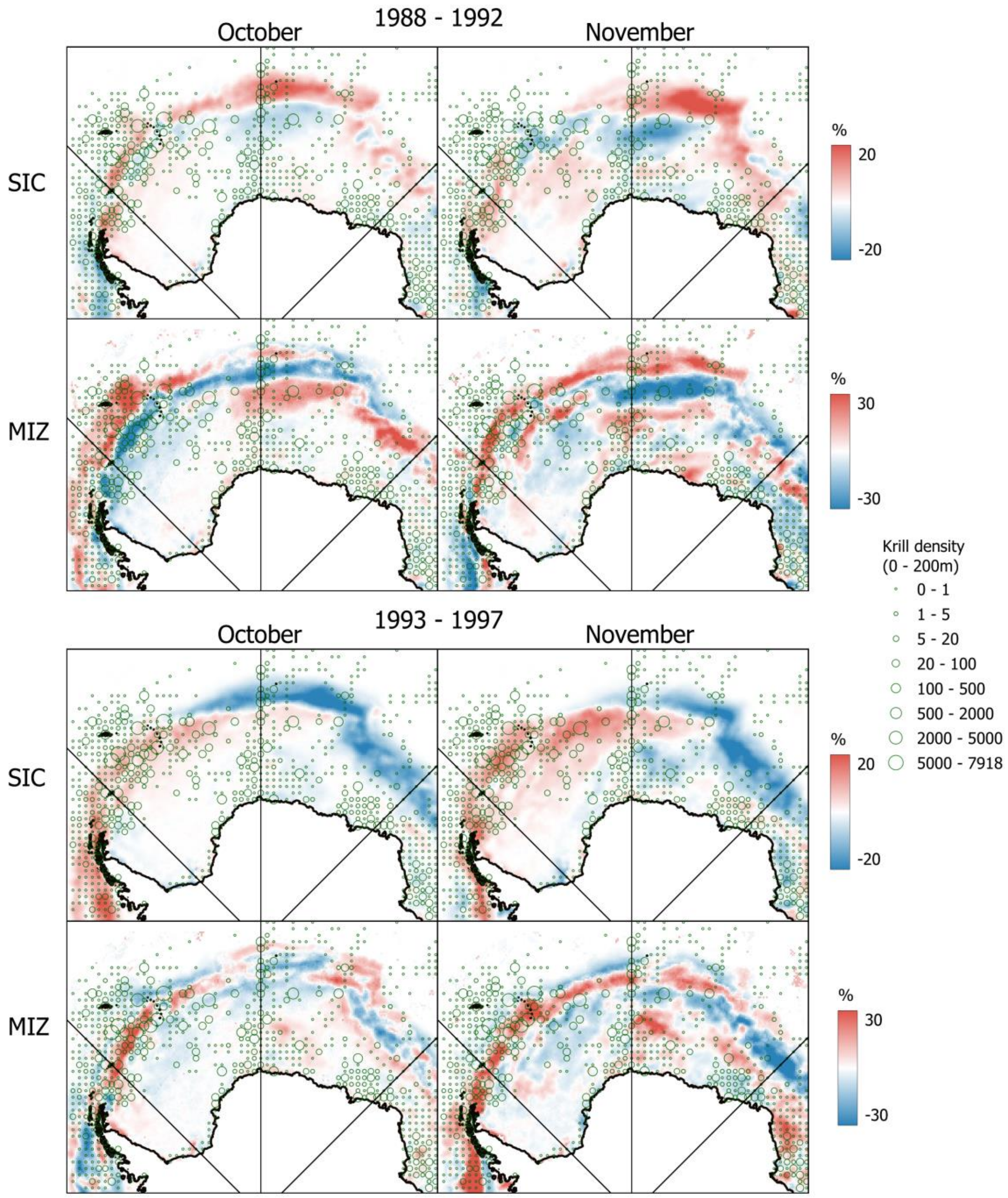


Figure A6. Sea ice concentration (SIC) and marginal ice zone (MIZ) indicator anomalies. The two periods of reduced sea ice (1988 – 1992 and 1993 – 1997) are presented here to compare the spatial configuration in anomalies. The anomalies represent 5-year means compared to the 1988 – 2020 mean. Antarctic krill densities from surveys between 1926 – 2016 are also presented.

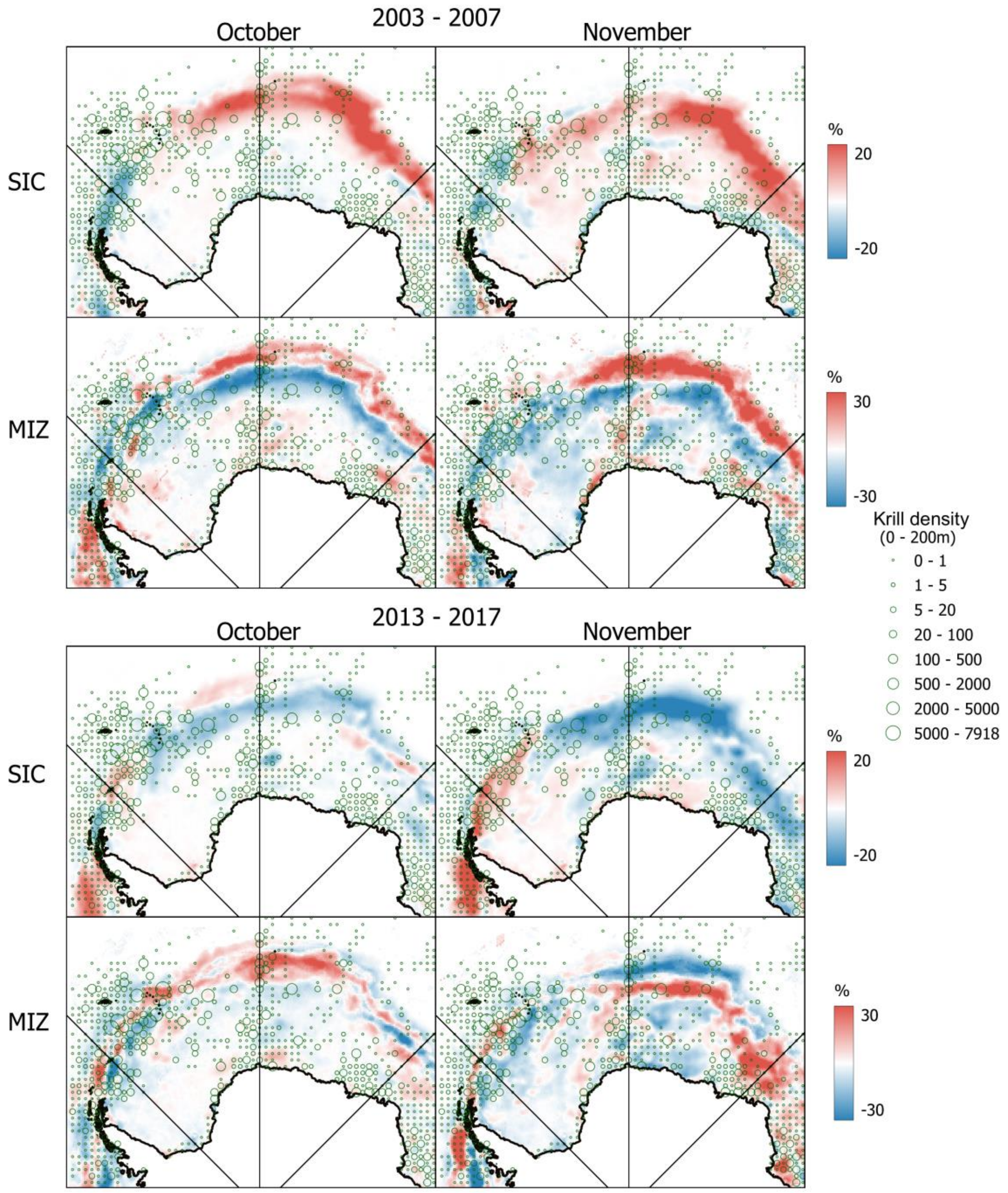


Figure A7. Sea ice concentration (SIC) and marginal ice zone (MIZ) indicator anomalies. The two periods of reduced sea ice (2003 – 2007 and 2013 – 2017) are presented here to compare the spatial configuration in anomalies. The anomalies represent 5-year means compared to the 1988 – 2020 mean. Antarctic krill densities from surveys between 1926 – 2016 are also presented.

7.2 Appendix B: THE OCEANOGRAPHPIC CHARACTERISTICS OF SOUTHERN RIGHT WHALE (EUBALAENA AUSTRALIS) MID-LATITUDE FORAGING GROUNDS

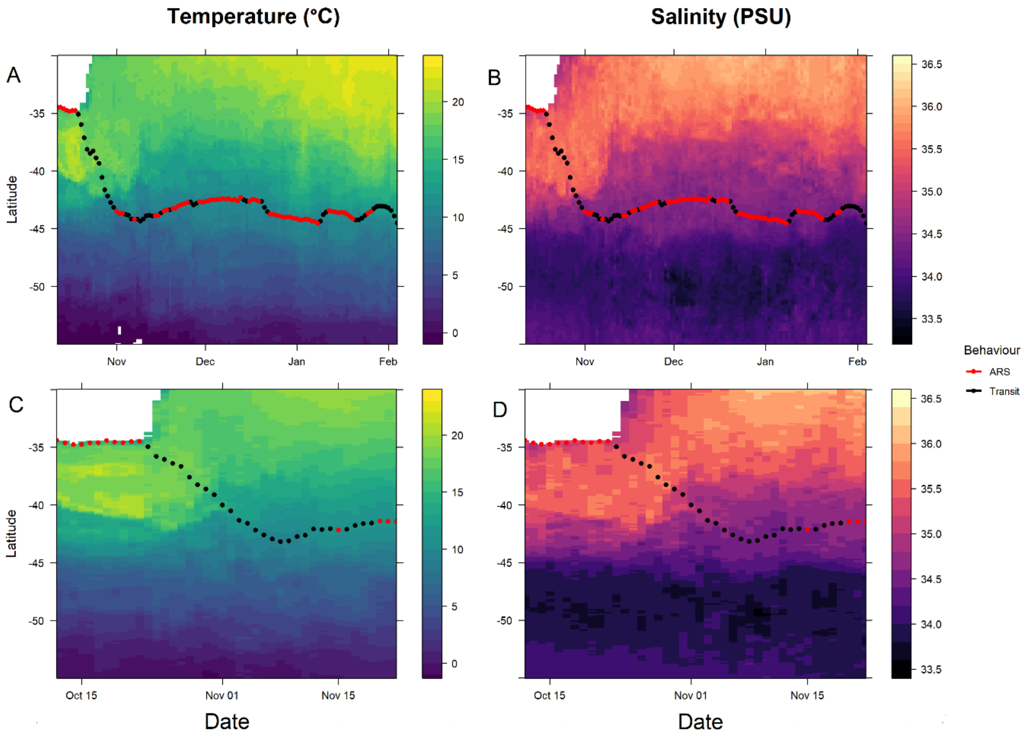
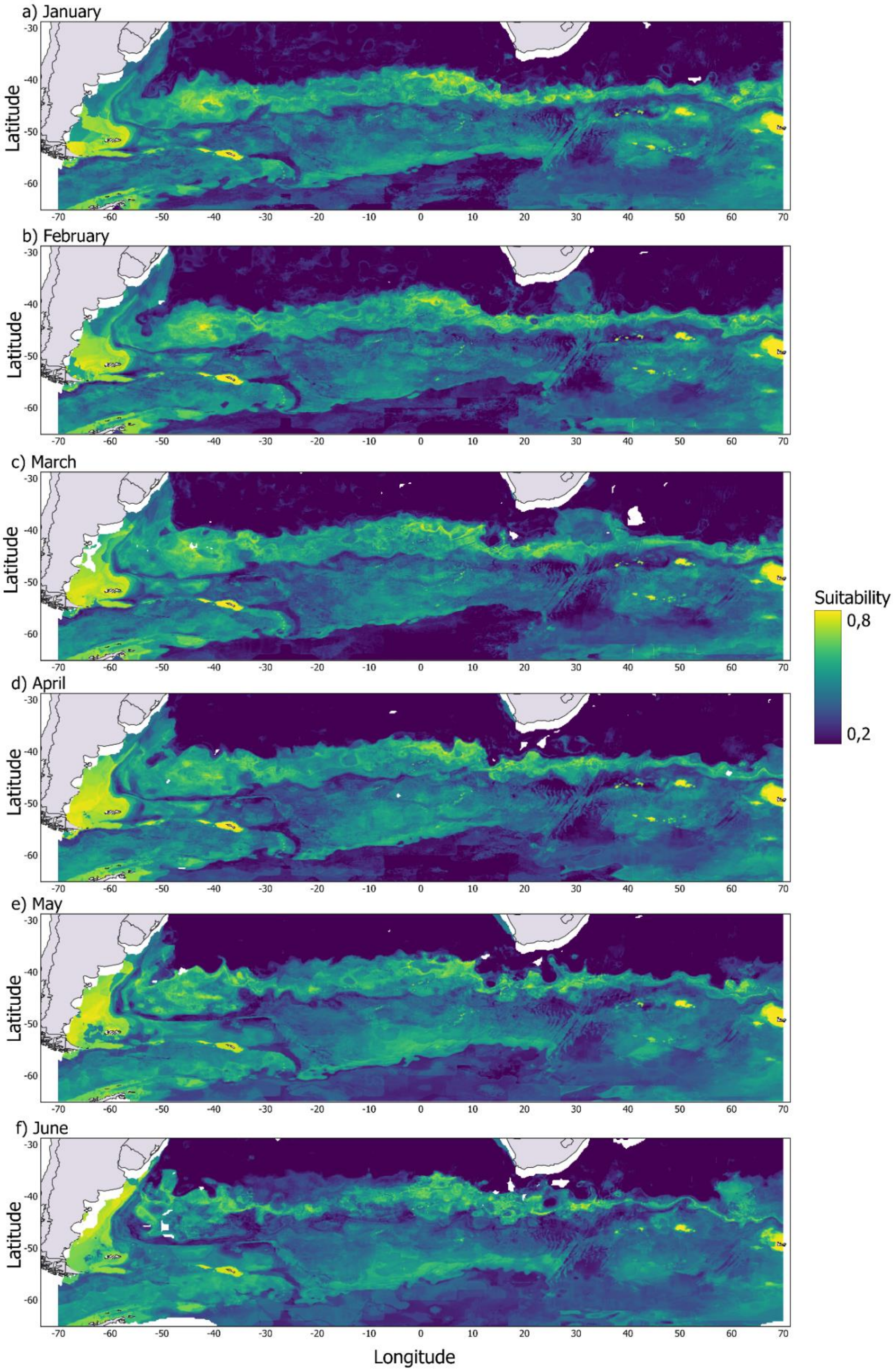


Figure B1. Hovmöller presentations of a) temperature and b) salinity and deepest daily dive for the date and position of whale 3.

7.3 Appendix C: OFFSHORE MIGRATORY BEHAVIOUR AND FORAGING HABITAT USE OF SOUTH AFRICAN SOUTHERN RIGHT WHALES (*Eubalaena australis*).



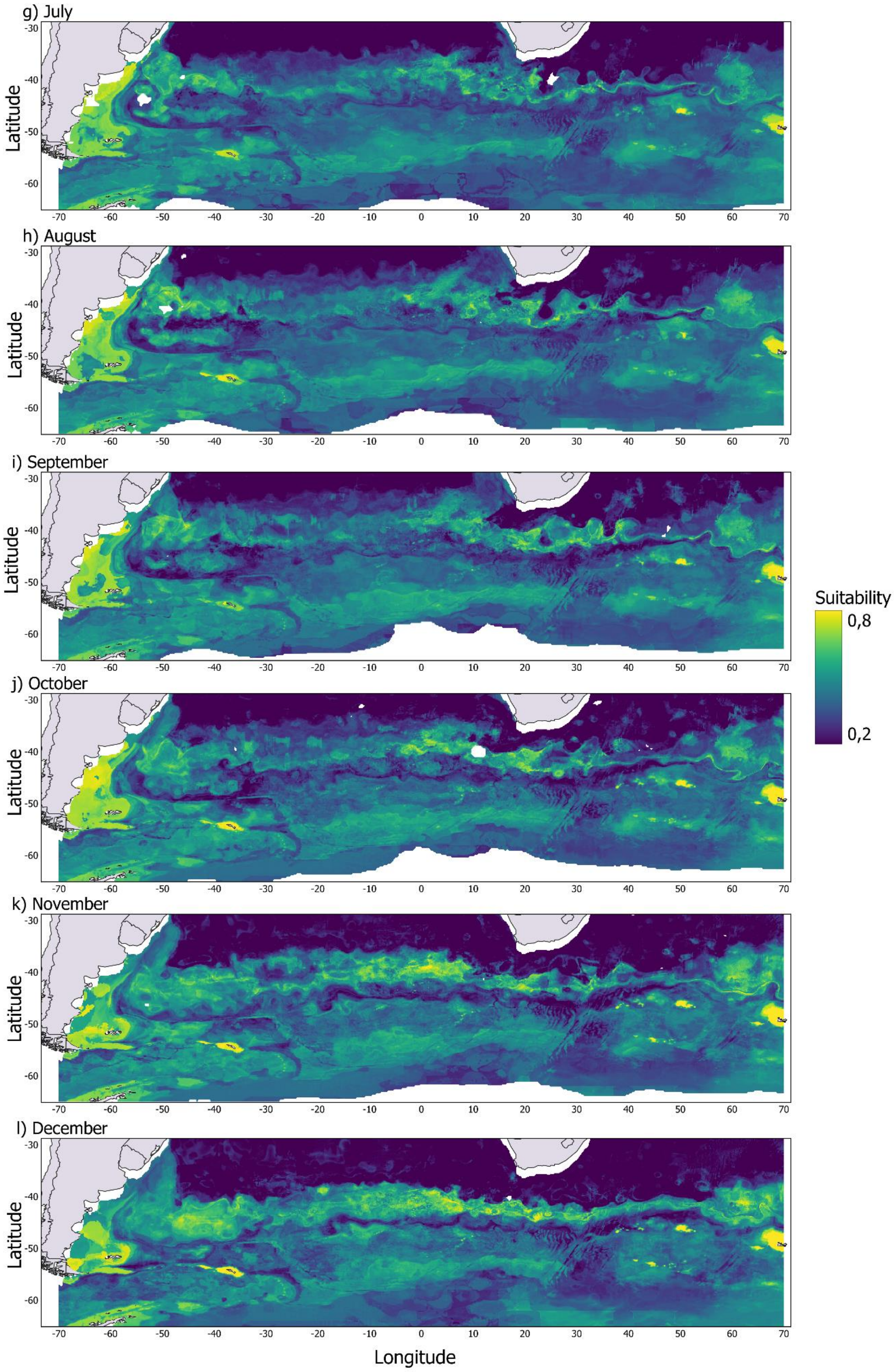


Figure C1. Monthly maps for a – l) January – December habitat suitability as predicted by random forests for 2022. These were created from the mean of each month of the two complete years of satellite telemetry data (2022 and 2023).