An investigation on humpback whales' distribution in relation to Antarctic sea ice in the IDCR/SOWER dataset

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Abstract

Existing literature has identified humpback whales (*Megaptera novaeangliae*) as climate sentinels since their feeding ecology is inextricably linked to the oceanic features around Antarctica, and to the seasonal sea ice. The changing Antarctic cryosphere in response to climate change threatens not only their habitat but also their prey resources. Understanding the interaction between the changing Antarctic Sea ice and its influence on the recovering humpback whales' distribution and behaviour is fundamental. Long-term ecological research offers the potential to understand ecological interactions and variability therein, over time scales relevant to both the life history of the animals and their physical environment. Implemented to assess the effectiveness of the moratorium on baleen whale densities, the IDCR/SOWER dataset is the sole cetacean long-term dataset containing in-depth information about the recent status of all Southern Ocean baleen whales. This study examines the potential utility of this dataset beyond its original scope, specifically assessing how it can contribute to climate research. Using the humpback whale sightings dataset, I prepared a workflow analysis to visually assess the distribution of humpback whales during the IDCR/SOWER surveys in relation to the sea ice from climate data records. The analysis was framed around the use of regional sectors typically used for sea ice research, rather than the feeding areas identified by the International Whaling Commission. The results show that although humpback whales indicate southward expansion as the sea ice retreats, the influence of interannual changes in sea ice on sightings is not uniform, and evident only in a few sectors. Taking into consideration the caveats of using presence/absence whale distribution data, this study represents a significant step forward in demonstrating the potential of this dataset for interdisciplinary research on polar environments beyond its original intention.

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1. Introduction

The Southern Ocean (SO), dominated by the Antarctic Circumpolar Current (ACC), plays a significant role in the global ocean circulation and climate systems (Turner et al., 2009; Constable et al., 2014; Rogers et al., 2020). The observed trends in multi-decadal variability within this region suggest a major influence from both natural and anthropogenic forces (Zhang et al., 2019). The localized, amplified warming of the southern polar region over the last three decades has altered the patterns of climate signals inducing more frequent occurrence of El Niño-Southern Oscillation (ENSO) events and positive Southern Annular Mode (SAM) (Turner et al., 2014; Clem et al., 2020; Crosta et al., 2021).

These anomalies have had implications for the physical environment of the Southern Ocean and around Antarctica, subsequently impacting crucial features and processes that define and provide habitats for numerous species found in the marine ecosystem of this region (Ainley et al., 2012; Bronselaer et al., 2018). Among the most obvious effects observed to date are increased sea surface temperature, a poleward shift of frontal systems, modifications of sea-ice dynamics, and changes in nutrient availability (Constable et al., 2014; Turner et al., 2014; Gutt et al., 2015; Stammerjohn & Maksym, 2017; Meynecke et al., 2020). According to Gutt et al. (2015) and Rogers et al. (2020), these climate-driven changes already and are projected to further disrupt the habitats and functioning of the Antarctic marine ecosystem.

This ecosystem has been subjected to perturbations due to the historical exploitation of top predators such as whales and seals, with some populations nearing extinction in the 20th century (Trathan & Reid, 2009; Ainley, 2010). This period coincides with unprecedented climatic changes, which have further affected the ecosystem, leaving it highly modified and altered in terms of its structure and resilience (Croxall & Nicol, 2004; Nicol et al., 2007). Specifically, Gutt et al (2015) quantitative assessment highlights that areas influenced by changes in sea ice, both historically and projected into the future, are notably much larger than those affected by sea surface temperature increase. This poses a significant threat considering that the Antarctic sea-ice ecosystem supports species populations that are exclusively reliant on sea ice throughout their life cycles, top predators that use it for breeding, or resting, as well as cetaceans which undertake annual migrations to Antarctica for feeding purposes.

I, hereafter, refer to the various processes and changes occurring within the sea ice environment over time as "sea ice dynamics". In this context, this is an umbrella term for all the classic sea ice variables (derived from sea ice concentrations) often used as sea ice habitat descriptors and are affected by factors like seasonal changes, climate patterns, and oceanic currents. Examples include sea ice extent, thickness, duration, timing and rate of advance and retreat.

This thesis explores the relationship between the sea-ice environment and one specific group of baleen whales, humpback whales (*Megaptera novaeangliae*). Baleen whales inhabit all major oceans and adapt to various ecosystems and are known for their extensive migrations over large distances throughout their lifespan (Schall et al., 2020). Their migrations are characterised by strong site fidelity to the same routes, breeding and feeding grounds (Aidley, 1981; Horton et al., 2017). Whales' habitat preference in feeding grounds is driven by multiple factors, including the availability of prey and environmental conditions such as temperature, bathymetry, sea ice and hydrodynamics (Meynecke et al., 2020; Henderson et al., 2023b).

Following the implementation of a moratorium on commercial whaling in the 1980s, whale populations have been recovering with the humpback whales demonstrating a relatively fast recovery rate after full protection was implemented (Zerbini et al., 2019; Meynecke et al., 2020; Johannessen et al., 2022). Could the simultaneous increase in whale populations and observed changes in their biophysical environment, potentially affect the balance of the Antarctic sea ice ecosystem, despite the direct correlation between these two trends? These interactions are not necessarily linear and may involve cascading effects, where shifts in one component, such as predator populations or sea ice cover, indirectly affect other ecosystem processes, including prey availability and nutrient cycling (Smetacek & Nicol, 2005). This necessitates the need to study humpback whales' behavioural responses to the changing climate. The limited accessibility of this region for conducting field observations limits our understanding of the response of the Antarctic ecosystem to climate change.

Of all baleen whales, humpback whales are the best studied (Ralls & Mesnick, 2019). Existing literature well defines large-scale spatial patterns for humpback whales and shows that the environmental drivers of their distribution, movement, and reproduction are tightly coupled with oceanographic features (Meynecke et al., 2020; Meynecke et al., 2021). Research on predator-prey interactions in the Southern Ocean reveals that all Southern Hemisphere humpback populations have broad longitudinal ranges, occupying distinct foraging niches directly linked to prey availability (Murphy, 1995; Trathan et al., 2007; Trathan & Hill, 2016).

This makes humpback whales an ideal species for studying the potential impacts of climate-induced sea ice changes on marine ecosystems. A comprehensive understanding of an animal's ecology allows for the prediction of their spatial and temporal distribution and the identification of their potential responses to changes in the environment (Potts & Börger, 2023). The ecology of humpback whales inextricably links them to the sea ice dynamics of the Antarctic (Bengtson Nash et al., 2018; Druskat et al., 2019). This forms the foundational premise of this study, where knowledge of both ecological and cryosphere factors will be used to study the distribution of humpback whales in relation to the Antarctic Sea ice.

Using historical whale observations of occurrence originally designed to assess baleen whales' density, the project aims to set-up an investigative framework that will contribute to further the understanding of humpback whales' relationship with Antarctic sea ice. To demonstrate the potential of this framework, this thesis will focus on two initial key questions:

1) How do humpback whale sightings relate to Antarctic sea ice patterns?
2) Do humpback whales sightings follow closely the spatio-temporal variations of the sea-ice edge?

1.1 Humpback Whales

1.1.1 The Feeding Ecology of Humpback Whales

These whales are among the most recognizable baleen whale species, primarily due to the distinctive shape of their fins, such as their pectoral fins, which account for about one-third of their body length (Gales & Gales, 2011). Currently, seven stocks (stocks A to G, Figure 1) of the Southern Hemisphere humpback population are recognized by the International Whaling Commission (IWC) based on the geographical location of their breeding grounds (IWC, 1998).Recovery patterns following the whaling ban vary across populations, with some population reaching about 90% pre-exploitation levels (e.g., stock D) while some are still classified as “Endangered and Vulnerable” under the Red List (stock E and F) (Seyboth et al., 2023). Undertaking one of the longest marine mammal migrations, these stocks seasonally migrate between their low-latitude breeding grounds and mid-high latitude feeding grounds. Contrary to the Northern Hemisphere counterparts, despite supplementary feeding outside the traditional areas being recorded (Seyboth et al., 2023), the Southern Hemisphere humpback whales display high site-fidelity i.e., using the same migratory corridors (Horton et al., 2017).

Their strong fidelity to breeding grounds and migratory routes connects these stocks to six IWC feeding areas (Areas I to VI) in the Antarctic (Donovan, 1991), as shown on Figure 1. Historically, the demarcation of these feeding grounds is based on the premise that humpback whales migrate directly from their breeding to feeding grounds (Leaper & Miller, 2011), as direct migratory links have been established (Stevick et al., 2004; Zerbini et al., 2006; Barendse et al., 2013). This classification assumes that these stocks does not overlap when inhabiting the Antarctic feeding grounds (Branch, 2011), however evidence indicating intermixing of these stocks in feeding grounds have emerged in recent years (Ramos et al., 2023; Seyboth et al., 2023). Donovan (1991) describes these stock boundaries as "best guesses" and/or as founded on a conservative principle from a management standpoint more than the ecological perspective.

Globally classified as generalist, filter-feeders (consuming small planktonic crustaceans and fish), studies on their dietary habits in the Antarctic reveal that they exclusively feed on euphausiids (Eisenmann et al., 2016; Groß et al., 2020a; Rogers et al., 2020; Nash et al., 2023). The Antarctic krill (*Euphausia superba),* a keystone species in the Antarctic sea-ice ecosystem, is reliant on sea ice for most of its key life-cycle phases (Atkinson et al., 2019; Steiner et al., 2021). Such that, its abundance depends on sea ice and also, it exhibits a circumpolar distribution closely aligned with the seasonal extent of sea ice, even observed changes in its distribution over the recent decades has been linked to the changing sea ice dynamics (i.e., extent, thickness, and duration) (Atkinson et al., 2019; Cavan et al., 2019; Steiner et al., 2021; Swadling et al., 2023).

Humpback whales, as "capital-breeders," store energy accumulated during the intensive summer feeding in their blubber reserves and use these reserves as their primary energy source throughout migration and breeding activities (Irvine et al., 2017; Groß et al., 2021). This reliance on prey availability makes them vulnerable to variability and long-term changes in the Antarctic sea ice (Steiner et al., 2021; Baines et al., 2022), as sea ice dynamics not only influence their spatial and temporal distribution within feeding grounds but also impact their nutrition, therefore affecting nutrition and reproductive success (Simmonds & Isaac, 2007; Seyboth et al., 2021b).

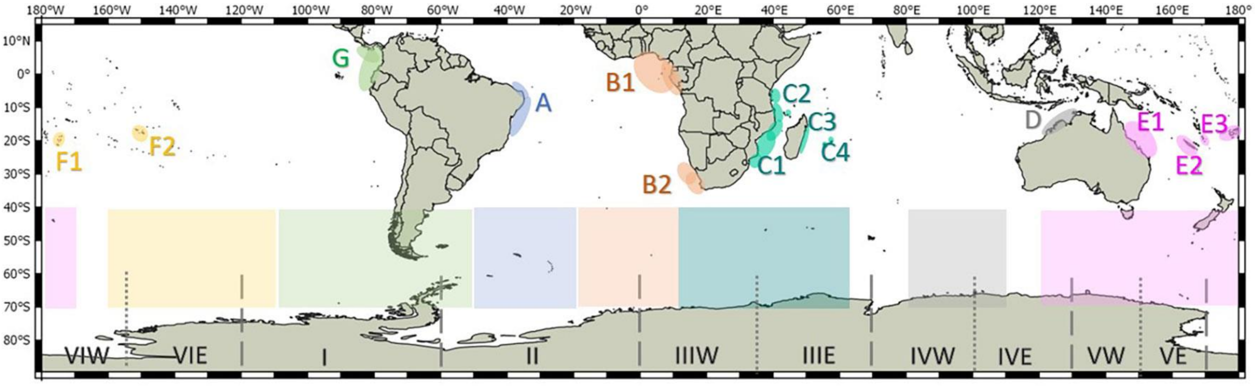


Figure 1.The seven stocks (A-G) of humpback whales recognized by the IWC and their feeding grounds in the Southern Hemisphere. Some stocks have further been divided into sub-stocks, based on genetic data or mark-recapture or whaling data. Color-coded to show which correspo Image source: (Seyboth et al., 2023).

Based on the literature from the past four decades reviewed by Meynecke et al. (2021), the environmental drivers of humpback whales habitats depend on whether they are feeding, migrating, or breeding and can be best described using combination of multiple drivers (Figure 2). On the feeding grounds, these factors are generally associated with high prey concentrations. Due to sea ice variability being heterogeneous around Antarctica, the type, strength, and role of the same environmental drivers in relation to HW distribution may depend on finer-scale regional ocean features.

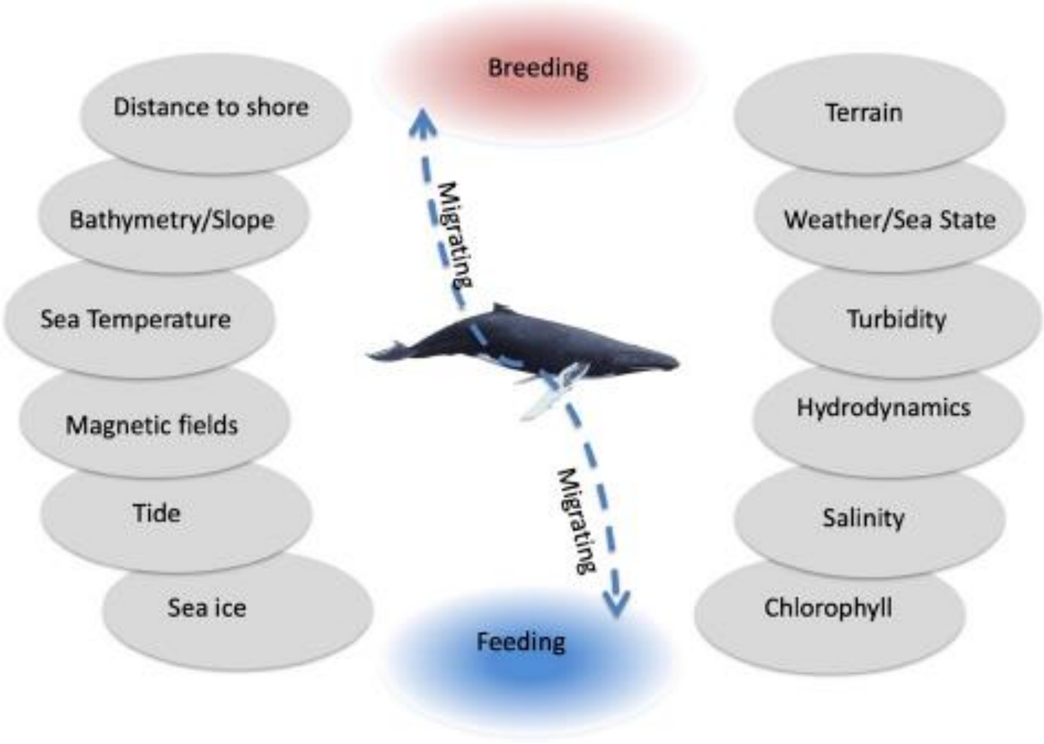


Figure 2. The main environmental drivers in order of relevance to humpback whale behavioural modes (i.e., breeding, migrating, and feeding). Adapted from (J.-O. Meynecke et al., 2021)

1.1.2 Methods Used for Humpback Whales research.

Several research methods have been used in research to enhance our understanding of humpback whale population dynamics. These methods include seasonal sightings surveys which are shore-based observations (e.g., Best et al. (1998)) and/or cruise-based programs like the IDCR/SOWER. Other methods include natural marking through photo-identification, tracking and monitoring through technologies like genetic sampling (e.g., Eisenmann et al. (2016) & Groß et al. (2021)), satellite tagging (Dalla Rosa et al., 2008), time-depth recorders (Heide-Jørgensen & Laidre, 2015), aerial surveys (Andriolo et al., 2006), and acoustic studies (Clark & Clapham, 2004) . While whale tagging dates back to the early 20th century (Brown, 1978), tagging methods have since advanced significantly and gained traction in recent years (Kennedy & Clapham, 2017). These advances involve attaching small devices such as satellite tags to track the movements and behaviours of individual whales. The collected data provides detailed individual information on whale distribution, seasonal movements, migration patterns, and behaviour. This level of detail is analysed to identify seasonal patterns in species distributions or gain insights into habitat use and preferences (Willson et al., 2018)

However, cruise-based sightings remain relevant as they offer a complementary set of advantages. They provide valuable ancillary data on oceanographic variables, prey availability, and other ecological parameters essential for ecosystem management (Gilman et al., 2017). Vessel-based surveys are commonly utilized, especially in regions with limited information regarding whale presence, distribution, and density (Henderson et al., 2023a). In this approach, transect lines are systematically designed to ensure comprehensive coverage of the targeted area. Researchers, aboard a dedicated vessel, navigate these lines, documenting all observations along the way.

Combining satellite telemetry with these other research techniques offers a powerful way to study large mammals, offering detailed individual data on whale movements and behaviour, and their ecological interactions (Mull et al., 2022). This integrated approach allows researchers to gain a more complete picture of top-predator ecology, including humpback whales, thereby informing more effective conservation strategies (Louzao et al., 2009; Thums et al., 2018; Fitzmaurice & Steenkamp, 2023).

1.1.3 The role of humpback whales in the Antarctic sea-ice ecosystem

Primarily recognized for their critical ecological role as top predators, whales have been the focus of both historic and more recent long-term datasets in the Southern Hemisphere (e.g., as discussed in Leaper et al. (2008) and Ferguson et al. (2009)). These datasets have proven invaluable for studying whale population dynamics, contributing to a broader understanding of the significant role whales play within ecosystems (Seyboth et al., 2023). Recent research has identified whales not only as top predators but also as ecosystem engineers, forming an integral part of the Southern Ocean's biochemistry (Pershing et al., 2010; Lavery et al., 2014; Ratnarajah et al., 2014; Roman et al., 2014). An ecosystem engineer is an organism capable of altering, maintaining, or creating habitats through its interaction with the physical environment, and thereby indirectly affecting other organisms (Altieri, 2015).

Among their many ecological roles in feeding areas, baleen whales act as nutrient recyclers, re-fertilizing the photic zone and promoting primary productivity. They contribute to nutrient distribution through processes such as the "whale pump," wherein they release nutrients like iron, carbon, nitrogen, and sulphur from deep, nutrient-rich waters into shallower waters through feeding and excretion. These activities indirectly contribute to carbon sequestration, playing a crucial role in maintaining the balance of the Antarctic ecosystem (Roman et al., 2014; Meynecke et al., 2023).

Considering their migratory patterns and ecology, humpback whales have been identified as sentinels of the Antarctic sea-ice ecosystem. This recognition stems from their sensitivity to changes in sea-ice extent and shifts in krill, as this is closely associated with their foraging habitats in the Antarctic feeding grounds (Andrews-Goff et al., 2018; Schall et al., 2020; Nash et al., 2023). Based on this, humpback whales can therefore be regarded as climate sentinels. Hazen et al. (2019) describes climate sentinels as marine-top predators that respond both to climate and ecosystem variability. Understanding the adaptation of whales to climate change is crucial because alterations in their migratory patterns and dietary habits can have far-reaching repercussions for marine ecosystems. These shifts can also serve as valuable indicators of climate change. It has become evident that a comprehensive understanding of whale ecology can be utilized as a tool to advance our comprehension of climate dynamics over Antarctica. Humpback whales, being highly responsive to environmental changes, serve as indicators of shifts in the Antarctic ecosystem, providing valuable insights into the broader impacts of climate change on this region.

1.2 The Antarctic Sea Ice

1.2.1 Reliability of Satellite Observations over Antarctica

Due to Antarctica's remote location, obtaining quantitative in-situ observations is logistically extremely difficult (Kohout et al., 2016; Arndt et al., 2020) and this introduced a knowledge gap in understanding the conditions influencing Antarctic sea ice dynamics (Himmich et al., 2023). To overcome this limitation, prior to the earth observations era, numerous methods were used to infer sea ice conditions in the polar regions, both directly and indirectly (Polyak et al., 2010). Examples include the use of in-situ observations, marine sedimentary records, historic whaling records, snow accumulation, and polar ice cores as proxies for sea ice conditions and extent (Mackintosh & Herdman, 1940; Abram et al., 2013; Thomas et al., 2019).

Most methods used before the satellite era indicated a decline in sea ice and a southward shift of the sea ice edge between the 1950s and 1970s (De La Mare, 2009). The accuracy of these predictions faced criticism, not only due to the spatial and temporal sporadic nature of the observations (Abram et al., 2013) but also because the purely biological approaches, such as using whale-catch records as proxy of sea ice edge (Vaughan, 2000; Ackley et al., 2003), inherently possess limited spatial and temporal scope. These constraints arise from many factors including catch restrictions, the uneven distribution of catch effort, and catch selectivity, all of which reduce the comprehensiveness and representativeness of the data.

To overcome the shortcomings of in-situ observations, the field of earth observations has continuously made significant advancements in accurately capturing sea ice dynamics since the introduction of the first passive microwave Nimbus-5 satellite Electrically Scanning Microwave Radiometer (ESMR) data in 1979 (Takenobu, 2009). Compared to the past four decades, sea ice remote sensing is now a well-established application of satellite observations. Passive microwave technology, in particular, has played a crucial role in retrieving essential sea ice parameters, with a notable focus on sea ice concentration (SIC) (Sandven et al., 2023). One of the key advantages of passive microwave sensors is their ability to penetrate cloud cover and provide consistent observations under various weather conditions, ensuring reliable monitoring even in the frequently overcast polar regions (Gabarró et al., 2023).Currently, the monitoring and interpretation of the changing sea ice dynamics, primarily rely on earth observation products derived from these remote sensing technologies (Sandven & Johannessen, 2006; Gabarró et al., 2023).

For instance, attempts to accurately capture and quantify regional and annual variability involve using sea ice variables derived from SIC as proxies for the marginal ice zone (MIZ) and sea ice edge conditions (Smith et al., 1998; Stammerjohn et al., 2008). SIC represents the percentage of ice cover within a single cell on a gridded map, and metrics derived from SIC are typically a threshold of ice concentration (e.g., sea ice extent, area and MIZ)(Hobbs et al., 2016). The sea ice extent (SIE) is computed by summing the grid cell area of all cells that has 15% or greater sea ice concentrations and the MIZ, which is the transitional region between the open ocean and pack ice, ranging from 15% to 80% concentration.

Recent concerns about the reliability of this proxy in the Southern Ocean have been raised by Vichi (2022), given the region's distinctive and expansive circumpolar MIZ. Vichi argues that utilizing a threshold-based concentration criterion may not effectively capture the variability of Antarctic sea ice, considering the heterogeneity of ice types in this region. As a solution, Vichi proposed an alternative MIZ indicator that can reliably capture trends in ice variability when conducting climatological assessments and regional analyses in the Southern Ocean. This further highlights the ongoing efforts to refine and enhance earth observation methodologies over Antarctica to improve our understanding of its complex sea ice dynamics.

1.2.2 Observed Trends in Antarctic sea ice.

Since the first satellite observations became available, in contrast to Arctic Sea ice, Antarctic Sea ice does not display a clear long-term declining trend but instead exhibits significant year-to-year variability with strong spatial heterogeneity (Constable et al., 2014; Stammerjohn & Maksym, 2017). Over the period since 1979, the overall trend in Antarctica indicates that sea ice cover has increased by about 1.6±0.4% per decade, with a climatological seasonal SIE cycle (Figure 3) expanding to more than 19 million km^2 each winter and contracting by about 3–4 million km^2 each summer (Parkinson, 2019; Crosta et al., 2021). However, recent studies have shown an intense decrease in sea ice cover, with the annual mean Antarctic sea ice extent recording successive low years post-2014, with a record low in 2023 (Parkinson, 2019; Clem et al., 2020; Clem et al., 2023; Gilbert & Holmes, 2024). This observed decline has been attributed to the effects of ocean and atmospheric warming (Purich & Doddridge, 2023).

Compared to the Arctic, most Antarctic Sea ice is seasonal, except for the Weddell Sea, which comprises multi-year sea ice and accounts for approximately 40% of the total summer sea ice in Antarctica. Additionally, it holds the largest circumpolar marginal ice zone, which is intensely affected by air-sea exchanges (Vichi, 2022). Thus, seasonality and regional variability constitute critical factors affecting the Antarctic SIE.

The observed variability, occurring at regional, interannual, and long-term scales, is attributed to the interaction between atmospheric, oceanic, and cryospheric processes. These processes operate differently depending on the region and contribute differently to the overall variability (Hobbs et al., 2016). Atmospheric drivers, such as local changes in wind patterns and shifts in large-scale zonal winds dominant over the Southern Hemisphere like the Southern Annular Mode (SAM) and the El Niño–Southern Oscillation (ENSO) (Raphael & Hobbs, 2014; Stammerjohn & Maksym, 2017), are primarily responsible for interannual variability. Meanwhile, oceanic drivers, including the vertical structure of the near-surface water column (Martinson & Iannuzzi, 1998), cryospheric factors like melting ice shelves (Bintanja et al., 2015), dynamic and thermodynamic processes (Massom & Stammerjohn, 2010; Himmich et al., 2023), contribute significantly to the large annual cycle of Antarctic sea ice.

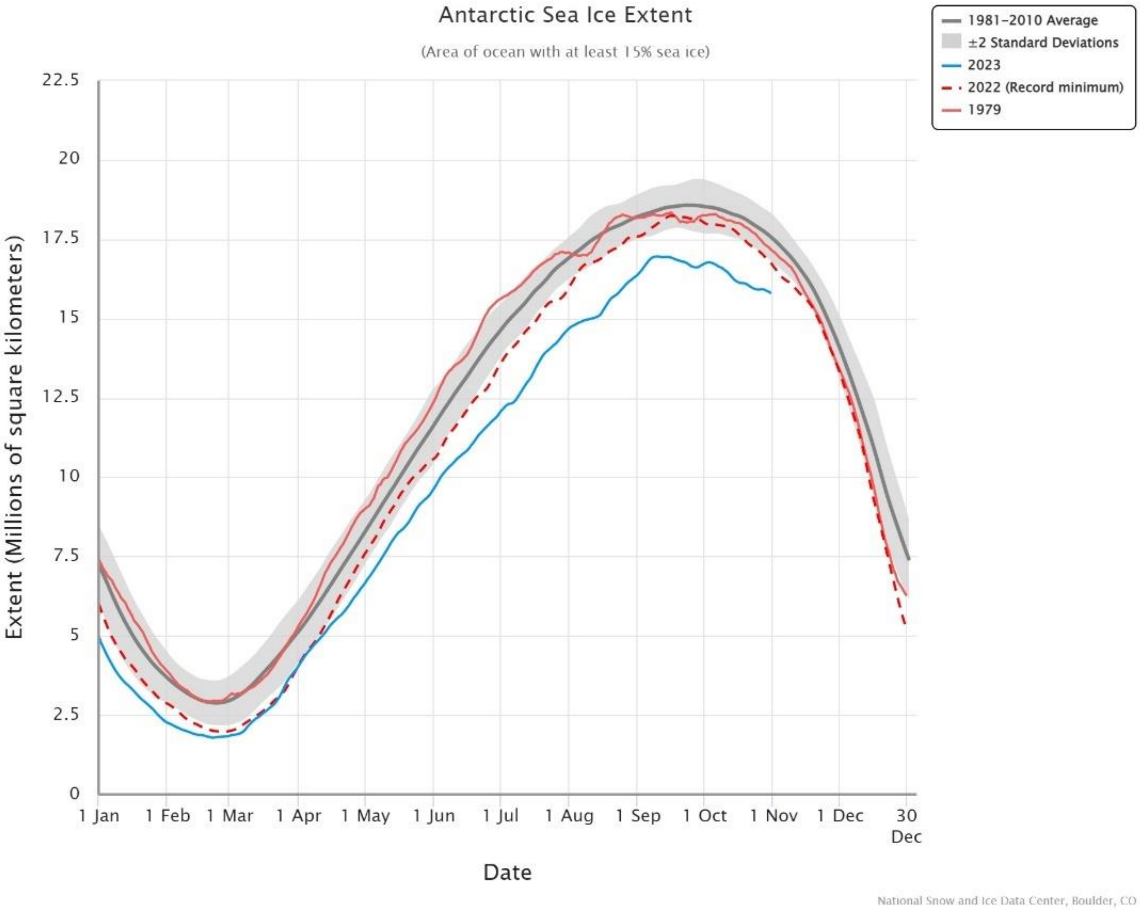


Figure 3. Climatological seasonal cycle of Antarctic sea ice extent for period 1981-2010, based on passive microwave satellite derived SIC greater than 15%. Blue line denotes SIC for 2023 as the year with the lowest minimum and maximum extent ever recorded. *Image retrieved from the NSIDC (https://nsidc.org/arcticseaicenews/charctic-interactive-sea-ice-graph/).*

To examine the regional variability of Antarctic sea ice, studies conducted prior to 2014 relied on regions defined geographically. However, Raphael and Hobbs (2014) introduced a significant advancement as they redefined new ice sectors based on distinct sea ice regimes, utilizing a decorrelation length scale. This scale measures how quickly the correlation between sea ice extent measurements decreases by the longitude. Clear dips or minima on the graph (Figure 4) indicate where sea ice regimes change noticeably, suggesting boundaries between different sectors with distinct sea ice patterns. This redefinition was crucial for accurately capturing the non-uniform patterns of key sea ice seasons in each region (i.e., the periods of retreat and advance, including ice duration).

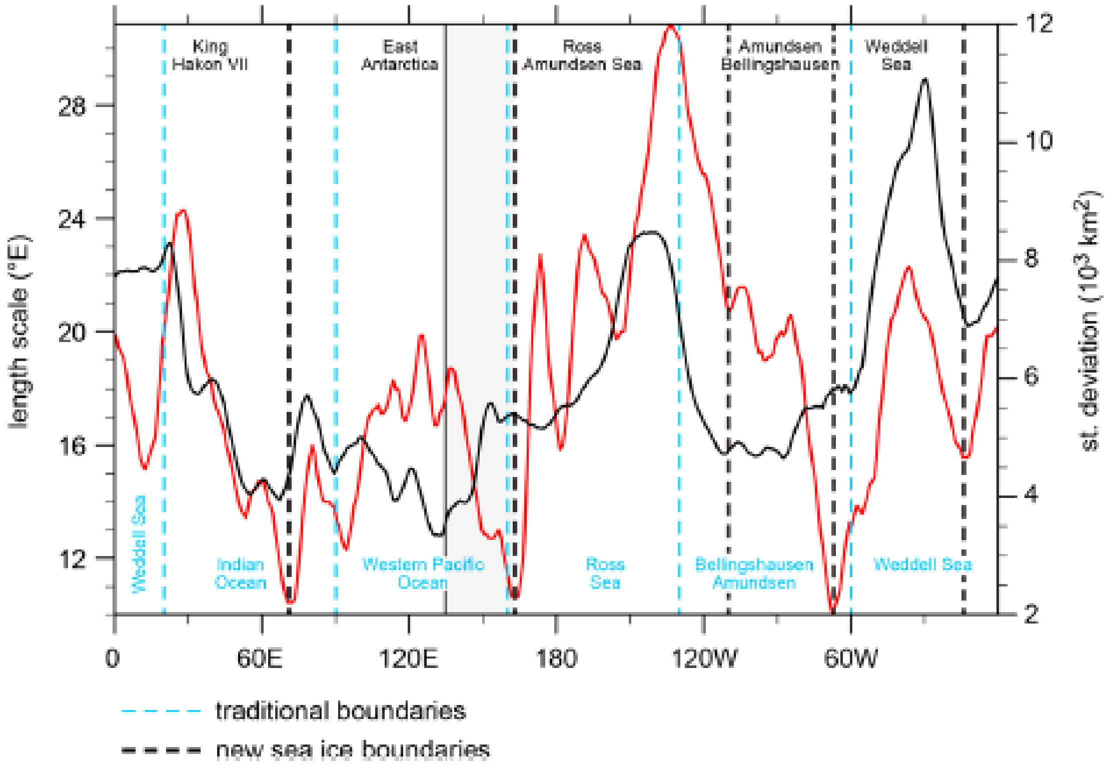


Figure 4. Antarctic sea ice regions as defined by Raphael and Hobbs (2014). The black solid line represents the standard deviation of sea ice extent anomalies by longitude, while the red line indicates the decorrelation length scales.

Antarctic sea ice covers an extensive region of the Southern Ocean and plays a pivotal role in shaping high latitude SO ecosystems and climate (Thomas & Dieckmann, 2008). It contributes significantly to primary production and influences key environmental factors, while also playing a pivotal role in moderating air-sea interactions. Understanding sea ice dynamics and trends within each sector is crucial, as this helps disentangle what drives the regional differences and how this may affect environmental conditions that shape the Antarctic sea-ice ecosystems.

1.2.3 The role of sea ice in structuring the Antarctica ecosystem.

The presence and seasonal variability of Antarctic sea ice impact nutrient dynamics, light availability, habitat suitability, and the structure of food webs within the Southern Ocean (Gutt et al., 2015; Fraser et al., 2023; Swadling et al., 2023). Changes in SIE, affect krill abundance, which potentially influence the populations of krill-dependent species higher up in the food web, such as whales, seals, and penguins (Figure 5). For example, during winter, the sea ice cover acts as a nutrient-rich substrate, creating a critical habitat for a thriving population of microbial communities. This, in turn, serves as the main food source for pelagic herbivores like the Antarctic krill, particularly when the water column has limited food resources. Additionally, sea ice provides shelter, resting, breeding, and feeding ground for larger predators such as seals, penguins, and whales (Stammerjohn & Maksym, 2017; Steiner et al., 2021).

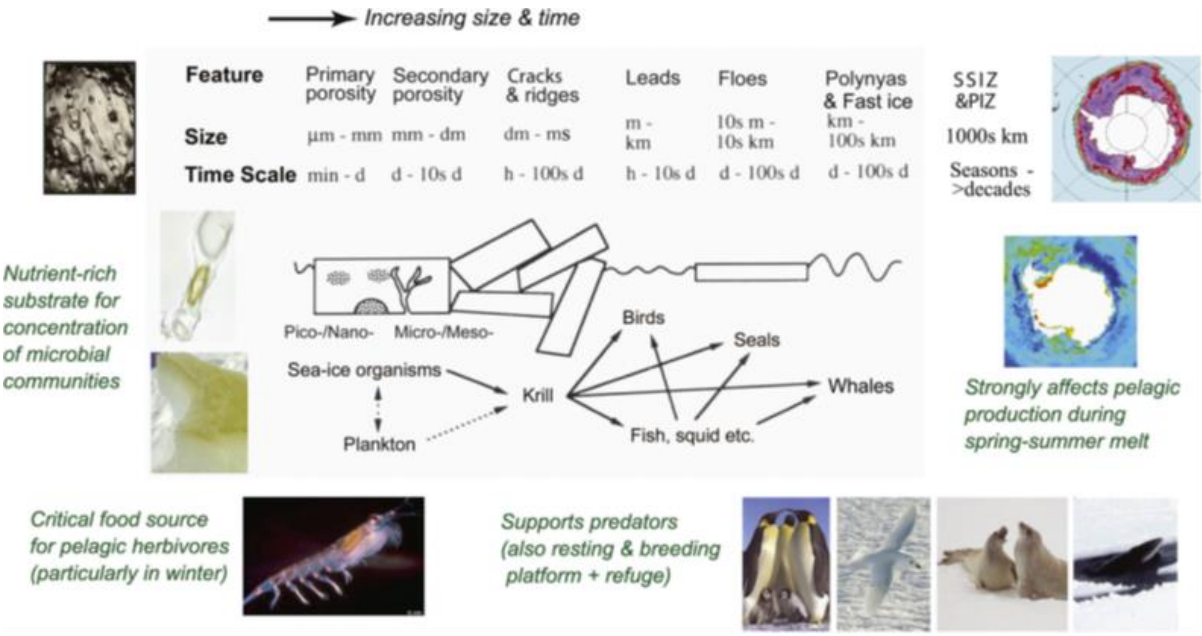


Figure 5. The influence of Antarctic sea ice on the different trophic levels of the food web in this region (Source: Massom and Stammerjohn (2010)).

In summer, as the sea ice melts, an increased number of polynyas are found along the coast, associated with enhanced primary productivity (Smith et al., 2010; Moreau et al., 2019). Any alterations in sea ice, whether in extent, concentration, thickness, dynamics, or spatio-temporal characteristics, have far-reaching consequences across the entire marine food web and ecosystem as different ice types support varied species (Massom & Stammerjohn, 2010; Swadling et al., 2023). According to Constable et al. (2014), the regional variability around the Antarctica could result in non-uniform responses from the biota, with some being more vulnerable than others. As introduced earlier, regional differences affect habitat quality for marine mammals, and ultimately their foraging success (Speakman et al., 2020).

1.3 Previous Research on Humpback Whales and Sea Ice

1.3.1. Existing literature on environmental drivers of humpback whale behaviour and distribution during feeding.

Most studies reveal that the environmental conditions relevant to the HW foraging behaviour and feeding grounds habitat selection over the Southern Ocean are mostly areas where there is high marine productivity (i.e., areas of upwelling and/or high chlorophyll-a concentrations following sea ice retreat), where prey can be found in abundance (Owen et al., 2017; Bestley et al., 2019; Riekkola et al., 2019). However, it is important to acknowledge that quantifying prey abundance over the Antarctic region presents a substantial challenge.

To address this limitation, chlorophyll data from space are often employed as a proxy for primary production. However, this approach introduces uncertainties, as whales do not directly consume chlorophyll but rather feed on krill ,which may not always be directly correlated with surface chlorophyll concentrations. Relying solely on chlorophyll as a proxy for prey productivity can result to mismatches in both timing and location. Therefore, it is important to account for the spatial, temporal, and trophic lags between chlorophyll concentrations and actual prey availability when studying humpback whale feeding ecology, as these lags can influence the effectiveness of using chlorophyll as a proxy for whale prey.

For instance, a study conducted by Andrews-Goff et al. (2018) observed no discernible relationship between seasonal chlorophyll-a levels and HW foraging grounds over the Antarctic. According to Andrews-Goff et al. (2018), the foraging habitat of humpback whales in the Antarctic is strongly associated with the marginal ice zone. Using a Generalized Additive Mixed Model (GAMM) that included all environmental variables that potentially had an explanatory power on their inferred foraging behaviour, proximity to the ice edge (~65 km away), the rate at which the ice is melting, and the fluctuations in ice concentration observed two months prior to their arrival in the region were identified as the key environmental factors characterizing the Antarctic foraging habitat. Findings of some studies (Reisinger et al., 2021; Bamford et al., 2022; Bedriñana-Romano et al., 2022), also suggest that the foraging activities of these whales occur in high densities near the sea ice edge and/or along coastal regions, particularly those adjacent to sub-Antarctic islands (except for the Ross Sea and Weddell seas, due to their high ice concentrations (Branch, 2011)).

Using a similar approach, Bassoi et al. (2020) found SST, topography, and distance to fronts to be the most influential covariates associated with humpback distribution. These findings align with those of Naganobu et al. (2006), who also identified close interactions between oceanography of the surface layer (represented as an environmental index that integrated temperature means from 0 to 200 m in depth (ITEM-200)) and the distribution of krill, and baleen whales as predators. According to Naganobu et al. (2006), humpback whales were distributed in high density in waters where the ITEM-200 = 0°C, which coincided with the Antarctic Circumpolar Current (ACC), melting marginal waters of sea ice as well as relatively high chlorophyll-a levels.

Recent studies (Mori et al., 2019; Bedriñana-Romano et al., 2022; A. F. Henderson et al., 2023) have recorded a southward shift in the foraging activities of these whales, presumed to be a response to the recent low sea-ice extent recorded, which has induced a shift in krill populations. As stated by Thomas et al. (2015) and Friedlaender et al. (2018), these observed shifts in ocean productivity are most likely due to climate change and have also influenced the recent changes or anomalies in migration patterns and feeding ground of whales. A review by Seyboth et al. (2023), on supplementary feeding beyond the Southern Ocean and plasticity shown by these species also indicate that the changing environmental conditions influence humpback whale distribution and movement patterns. That is, it results in possible suppression of migration or interchange/ overlapping of stocks in feeding grounds.

Furthermore, Reisinger et al. (2021) using regional models that employed an ensemble of machine learning algorithms, reported that HW inhabiting the Antarctic exhibit a preference for open water zones in close proximity to the sea ice edge although there is heterogeneity in their circumpolar distribution. Their distribution patterns were observed to shift southwards as the sea ice extent receded, as corroborated by earlier research (Bombosch et al., 2014; Andrews-Goff et al., 2018). Similar behaviour has been reported for fur seals in winter, but not for other baleen whales like minke whales' which are consistently associated with pack ice throughout all seasons (Ribic et al., 1991). The overlapping and time-lagged effects of factors associated with prey availability and feeding events, make it challenging to disentangle the natural variability of distribution patterns from climate change impacts (Meynecke et al., 2020; Meynecke et al., 2021).

Genetic, isotope, and fatty acid studies of humpback whales have also highlighted that the changing sea ice dynamics have led to changes in prey availability and abundance. Groß et al.

(2020b) discovered some variations in feeding behaviour, though Antarctic krill remains the primary prey for humpback whales. They attributed the observed variability in the whales' fatty acid profiles more to changes in the krill population than to alterations in the whales' diet. Studies by Kershaw et al. (2021) and Seyboth et al. (2021a) linked the decline in reproductive success of humpback whales to shifts in prey availability within their feeding grounds, which is induced by changing environmental conditions.

Most research supports the idea that humpback whales have a relatively narrow feeding niche, primarily relying on Antarctic krill to replenish their blubber stores (Nowacek et al., 2011; Owen, 2014; Curtice et al., 2015; Baines et al., 2022). This conventional feeding-fasting model is based on historical whaling records and shapes our current understanding of whale migration. However, recent studies have reported on a few populations feeding along their migration routes (Seyboth et al., 2023). Although feeding behaviour in low- and mid-latitude areas has been identified in earlier studies (Baraff et al., 1991; Gendron, 1993; Danilewicz et al., 2009), Eisenmann et al. (2016) were the first study to use baleen plate analysis to explore the feeding relationships and dietary habits of Southern Hemisphere humpback whales. Findings by Fleming et al. (2016), further showed that humpback whales can exhibit behavioural and dietary plasticity when environmental conditions are unfavourable for common target prey species (i.e., shifting from krill to schooling fish due to increased SST).

Whether this emerging evidence of some populations deviating from the classical feeding ecology model constitutes proof of a response to a changing environment due to climate change or results from the recovering whale populations remains unclear. This further emphasizes the need to understand how the changing multiple environmental drivers, including the effects of past whaling, are influencing the distribution and habitat selection of humpback whales. Thus, disentangling the impacts of climate change from those of historical perturbations and/or natural variability of humpback population dynamics.

The examples mentioned above highlight several assessments of the environmental conditions influencing humpback whales in Antarctic feeding grounds. A common thread among them is their focus either on specific locations, stock populations and/or for relatively short periods of time. This narrow focus could potentially lead to incomplete or biased assessments of the drivers influencing humpback whale populations, hindering efforts to develop comprehensive conservation and management strategies. Additionally, it may conceal the broader ecological context in which these whales operate, thereby limiting our ability to predict and mitigate the impacts of environmental changes on their populations effectively.

1.3.2 The use of long-term ecological research in climate studies

Long-term ecological research programs serve as invaluable tools for tracking changes in the movement and distribution of highly mobile diving marine mammals that spend relatively little time on the surface, such as humpback whales (Ferguson et al., 2009; Friedlaender et al., 2018). One such program is the International Decade of Cetacean Research, Southern Ocean Whale and Ecosystem Research Programme (IDCR/SOWER), a multi-year initiative implemented by the International Whaling Commission (IWC). This program represents the sole cetacean sighting dataset that offers comprehensive, large-scale insights into the historical status of Southern Hemisphere humpback whales in the Southern Ocean (Bombosch et al., 2014; Friedlaender et al., 2018).

The initial goal of the IDCR was to provide reliable population estimates for minke whales in the Southern Ocean, using systematic sightings and marking techniques, independent of whaling operations, to support the management and conservation of the species (Best & Ohsumi, 1980). However, as the needs of the IWC evolved, its design was adapted to focus on assessing the effects of the 1985 whaling moratorium on all cetacean populations, while minke whales remained the primary focus (Ensor et al., 2009). Data from these surveys have been standardised, validated, and stored in the IWC database as described Burt (2004). It is not publicly available but can be requested from the IWC secretariat. Due to this, this dataset has not been of immediate exploitation and has mostly been utilized by individuals affiliated with whale ecology and/or associated with the IWC. It has been primarily exploited to assess the density distribution of baleen whales in the Antarctic region (Kasamatsu, 1996; Kasamatsu, 2000; Kasamatsu et al., 2000; Branch & Butterworth, 2001a; Matsuoka et al., 2003; Branch, 2007, 2011; Murase et al., 2020).

The structure of the dataset complicates its integration with other environmental information, thus requiring an initial pre-processing work to make it usable. These challenges, arising from the biases present in the data, are discussed on page 47. This work aims at highlighting the full potential of this dataset through a preliminary investigation of humpback whales' occurrence in relation to environmental data. The objective of the study is to capitalize on the wealth of the IDCR/SOWER dataset in ways that extend it beyond its initial scope, specifically by assessing the relationship between the sightings dataset and satellite-derived observations of sea ice. This integrated approach has the potential to offer valuable insights into the changing climate over time, even in complex and dynamic environments like the Southern Ocean, as well as highlight the power of interdisciplinary research.

2. Materials and Methods

2.1 Description of the study area and survey design

The IDCR/SOWER Project was initiated to investigate the resources, ecology, and habitat of whale species in the Southern Ocean. It comprises 31 separate multi-vessel surveys conducted annually from 1978 to 2010. The primary objective was to assess whether whale populations were recovering following the whaling ban established in 1986 by the IWC, with a particular emphasis on estimating the abundance of Antarctic minke whales (Kasamatsu, 1996; Kasamatsu, 2000; Kasamatsu et al., 2000; Matsuoka et al., 2003). All cetaceans , including other baleen whales such as blue whales, humpback whales, and southern right whales, were also subjects of research.

Surveys conducted under the project were strategically designed to maximize spatial coverage. They encircled the Antarctic during three circumpolar series, crisscrossing strata of the open-ocean area south of 60°S. All IWC Antarctic Management Areas (refer to Figure 6) were surveyed during this period, with some areas receiving more frequent visits than others. During the first circumpolar period (CPI: 1978/79–1983/84) and the second (CPII: 1985/86–1990/91), longitudinal coverage took precedence over latitudinal coverage and a northern boundary of each area was established arbitrarily. In the third circumpolar series (CPIII), which began in 1991/92–2003/04, the focus shifted to prioritize latitudinal coverage (from the ice-edge to 60°S), leading to the expansion of the southern stratum further north and additional coverage of northern waters compared to the first and second circumpolar cruises. The cruise tracks and strata covered since the first survey till 2003/04 have been used to derive whale densities (Branch, 2011). Branch and Butterworth (2001a) described the sampling methods used during these three circumpolar surveys. The survey cruises carried out from 2004/05 to 2009/10 included a series of experiments that adopted new survey methodologies to address the shortcomings identified in previous analyses of abundance data. Raw data collected during each cruise include sightings of all cetaceans, information on the survey effort, weather conditions, ice-edge conditions.

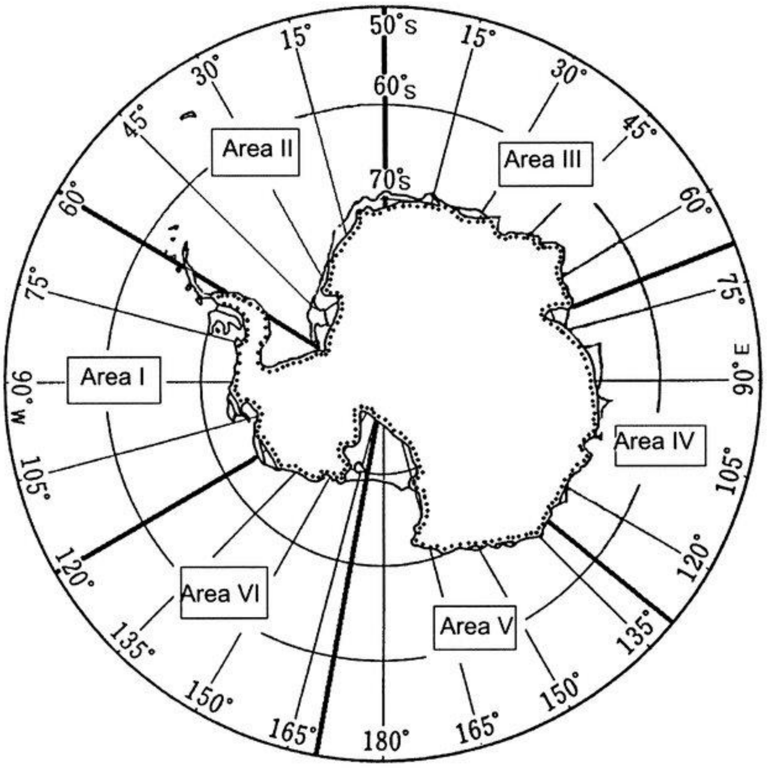


Figure 6. The six IWC Areas for the management of baleen whale species (except Bryde's whale). Source: (Matsuoka et al., 2003)

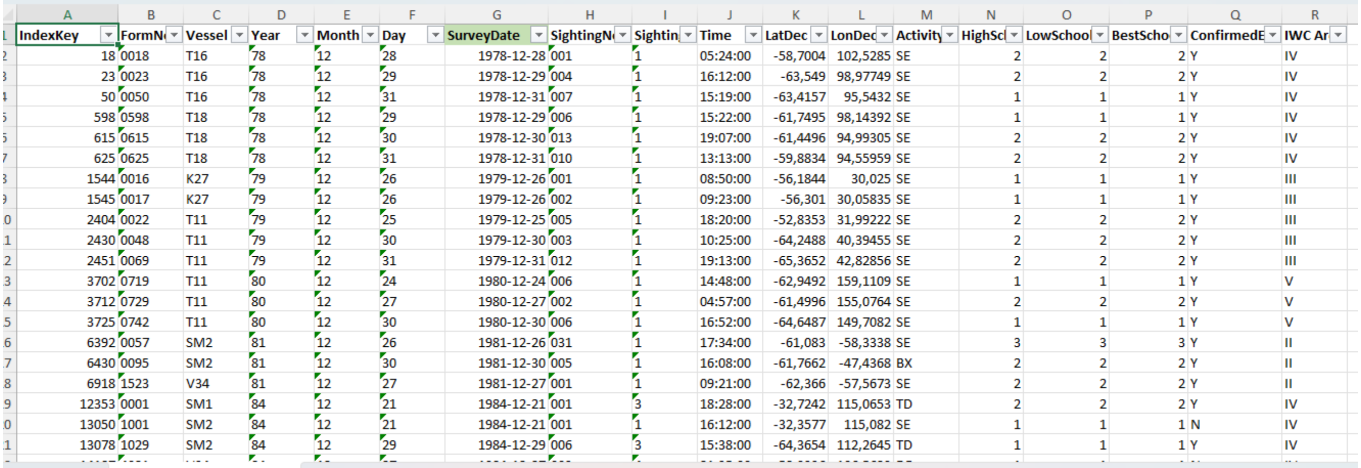
2.2 HW sightings data

During each survey, two (or more in some cases) vessels collected sightings data through various survey modes. All surveys were initially carried out in closing mode (during CPI), in which the vessel would turn off the track line to confirm a sighting. Subsequent surveys alternated between passing and closing modes. During the passing mode, the vessel continued along its track line after a sighting, with topmen in the barrel maintaining their full searching effort while those on the upper bridge focused on tracking and identifying the sighting. In this mode, often referred to as “IO mode”, the effort involved an additional Independent Observer (IO) stationed on a different platform on the main mast. The IO was positioned separately to independently verify the sightings, minimizing bias and enhancing the reliability and accuracy of the data through an additional assessment of the whale group (Matsuoka et al., 2003).

The sightings were categorized into primary sightings, when full searching effort was applied, and secondary sightings, which encompassed all other sightings recorded during experiments and during other non-primary activities such as closing on a sighting to confirm another group, drifting, or steaming with the topmen down. Because the main objective of this work is assessing distribution on a spatial and temporal context, all the sightings were included in the analysis.

Sourced from the IDCR/SOWER dataset available in the IWC database, the sightings (presence-only) data (Table 1), were requested from IWC by Dr Elisa Seyboth from the University of Pretoria. Each recorded sighting of a cetacean corresponds to a unique index key, which is connected to a header key linking it to related effort and weather data. The sightings entries contain details on position, date, time, observer information, and extra information important for estimating abundance like whale size (minimum and maximum length), school size, and any duplicate records. Starting from the 1990/91 survey, supplementary details regarding behavioural observations, such as 'Pod/General Behaviour' and swimming activities, have also been documented. Prior to the application of this dataset in the current study, it was further filtered and sorted according to the Whales and Climate dataset structure[1].

Table 1. Snapshot of the IDCR/SOWER dataset revised following the Whales and Climate dataset structure.



A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
IndexKey	FormN	Vessel	Year	Month	Day	SurveyDate	SightingN	Sightin	Time	LatDec	LonDec	Activity	HighSc	LowSchool	BestScho	ConfirmedE	IWC Ar
18	0018	T16	78	12	28	1978-12-28	001	1	05:24:00	-58,7004	102,5285	SE	2	2	2	Y	IV
23	0023	T16	78	12	29	1978-12-29	004	1	16:12:00	-63,549	98,97749	SE	2	2	2	Y	IV
50	0050	T16	78	12	31	1978-12-31	007	1	15:19:00	-63,4157	95,5432	SE	1	1	1	Y	IV
598	0598	T18	78	12	29	1978-12-29	006	1	15:22:00	-61,7495	98,14392	SE	1	1	1	Y	IV
615	0615	T18	78	12	30	1978-12-30	013	1	19:07:00	-61,4496	94,99305	SE	2	2	2	Y	IV
625	0625	T18	78	12	31	1978-12-31	010	1	13:13:00	-59,8834	94,55959	SE	2	2	2	Y	IV
1544	0016	K27	79	12	26	1979-12-26	001	1	08:50:00	-56,1844	30,025	SE	1	1	1	Y	III
1545	0017	K27	79	12	26	1979-12-26	002	1	09:23:00	-56,301	30,05835	SE	1	1	1	Y	III
2404	0022	T11	79	12	25	1979-12-25	005	1	18:20:00	-52,8353	31,99222	SE	2	2	2	Y	III
2430	0048	T11	79	12	30	1979-12-30	003	1	10:25:00	-64,2488	40,39455	SE	2	2	2	Y	III
2451	0069	T11	79	12	31	1979-12-31	012	1	19:13:00	-65,3652	42,82856	SE	2	2	2	Y	III
3702	0719	T11	80	12	24	1980-12-24	006	1	14:48:00	-62,9492	159,1109	SE	1	1	1	Y	V
3712	0729	T11	80	12	27	1980-12-27	002	1	04:57:00	-61,4996	155,0764	SE	2	2	2	Y	V
3725	0742	T11	80	12	30	1980-12-30	006	1	16:52:00	-64,6487	149,7082	SE	1	1	1	Y	V
6392	0057	SM2	81	12	26	1981-12-26	031	1	17:34:00	-61,083	-58,3338	SE	3	3	3	Y	II
6430	0095	SM2	81	12	30	1981-12-30	005	1	16:08:00	-61,7662	-47,4368	BX	2	2	2	Y	II
6918	1523	V34	81	12	27	1981-12-27	001	1	09:21:00	-62,366	-57,5673	SE	2	2	2	Y	II
12353	0001	SM1	84	12	21	1984-12-21	001	3	18:28:00	-32,7242	115,0653	TD	2	2	2	Y	IV
13050	1001	SM2	84	12	21	1984-12-21	001	1	16:12:00	-32,3577	115,082	SE	1	1	1	N	IV
13078	1029	SM2	84	12	29	1984-12-29	006	3	15:38:00	-64,3654	112,2645	TD	1	1	1	Y	IV

2.3 Sea Ice Data:

The sea ice data used in this study were extracted from the NOAA/NSIDC Climate Data Record of Passive Microwave Sea Ice Concentration, Version 4 (Meier, 2021). The dataset contains sea ice concentrations which are estimates of the fraction of ocean area covered by sea ice. I used monthly data covering the ocean surface area from 39.36°S to 89.84°S in the Southern

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[1] https://whalesandclimate.org/portfolio/ : Whales and Climate data portal.

Hemisphere. This product leverages on two well-established and well-validated concentration algorithms, the NASA Team (NT) algorithm and NASA Bootstrap (BT) algorithm. An additional advantage is that the SMMR data have been added to the period of record such that the monthly CDR variable spans from November 1978 through to the most recent processing; covering the entire period of interest (Meier, 2021).

The dataset uses a grid on a polar stereographic projection, with a spatial resolution of 25 km x 25 km. The variable of interest is the monthly average of the daily CDR sea ice concentrations (cdr_seaice_conc). It consists of aggregated monthly files with spatial dimensions (x and y grid) and a time dimension indicating the number of months. The presence of gaps in the data is negligible because the CDR uses gap-filling procedures; only 12 out of 3412 sightings recorded had no sea ice data due to missing or corrupt data. They correspond with the observing period 1987/12/03 – 1988/01/13.

2.4 Data analysis

Data wrangling and visualization of both sea ice and sightings data were conducted using Python, utilizing libraries such as Pandas, Matplotlib and Cartopy. For whale sightings, the data was initially pre-processed and organized according to the guidelines of the Whales and Climate Project database structure (https://whalesandclimate.org/portfolio/). Further data manipulation involved using *dataframes* and dictionaries to add variables such as survey seasons (defined as a combination of two consecutive years spanning December to February) and assign sectors to each observation based on predefined geographical ranges. A size-encoded *heatmap* depicting the number of whale sightings per IWC area (presence only) across different survey seasons was generated to explore the overall spatial and temporal patterns of whale sightings.

Pre-processing of the sea ice data included applying a scaling factor and adjusting flag values to ensure consistency and facilitate meaningful comparisons. To analyse how sea ice evolved over time and for identification of fine-scale patterns in each region, line plots were utilized to present the monthly extent anomalies for the study period and annual cycles of sea ice each IWC Area and ice sector. Anomalies were sliced to focus on the survey seasons period, from December to February, and presented as a bar plot highlighting deviations from the monthly climatological mean. The years 1981-2010 were used as the reference period for calculating the anomalies.

Next, a comparative analysis of whale sightings' latitudinal distributions between sectors during the feeding season was conducted using *violin plots*. Further examination of the sightings data within ice sectors included determining the whales’ median latitude per month for each season, the total number of unique days in which whales were recorded and the total count size per survey season. The output was presented in a table and aided in selecting years (together with the criteria described below).

To assess humpback whales’ distribution in relation to sea ice, visual analyses of sea ice anomalies, whale sightings, and vessel track lines were presented using a grid of subplots. Track line data of the cruise surveys were included to aid in identifying presence/absence where surveys were conducted but no sightings were made. A loop iterated over a predefined set of different combinations of years and summer months, filtering and processing relevant data subsets. Iteration produced a subplot within a grid including timestamps and geographic features (e.g., land, coastlines, latitudes), enhancing the interpretability of the plots. For each survey season, 5 months were visualized. The inclusion of the two months pre-survey season (October and November) in the combined analyses was done to investigate if any lagged sea ice effects were present. Since sea ice was the variable of interest, sightings only south the latitude 55°S were analysed in combined analyses. This is the northernmost latitude Antarctic sea ice extent reaches in winter (Eayrs et al., 2019). By organizing the data in this manner, the structure facilitated systematic comparisons across different years and months. This approach allowed for easier tracking and identification of patterns and trends over time.

All years and regions were included in the analysis and the regions not presented in the main text are available in the Appendix. In Chapter 3, I present and discuss three sectors selected for their unique combined features: the Amundsen-Bellingshausen (AB) sector (130°W to 170°W), which have negative sea ice trends and smaller SIE; the Ross-Amundsen (RA) sector (165 ° E to 130° W), which is representative of the behaviour of the majority of the Antarctic sea ice; and the East Antarctic (EA) sector, representing sectors on the east part of Antarctica where the greatest number of humpback whale sightings were recorded. The selection of survey seasons to present was based on whale data, and the criteria for selection included:

1. The survey season had to have data for at least two of the three summer months (December to February).

2. High count size/ number of unique days with recorded sightings; a preference for seasons with higher total counts/ number of unique days of sightings recorded. It is important to mention that this does not reflect effort/encounter rate but determined so to aid in selecting years with substantial data.
3. Differences in mean latitudes observed across seasons.
4. At least one survey during each circumpolar period.

The survey had to meet a minimum of three of these requirements, as some were not applicable in some sectors (e.g., the AB sector had no sightings recorded in December for all the seasons surveyed). In cases where seasons had minimal differences or did not meet the minimum requirements, a season sharing common variables with a season already selected for meeting the minimum requirements was also included to ensure comparability. This included taking the sea ice anomalies conditions into consideration. All conditions were assessed where possible, including years characterized by negative, positive, or neutral summer anomalies. By neutral summer anomalies, I refer to survey seasons where there is a combination of both above- and below-average anomalies, resulting in no clear trend. Throughout the analysis, considerations were made for potential biases in the data and were taken into account when interpreting the results.

3. Results

3.1 Sightings data

The spatial distribution of humpback whale sightings across the Antarctic feeding grounds reveals monthly disaggregation, with a southward shift in sightings over the months. February shows the highest concentration of sightings south of 60°S, compared to January and December (Figure 7). The total count of sightings recorded during the entire survey period is 3408. Each survey season spanned three months (December, January, and February), with the highest number of sightings recorded in the middle of the summer season, represented by percentages of 8.4%, 52.1%, and 39.6%, respectively.

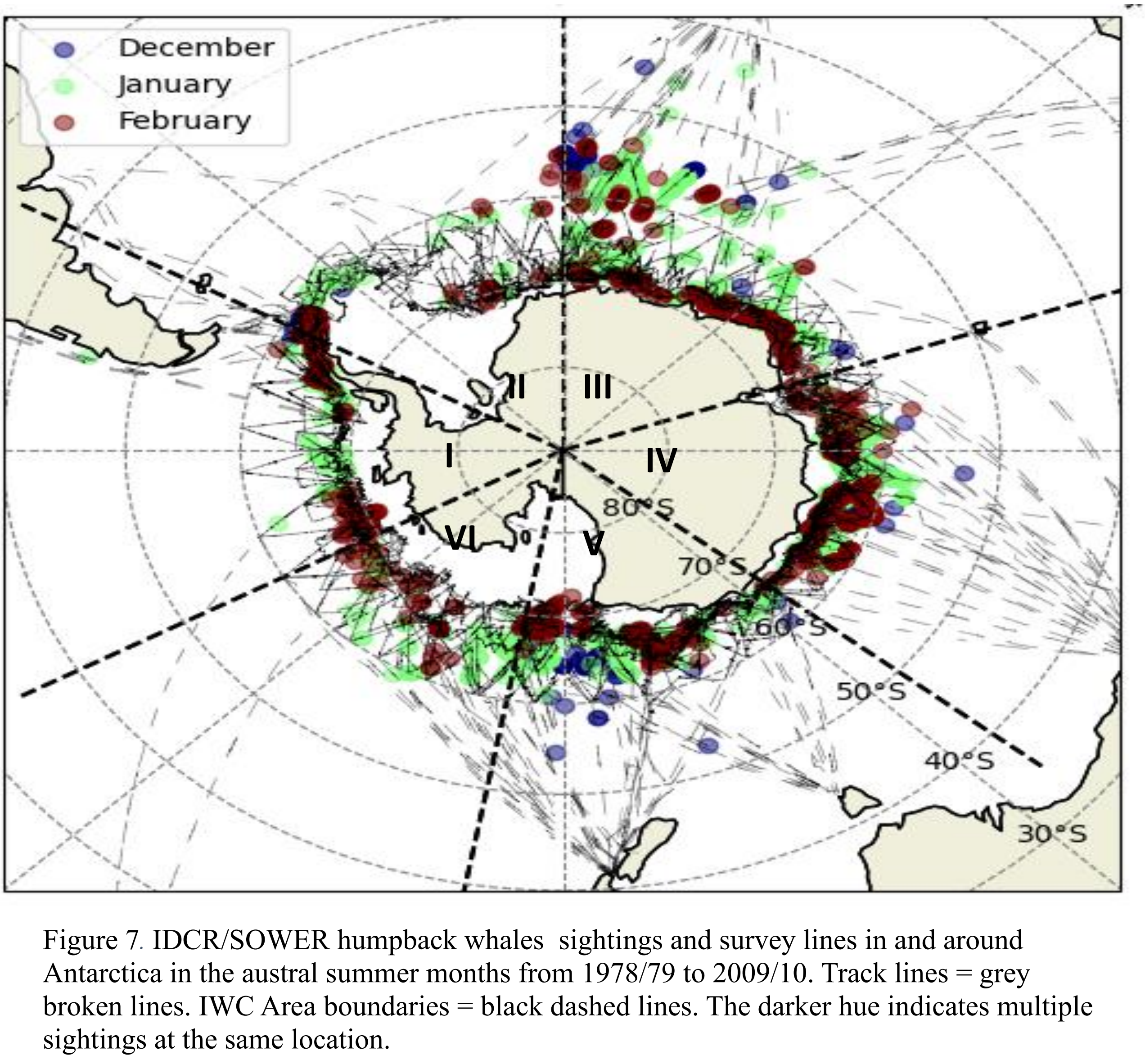


Figure 7. IDCR/SOWER humpback whales sightings and survey lines in and around Antarctica in the austral summer months from 1978/79 to 2009/10. Track lines = grey broken lines. IWC Area boundaries = black dashed lines. The darker hue indicates multiple sightings at the same location.

The distribution of sightings per year and area is shown in Fig. 8. The number of whales sighted between the first survey and the 1997/98 survey remained consistently low, with total sightings recorded being less than 65 per season, except for the 1988/89 survey season in Area IV. Of the six IWC Areas, I, II, and VI had the fewest seasons surveyed, with Areas I and II having 5 and 6 seasons respectively, and none conducted post-2000/01. Areas III, IV, and V, which were more frequently surveyed, recorded a sudden increase in sightings during the last decade of the study period.

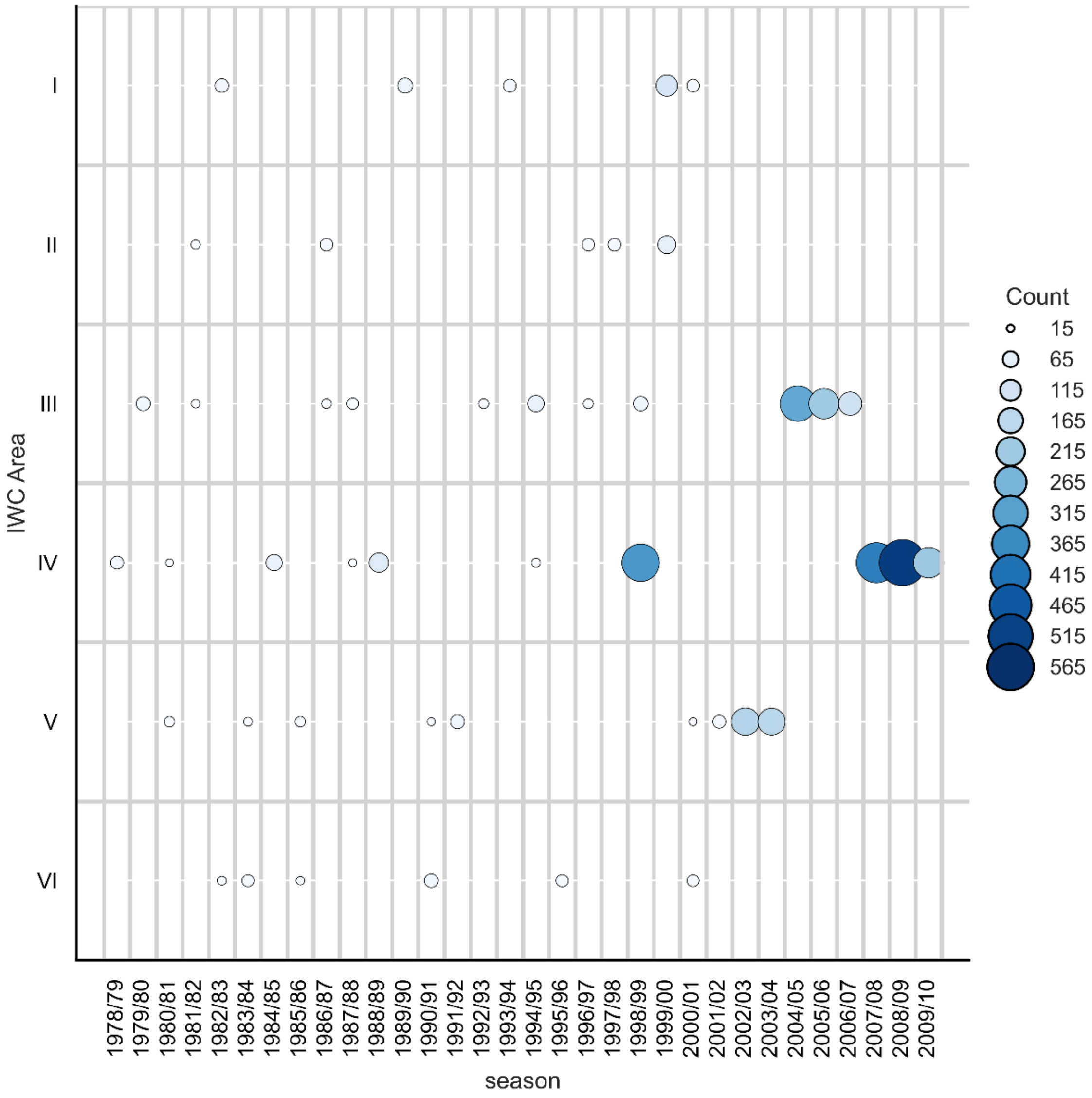


Figure 8. Number of sightings per survey season in each IWC Area. The first category comprises 1 to 15 sightings; blank spaces indicate areas that were not surveyed during that season.

3.2 Sea ice extent and choice of sectors

Sea ice extent was calculated as explained in Sec, 2.x for the whole Antarctic region and for the sectors defined in Raphael and Hobbs (2014) (hereafter referred to as "the ice sectors", Sec. 1.2.2 and Fig. 4) and IWC Areas (1991). The monthly anomalies of sea ice extent during the period of the surveys show a minimal positive long-term trend but exhibits high interannual variability (Fig. 9). This is aligned with the literature prior to the 2017 period (Parkinson, 2019). However, Antarctic sea ice is known for its large regional differences; hence a sector-based analysis is necessary.

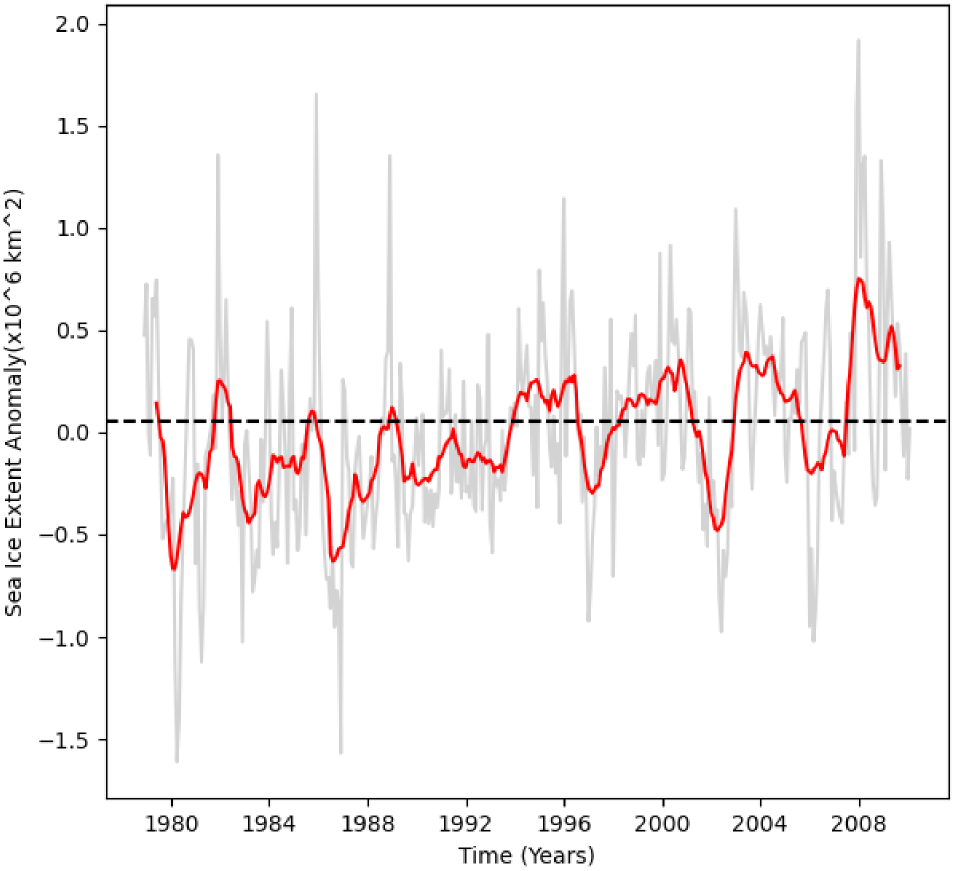


Figure 9. Monthly Antarctic sea ice extent anomalies stretching from November 1978 to February 2010 (grey line), calculated from a climatological baseline of 1981-2010 (black line). The red line shows the 4 months running mean anomaly.

The geographical locations of the Antarctic sea ice sectors and the IWC Areas are shown in Figure 10. All IWC Areas, except Areas III and IV, span across two ice sectors. Area I predominantly occupies the Amundsen-Bellingshausen (AB) sector, with a minor overlap of approximately 10 degrees into the Weddell Sea. Area VI largely spans the Ross-Amundsen

(RA) sector with a similar overlap into the AB sector. Area V substantially extends over both the East Antarctica (EA) sector (35 degrees) and the RA sector (65 degrees). These ice sectors have distinct seasonal cycles of sea ice with differences in extent, duration, and timing of advance and retreat (Figure 11, top panel). Of all the sectors, the AB and EA sectors have the smallest ice extents, with the AB sector retreating the earliest. The RA sector is characterized by an earliest advance and a later retreat.

When viewed through the lens of the IWC Areas, sea ice seasonality is also apparent as all IWC Areas have different annual seasonal cycles (Fig.11, bottom panel). The intersection of sectors has been graphically presented by combining the line colours in the plot. For areas that extend over two sectors, the influence of multiple sea ice sectors is evident in their seasonal cycles. For example, the summer extent of Area II resembles that of the Weddell Sea, but the overall extent is much larger, with the winter maximum resembling that of King Hakon VII. The degree of influence varies depending on the longitudinal coverage of the ice sector. For instance, the influence of the early advancing RA sector is evident in the cycles of Areas V and VI, with the latter having a stronger resemblance.

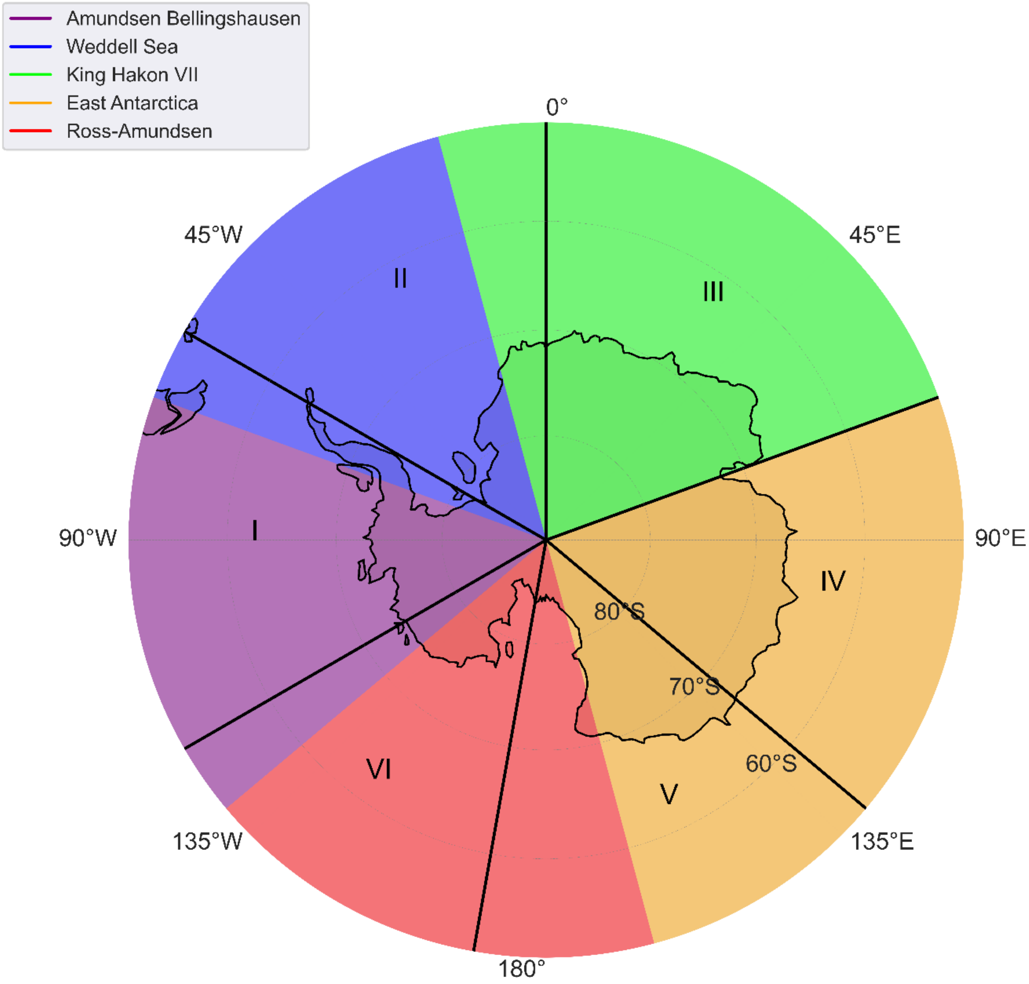
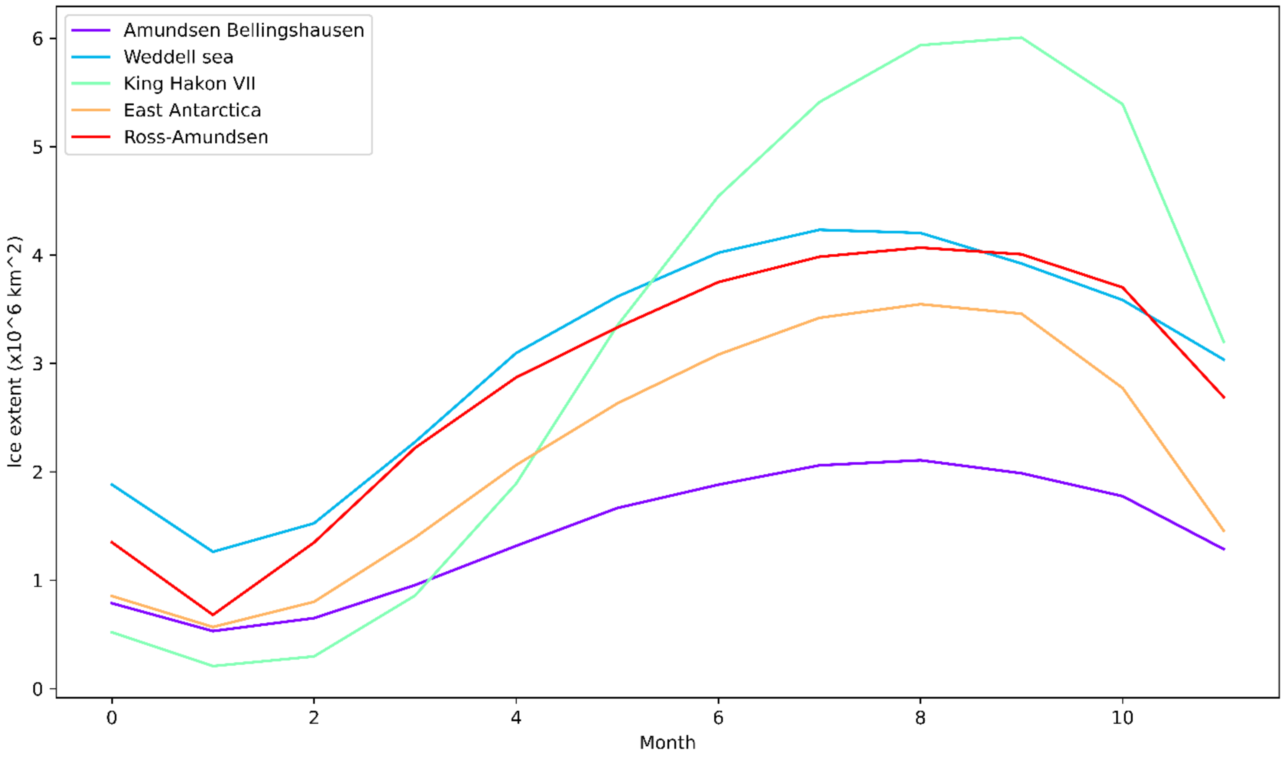


Figure 10. Comparison of the geographical location of the ice sectors as defined in Raphael and Hobbs (2014) and IWC Areas as defined by IWC (1991). Ice sectors are defined using colour and named as in the legend; black vertical lines represent the IWC Areas boundaries and roman numerals are the area numbers.



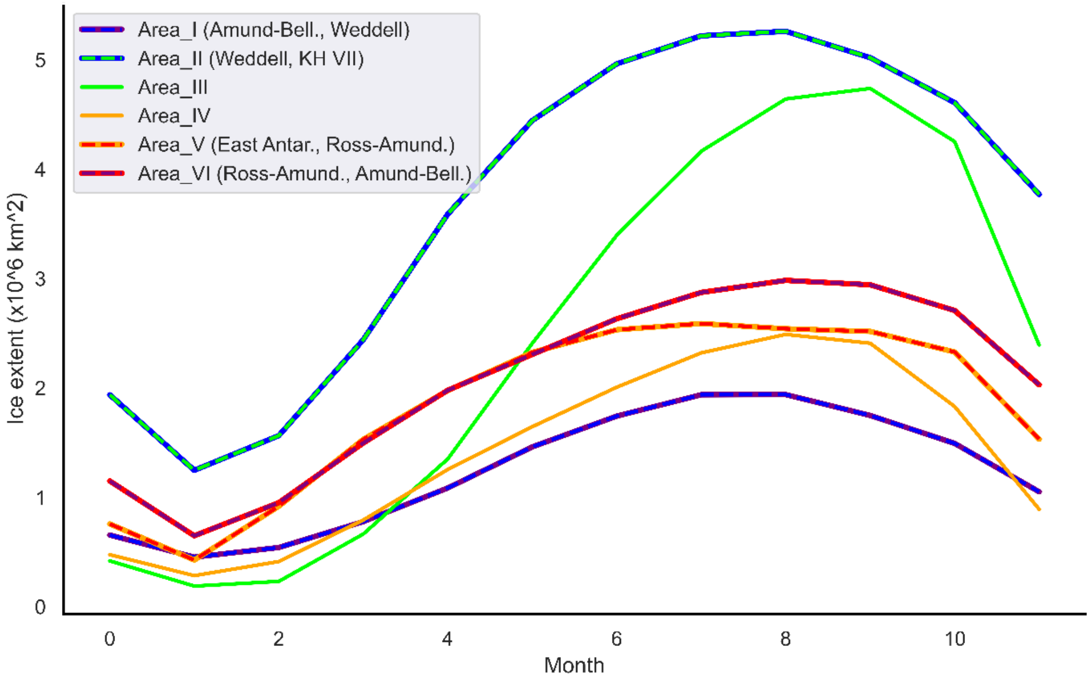


Figure 11. Annual seasonal cycle of sea ice extent in the sectors defined by Rafael and Hobbs (2014, top) and IWC Areas (bottom). The dashed line colours in the bottom panel are determined by the overlap of sectors from the top panel (also refer to Figure 10).

The influence of multiple sectors on the sea ice trends obtained within each IWC Area is also evident. Summer anomalies of the Amundsen Bellingshausen (a) and Ross Amundsen (b) ice sectors are shown in Figure 12. During the first circumpolar set of IDCR observations in the early 80's, the summer anomalies of the RA sector were dominated by negative anomalies. Thereafter, there was an increase in positive anomalies, which became more dominant from 1988/89 onwards. In contrast, the AB sector initially experienced very few negative anomalies, which only became frequent post-1990. During the last set of survey seasons, this sector was dominated by negative anomalies. When the same diagnostics are calculated with the IWC sectors, the summer anomalies for Area VI (Figure 13), which span the two sectors illustrated in Figure 12, showed no clear long-term trends with the occurrence of alternating negative and positive anomalies. Initially dominated by positive anomalies for the first five years, the anomalies then shifted to negative anomalies for the next five years, continuing this cycle until the end of the study period. Overall, the zoning of IWC Areas when used to examine sea ice trends adds more complexity as they do not align perfectly with sea ice sectors that are identified through coherent dynamics and trends by Rafael and Hobbs (2014).

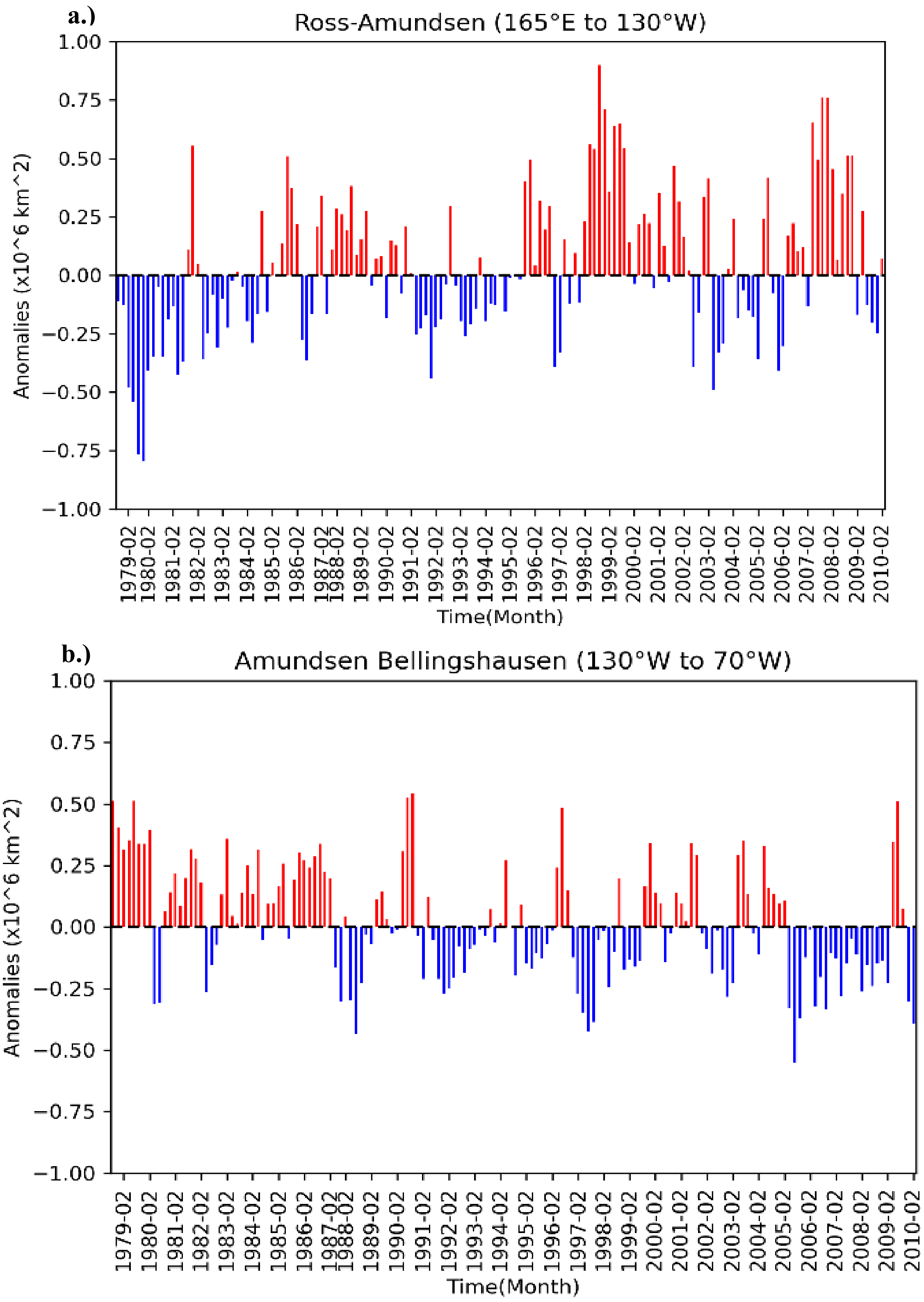


Figure 12. Summer (December to February) anomalies of two adjacent sectors with contrasting ice trends: a) The Ross-Amundsen sector and b) the Amundsen-Bellingshausen sector

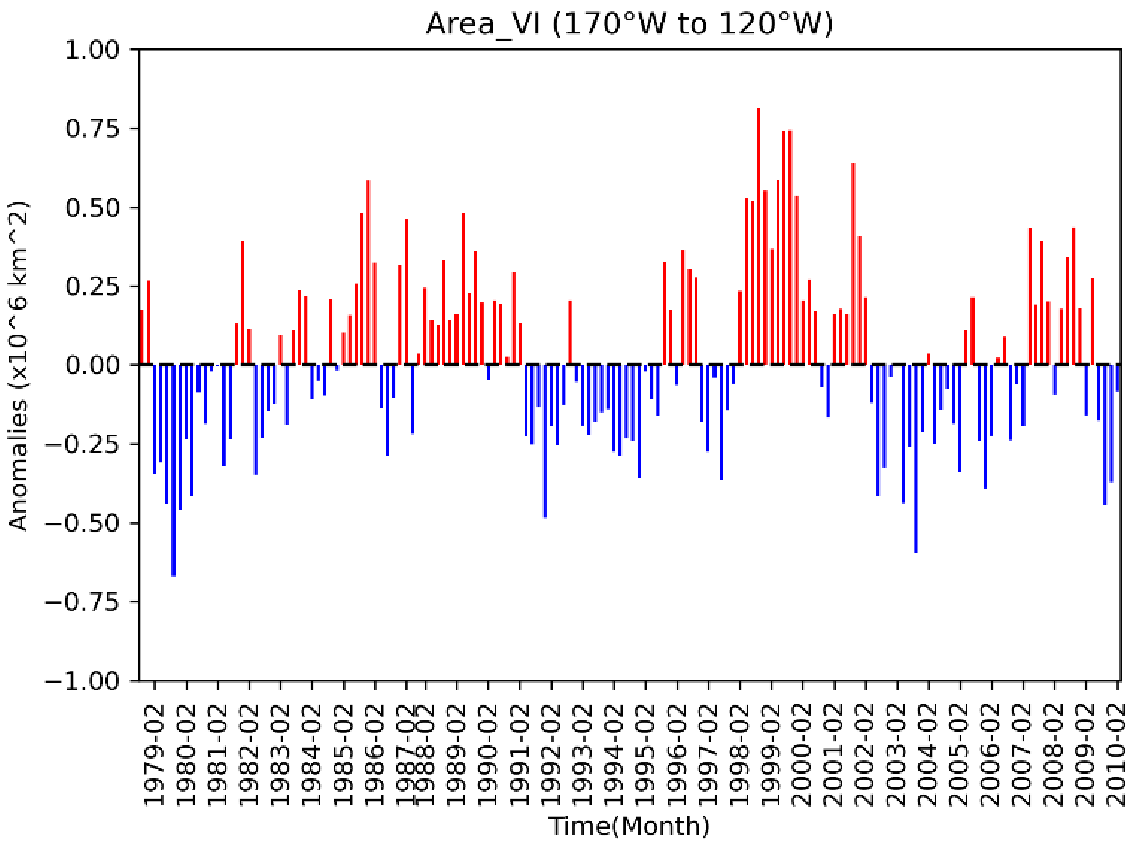


Figure 13. Summer (December-January-February) sea ice concentration anomalies in IWC Area VI, which spans over the two ice sectors depicted in Fig.12

3.3 Distribution of sightings within the ice sectors

Sightings previously grouped within a single IWC area were now regrouped according to the sea ice sectors (Fig. 14). For instance, sightings from Area I were primarily in the Amundsen Bellingshausen sector, with a few seasons (1983/84, 1990/91, and 2000/01) from Area VI. The remaining seasons from Area VI were within the Ross-Amundsen sector, which had the majority of sightings from Area V. Minimal changes in groupings were noted in areas which are confined within a single ice sector. That is, areas III and IV overlap with King Hakon VII and East Antarctica, respectively.

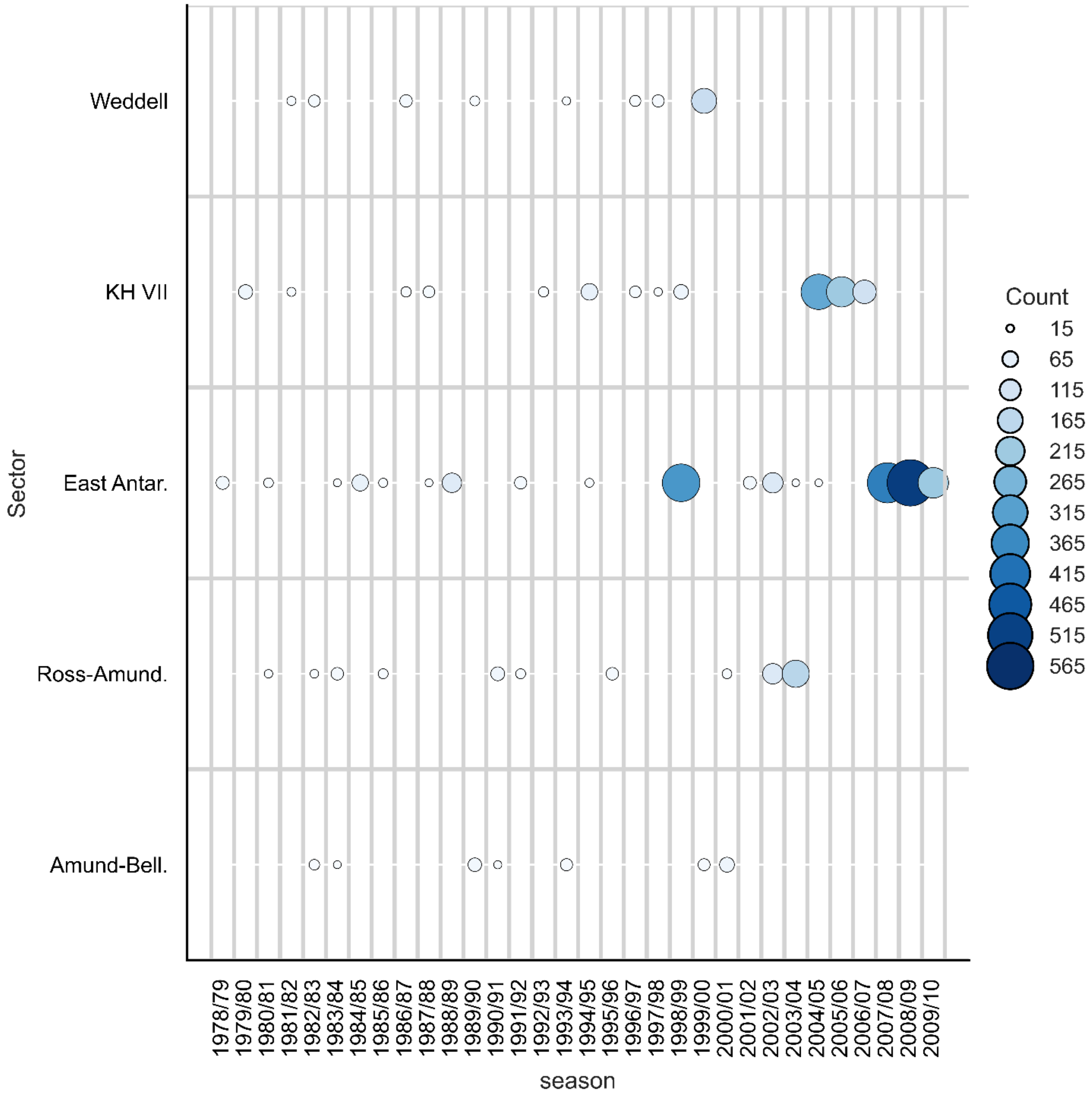


Figure 14. Frequency of humpback whale sightings within each sea ice sector per season surveyed.

The assessment of the sighting distributions through violin plots revealed variability between sector, month, and the median latitude occupied (Fig. 15). In all sectors except the RA, the December median latitude of the distributions was north of 65°S. As hinted visually when presenting Figure 7, a notable southward shift in the median latitude from December to January was observed in all sectors except the AB sector, where no sightings were recorded in December for any survey season. The AB sector, which has the smallest sea ice extent seasonality (Fig. 11) also had a narrower latitudinal range of the sightings, approximately between 62°S and 69°S for the entire season. A relatively minor southward shift from January to February was observed only in the EA and Weddell sectors.

In contrast, a northward shift in the median latitude in February was observed in the distribution of whales from the RA and KH VII sectors, resulting in a bimodal distribution.

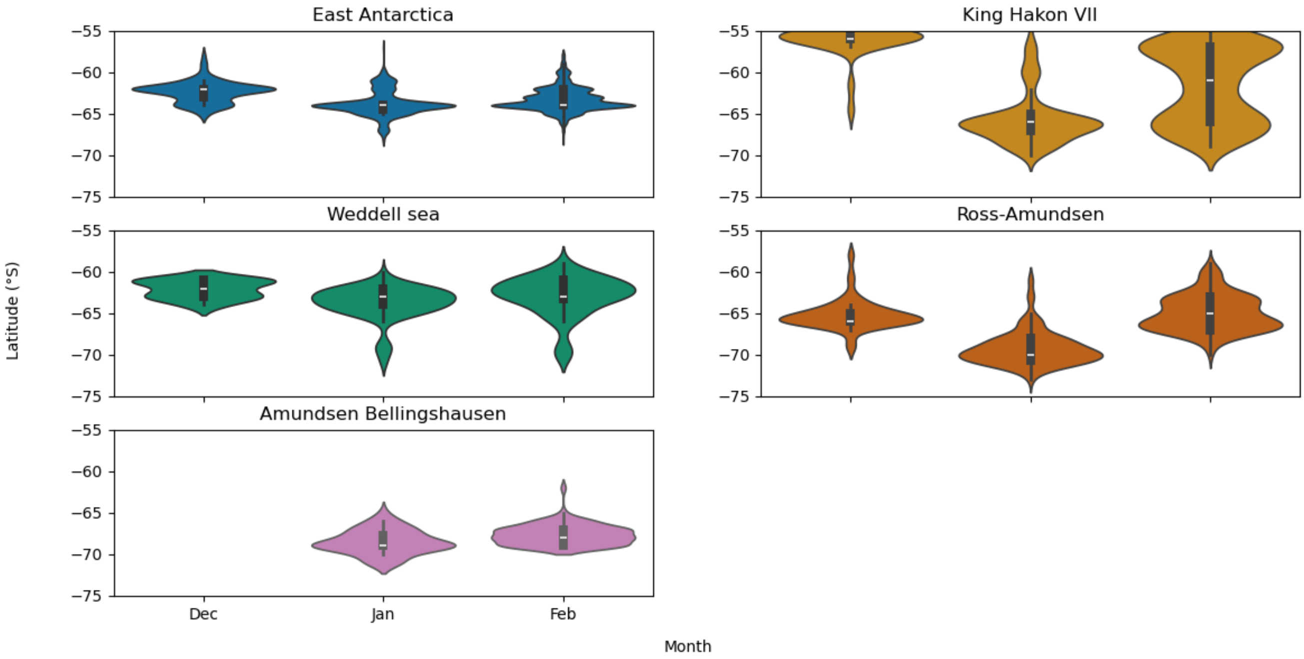


Figure 15. Temporal distribution of humpback whales sightings for all the survey seasons (December, January, and February) across different sea ice sectors.

From further examination of sightings distribution within the ice sectors (Table 2) and the criteria discussed in Chapter 2 survey seasons were selected and are highlighted in bold. These surveys seasons were selected based on the premise that they had sufficient data and were comparable in terms of spatial coverage of the surveys, thus enabling analyses of sightings and sea ice conditions over time. Sea ice concentration anomalies and humpback whale sighting locations demonstrate regional variation across ice sectors in the Antarctic feeding grounds (Figures 16, 17, and 18). To gain a broader overview of the sea ice conditions associated to whale presence, sea ice concentration anomalies from two months prior to the survey period were included, and only sightings south of 60°S were visualized. Survey paths were included to illustrate the areas covered (i.e., giving a qualitative idea of the survey effort) since this dataset is used as presence-only data. Presence-only datasets add complexity to the analysis because they lack information on where whales were not observed. This limitation can pose challenges for interpreting spatial patterns, as the absence of sightings does not necessarily indicate the absence of whales. Additionally, while whale sightings are sometimes spread out and easily distinguishable, in denser areas, they appeared clustered graphically as a single large point, and survey paths were not always clearly visible.

Despite these challenges, the analysis accounted for underlying biases, such as sampling effort variations, to provide as accurate a representation as possible (see chapter 4).The survey design, which prioritized coverage of strata south of 60°S and near the sea ice edge, combined with the known feeding behaviour of humpback whales, allows for reasonable interpretation of consistent whale aggregations around specific areas as indication that those areas are reliable prey sources for humpback whales. Given the nature of the dataset, these figures are the best compromise as they highlight key observations and provide context of how humpback whales are distributed with respect to larger scale sea ice conditions.

Table *2*. Examination of the median latitude of sightings south of 55°S for all months per survey season. Total number of days with whales sightings and the total number of sightings recorded in each survey season. Gaps/blanks = no survey conducted (except for the December in the Amundsen Bellingshausen sector).

Sector	season	Median latitude per survey season			Total Unique Days with sightings	Total Sightings Counted
		Dec	Jan	Feb		
Weddell sea	**1981/82**	-62	-62		6	7
	1982/83		-64		7	21
	1986/87	-61	-61		9	25
	1989/90	-63	-63		5	11
	1993/94			-66	3	4
	1996/97		-70	-69	9	17
	1997/98		-63		4	23
	1999/00			-63	9	142
King Hakon VII	**1979/80**	-60	-66	-68	19	36
	1981/82			-64	2	2
	1986/87		-69	-57	6	13
	1987/88	-61	-65		11	19
	1992/93		-66	-59	10	12
	1994/95		-62	-65	17	55
	1996/97		-61	-58	8	18
	1997/98			-56	2	4
	1998/99		-65		9	38
	2004/05		-56	-66	25	293
	2005/06	-55	-57	-69	31	207
	2006/07	-56	-67	-63	25	118

Sector	season	Median latitude per survey season			Total Unique Days with sightings	Total Sightings Counted
		Dec	Jan	Feb		
Amundsen Bellingshausen	**1982/83**		-67	-69	12	14
	1983/84			-67	2	2
	1989/90		-69	-68	11	32
	1990/91			-66	2	3
	1993/94		-68	-69	12	23
	1999/00		-67	-65	11	22
	2000/01		-68	-69	17	44
East Antarctica	**1978/79**	-62	-64	-64	18	29
	1980/81	-63	-66		7	10
	1983/84		-68		1	2
	1984/85	-62	-63	-64	26	51
	1985/86	-65	-65		4	7
	1987/88	-58			1	1
	1988/89	-62	-62	-65	13	79
	1991/92		-65		4	24
	1994/95			-63	5	6
	1998/99		-63	-62	27	337
	2001/02	-64	-64	-66	12	28
	2002/03		-65	-66	17	89
	2004/05			-57	1	1
	2007/08	-63	-63	-65	32	387
	2008/09		-64	-64	24	521
	2009/10		-64	-64	27	218
Ross-Amundsen	1980/81		-68	-67	4	4
	1982/83			-70	3	5
	1983/84		-66	-68	15	25
	1985/86		-69	-69	18	11
	1990/91		-65	-67	12	33
	1991/92		-67	-72	5	11
	1995/96		-66	-66	13	25
	2000/01		-64		7	10
	2002/03	-64	-65		21	90
	2003/04	-66	-65	-70	22	170

For the Amundsen-Bellingshausen sector, survey seasons 1982/83, 1989/90, 1993/94, and 2000/01 are presented (Fig. 16). The 1982/83, 1989/90, and 2000/01 survey seasons were chosen because they provide data for both January and February for CPI, CPII, and CPIII, respectively, and were seasons with a high total count of sightings and unique survey days in their circumpolar set. The 2000/01 season had the highest count size in this sector. The 1993/94 season was selected because its count size was higher than that of 1982/83 despite having the same number of days where sightings were recorded. A similar approach was used to select the presented survey seasons for the other sectors.

In the Amundsen Bellingshausen (AB) sector, the presence of both positive and negative anomalies of sea ice concentration was observed, however no substantial differences were observed in whale distribution patterns by latitude despite variations in region of occurrence or intensity of anomalies. For example, in 1982/83, negative anomalies were recorded around the Amundsen Sea with a band of below-average conditions near sea ice edge, while for the 1989/90 survey season, positive anomalies dominated near the Antarctic Peninsula for the months prior to the surveys and during the summer months.

Despite these differences, humpback whale sightings in this sector were confined within a narrower latitudinal range, north of the sea ice edge in both seasons. Similarly, the 2000/01 survey season experienced a combination of contrasting sea ice anomalies, with increasing positive anomalies observed from December to February. However, during this season, whales were recorded only towards the Amundsen Sea and further offshore in both January and February. A common pattern observed across these three survey seasons is that, in February, whales were recorded at varying distances from the sea ice edge but tended to shift further east towards the 120° longitude.

In contrast, the 1993/94 survey season, characterized by persistent negative sea ice anomalies, saw whales recorded closer to the Western Antarctic Peninsula (WAP) in February. Sightings appear to be more present near sea ice edge only for a survey season conducted during CPI, i.e., 1982/83. For other circumpolar surveys, they remained dispersed within these narrow ranges and were constantly in areas that were covered by ice in months preceding the survey seasons with shift following melting ice at a distance. Similar to the AB sector, there were no remarkable features in the overall distribution patterns of humpback whales in the Ross-Amundsen Sector (Fig. 15). Sightings were also not more frequent near the sea ice edge but tended to return to previously occupied areas.

Throughout the study period, no sightings were made south of 72°S, instead they remained non-uniformly distributed north of it in all seasons surveyed. In contrast to the AB sector, the distance between the sea ice edge and sightings increased as the season progressed. Except in the recent survey seasons where sightings were noted in December and a southward shift in sightings occurred in the late survey seasons, albeit at a slight distance. For CPI and CPII, sightings were widely distributed between approximately 170°W and 135°W but shifted towards the 180° longitude in the recent circumpolar set (CPIII). These minor expansions in the late surveys occurred during survey season where increased above-average sea ice conditions in the Ross Sea were observed.

East Antarctica stands out as one of the two sectors where evident increases in sightings were observed over time (Figure 14). Sightings recorded during CPII (1988/89) were twice those recorded in CPI (1978/79), with a fourfold increase in CPIII (1998/99). This increase in sightings saw a notable shift from being distributed around 90°E to between ~100°E and ~135°E. As shown in Figure 18, despite variations in survey methods, humpback whale distribution during the circumpolar sets remained relatively wide throughout the survey seasons, primarily in the vicinity of areas covered by positive ice anomalies two months prior. The 2008/09 survey season recorded the highest number of sightings and is the only season where humpback whales clustered within a closer distance to the sea ice edge, concentrated around 90°E and remained there throughout the season.

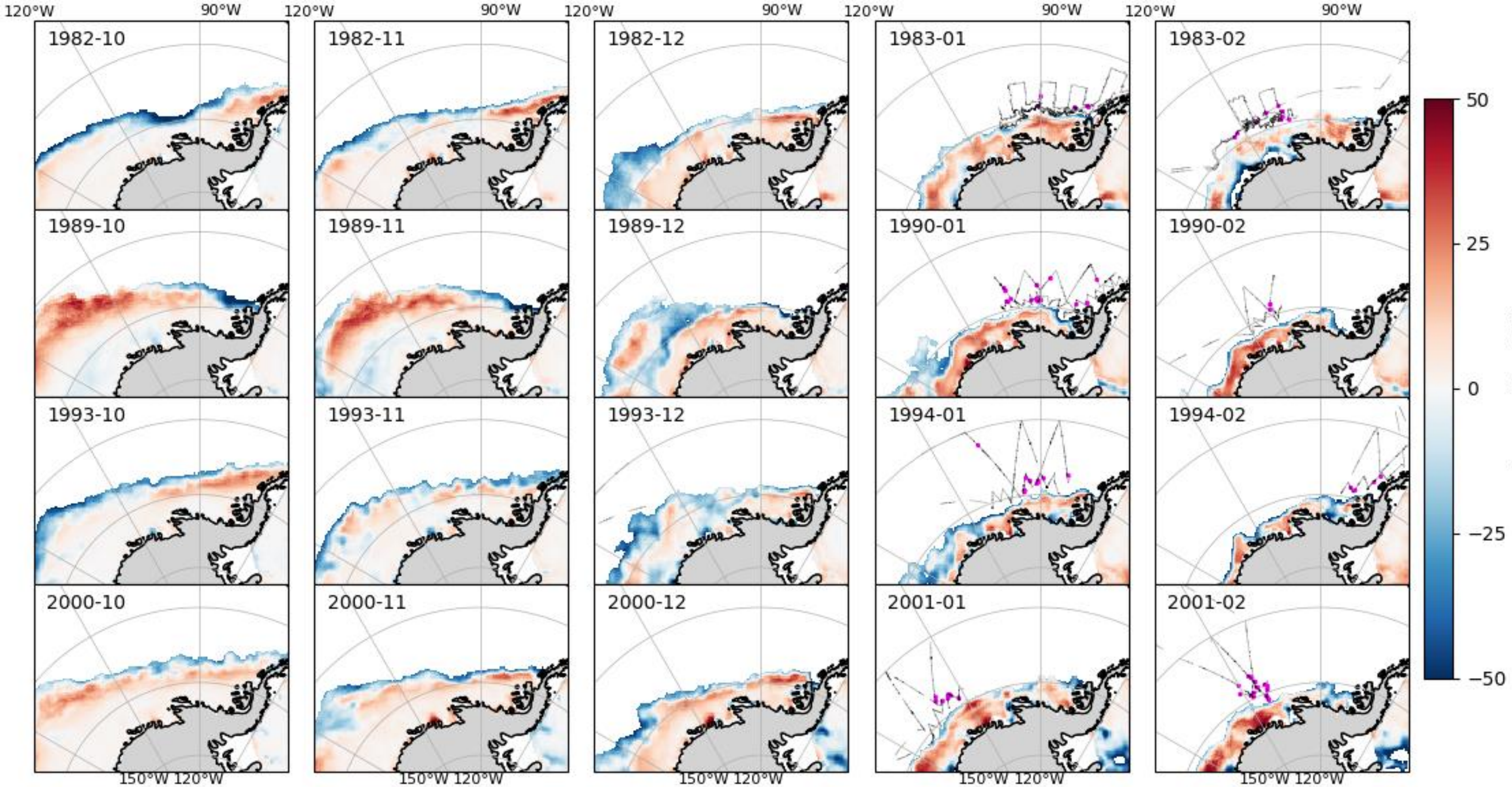


Figure 16. Humpback whales' distribution in relation to sea ice anomalies in the Amundsen-Bellingshausen sector (130° W to 70° W). The shown parallel is 60°S. In magenta are the humpback whale sightings from the IDCR/SOWER data and the black lines are the cruise track lines.

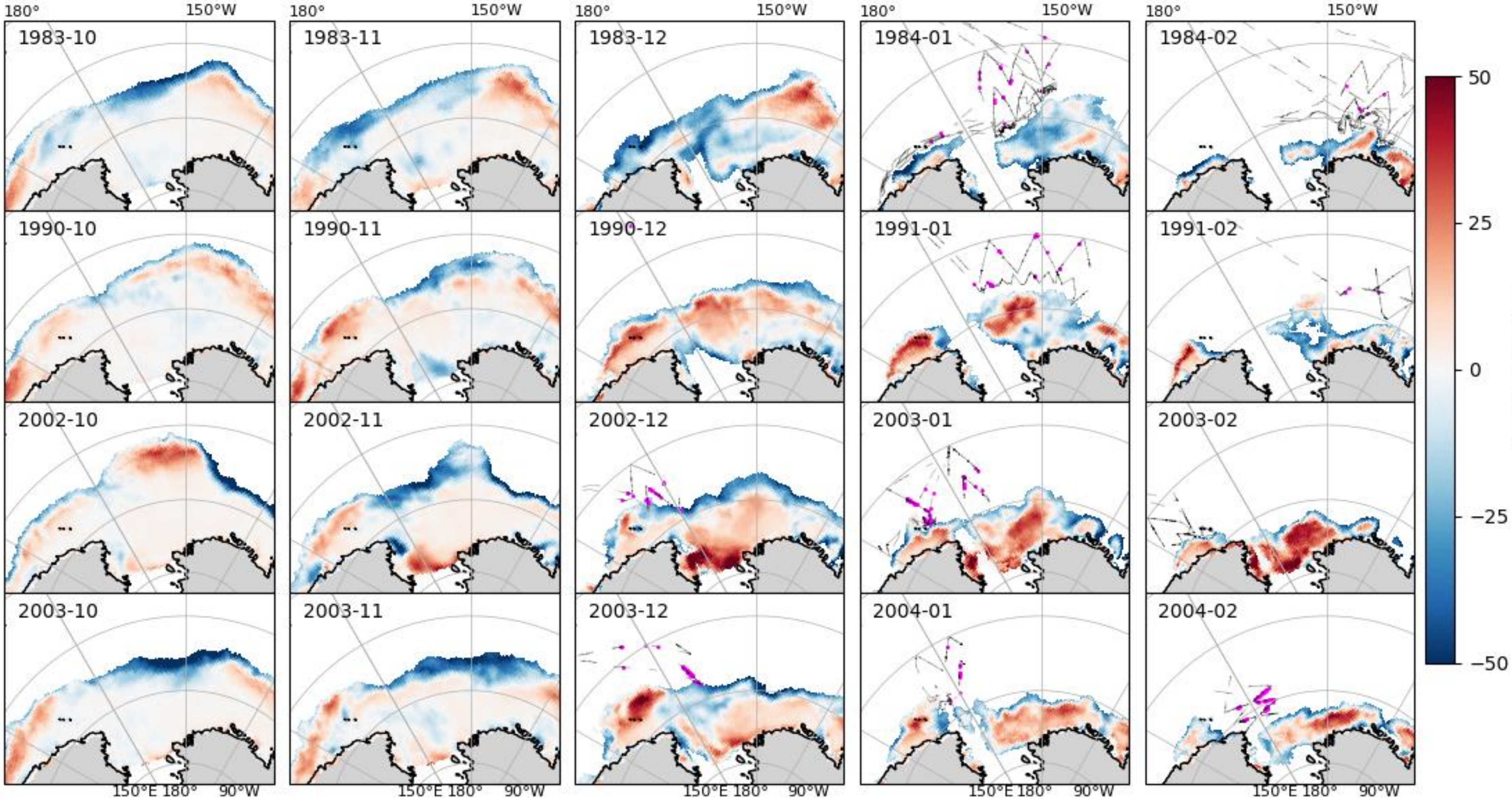


Figure 17. Humpback whales' distribution in relation to sea ice anomalies in the Ross-Amundsen sector (165 ° E to 130° W). The shown parallel is 60°S. In magenta are the humpback whale sightings from the IDCR/SOWER data and the black lines are the cruise track lines.

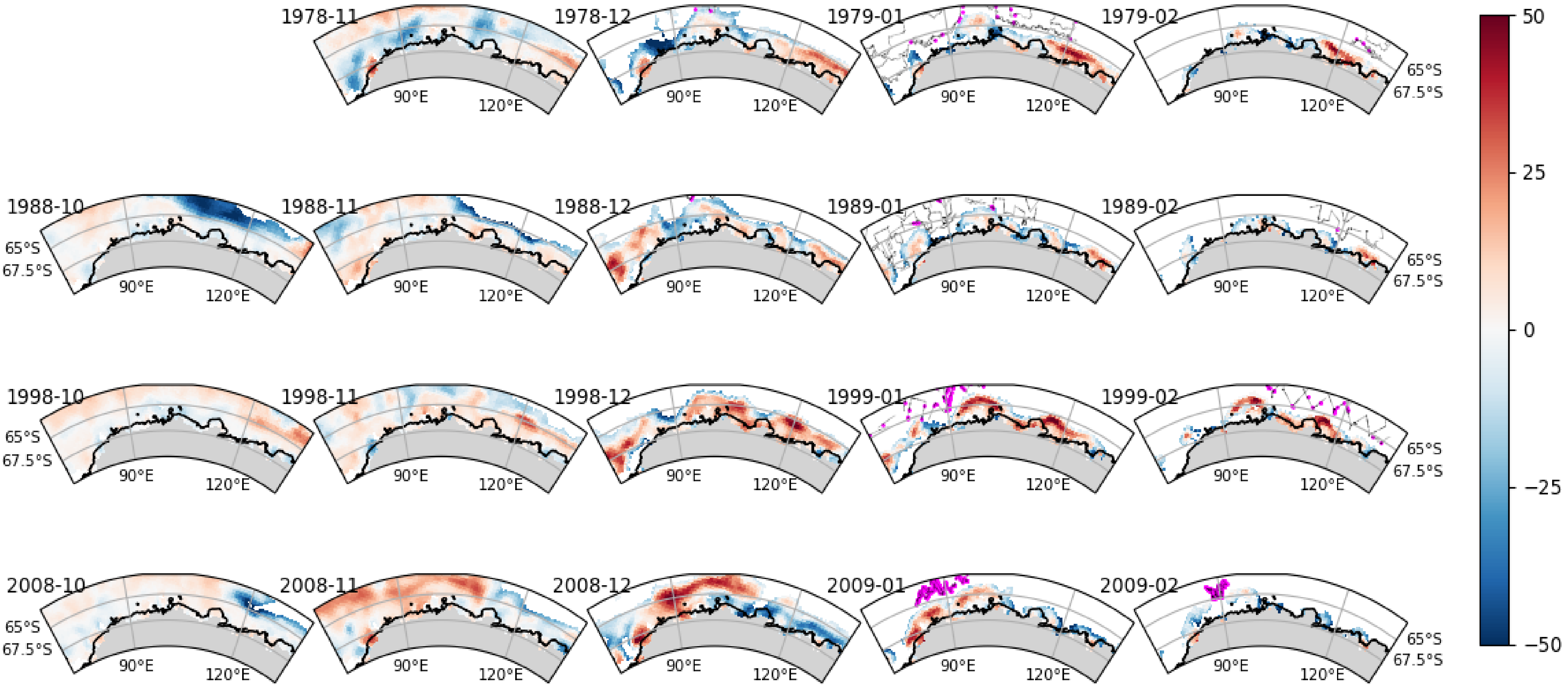


Figure 18. Humpback whales' distribution in relation to sea ice anomalies in the East Antarctica sector south of 65°S (70° E to 165° E). The empty plot is due unavailability of sea ice concentration records for that period since CDRs of sea ice only extend from 25 October 1978. In magenta are the humpback whale sightings from the IDCR/SOWER data and the black lines are the cruise track lines.

4. Discussion

4.1 IWC Boundaries and Sea Ice Sectors

The six IWC areas were established as management boundaries based on multi-species whaling catches, and existing literature indicates no differences between the environmental conditions and feeding ecology of these stocks (Donovan, 1991). Several environmental factors are known to affect HW behaviour (Meynecke et al., 2022), and sea ice is considered one major driver during the feeding period. Most studies use the IWC areas for regional analyses of whales' behaviour in their feeding grounds (Branch & Butterworth, 2001b; Rock et al., 2006; Branch, 2007, 2011; Matsuoka et al., 2011; Hakamada & Matsuoka, 2014; Murase et al., 2014). Some studies have proposed redefinition of the existing area boundaries because of increasing evidence of the porous boundaries and interchange between recognized stocks during feeding (Dalla Rosa et al., 2008; Pastene et al., 2011; Marcondes et al., 2021). However, none of the proposals have investigated the influence of sea ice at the larger scales because the division of IWC Areas did not consider Antarctica's regional sea ice variability.

This work represents a preliminary attempt at combining the analysis of sea-ice extent and concentration variability with the most extensive dataset of HW sightings. The standard division of the IWC areas poses a challenge when attempting to find relationships between the sea ice environment and the whales' behaviour within the feeding grounds from an environmental perspective. This work demonstrated that only few annual cycles computed over the IWC areas are similar to those obtained from the standard sea ice sectors, as depicted in Figure 11. The distinct patterns of localized sea ice variability within each of the five sectors yield different sea ice annual cycles. These large-scale trends reflect the complex patterns of change in the sea ice dynamics, such as rate and timing of sea ice advance, retreat, and duration, occurring within each sector (Smith & Comiso, 2008; Constable et al., 2014; Gutt et al., 2015; Fraser et al., 2023; Swadling et al., 2023).

Therefore, because a single IWC area encompasses contrasting sea-ice sectors, the average spatial and temporal variability is affected by the presence of different sea ice dynamics. For instance, Area VI spans over two sectors with very contrasting sea ice conditions; the Ross-Amundsen, known for its early advance and later retreat which has been dominated by positive anomalies in the last decade, and the Amundsen Bellingshausen sector which has a negative monthly extent trend with a later advance and earlier retreat, hence has a shorter duration. The extent and seasonality of Area VI sea-ice features is influenced by both these different trends despite that only a small portion of this area is overlapping the AB sector, as evident in the summer anomalies (Figure 13). Physical conditions that determine habitat and food availability are then more likely to differ even within a single area as some parts experience earlier or later retreat compared to others resulting in patchy distribution of ice cover and food resources.

Consequently, this may induce non-uniform behavioural responses from species of the same population regardless of the occupied IWC area being the same, as behaviour of migratory species is driven by a combination of both internal and external cues (Constable et al., 2014, (Raphael & Hobbs, 2014; Raphael et al., 2020). Perhaps even more important to humpback whales is the timing and period of sea-ice retreat, which signals the commencement and duration of the feeding season in the Antarctic waters (Horton et al., 2017; Bengtson Nash et al., 2018; Druskat et al., 2019; Nash et al., 2023). This highlights the complexities of considering uniform sea ice dynamics within a single IWC area, which makes it difficult to identify clear cause-and-effect relationships between humpback whales and sea ice. Similar observations were reported by Beekmans et al. (2010), as they noted the challenge of detecting consistent qualitative relationships between minke whales and their environment within prescribed management areas over various survey years.

In this study, ice sectors were used instead of IWC areas, and the distribution of humpback whales sightings from IDCR/SOWER were reprocessed in relation to known sectors in which sea ice thermodynamic and dynamics are assumed to be more coherent (Massom & Stammerjohn, 2010). Given that much of our current knowledge on response of marine ecosystems in the Antarctic to regional shifts on the krill abundance and their habitat quality has been linked to variability and seasonality in sea ice (Ducklow et al., 2007; Ducklow et al., 2012; Constable et al., 2014; Loeb & Santora, 2015; Atkinson et al., 2019), using defined sea ice sectors was therefore more ideal because sea ice patterns and their influence on factors effecting humpback whales' distribution are more uniform within ice sectors than within IWC areas.

By analysing anomalies in sea ice extent, this study offers a detailed perspective on how these anomalies influence the latitude of the sea ice edge—relationships that may not be fully captured by threshold-based methods (e.g., SIC), especially given the high temporal variability observed in overall sea ice trends (Fig. 9) and within individual sectors (e.g., Fig. 12). Positive anomalies, which increase spatial ice coverage, lead to a more northward shift in the ice edge. In contrast, persistent negative anomalies a result in a poleward retreat, reducing suitable habitat for whales(Stammerjohn et al., 2008; Massom & Stammerjohn, 2010). Based on this premise, if shifts in humpback whale sightings align with these changes in ice extent, it suggests that variations in the latitude of the ice edge, driven by anomalies, may influence humpback whale distribution.

4.2 Distribution of humpback whales sightings in relation to sea ice

While the observed patterns could reflect the distribution of survey effort, given that the vessels did not penetrate the sea ice and the surveys were designed to be conducted north of the sea ice extent, findings from this study align with existing literature. This literature indicates that humpback whales tend to prefer open water but follow the sea ice edge to capitalize on the abundance of krill when the sea ice melts (Friedlaender et al., 2006; Vigness-Raposa et al., 2010; Kennedy, 2013; Zerbini et al., 2020; Seyboth et al., 2023).

The patterns observed in the IDCR/SOWER database support this, with humpback whales consistently found in open waters, often in areas that were previously covered by ice. In sectors where sightings' distribution visually correlated with sea ice changes (i.e., the Amundsen-Bellingshausen and East Antarctica), sightings moved further south as the sea ice retreated while maintaining distance from sea ice edge. Additionally, shifts in the latitudinal and longitudinal ranges corresponded to presence of above and /or below-average ice conditions.

This study represents a preliminary investigation on the potential uses of the IDCR/SOWER database. From this initial assessment, it appeared that humpback whales generally did not cluster near sea ice edge. Instead, they were dispersed within their latitudinal ranges. During CPI, sightings closely aligned with the vessel track creating an appearance of higher concentrations near the sea ice edge due to the survey method closely tracking the sea ice edge. Branch (2011) reported on the pronounced peak in sightings directly on the track line during CPI, attributing this to the observers' tendency to round small sighting angles to the nearest 10-degree interval. The overrepresentation of sightings near the trackline was also evident in subsequent circumpolar surveys. This could partly reflect biases related to the use of reticle binoculars, which were routinely used during surveys (Leaper & Gordon, 2001; Matsuoka et al., 2003). Reticle binoculars' limited field of view, combined with overlapping observation fields from both sides of the vessel, likely concentrated observation effort near the trackline.

During the first two months, sightings occurred over wider latitudinal ranges compared to February, when they were recorded in narrower latitudinal ranges closer to the Antarctica continent, except in the King Hakon and East Antarctica sectors. In these two sectors, high densities and localised distributions of humpback were recorded around specific longitudes and coastal polynyas, e.g. around 90°E in East Antarctica. Notably, in the late experimental surveys in the EA sector, increased sightings were recorded and clustered near sea ice edge. These findings are consistent with previous studies by (Kasamatsu, 1996; Gales et al., 2011; Gales & Gales, 2011; Bombosch et al., 2014), which also reported similar patterns in humpback whale sightings.

Humpback whales' distribution in the Southern Ocean feeding grounds can be categorised into two main behavioural states: transiting and foraging (area-restricted search) (Weinstein et al., 2017; Andrews-Goff et al., 2018). Behaviour south of 60°S is largely foraging and since humpback whales demonstrate behavioural plasticity during foraging Riekkola et al. (2019), the observed changes in the temporal and spatial distribution may reflect fluctuations in prey and habitat availability. According to Bombosch et al. (2014), these patterns also correspond to suitable habitat availability. Their study indicated that maximum habitat suitability occurs in January and decreases as the season progresses, with the most favourable conditions forming a narrow band around the Antarctic coastline by February. Furthermore, these maps showed that habitat conditions in Amundsen-Bellingshausen only become favourable in January. This may be the reason for the absence of sightings in December within the Amundsen-Bellingshausen sector (ABS) throughout our study period.

Kasamatsu (1996) attributed the peak in January sightings in the IDCR dataset to the age and sex-segregation in the migrations of humpback whale populations. He suggested that early feeding begins when the first group of whales arrives in the feeding grounds from November to early December and the arrival of the second group between mid-December and early January marks the commencement of main feeding period. Nichols et al. (2022) further suggested that the decline in February sightings and their narrow latitudinal occurrence may indicate that foraging efforts and presence reduce as the season progresses. All these arguments are consistent with the qualitative findings of this study. The number of sightings recorded increased from December to January, followed by a decline in February.

To reduce predator-prey mismatches, humpback whales time their arrival on feeding grounds and balance the time spent on foraging behaviour to exploit the habitat optimally (Bierlich et al., 2022). This behavioural pattern is typical for long-distance migrating top predators and has been documented also for species such as birds (Nakano et al., 1999; Fraser & Huntingford, 2010). Using their memory, maternally derived fidelity and environmental cues, humpback whales target known prey hotspots during foraging, and are able to adjust their movement and behaviour in response to complex or patchy environments(Arthur et al., 2016; Riekkola et al., 2019). Findings of this study largely supports this as the influence of changing sea ice dynamics on humpback whale distribution patterns appeared to be greater in the AB and EA sectors, which are characterized by higher variability of the sea ice environment (Vichi, 2022).

The AB sector is characterized by high nutrient levels but low productivity due to vertical mixing and limited light availability(Stambler, 2003). However, productivity rates vary across spatial scales, with localized high productivity observed along onshore-offshore gradients. For instance, high abundances of krill are found inshore during summer around the Western Antarctic Peninsula (WAP) and off the continental shelf in the Bellingshausen Sea (Ross et al., 2008; Perry et al., 2019). The small-scale spatial variability in the AB sector, typical of sea ice habitats (Convey & Peck, 2019), reflects its subdivision into distinct ecological regions shaped by local physical and biological conditions such as light gradients, salinity, and nutrient availability. Shorter ice duration coupled with an early sea-ice retreat, are deemed unfavourable for krill reproduction (Loeb & Santora, 2015; Atkinson et al., 2019).This preliminary analysis indicates that humpback whales followed the melting sea ice and only reached the coastline during the years characterized by persistent occurrence of negative anomalies which resulted in early sea ice retreat. For instance, in the AB sector, one explanation for the lack of major differences in humpback whale distribution patterns when above- or below-average ice conditions were present is that krill recruitment in the spawning hotspots or nursery grounds of this sector is influenced by ice conditions from both the highly variable Bellingshausen and Amundsen Seas (Wiedenmann et al., 2009; Veytia et al., 2021). If one sub-region experiences below-average ice conditions, an average or above-average conditions in the other can mitigate the effects (Wiedenmann et al., 2009), and become a favourable habitat for whales.

On a regional scale, the ice sectors in the South Pacific (i.e., Amundsen-Bellingshausen Sea and Ross-Amundsen sectors) exhibit relatively homogeneous patterns of change in sea ice seasonality (Constable et al., 2003; Constable et al., 2014). Conversely, East Antarctic sea ice trends are more complex as they comprise mixed signals due to pockets of strongly positive and negative trends, resulting in large spatio-temporal variability in sea ice seasonality and areas of enhanced productivity hotspots within the marginal ice zone (Massom et al., 2013; Hobbs et al., 2016). Riekkola et al. (2019) suggested that the consistent wider latitudinal range throughout summer in this sector indicates patchy prey distribution, as whales are forced to constantly move long distances to find food between these pockets.

Sightings data obtained from JARPA surveys (Japanese Whale Research Program under Special Permit in the Antarctic) demonstrated that, before the late 1990s, humpback whales within Area IV were rarely observed near the shelf during the feeding season. It was only post-2001 that they expanded their habitat closer to the coastline, subsequently occupying the entire survey area (Matsuoka & Hakamada, 2008; Matsuoka et al., 2011; Murase et al., 2014; Naganobu et al., 2014). The increased occurrence of sightings near the ice edge and/or their latitudinal shifts in the recent survey period has also been reported in JARPA surveys as observed in this study.

According to Matsuoka et al. (2011), this could be attributed to whale population size expansion and partly to the changing oceanographic conditions caused by occurrence of ENSO events. And as a result, humpback whales from this sector may prioritize feeding by timing their arrival at higher latitudes and spending more time near areas with positive sea ice anomalies to take advantage of increased productivity. For example, sightings recorded in the EA sector during the 2008/09 survey season (Figure 18) were clustered near the sea ice edge, corresponding to a season with the highest number of sightings and positive sea ice concentration anomalies.

In contrast to humpback whales from the AB and EA sectors, which rely on sea ice dynamics for prey availability, humpback whales in Ross-Amundsen (RA) sector have been reported to return to established productivity hotspots (Andrews-Goff et al., 2018; Riekkola et al., 2019). Similar trends are observed in the King Hakon VII ice sector, where the occurrence of whales was often around the Maud rise polynya, a known 'prey hotspot'(Kawamura, 1994; Tynan, 1998; Thiele et al., 2004; Andrews-Goff et al., 2018; Swadling et al., 2023).Despite of the Antarctic continental shelf reaching its maximum production and chlorophyll-a concentrations in January (Constable et al., 2003; Constable et al., 2014), humpback whales in the RA sector were notably absent in the Ross Sea and consistently remained farther north of the continental shelf break (north of ~70°S). This pattern, reported in previous studies by Branch (2011) and from other long-term ecological research program such as JARPA surveys (Matsuoka & Hakamada, 2008), may reflect the distribution of krill species, with Antarctic krill dominating north of 73°S. Reports by Naganobu et al. (2006) and Murase et al. (2006) support this, suggesting that Antarctic krill are present around the continental shelf but not south of 74°S in the Ross Sea.

4.3 Potential of the IDCR/SOWER dataset

The analysis of humpback whale sightings from the IDCR/SOWER dataset presented several complexities stemming from biases inherent in the data and its original design. Since the program's goal was to estimate the population densities of all cetaceans following their over-exploitation and the implementation of the whaling moratorium, the cruise surveys prioritized recording attributes relevant to abundance estimation. Specific biases include:

(1) changes in survey methodology over time, including varying spatial coverage, survey effort and duration, may have influenced the observed latitudinal range expansions. The survey design focused on establishing density boundaries, by following the sea ice edge with limited coverage of the entire feeding grounds south of 60°S. This is particularly true in sectors with lesser seasonal variations in sea ice edge median latitudes or where whales occupy wider latitudinal ranges, such as East Antarctica and Ross Amundsen sectors (Areas IV and V);

(2) observational constraints- availability and perception biases introduced by survey methodologies impacted data accuracy. For example, the use of reticle binoculars, although vital for distance measurements, limited observers' field of view. Additionally, overlapping observation fields near the trackline likely led to an overrepresentation of whale sightings close to the vessel, particularly in areas with high densities of whales;

(3) The use of presence-only data in this study introduced potential biases, as the absence of whale sightings does not necessarily indicate the absence of whales in a given area. This limits the ability to identify regions where whales were not observed, which could provide a more comprehensive understanding of their spatial distribution. However, given that humpback whale feeding behaviour is associated with area-restricted search and super-group feeding south of 60°S, aggregations of sightings in specific locations are sufficient to infer that these areas are reliable feeding grounds for humpback whales. While presence/absence data could offer additional insights the relationship between whale distribution and the sea ice edge, the use of presence-only data sufficed for investigating whether humpback whales utilize areas near the sea ice edge as main feeding habitats;

(4) information relevant for species distribution, such as general or pod behaviour was sparsely collected as priority was given to information important for density assessments, making it challenging to discern if the sightings was recorded in transiting

or foraging mode. This gap complicates efforts to determine how observed aggregations relate to feeding behaviour or habitat use;

(5) lastly, some sectors were only surveyed during seasons with similar sea ice conditions, limiting the ability to analyse humpback whale distribution patterns in all possible sea ice conditions.

Despite these challenges, this study represents the first necessary step towards expanding the usage of the IDCR/SOWER data in the context of a changing Antarctic sea ice. The findings demonstrate that, despite these biases and limitations, the IDCR/SOWER sightings dataset can be valuable for interdisciplinary research. By integrating additional covariate data from satellite, atmospheric reanalyses or directly from the cruise logs, such as wind direction and speed, sea surface temperature, air temperature, ice cover, sea state, researchers can begin to understand whale sightings in relation to environmental variables. Linking these data by means of *Headerkeys* (which are unique to each sighting) can connect humpback whale sightings with survey effort and weather conditions, facilitating more insights on whale distribution patterns.

Additionally, the study highlights the need for wider access to this dataset to enable collaborative research efforts. This dataset is currently available on demand through the IWC, which makes it accessible only to researchers from IWC member nations. Making the data publicly available would allow researchers from various fields to combine interdisciplinary expertise and resources, leading to innovative analyses and interpretations. The integration of machine learning algorithms and distribution models could further aid in quantifying and eliminating data bias in these integrated datasets. These modern quantitative approaches can address various errors and biases commonly found in ecological datasets (Bird et al., 2014). Thus, this study not only identifies the limitations and biases in the current data but also a significant step forward in demonstrating the potential of the IDCR/SOWER dataset for interdisciplinary research, providing a foundation for future studies to build a more comprehensive understanding of humpback whale distribution in relation to environmental variables.

5. Conclusion

This study represents an important step in utilizing the under-exploited IDCR/SOWER dataset and exploring its potential use for Antarctic climate research. Using humpback whales sightings dataset, a qualitative approach was used to assess their distribution in relation to sea ice. The results indicate that utilizing the standard IWC feeding areas to investigate environmental drivers of humpback whale distribution may not be ideal. These areas were primarily established based on historical catch data and management purposes, rather than for studying the ecological or behavioural patterns of whales in feeding grounds. Not only do most IWC areas span over two sectors known for their contrasting sea-ice features, but recent studies also proposed the redefinition of boundaries due to increasing evidence of breeding stocks overlapping and exchanging during feeding.

Given the spatial heterogeneity of Antarctic sea ice and how existing literature has linked humpback whale feeding ecology patterns to key Antarctic sea ice seasons, this study focused on broader spatial patterns using sea ice sectors. However, it is important to note that examining it from a regional perspective may mask finer variations in whale distribution. Therefore, future studies could capture these finer variations by using more refined spatial stratification, such as 10° longitudinal sectors, and quantitatively defining the latitude of the sea ice edge. Tracking how the position of the ice edge shifts over time would offer a more dynamic and localized perspective on the role of sea ice in shaping humpback whale feeding habitats and its impact on whale distribution.

There is no doubt that sea ice plays a significant role in humpback whales' feeding ecology. This analysis indicates that humpback whales exhibit regional differences in their distribution patterns, with their distribution being more uniform within an ice sector than at the circumpolar level. Despite the analysis being qualitative, a few patterns were identified. The changes in whale distribution could be related to the contrasting features of sea ice dynamics in the various sectors, which ultimately affect prey availability: namely, the regional variations of seasonal ice extent, lagged effects of interannual sea ice concentration anomalies, and distance between sightings and the marginal ice edge. Although this is a conservative stance, as the precise distance between the sea ice edge and sightings was not determined, it was evident in all cases that whales do not preferentially occupy areas directly adjacent to the observed ice edge, but they are rather found in earlier developed marginal ice zones and within a variable distance from the sea ice edge.

This suggests that humpback whales' distribution may be more closely linked to factors such as prey availability, including krill densities, which can vary independently of ice edge proximity. These findings corroborates the notion that regions associated with high densities of krill such as the eastern Weddell Gyre, the Antarctic Circumpolar Current, and the southern Kerguelen Plateau serve as reliable sources of high-quality feeding areas for humpback whales, although some of these areas exist at significant distances from the ice edges (Bestley et al., 2019; Baines et al., 2022; Moreau et al., 2023). A more detailed analysis, incorporating co-variates related to prey availability (e.g., chlorophyll-a, SST and bathymetry), is possible in future work now that the dataset has been pre-processed and aligned with satellite sea-ice data.

At a regional scale, some ice sectors are more likely to experience alterations in marginal ice zone dynamics. For example, the anticipated decline in sea-ice extent for the AB sector which supports the F2 and G stocks, would result in the reduction of the total marginal ice zone area, which in turn is expected to decrease productivity in the marginal ice zone (Constable et al., 2014). This poses a challenge as the sector is characterised low chlorophyll-a concentrations (Stambler, 2003), and the humpback whales of this sector rely on the marginal ice zones for feeding. Additionally, the Oceania breeding stocks, which include the whales from the F2 stock, are still listed as 'Endangered' (Seyboth et al., 2023) and their recovery rate may be affected. The frequent occurrence of ENSO events as a response to the warming prompt ice shelves loss, as observed in WAP, thus also threatening habitat availability for humpback whales which are known for site fidelity.

Climate-induced changes in Antarctic sea ice affect both prey availability and habitat availability for humpback whales. Of all Southern Ocean biogeographic zones, dominated by *E. superba* and copepods, marginal ice zones have the highest seasonal primary productivity (Constable et al., 2003). Consequently, these whales are consistently found in these open waters, north of the sea ice edge, feeding upon Antarctic krill. In contrast to minke whales, who seek shelter in sea ice, humpback whales are not only found in closer proximity to sea ice (Ainley et al., 2012; Friedlaender et al., 2006; Thiele et al., 2004). To give a preliminary answer to my question 2 on whether humpback whales sightings follow closely the spatio-temporal variations of the sea-ice edge, I can conclude that focusing on the wider seasonally varying MIZ region may be of higher relevance than focusing on the edge alone.

This work did not specifically target the relationship between humpback whales and the spatial variability in the distribution of the MIZ relative to the total sea ice extent around Antarctica. In regions such as the Ross Sea and East Antarctica, the MIZ constitutes more than half of the total sea ice extent (Vichi, 2022). This implies that ecosystems supported by these sectors are potentially more vulnerable to climate-induced changes in Antarctic sea ice. Further research could consider other definitions of the MIZ around Antarctica for the same period of study. For instance, observing how MIZ characteristics changed over the years within each ice sector and if the positions of sightings in the IDCR/SOWER data changed in response to that, thus providing insights on if and how humpback whales have been affected by the changing ice dynamics to date, and how the population may respond in the future.

Appendix

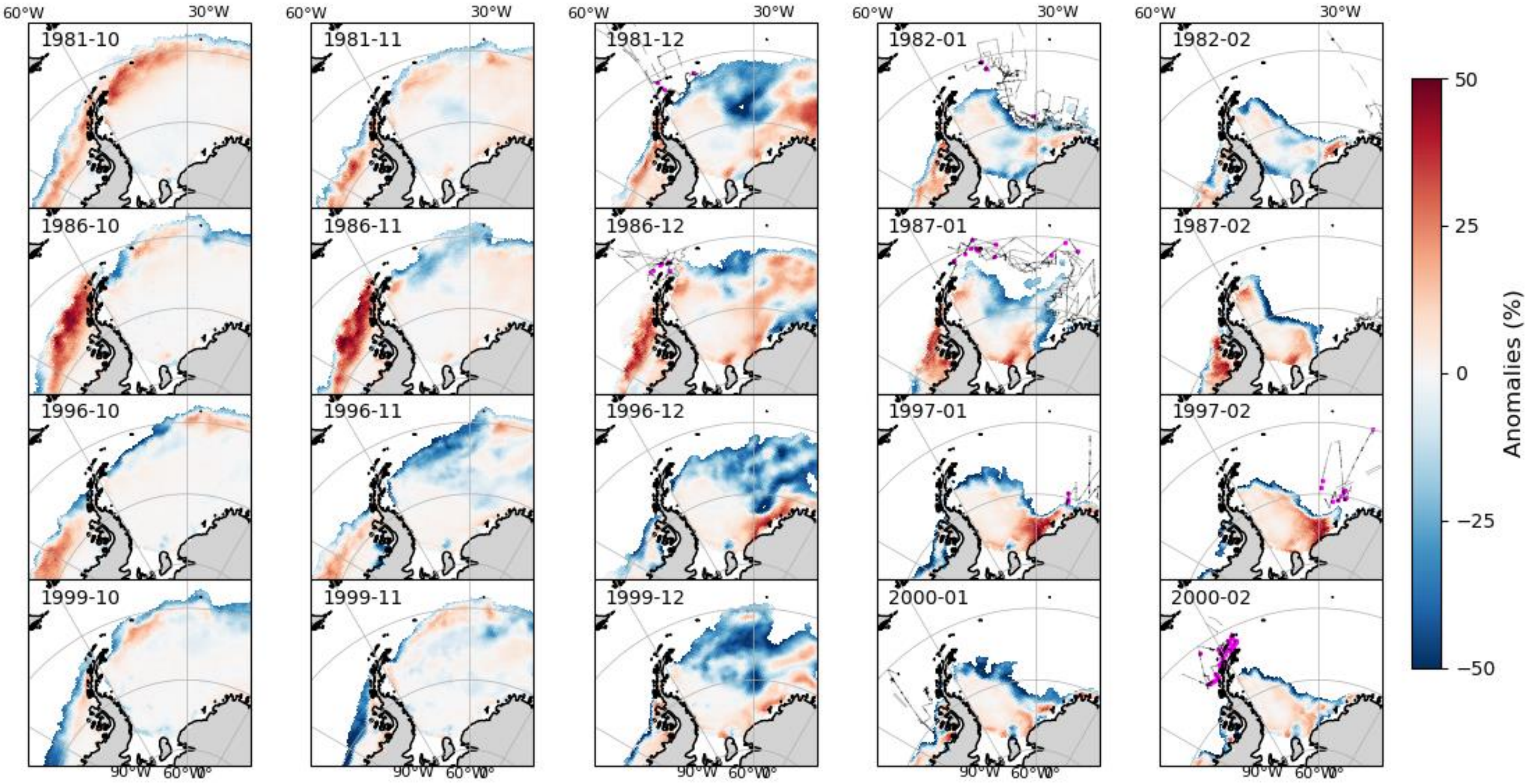


Figure 19. Humpback whales' distribution in relation to sea ice anomalies in the Weddell Sea sector (70 ° W to 15 W). The shown parallel is 60°S. In magenta are the humpback whale sightings from the IDCR/SOWER data and the black lines are the cruise track lines.

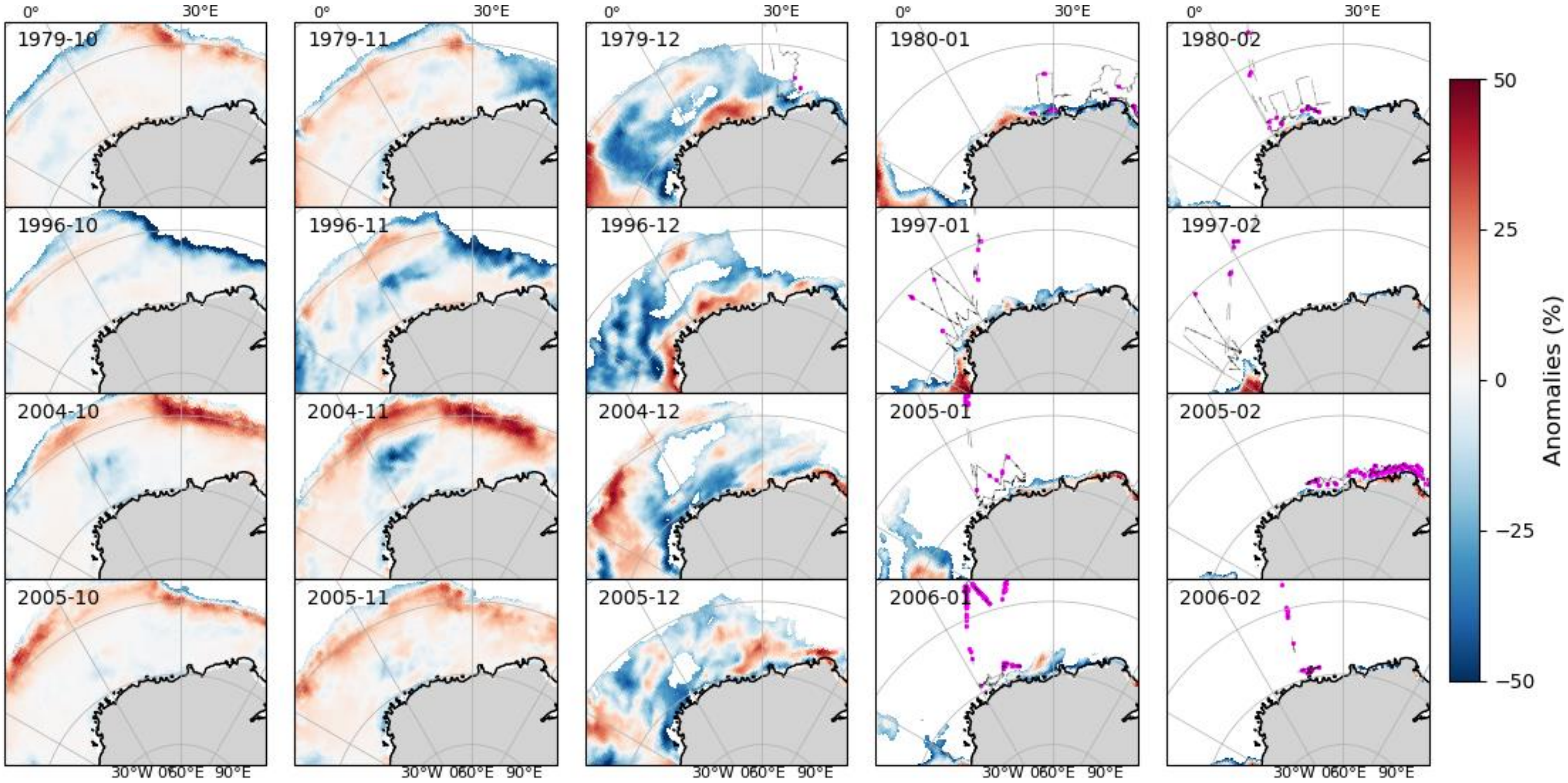


Figure 20. Humpback whales' distribution in relation to sea ice anomalies in the King Hakon VII (15 ° W to 70° E). The shown parallel is 60°S. In magenta are the humpback whale sightings from the IDCR/SOWER data and the black lines are the cruise track lines.

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