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Master's thesis in Biology, BIO-3950, August 2021

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Cover photo: Gentoo penguin (*Pygoscelis papua*) in the West Antarctic Peninsula in December 2019.
Photograph by Victoria Ollus.

# Acknowledgements

I am grateful to my supervisors Ulf Lindstrøm, Martin Biuw and Andrew Lowther for trusting me with this exciting project and for the opportunity to experience such a unique ecosystem. Thank you also for your guidance and encouragement along the way, it has been a rewarding learning process, and a privilege to work with such great scientists.

I would like to thank Hurtigruten and Chief Scientist Verena Meraldi for welcoming us onboard MS Midnatsol and MS Fram for data collection. I also wish to thank the captains, crews, and expedition teams for their hospitality and assistance, and for sharing their knowledge and experiences.

A special thank you to Elling Johannessen, Popi Gkikopoulou, Lucía Martín López and Chris Oosthuizen, for your valuable input in collecting the data, and for many good conversations and laughs in the field and in the office.

I sincerely appreciate the help of Tone Reiertsen, who always took the time to discuss seabird ecology with me and came with insightful comments, as well as the help of Raúl Primicerio, who taught me a lot about multivariate analyses and permutation design. Thank you kindly.

Lastly, I wish to thank my family and friends for encouraging me to follow my own path and supporting me along the way. I am grateful to my mother for instilling in me a deep admiration for the natural world, and to my father for awakening my curiosity for the underwater world at an early age.

# Abstract

Seabird distributions reflect physical and biological features of the marine environment and their variability on different spatial and temporal scales. Different species assemblages are associated with specific oceanic habitats and concentrations of birds typically occur in areas of high biological productivity. Here I explore seabird distributions and habitat use relative to biophysical cues of biological productivity throughout the Antarctic Peninsula and Scotia Sea in austral summer. Data on seabird at-sea distributions were collected through strip-transect counts using tourism vessels as opportunistic sampling platforms. Multivariate statistical methods and generalized additive models (GAM) were used to relate seabird guild composition, abundance, and species richness to environmental covariates. Sea surface temperature (SST) and distance to coast were the most important predictors of seabird distributions. Species assemblages differed between oceanographic zones and increased abundance and species richness was encountered in generally productive areas, such as coastal regions and oceanographic fronts. Coastal areas, particularly South Georgia, were important for seabirds at the time of our survey, which coincided with the breeding season for several bird species in the area. These findings highlight the importance of environmental features on seabird distributions and habitat use. Fine-resolution community-level data on marine top predator distributions are needed when assessing change, predicting habitat shifts, and ultimately to base successful conservation measures and management decisions on. This study shows that seabird distribution data collected cost-effectively using tourism vessels as platforms of opportunity can be a valuable addition to structured surveys.

*Keywords: spatial ecology, habitat use, biogeography, community composition, species richness, marine predators, seabirds, Southern Ocean*

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# 1 Introduction

Marine ecosystems around the world are under pressures from climate change and increasing human activities, causing loss of habitat and biodiversity and changes in food webs and species distributions (e.g., Myers & Worm 2003, Scheffer *et al.* 2005, Hoegh-Guldberg & Bruno 2010, Bindoff *et al.* 2019). In the Southern Ocean ecosystems, pressures include warming, sea ice reduction, acidification, and increasing commercial fisheries (Barbraud *et al.* 2012, Chown & Brooks 2019, Meredith *et al.* 2019, Bestley *et al.* 2020). A warming climate is expected to change predator distributions in the Southern Ocean (Meredith *et al.* 2019, Hindell *et al.* 2020), and changes related to temperature increase have already been detected for example in the southern Indian Ocean (Péron *et al.* 2010). The Scotia Sea and the Antarctic Peninsula belong to the fastest warming regions on Earth, and major changes are predicted in the area (e.g., Meredith *et al.* 2019). To comprehend the effects of large-scale environmental changes on marine ecosystems, we need to understand species interactions and the factors affecting the spatial distributions of top predators such as seabirds (González-Solís & Shaffer 2009).

Because the oceanic environment is a dynamic system, affecting prey distributions through both active and passive processes and on different spatial and temporal scales, predators must be able to track biological productivity (e.g., Fauchald 2009, Planque *et al.* 2011). The Ideal Free Distribution theory (Fretwell & Lucas 1970) predicts closely overlapping distributions of a predator and its preferred prey. But several factors including spatial constraints, species interactions and density-dependent processes make the distributions of prey and predators more complex and variable (Abrams 2007, Creel & Christianson 2008, Fauchald 2009, Planque *et al.* 2011). The association between prey and predator typically becomes stronger and more stable with increasing spatial and temporal scales (reviewed by Fauchald 2009). On larger spatial scale, Area Restricted Search tends to concentrate seabirds at patches of prey, whereas a two-way spatial game between prey and predator leads to less predictable distributions on smaller scales (Fauchald 1999, Abrams 2007, Fauchald 2009).

As top predators, seabirds are typically responsive to bottom-up processes (e.g., Piatt, Sydeman & Wiese 2007, Reiertsen *et al.* 2014), and coupled with their sometimes extreme mobility and ease of visibility, renders them suitable as ecosystem sentinels (Furness & Camphuysen 1997, Piatt, Sydeman & Wiese 2007, Einoder 2009). However, knowledge of the ecology and distribution of seabird species, as well as of the confounding effects from environmental variability and species interactions, is a prerequisite for choosing indicators that reflect the actual processes of interest (Einoder 2009). The ability to shift between prey species varies between species of seabirds, making specialist species generally better indicators of change (Furness & Camphuysen 1997, Einoder 2009, Moreno *et al.* 2016). Further, in a community- or ecosystem level approach, combining data from species with different diets produces indices that are less sensitive to factors affecting individual species (e.g., Hindell *et al.* 2020).

The association between seabird guilds and biophysical characteristics of the marine environment has been studied extensively during several decades (e.g., Pocklington 1979, Abrams 1985, Hunt *et al.* 1990, Amorim *et al.* 2009, Serratosa *et al.* 2020) and the heterogeneity of these features is known to be reflected in species distributions (e.g., Nelson 1980, Hunt *et al.* 1999, Ballance 2007, Bost *et al.* 2009, Ribic *et al.* 2011, Fauchald & Ziryanov *et al.* 2011). On a meso-scale, at continental edges and oceanic fronts, upwelling creates nutrient rich areas where prey, and therefor predators, tend to concentrate (Nelson 1980, Bost *et al.* 2009, Bestley 2020). On a local scale, seabirds may benefit from conspecifics or different species of seabirds in finding prey, or from marine mammals or fish (e.g., Ballance 2007, Fauchald & Ziryanov *et al.* 2011, Veit & Harrison 2017). Conspecifics or other species may passively provide cues of patches of prey, known as local enhancement (Grünbaum & Veit 2003, Veit & Harrison 2017). Alternatively, they can actively cooperate in herding prey, or, in the case of cetaceans and fish, leave floating offal behind and drive prey towards the surface where it becomes available for seabirds, known as facilitation (Harrison *et al.* 1991, Veit & Harrison 2017). The more elusive the prey patches are on a small scale, the more important local enhancement becomes in finding profitable patches, which might lead to high concentrations of seabirds but with weak overlap with actual prey distribution (Fauchald & Skov *et al.* 2011).

The Scotia Sea in the Southern Ocean is an important area for seabirds, with representatives of all major taxonomic groups (e.g., Shirihai 2007, Hindell *et al.* 2020). Due to their differing geographical location and climate, the ocean areas around the northern West Antarctic Peninsula (AP), South Georgia (SG) and Falkland Islands (FI) host differing seabird communities. In austral summer the Southern Ocean is a very productive system, attracting foragers that spend austral winters at lower latitudes. Some bird species, like the south polar skua (*Catharacta maccormicki*) (Shirihai 2007) and Wilson's storm-petrel (*Oceanites oceanicus*) (Nelson 1980, Shirihai 2007), migrate long distances to breed at the rich waters around Antarctica. Others migrate to feed outside their breeding season, like the arctic tern (*Sterna paradisaea*) (Egevang *et al*. 2010, McKnight *et al.* 2013). The seabird assemblages in the Scotia Sea and around the AP in austral summer therefor consist of both visitors and year-round residents, of which some are non-breeders, spending their time foraging at sea, and some are breeders and consequently central-place foragers, spatially constrained by their nesting sites (e.g., Gaston 2004). Breeding seabirds travel between colonies on land and food sources at sea and have elevated energetic demands (Markones *et al.* 2012). There is both inter- and intraspecific variation in foraging range inside and outside breeding seasons (Phillips *et al.* 2017), some species of seabirds are mostly pelagic while others are coastal, and some species roam vast ocean areas while others search more restricted areas (Nelson 1980, Fauchald & Ziryanov *et al.* 2011, Weimerskirch *et al.* 2014).

The strongest predictors of seabird distribution patterns tend to relate to prey distributions (e.g., Ballance 2007). In the efficient short-chained food web of the Scotia Sea and Antarctic Peninsula region, Antarctic krill (*Euphausia superba*; hereafter krill) is an important key stone species at the mid-trophic level (McCormack *et al.* 2021). But other crustaceans, fish and cephalopods comprise important prey for several seabirds in the area, such as albatrosses and terns (e.g., Griffiths 1982, Barrera-Oro 2002, Xavier *et al.* 2003, Alvito *et al.* 2015, Moreno *et al.* 2016). Large schools of krill attract a variety of seabirds (Shirihai 2007, Bost *et al.* 2009, Joiris & Dochy 2013), as well as fish that in turn serve as food for seabirds looking for larger prey (reviewed by Barrera-Oro 2002). Krill is particularly abundant in the Antarctic Peninsula and southern Scotia Sea area (CCAMLR 2019, Krafft *et al.* 2019, Perry *et al.* 2019), where its fishery consequently focuses and coincides with the highest abundance of krill predators around Antarctica (Hewitt *et al.* 2004, Nicol *et al.* 2012, Hinke *et al.* 2017, Warwick-Evans *et al.* 2019). A growing krill fishery has the potential of posing an indirect threat to seabird populations in the area by enhancing intra and inter-species competition (e.g., Trites *et al.* 2006, Bertrand *et al.* 2012, Bestley *et al.* 2020). As populations of the great whales recover from earlier exploitation, they also add competition by demanding their fair share of the krill stock (Reilly *et al.* 2004, Tulloch et al. 2019). Thus, with the additional pressures from rapid climate change (Meredith & King 2005, Kawaguchi & Nicol 2009, Nicol *et al.* 2012, Kawaguchi *et al.* 2013, Meredith *et al.* 2019), and with the changes that have been proposed to already have taken place (Reid & Croxall 2001, Atkinson *et al.* 2004, Atkinson *et al.* 2019, but see also Meredith *et al.* 2019), the AP and Southern Scotia Sea are consequently in need of effective ecosystem-based management (e.g., Hinke *et al.* 2017). Despite the considerable attention given to marine top predators, substantial information gaps on their distribution and habitat use remain and need to be filled in order to inform management of the area (reviewed by Bestley *et al.* 2020).

In light of this, fine-resolution distributional information on krill predators such as seabirds is needed in the implementation of successful conservation measures (Frederiksen *et al*. 2012, Bestley *et al.* 2020) and for appropriately managing fishing activities in time and space (Warwick-Evans *et al*. 2019). To ensure unbiased coverage and attain randomized data, at-sea counts of seabirds are typically conducted along systematic transects (e.g., Ainley *et al.* 1993, Santora & Veit 2013, Goyert *et al.* 2016, Bolduc & Fifield 2017). Usually the strip-transect method is used, in which birds are counted within a predetermined distance from the moving vessel (variants of the method have been described among others by Tasker *et al.* 1984, Spear

& Ainley 1992, van Franeker 1994, Spear *et al.* 2004, Ballance 2007, Hyrenbach *et al.* 2007). The operation of dedicated research vessels is costly however, particularly in remote areas, which limits the spatial and temporal extent and repetition of surveys. Tourism vessels operate on repeated routes throughout seasons and on a yearly basis, and as opportunistic platforms for researchers, tourist vessels offer relaxation of the economic constraints posed on data collection, allowing larger data sets with better spatial and temporal coverage to be collected. This is a considerable advantage particularly in areas that are difficult to access and hence sparsely sampled, and in areas of rapid environmental change for which there is an urgent need for ecological knowledge to base management decisions on.

The objective of this study is to match the variation in space use and community composition of seabirds to various physical and biological variables which in turn may act as cues for biological production. I hypothesize that (1) physical and biological environmental features drive species-specific seabird distributions and hence community composition, and (2) seabird abundance and diversity are higher in areas of assumed high biological productivity. Tourism vessels are used as opportunistic sampling platforms and their usefulness for collecting community-level data on seabird at-sea distributions is assessed.

# 2 Methods

## 2.1 Study area

The Scotia Sea is situated in the Atlantic part of the Southern Ocean (Figure 1, inset). It is characterized by a circumpolar eastward water movement, the Antarctic Circumpolar Current (ACC), and by four circumpolar frontal systems which are from north to south the Subantarctic Front (SAF), the Polar front (PF), the southern Antarctic Circumpolar Current front (sACCf), and the southern boundary of the ACC (sbACC) (Orsi *et al.* 1995). The sbACC marks the transition from a circumpolar eastward water flow to a more complex and variable hydrography of the shelf waters (Orsi *et al.* 1995, Amos 2001, Thompson *et al.* 2009). The cold surface water south of the PF is called Antarctic Surface Water and has a higher nutrient content than the Subantarctic Surface Water found north of the PF (Sievers & Nowlin 1984, Prézelin *et al.* 2000). The southern Scotia Sea and the Antarctic Peninsula region are particularly productive (Prézelin *et al.* 2000, Atkinson *et al.* 2001, Kahru *et al.* 2007, Piñones *et al.* 2011, Sanchez *et al.* 2019). The study area is located between longitudes 35 and 68°W, and latitudes 51 and 66°S, and consists of both shelf waters and deep sea, crosses all fronts of the ACC, and stretches over different climate regimes (Figure 1).

## 2.2 Seabird surveys

At-sea surveys were conducted from two cruise ships (MS Fram and MS Midnatsol, Hurtigruten AS) which ran regular trips throughout the Scotia Sea and the northern AP during the austral summer of 2019-2020. Observations on MS Midnatsol were done during three consecutive trips from Ushuaia to West Antarctic Peninsula and back, between 23 November to 28 December 2019. On MS Fram, observations were done during two consecutive trips from Ushuaia, via the Falkland Islands and South Georgia, to the Antarctic Peninsula and back to Ushuaia, between 10 December 2019 to 19 January 2020. The vessels' track lines are presented in Figure 1 (for a closer look of the northern Antarctic Peninsula see Appendix Figure S1).

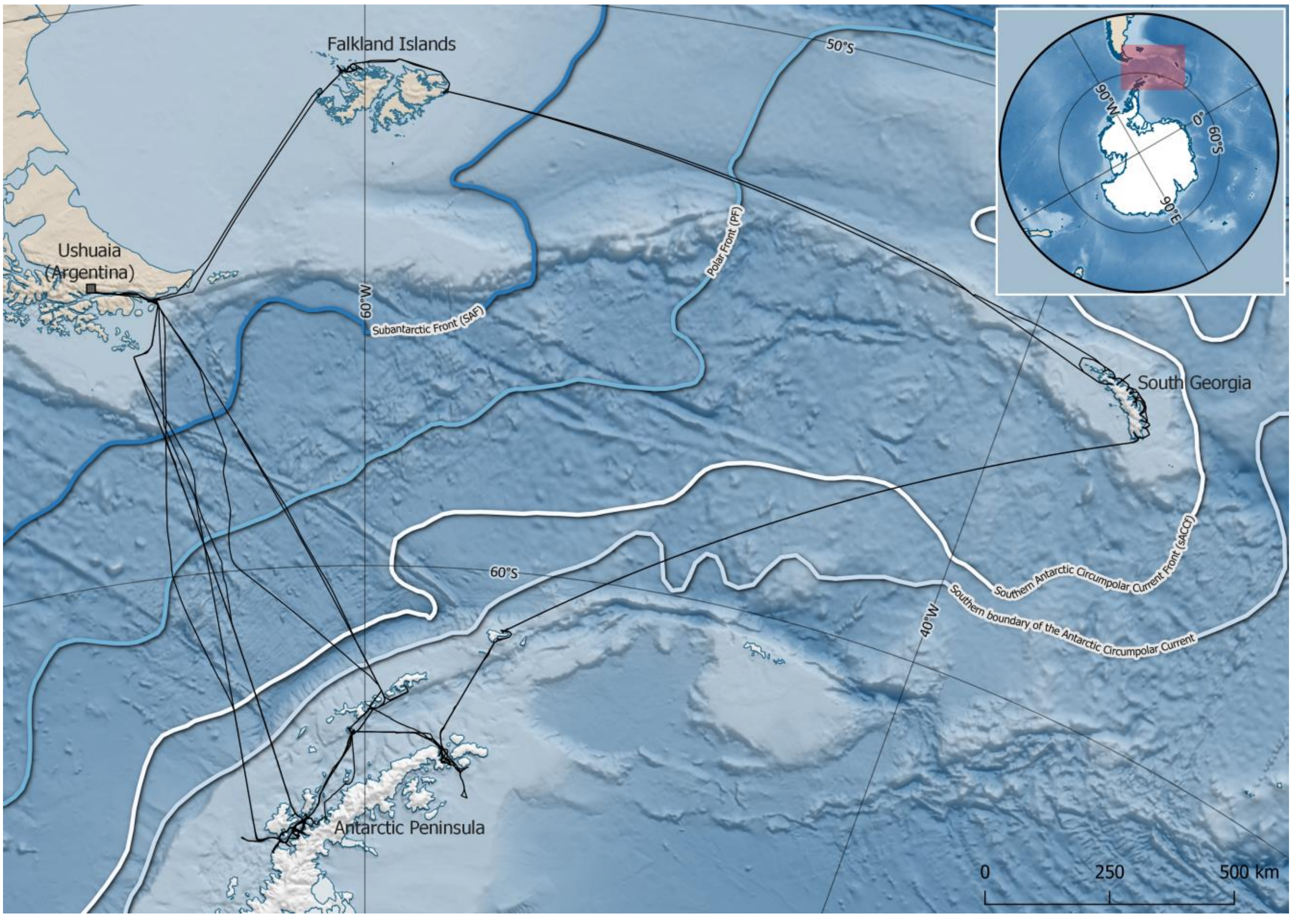

***Figure 1.*** *Study area with track lines of the vessels indicated as black lines. The map was created using Quantarctica (Matsuoka et al. 2018) in QGIS (QGIS.org 2019).*

Surveys were conducted using a continuous strip-transect count methodology (Tasker *et al.* 1984, Van Franeker 1994, Spear *et al.* 2004, Ballance 2007, Buckland *et al.* 2015). On each ship, a team of two to three observers took turns counting seabirds in continuous 10-minute strip-transects from the bridge, approximately 15 meters above sea surface. Strip-transect counts were made along transects of 300 meters width, in time intervals of 10 minutes once every hour, but only when the ship was in transit and under satisfying weather conditions (visibility > 300 meters). Ten-minute counts of birds at sea have been identified as an appropriate approach for capturing the variation in seabird communities in waters of great environmental variability (reviewed by Tasker *et al.* 1984) and leaving 40-60 minutes between counts reduces autocorrelation between observation periods (Hyrenbach 2001). A strip width of 300 meters has previously been identified as optimal for bird counts at sea when visibility is good (e.g., Ballance 2007, Bolduc & Fifield 2017) and was used here, as even the smallest birds (storm petrels) can be identified with certainty at this distance. The transect extended from the bow in a 90° arc to the side with better visibility (least glare), either the starboard (0°-90°) or to the port side (270°-360°). Observations of seabirds were done primarily unaided, and binoculars (Opticron Marine PS II 7x50) were used for species identification when required.

Some species-specific biases in seabird counts were expected, due to species-specific behaviour and methodology used; the most conspicuous bias is related to multiple counting of individuals because they follow the ship. Many birds tend to follow ships at sea, and while doing so some species circulate the vessel entering and exiting the strip repeatedly (Spear & Ainley 1992, Hyrenbach 2001). We noticed this kind of behaviour in cape petrels (*Daption capense*) for example but did not keep track of ship-following or -circulating individuals during strip-transect counts. Hence, counts of species attracted to ships are expected to be inflated. Further, flying birds moving faster than the vessel or perpendicular to the strip-transect are more likely to enter the strip-transect than swimming birds or birds resting on the sea surface. Consequently, the number of birds flying through a continuously counted strip-transect is higher than in any moment of time, and the flux of birds inside the strip-transect leads to a positive bias in flying birds in absolute density estimations, if not accounted for with methods described by Tasker *et al.* (1984), Spear & Ainley (1992) or van Franeker (1994). In this study we were interested in relative abundances, and since these methods are effort intensive in areas where bird densities are high, like ours, a positive bias for some species was considered acceptable.

Start time (UTC) for each strip-transect count and observed species with number of individuals were stored using Logger 2010 software (Gillespie *et al.* 2010) on a portable laptop (Dell

Precision 5520). The position of the vessels was logged continuously (on a temporal resolution of 1 minute) onboard together with time and speed data using a Globalsat USB GPS receiver, so that observation data could be related to geographical position. Not all species could be reliably identified to the species level, and the taxonomic groups used for data analysis are presented in Appendix Table S1.

## 2.3 Environmental predictors of seabird distribution

Marine predators such as seabirds track biological productivity (e.g., Fauchald *et al.* 2000, Bost *et al.* 2009). Because productivity and prey availability were not possible to assess during the survey, we relate seabird distributions to food availability using a suite of environmental predictors widely considered as cues for biological production (e.g., Abrams & Miller 1986, Wahl *et al.* 1989, Bost *et al.* 2009, Tittensor *et al.* 2010, Piñones *et al.* 2011, Lowther *et al.* 2014, Serratosa *et al.* 2020). These are 1) distance to coast (km), 2) bathymetric depth (m) and slope (degrees of inclination), 3) sea surface temperature ($^{o}$C) and its gradient over space defining mesoscale (>100 km) oceanographic fronts, 4) Lagrangian Coherent Structures defining sub-mesoscale (>10 km) regions of particle retention (Finite-Size Lyapunov Exponents, FSLE), and 5) concurrent abundance of cetaceans (number of observed baleen and toothed whales per nautical mile). In addition, the speed of the observation platform (vessel speed, knots) was included as a control variable in statistical analyses due to its positive affect on strip-transect length and negative affect on seabird flux within the transect counted (e.g., Spear *et al.* 2004).

*Distance to coast*

Distance to coast has been described as an important predictor of biological productivity and species assemblages (e.g., Doty & Oguri 1956, Abrams & Miller 1986), and the distance to land-based colonies is an important limiting factor of the spatial distribution of breeding seabirds (Gaston 2004). Distance to coast was calculated as the shortest distance (km) from the start point of a strip-transect to the nearest land mass (island or mainland).

### *Bathymetric depth and slope*

Bathymetric data from a 1 arc-minute (~1000m) resolution bathymetric model were used (ETOPO 1; Amante & Eakins 2009) to generate 1 arc-minute resolution raster layers from which bathymetric depth was extracted for each strip-transect. A high bathymetric slope indicates potential areas of upwelling, where nutrients are brought up to the photic water layer, increasing primary production (e.g., Prézelin *et al.* 2000). A raster layer for seabed slope was created based on bathymetric data in Quantarctica (elevation raster of 2000m resolution, Matsuoka *et al.* 2018) using the 'slope' function in QGIS (v 3.10.1; QGIS.org 2019). Values of seabed slope as degrees of inclination to the horizontal was then derived for the position of each strip-transect from the created raster.

### *Sea Surface Temperature and its gradient over space*

Different water masses, typically identified through differences in sea surface temperature (SST), have repeatedly been recognized as an important factor in shaping seabird distributions (e.g., Griffiths *et al.* 1982). Daily SST data were downloaded from the Physical Oceanography Distributed Active Archive Center (UK Met Office 2012) with values on a 0.054-degree grid (spatial resolution 0.05 degrees Latitude * 0.05 degrees Longitude), from which SST values were extracted for each strip-transect based on date and coordinates. A high SST gradient is indicative of oceanographic fronts, where water mixing and upwelling support higher primary production (Hunt *et al.* 1999, Kahru *et al.* 2007). The sea surface temperature gradient was calculated as the spatial change in SST.

### *Lagrangian Coherent Structures*

FSLE show particle retention and are calculated based on surface water flow. Areas of low values of FSLE are created in convergencies of surface flow, where passive food particles such as phytoplankton and weakly swimming zooplankton have a longer retention time (for example, absolute FSLE values >$0.1d^{-1}$ typically characterize retention rates at approximately monthly timescales) and are consequently concentrated (https://www.aviso.altimetry.fr/; Lowther *et al.* 2014). Seabirds are, along with other marine predators, attracted to these productive areas for feeding (Kai *et al.* 2009, Piñones *et al.* 2011, Lowther *et al.* 2014). FSLE values were obtained for each strip-transect from a 0.04-degree grid with daily FSLE data (https://www.aviso.altimetry.fr/).

*Cetacean abundance*

Cetaceans use same food resources as most seabirds, and in addition to being attracted to the same food patches, whales provide visual cues of prey patches (local enhancement) and drive prey towards the surface where it can be accessed by seabirds (facilitation), making many seabirds attracted to feeding cetaceans (Enticott 1986, Veit & Harrison 2017). There is a growing documentation on observations of seabirds associating with cetaceans for such opportunities (e.g., Martin 1986, Ridoux 1987, Sakamoto *et al.* 2009) and studies on associations between seabirds and cetaceans in the African (Griffiths 1982, Enticott 1986) and Australian (Hodges & Woehler 1994) sectors of the Southern Ocean show that seabirds frequently associate with orcas (*Orcinus orca*) and dolphins (Delphinidae). We also collected data on marine mammal distributions (Deehr Johannessen 2020) using the line transect method (Buckland *et al.* 2015) and these data were used to relate seabird distributions to concurrent abundances of baleen whales (Mysticeti) and toothed whales (Odontoceti). For every strip-transect, the number of whales observed during a 30-minute period from 10 minutes before to 10 minutes after the strip-transect count, were summed and standardized by distance travelled (whales observed per nautical mile).

## 2.4 Statistical analyses

The data were processed and analysed using QGIS (http://qgis.osgeo.org) and R (R Core Team 2020, https://www.r-project.org). The ‘LoggeR’ package (Biuw 2019) was used to bring data from the Logger program to R. The ‘geosphere’ package (Hijmans 2019) was used to calculate distances to the nearest coast, based on the coordinates for the start points of the strip-transects and the coordinates for the coastline in Norwegian Polar Institute’s Quantarctica package (Matsuoka *et al.* 2018) for QGIS (v 3.10.1; QGIS.org 2019). The R package ‘marmap’ (Pante & Simon-Bouhet 2013) was used to import bathymetric data (ETOPO 1; Amante & Eakins 2009) for the start point coordinates of each strip-transect, while the ‘terrain’ function in the ‘raster’ package for R (Hijmans 2020) was used to calculate the temperature gradient based on the SST data used (UK Met Office 2012).

Collinearity between predictors was explored through pairwise correlations with Pearson’s and Spearman’s correlation factors (Appendix Figures S2-S7). Collinearity of $|r|<0.7$ between predictors in the same model was considered acceptable (Dormann *et al.* 2013). As expected, high collinearity was found between depth and distance to coast (Pearson $|r|=0.83$, Spearman $|r|=0.80$) and as a result one of the predictors was removed from analyses. Significance was assessed at $\alpha=0.05$.

### 2.4.1 Seabird guild composition

Multivariate methods offer tools for interpretation of community-level data. Community composition and environmental drivers of species assemblages were explored through Constrained Correspondence Analysis (CCA), which reduces the high dimensionality in community data in the space constrained by chosen predictors to a two-dimensional approximation (Quinn & Keough 2002, Greenacre & Primicerio 2013). The ‘vegan’ package (v2.5-6; Oksanen *et al.* 2019) was used for the multivariate analyses. CCA was performed on square root transformed species counts to homogenize variation in abundance between species (presented in results), as well as on untransformed species counts for comparison (presented in Appendix Figures S11-S13).

Because the strip-transects were irregularly spaced in space and time, traditional tests of autocorrelation would not be effective. Hence, a restricted permutation design in the form of sequential randomization was incorporated in the ANOVA of the CCAs to account for autocorrelation between consecutive strip-transects (Fortin & Jacquez 2000, Anderson 2001).

Model selection was done through forward selection and backward elimination (e.g., Borcard 2006). Variance Inflator Factors (VIFs) were checked for the CCA models in which both depth and distance to coast were included through model selection (Borcard 2006, Greenacre & Primicerio 2013), and the predictor with a higher VIF was removed from the final model.

Exploration of the whole data set showed that geography was the main explanatory factor of variation in seabird community composition. To explore variation on a smaller spatial scale, the study area was divided into regions (Figure 2). The regions explored separately were the Antarctic Peninsula (AP), the Drake Passage (DP), the Falkland Islands (FI), South Georgia (SG), and the ocean areas between Ushuaia and FI (U-FI), FI and SG (FI-SG), and SG and AP (SG-AP). Limits between coastal and pelagic regions are drawn arbitrarily at 15 km from the coast, but exceptions were made around the tip of South America where five coast-near (<15 km from land) observations were included in either DP (4 observations) or U-FI (1 observation), and in the Bransfield Strait where all observations were included in AP.

### 2.4.2 Seabird habitat use and aggregations

Seabird concentrations were explored visually by mapping species richness and seabird densities observed. For this purpose, the total counts of seabirds in each observation were divided by the area of the corresponding strip-transect to yield values of total seabird density (number of birds/km$^2$). Generalized Additive Models (GAMs) were used to explore non-linear univariate relationships between seabird aggregations and environmental predictors, with species richness and total seabird counts as responses. In addition, a smooth additive quantile regression model (QGAM) was used to explore predictors of high density aggregations of seabirds.

Data from the whole study area were used in the GAMs and the QGAM to allow for enough variation in predictor variables. Species richness (the sum of observed taxonomic groups as defined in Appendix Table S1) was chosen as a response variable instead of diversity indices, because species counts were biased towards ship-associated birds. The true species richness might have been higher however, as some species groups include two or more species. GAMs have been shown to be well-suited for analysis of at-sea counts of seabirds (Clarke *et al.* 2003) and was used here to find predictors of seabird aggregations. Due to species specific behaviour and flux, total counts are affected by biases from all species present and should be used as a measure of abundance with some caution. Vessel speed was included in the GAMs and the QGAM as a fixed variable to control for both the differences in strip-transect length, caused by changes in vessel speed, as well as increased flux at lower speed. Since strip length increases while flux decreases with vessel speed, these two effects of vessel speed are counteracting.

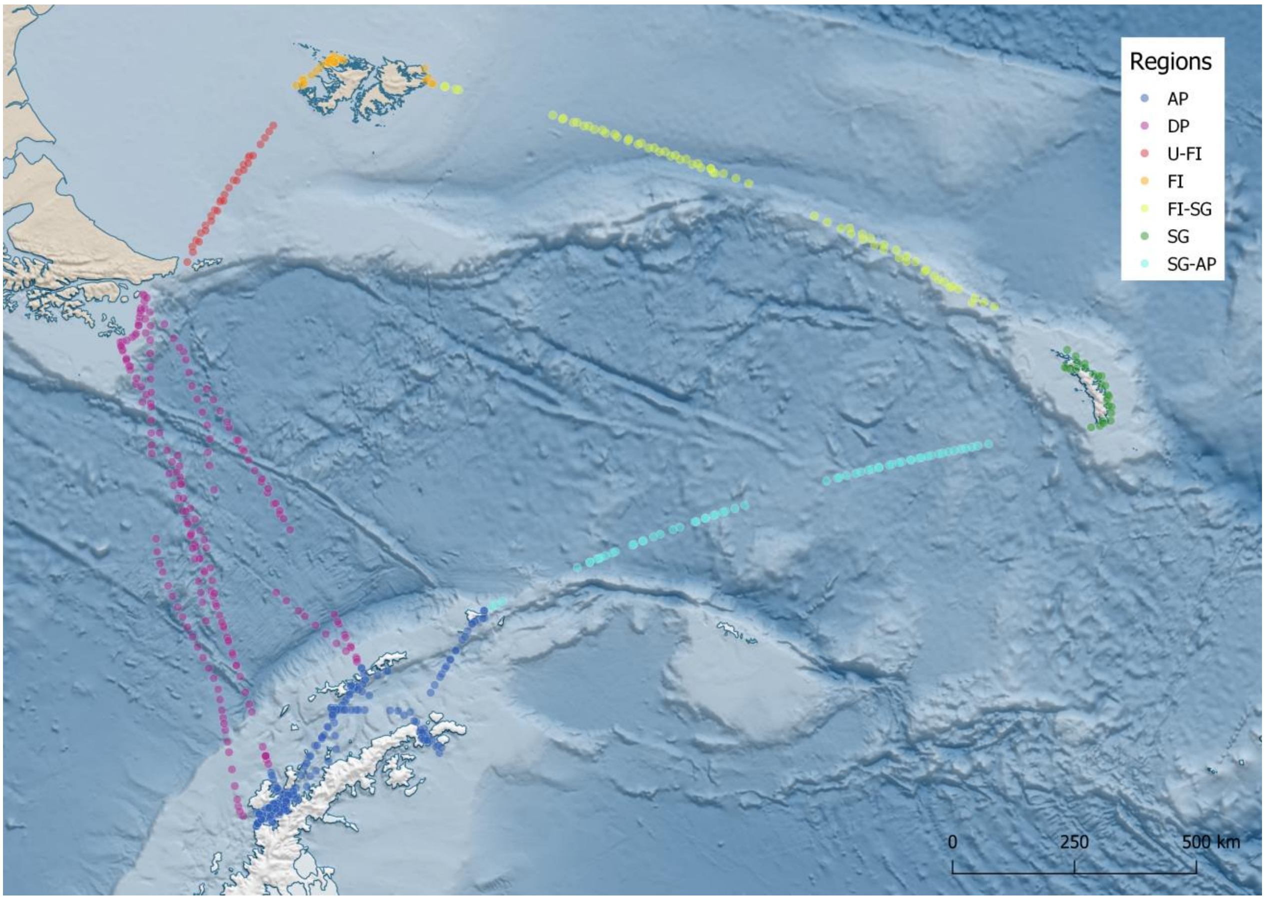

***Figure 2.*** *Strip-transects as points with colouring indicating region. The map was created using Quantarctica (Matsuoka et al. 2018) in QGIS (QGIS.org 2019).*

GAMs were fitted with untransformed response data using thin plate splines. For model selection in GAM, penalty was added to the null space by turning on the ‘select’ argument in the ‘gam’ function (Wood 2003, Wood 2011, Wood *et al.* 2016). Smooths with all basis functions in the null space are then penalized to zero and consequently dropped from the model. Depth was left out due to its covariance with distance to coast, which was considered ecologically more important in the breeding season. The distribution family used for the GAM for species richness was Poisson, while negative binomial was used for the GAM for total counts due to overdispersion. Restricted Maximum Likelihood (REML) estimation was used in both models, following recommendations (Wood 2011, Simpson 2018).

Temporal autocorrelation in species richness, total counts, and total density between strip-transects was explored through variograms (Appendix Figures S8-S10). Notable autocorrelation was not found in species richness, but in total seabird counts and densities autocorrelation occurred between observations made less than 5 hours apart on MS Midnatsol and less than 10 hours apart on MS Fram. Attempts to account for this temporal autocorrelation by fitting Generalized Additive Mixed Models (GAMMs, Wood 2004) using a CAR(1)-type of autocorrelation structure were not successful, probably because the non-linear trends and the autocorrelation operate on a similar temporal scale, making the model unable to separate trend and autocorrelation (Simpson 2018). As a result, the temporal autocorrelation was not accounted for.

For QGAM, the 90th percentile of total counts was used to explore the highest seabird concentrations inside the whole study area. The 90th percentile was chosen following the example of Tittensor *et al.* (2010) and Hindell *et al.* (2020). Prior to fitting the QGAM, the count data were log-transformed. Model selection was not possible to perform for the QGAM, but only significant model predictors will be presented in the results.

The GAMs and the QGAM were specified as

R ~ s(SST, bs='tp') + s(TG, bs='tp') + s(slope, bs='tp') + s(FSLE, bs='tp') + s(dist, bs='tp') + s(Mys, bs='tp') + s(Odo, bs='tp') + s(speed, bs='tp')

where R is the response variable and the model predictors are sea surface temperature SST, the SST gradient (TG), the bathymetric slope, FSLE, distance to coast (dist), abundances of baleen whales (Mys), abundances of toothed whales (Odo), and vessel speed. Packages ‘mgcv’ (v1.8-31; Wood 2011, Wood *et al.* 2016) and ‘QGAM’ (v1.3-2; Fasiolo *et al.* 2017) were used for fitting the GAMs and QGAMs, respectively.

# 3 Results

A total of 636 strip-transects (294 on MS Midnatsol and 342 on MS Fram) covering an area of 690 km² were counted (Figure 2), and a total of nineteen species and nine taxonomic groups were observed (Appendix Table S1). Our observations of threatened species (IUCN 2021) are presented in Appendix Figure S18. Because the study area was large and covered different climate regimes, very different seabird communities were included in this study.

## 3.1 Seabird guild composition

The model acquired through CCA for the whole study area (p=0.001) is presented in Figure 3 and explains about 11.4% of the variation in the data. Both forward selection and backward elimination gave the same model, from which depth was dropped due to having a higher VIF than distance to coast. The predictors of different species assemblages in the final model were SST (p=0.001), distance to coast (p=0.001), vessel speed (p=0.001), the abundance of baleen whales (p=0.014), and the bathymetric slope (p=0.006). Ellipses represent standard deviations of the observations in each region. The horizontal CCA1 axis represents a gradient in SST and a latitudinal gradient in community composition, while the vertical CCA2 axis represents a coastal-pelagic gradient, separating breeding coastal species from breeding pelagic species that can travel further in search for food. Observations appear in regional groups highlighting the spatial segregation of seabird species assemblages. Particularly communities in the AP and FI differentiate from the others. The AP in the south end of the study area stood out with its ice-associated species, while the FI which is situated north of the Subantarctic Front (SAF) formed a distinct group in the high temperature end. For the open ocean seabird communities, there was a latitudinal change in species assemblages between the northern and southern Scotia Sea. Communities in the AP were associated with a higher bathymetric slope, as well as with a higher abundance of baleen whales. Toothed whales were seen more rarely during this study, and the data were probably too sparce to detect an effect of their presence on seabirds. Vessel speed was included to control for the variation it causes in strip-transect length and bird flux.

Vessel speed was correlated with distance to coast (Pearson |r|=0.48, Spearman |r|=0.62), but both predictors were kept in the model since |r|<0.7 and the VIFs for all model predictors were <1.3. When performed with untransformed community data, the CCA showed an association of seabird communities in the FI with a stronger gradient in SST (TG) than in other regions (Appendix Figure S11), while an association between pelagic communities and an SST gradient was not found on the scale of the whole study area.

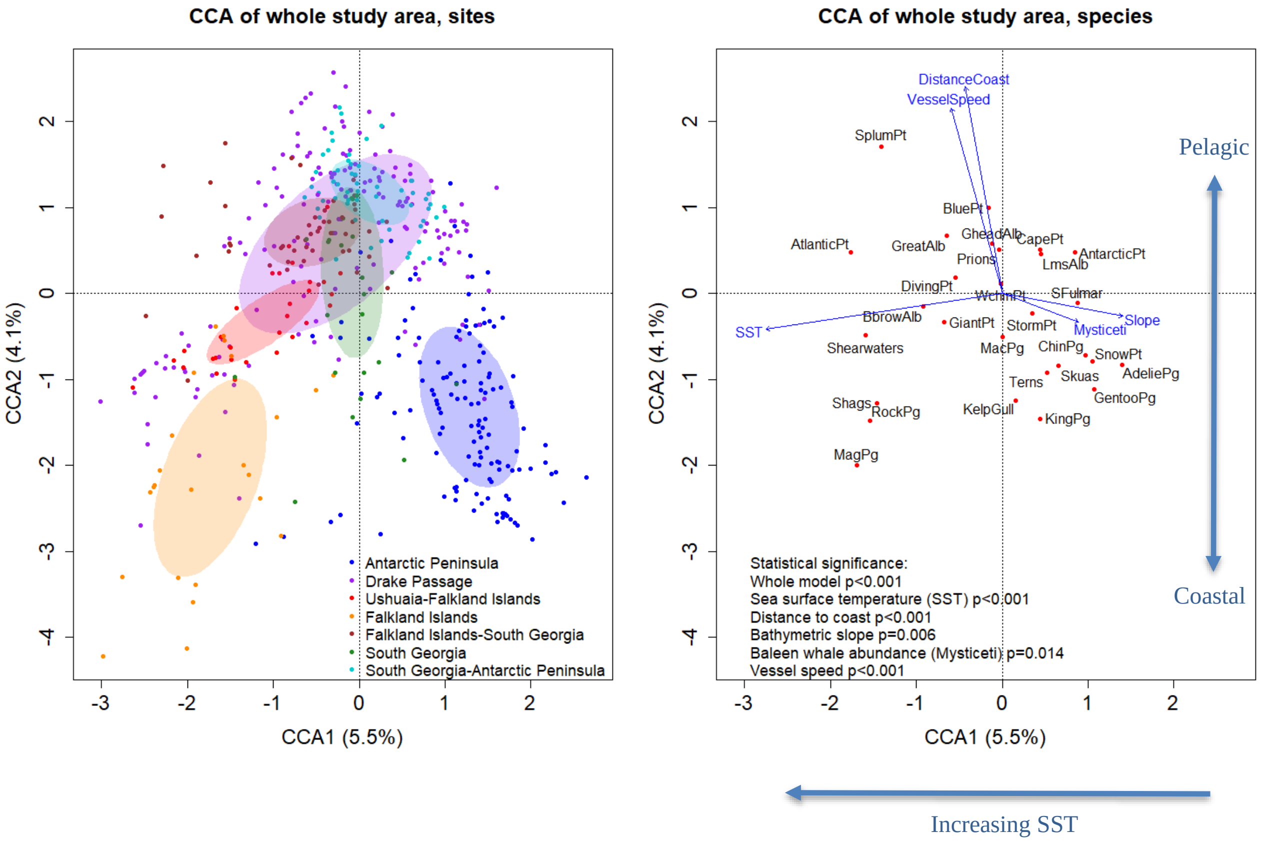

***Figure 3.*** *CCA ordination biplot of axes 1 and 2 for CCA of seabird communities in the whole study area, divided into two plots. The left hand side plot shows sites (strip-transects) as dots with colour indicating region, and ellipses representing standard deviations of observations inside each region. The right hand side plot shows species (red dots) and significant predictors (blue arrows). The significant predictors, which are sea surface temperature (SST), distance to coast (DistanceCoast), the bathymetric slope (Slope), baleen whale abundance (Mysticeti), and vessel speed (VesselSpeed), explained 11.4% of the total variation in community composition.*

To find the important environmental gradients on a smaller spatial scale, constrained correspondence analysis (CCA) was performed separately for each region. A restricted permutation design requires enough data to be able to perform enough permutations, however, and reliable results were acquired only for the AP and the DP. The CCA for the AP is presented in Figure 4. The model is significant ($p=0.001$) and explains about 7.4% of the variation in data. Both forward selection and backward elimination gave the same model. The predictors are SST ($p=0.001$), TG ($p=0.025$), and vessel speed ($p=0.002$). On a scale of the whole study area, the slope and baleen whale abundance were significant predictors of seabird communities and a higher slope a higher abundance of baleen whales were associated with species assemblages in the AP region (Figure 3), but no significant effects of these predictors were found on the scale of the AP region itself (Figure 4). When performed with untransformed data, FSLE was a significant predictor of seabird communities in the AP (Appendix Figure S12).

The CCA for the DP is presented in Figure 5. Both forward selection and backward elimination gave the same model ($p=0.001$), which explains about 17.3% of inertia. The only predictors of the model are SST ($p=0.001$) and distance to coast ($p<0.001$), which accounted for the main patterns also on the scale of the whole study area. Depth and distance to coast were strongly correlated also inside the DP region (Pearson's $|r|=0.71$ and Spearman's $|r|=0.65$, Appendix Figures S6 and S7, respectively) and depth was dropped due to having a higher VIF than distance to coast. In the final model, both predictors had VIFs <1.2. Untransformed data showed a very similar pattern, but with a weak effect of vessel speed on community composition in the DP (Appendix Figure S13).

On the scale of the whole study area, the use of square root transformed data did not change the results much from results given by untransformed data (Appendix Figure S11). But on a regional scale, results were sensitive to transformation and the models for transformed data explained less of the variation than the models for untransformed data (Appendix Figures S12 and S13), particularly for the AP region.

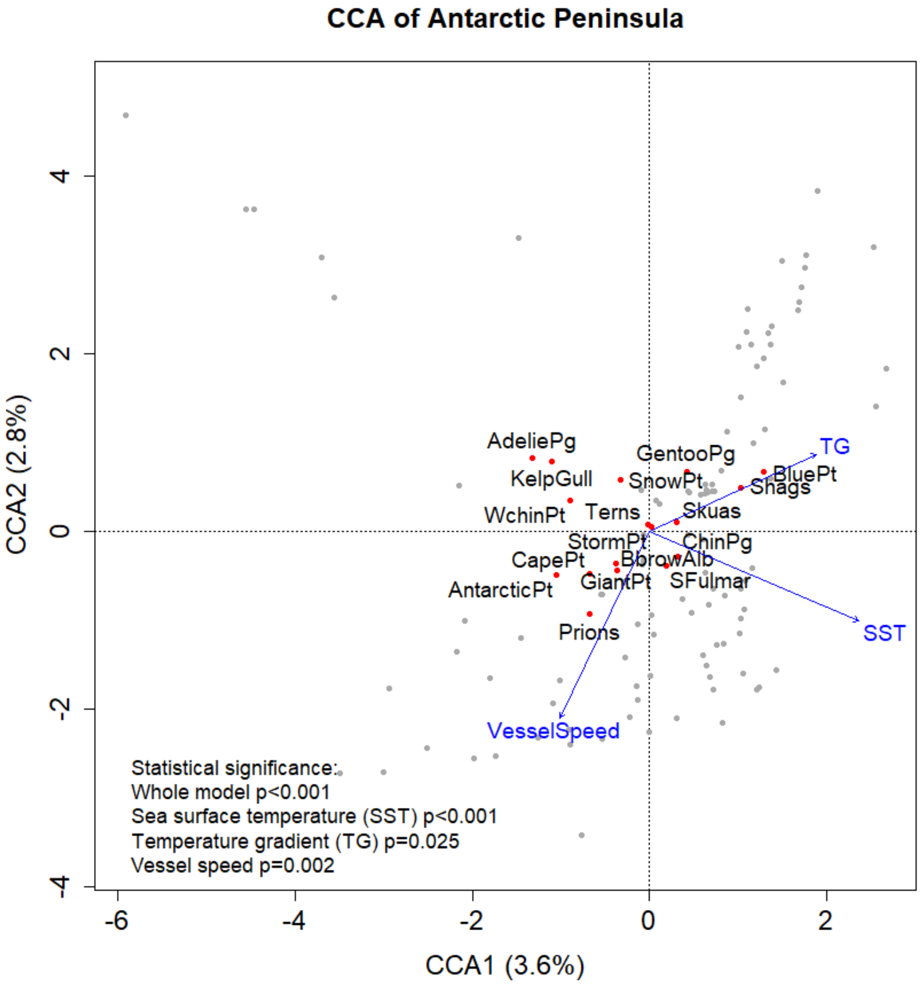

***Figure 4.*** *CCA ordination biplot of axes 1 and 2 for CCA of seabird communities in the Antarctic Peninsula region, performed on untransformed data. Sites (strip-transects) are shown as grey dots, species as red dots, and significant predictors as blue arrows. The significant predictors, which are sea surface temperature (SST), the SST gradient (TG), and vessel speed (VesselSpeed), explained 7.4% of the total variation in community composition.*

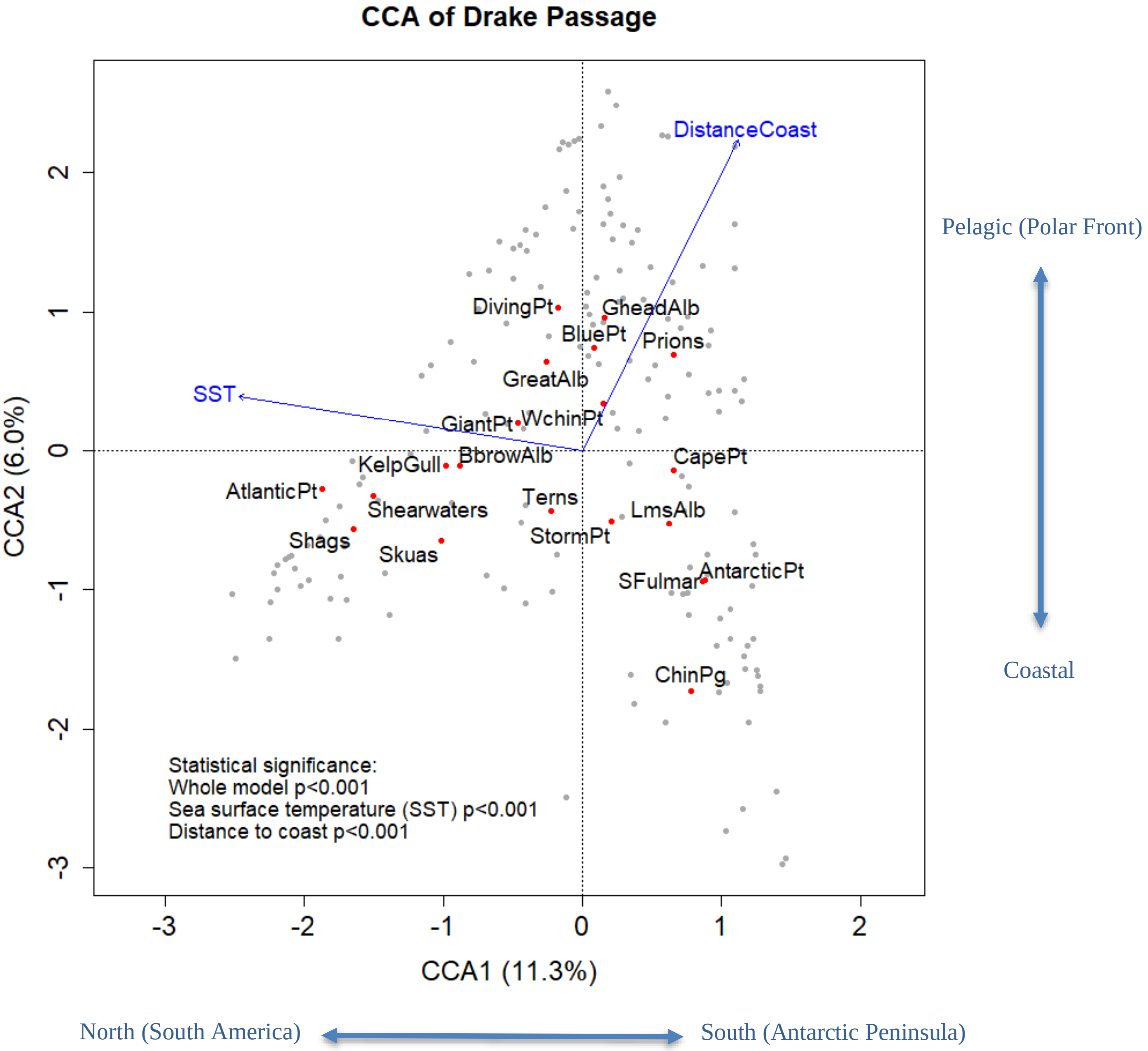

***Figure 5.*** *CCA ordination biplot of axes 1 and 2 for CCA of seabird communities in the Drake Passage, performed on untransformed data. Sites (strip-transects) are shown as grey dots, species as red dots, and significant predictors as blue arrows. The significant predictors, which are sea surface temperature (SST), and distance to coast (DistanceCoast), explained 17.3% of the total variation in community composition.*

## 3.2 Seabird habitat use and aggregations

Species richness varied between 0 and 10 and was highest around South Georgia (Figure 6). Total seabird densities were highest in SG and close to the mean positions of fronts (Figure 7). Figures 6 and 7 show the observed species richness and total densities, respectively, of seabirds in each strip-transect together with the mean positions of oceanographic fronts. Frontal systems are dynamic, and their mean position might not represent their position at the time of survey. However, due to the latitudinal constraint the DP poses on the ACC, the positions of the fronts in the DP are relatively constant (Brandon *et al.* 2004). Seabird aggregations seem to be

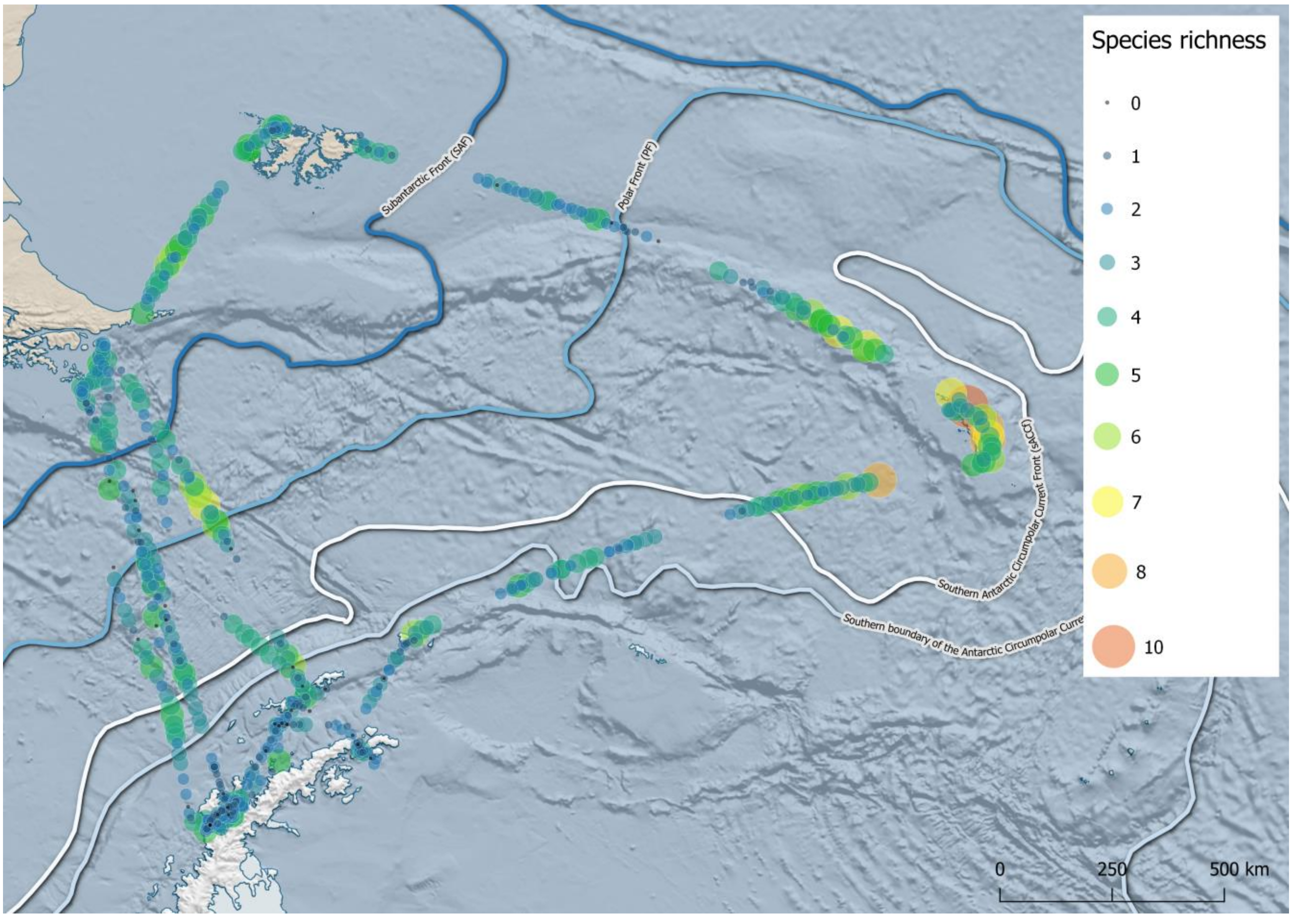

***Figure 6.*** *Species richness (number of taxonomic groups) in each strip-transect. Strip-transects are shown as dots, and the size and colour of the dots correspond to the number of taxonomic groups observed. The map was created using Quantarctica (Matsuoka et al. 2018) in QGIS (QGIS.org 2019).*

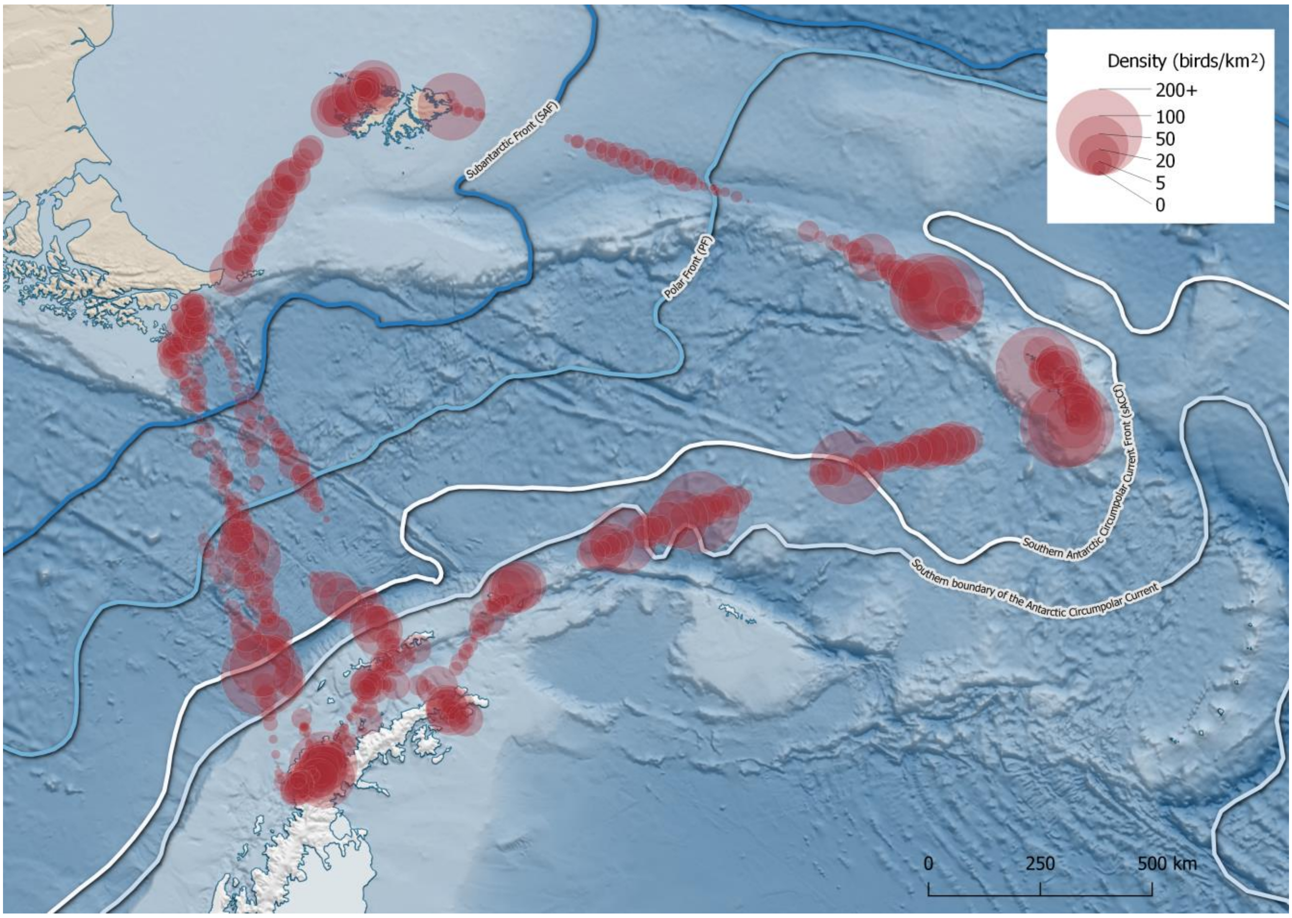

***Figure 7.*** *Total seabird densities, truncated at 200 birds/km² (which truncates four observations: two with over 1000 birds/km² in SG, one with 219 birds/km² in SG, and one with 210 birds/km² in FI-SG). Note that species-specific biases have not been accounted for in the calculated total density, leaving total density biased by the behaviour of species found in the community. The map was created using Quantarctica (Matsuoka et al. 2018) in QGIS (QGIS.org 2019).*

associated with coasts and oceanographic fronts, and South Georgia stands out as a particularly species-rich region with high densities of seabirds (Figures 6 and 7). South Georgia and open ocean areas close to SG and the sACCf experienced the highest species richness (Figure 6) and seabird densities (Figure 7), presumably because of the many seabird species breeding in SG. The polar front appears to create higher species richness in the DP, at least locally (Figure 6). Visual inspection of Figure 6 suggests that highest species richness in northern AP was observed around Elephant Island and the sbACC north of the South Shetland Islands. Observations with a species richness of five and above were also made northwest of the South American tip, on the way to the FI.

The significant predictors of species richness from the fitted GAM, SST ($p<0.001$), the SST gradient ($p=0.0413$) and the bathymetric slope ($p=0.0278$), explained 15.6% of the deviance (Figure 8). The species richness displayed a bimodal response in relation to SST and peaked at about 3°C and 9°C. In contrast, species richness declined linearly with an increasing bathymetric slope, while the SST gradient did not appear to cause any trend in species richness. In the diagnostic plots, model residuals look satisfactory, except for the residual vs linear predictor which appears to display a weak linear trend (Appendix Figure S14).

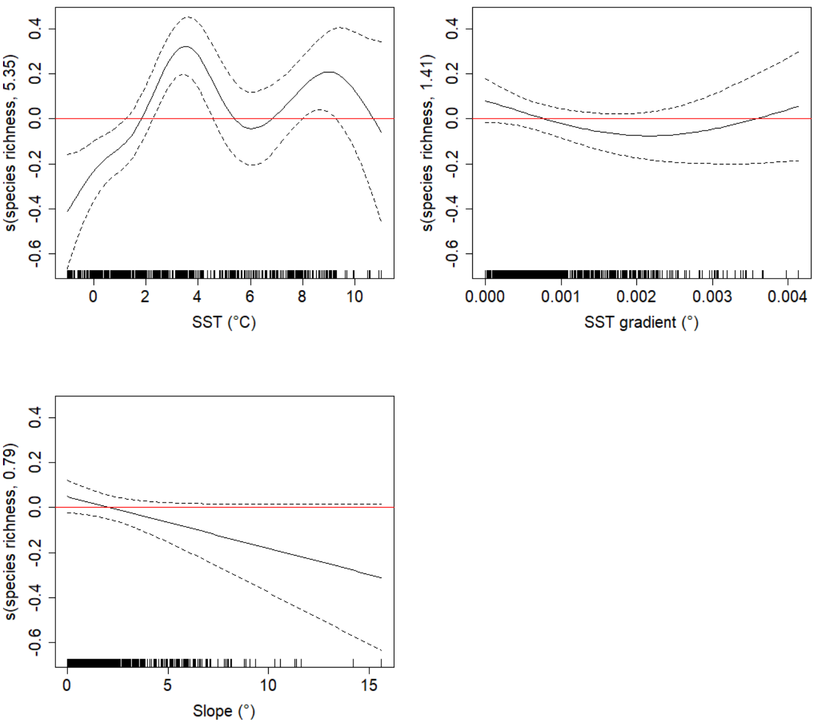

***Figure 8.*** *GAM smooth terms (s, linear predictor scale) of species richness as a function of significant explanatory variables (SST, SST gradient and Slope) with null space penalization. The dotted lines represent the lower and upper 2.5% percentiles of the confidence intervals.*

The significant predictors of seabird abundance from the fitted GAM, SST (p<0.001), slope (p<0.001), distance to coast (p<0.001), and vessel speed (p=0.004), explained 26.1% of the deviance (Figure 9). Observations of total seabird counts were temporally autocorrelated within time intervals of about 10 hours (Appendix Figure S10), which could lower the p-values. The residual plots for the model look satisfactory, however, except for the residual vs linear predictor which again appears to display a weak linear trend (Appendix Figure S15).

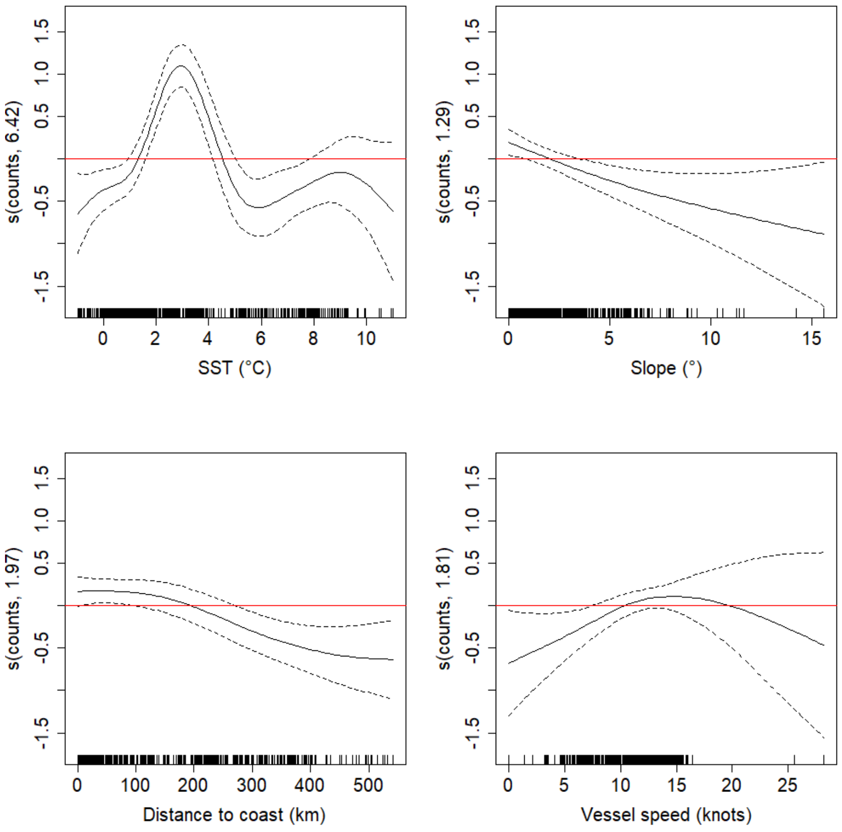

***Figure 9.*** *GAM smooth terms (s, linear predictor scale) of total counts as a function of significant explanatory variables (SST, slope, distance to coast and vessel speed) with null space penalization. The dotted lines represent the lower and upper 2.5% percentiles of the confidence intervals.*

Generally, seabird abundance increased closer to coasts. The peak in both species richness and abundance at sea surface temperatures around 3°C coincides with surface water temperatures close to the PF, as well as surface water temperatures close to SG (Appendix Figure S17 shows species richness and total density plotted against SST). Another increasing trend, although not significant, in species richness and abundance occurred at SST about 9°C and represents waters north of the SAF. A higher bathymetric slope had a slightly negative effect on both species richness and abundance, probably as a consequence of continental slopes lying quite far from the coasts of the study area.

The QGAM, which explored drivers of seabird abundance in high abundance areas, showed a significant effect of SST ($p<0.001$), distance to coast ($p=0.001$), FSLE ($p=0.016$), and slope ($p=0.007$) (Figure 10). The peak in abundance at SSTs about 3°C in the GAM was apparent also in QGAM. Low FSLE values are indicative of surface water convergence that aggregates passive particles. These particle-concentrating convergence areas had a slight positive effect on seabird abundance inside high abundance areas. Due to few strip-transects with low FSLE values, the effect of FSLE shows large variation at the low end of the spectrum, but particle retention on a monthly timescale (absolute FSLE values $>0.1d^{-1}$) had an aggregating effect on seabirds. Autocorrelation in the response variable could have lowered the significance levels of predictors in the QGAM, and although diagnostic plots look satisfactory (Appendix Figure S16), less strong relationships should be interpreted with caution.

SST was a significant predictor of both species richness and overall abundance, while total seabird counts showed a negative trend with increasing distance from coast and with a higher bathymetric slope. The maximum foraging range for most birds seems to be around 200 km from their colonies, and the negative effect of an increased slope on seabird abundance is probably due to most continental slopes lying outside this range. Surface water convergence had an aggregating effect on seabirds when examining the observations with highest overall abundance. SST and distance to coast were important predictors of seabird aggregations also inside high abundance areas, which occurred close to coasts and around a sea surface temperature of 3°C.

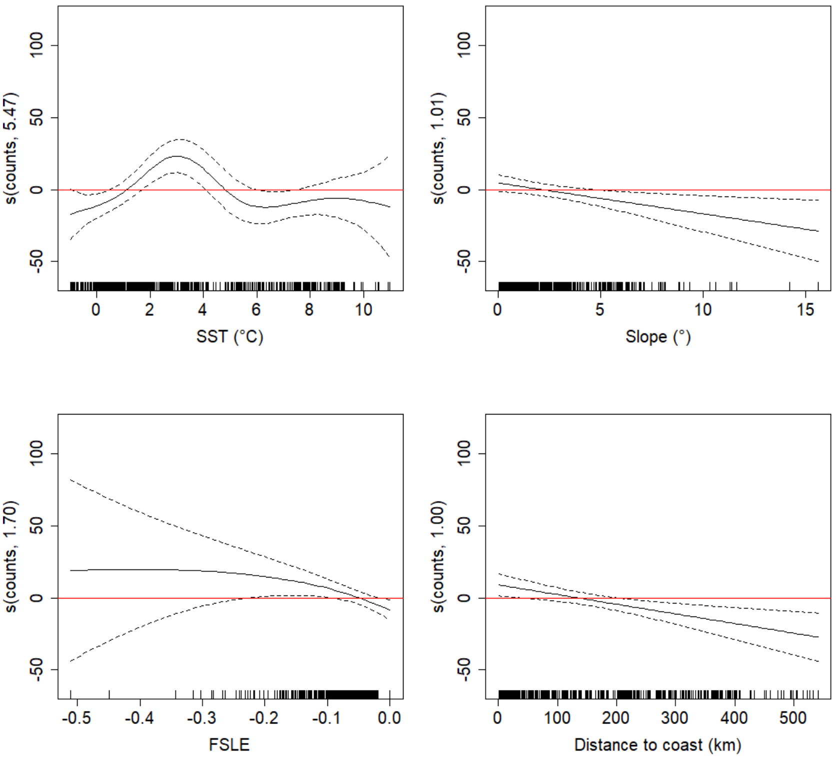

***Figure 10.*** *QGAM (qu=0.9) smooth terms (s, linear predictor scale) of total counts as a function of significant explanatory variables (SST, slope, FSLE and distance to coast). The dotted lines represent the lower and upper 2.5% percentiles of the confidence intervals. Low FSLE values are indicative of longer particle retention times.*

# 4 Discussion

## 4.1 Patterns and drivers of seabird guild composition and habitat use

This study shows a clear spatial pattern in seabird distributions across the Scotia Sea, with significant (1) oceanographic separation of avifauna and (2) higher aggregations (abundance and species richness) closer to coasts and in areas of increased hydrographic variability. Similar patterns were also found by Abrams (1985) in the African sector of the Southern Ocean. Species assemblages differed between the Antarctic Peninsula (AP), South Georgia (SG), and Falkland Islands (FI), while the different ocean areas had varying degrees of overlap generally characterized with a gradual north-south cline in species assemblages. Coastal communities in SG resembled those in open-ocean areas, presumably because of the many pelagic species breeding there (e.g., Shirihai 2007). Seabird guild composition and distributions were structured along geographical gradients, and gradients of both meso- and submesoscale biophysical cues (presumably reflecting areas of biological productivity; Abrams & Miller 1986, Enticott 1986, Ballance 2007, Kahru *et al.* 2007).

Sea surface temperature (SST) has been described as the most important predictor of marine biodiversity on a global scale (Tittensor *et al.* 2010) and was an important predictor of seabird aggregations also in this study. SST and distance to coast were the most important predictors of species assemblages, reflecting species-specific biogeography and life history traits. The results from this study are also consistent with results from other locations such as the South East Pacific (Serratosa *et al.* 2020), where SST and a pelagic-coastal gradient were important predictors of seabird community composition. Predator-habitat relationships generally reflect predator-prey relationships (e.g., Ballance 2007). Ocean surface temperature typically varies between water masses and gradients arise where water masses converge, creating oceanic habitats with physical characteristics occupied by different assemblages of prey species (Pocklington 1979, Chapman *et al.* 2020, Wahl *et al.* 1989, Jungblut *et al.* 2017). The coastal-pelagic gradient is another important factor affecting prey species present through gradients in productivity, bathymetry, and water characteristics (Doty & Oguri 1956, Abrams & Miller 1986), contributing to the differences in species assemblages between the pelagic and coastal habitats described in this study. Different predator guilds are consequently associated with specific ranges of geographical gradients through their diets and physiological and behavioural adaptations (Griffiths *et al.* 1982, Abrams 1985, Abrams & Miller 1986, Hunt *et al.* 1990, Joiris 1991, Ainley *et al.* 1993, Ainley *et al.* 1994, Ballance 2007, Fauchald & Ziryanov *et al.* 2011).

Our survey was conducted during the austral summer when many species of seabirds breed. Breeding poses a spatial constraint on seabirds (e.g., Gaston 2004, Amorim *et al.* 2009); the need to return to land to feed dependent offspring constrains how far and for how long adult birds can forage at sea. These restrictions lead to higher densities of some bird species in coastal waters (e.g., Abrams & Miller 1986), a pattern detected in this study with negative associations of species richness and abundance with distance from coast. For example, large numbers of pelagic species like grey-headed albatross and white-chinned petrel were observed in the coastal waters off SG. Land-breeding marine predators select breeding sites that, on average, provide appropriate access to sufficient, predictable food resources to enable successful fledging of offspring (Rosenberg & McKelvey 1999, Briscoe *et al.* 2018). Thus, while breeding places constraints on the duration and distance of at-sea foraging trips, breeding locations are typically located adjacent to marine areas of high food abundance which in turn is related to increased and seasonally predictable coastal productivity (caused by topographically induced water mixing and terrestrial runoff; Doty & Oguri 1956, Abrams & Miller 1986). Seabird communities in the coastal AP region were associated with topographic variability, which likely reflects the deep basins of Bransfield Strait and the deep fjords around coasts of AP. This, together with the fact that Bransfield Strait receives water from several distinct water masses, creates seasonal water mixing and gradients in SST that affect prey and hence seabird distributions (Hunt *et al.* 1990). Accordingly, a strong TG was a significant predictor of species assemblages inside the AP region.

Water characteristics such as temperature, salinity, and nutrient concentrations in the Southern Ocean show large latitudinal gradients, dividing the ocean into biogeographical zones (Grant *et al.* 2006). Seabird communities over temperate and Subantarctic waters north of the PF were dominated by black-browed and great albatrosses, shearwaters, Atlantic petrel, shags, and rockhopper and magellanic penguins, whos' diet consists mainly of cephalopods and fish (Appendix Table S1). Communities over Antarctic waters south of the PF, where krill is abundant, were on the other hand dominated by planktivores such as Adélie and chinstrap penguins, storm petrels, blue petrel, and prions. Snow and Antarctic petrels are mixed feeders that are adapted to hunting in pack ice where they find less competition (Griffiths *et al.* 1982, Ainley *et al.* 1993, Ainley *et al.* 1994) and were primarily observed in the AP region. Skuas were observed close to penguin colonies in the AP, where they feed on penguin eggs and chicks in austral summer (Shirihai 2007). These results support earlier studies that found associations of seabird guilds consisting of species with similar dietary preferences with water masses inhabited by preferred prey (Griffiths *et al.* 1982, Abrams 1985, Abrams & Miller 1986, Hunt *et al.* 1990, Joiris 1991).

Water mixing, revealed by a strong gradient in SST (TG), affected community composition on a regional scale in the AP. In the pelagic, strong gradients in SST are generally indicative of oceanographic fonts, which might act in two ways in shaping seabird distributions. First, as productive areas they can be associated with an elevated abundance of seabirds and other higher-level predators (e.g., Wahl *et al.* 1989, Bost *et al.* 2009) and second, they can act as avifaunal boundaries, separating different species assemblages (e.g., Pocklington 1979, Wahl *et al.* 1989), as has been described for the PF and the southern boundary of the Antarctic Circumpolar Current (sbACC) (Ribic *et al.* 2011). Ribic *et al.* (2011) found increased abundances of a few species, including diving petrels and blue petrel, at the PF and the sbACC, but the fronts' effect as boundaries for differing species assemblages were more pronounced. Seabirds breeding in the South Shetland Islands have been shown to use the sbACC as an important feeding ground (Santora & Veit 2013), pointing towards both a possible aggregating effect of the sbACC, and its possible role as a boundary for AP species in the breeding season. The role of fronts as boundaries could explain the higher importance of SST for community composition than that of the TG in our data. The TG did not manage to capture an effect of oceanographic fronts on pelagic communities, nor was there an effect of the TG on seabird abundance and species richness contrary to results from for example Serratosa *et al.* 2020. A possible explanation for the lack of association is that a frontal temperature gradient might not always be detectable at the surface (Chapman *et al.* 2020).

Other studies have shown a positive association of seabird abundance with areas of coastal upwelling, such as in the Eastern South Pacific Ocean (Serratosa *et al.* 2020). Interestingly, both the abundances and species richness of seabirds in this study appeared to decline in relation to higher bathymetric slopes which are typically associated with coastal upwelling. Potentially, this trend may be related to the overall lower species richness in the topographically complex AP compared to the sub-Antarctic areas (e.g., Hindell *et al.* 2020). The highest species richness and abundances were on the other hand found in SG, which lies on a large plateau. Because the AP hosts less flying seabird species causing flux in strip-transects, total bird counts might be biased against AP observations. Penguins on the other hand is a dominant group in the AP and have been suggested to dive as a response to ships (Jehl 1974, as cited in Tasker *et al.* 1984). Species richness in some strip-transects might have been underestimated as species that were hard to identify at sea were grouped together. For example, sympatric species of storm petrels are found in the AP and sympatric species of prions are found in SG and the FI (Shirihai 2007, Clarke *et al.* 2012). In the transects between land masses, only few strip-transects were situated at continental slopes, and a positive effect of slopes on seabird abundance in the pelagic might therefor not show in the results.

The associations between explanatory variables and seabird abundances found in this study may be exaggerated due to autocorrelation between observations. Lagrangian Coherent Structures such as Finite Scale Lyapunov Exponents (FSLE), were significant predictors of seabird aggregations within high abundance areas. Within these areas, FSLE values that suggested protracted retention of productivity were associated with observations of high seabird abundance, while shorter retention time was associated with lower abundance. In the AP region, biological hot spot areas have been shown to be associated with areas of higher particle residence times (Piñones *et al.* 2011). In line with this, but keeping in mind the point made about autocorrelation above, we show a weak aggregating effect of low FSLE on seabird abundance. This supports the findings of Piñones *et al.* (2011) and Lowther *et al.* (2014) which suggest that higher trophic level predators can track these dynamic structures. These findings are similar to findings in other locations such as in the Mozambique Channel, where the great frigatebird (*Fregata minor*) has been shown to be able to track dynamic structures where particles are concentrated by surface flow, identified by a low FSLE values (Kai *et al.* 2009). Prey are heterogeneously and dynamically distributed in the marine environment (Fauchald 2009), and variability in krill distribution occurs also at fine spatial and temporal scales (Bernard & Steinberg 2013). Hence, even though successful foraging depends on environmental predictability on a meso-scale, it also requires the ability to track dynamic prey patches on finer spatial and temporal scales.

Seabird communities in the AP were associated with higher baleen whale abundances than other regions. This association is probably due to the general high abundance of baleen whales in the AP region, particularly humpback whales (*Megaptera novaeangliae*) (Deehr Johannessen 2020). The AP region has repeatedly been recognized as a productive area with high krill availability, attracting both seabirds and baleen whales (e.g., Santora and Veit 2013). The association between baleen whales and seabirds around the AP probably reflects this attraction to a shared food resource rather than a direct association between the taxa, because whales were observed on a much larger scale (all the way to the horizon) than seabirds that were counted only up to 300 meters from the vessel. However, sharing the foraging ground, humpback whales in the AP likely create additional foraging opportunities for seabirds, while simultaneously being an important competitor for food (Croxall 1992). On a biogeographical scale, baleen whales were most strongly associated with penguins, but this association was not detected in the AP region itself. Coastally foraging humpback whales dwelling close to penguin colonies in the AP might have a negative rather than a positive effect on the penguins, since diving seabirds probably find the effects of competition more important than those of facilitation. Data on humpback whale distributions collected simultaneously with this study (Deehr Johannessen 2020) suggest that the whales feed close to penguin colonies (described in Harris *et al.* 2011, http://www.penguinmap.com/mapppd). With an increasing abundance of humpback whales in the AP (e.g., Pallin *et al.* 2018), penguins might face increased competition in the future.

The downside of ships of opportunity is that their predetermined routes do not allow complete randomization of sampling due to their lack of structured spatial coverage. In the case of our study, the routes allowed a representative data set to be collected by crossing all biogeographical regions in the study area (Grant *et al.* 2006) and covering both oceanic and coastal areas. However, our observations are likely to be biased towards coastal and particularly biodiverse areas. Because of migratory movements, seasonal variation is typical for large-scale distribution patterns of seabirds (e.g., Ballance 2007, Phillips *et al.* 2017). Studies in the Eastern South Pacific Ocean (Serratosa *et al.* 2020) and around the Azores (Amorim *et al.* 2009) have shown that time of year is an important variable affecting seabird community composition, overall abundance, and species richness. Here, we have explored an early summer season, when visitors to the areas are expected to influence community composition, species richness and total seabird abundance. In addition to seasonal variability, inter-annual variation in climate and oceanographic factors are reflected in predator habitat use (Ballance 2007, Lowther *et al.* 2018), adding another temporal scale to the variation in seabird distributions.

## 4.2 Areas of importance and implications for ecosystem management

Both species richness and seabird densities were particularly high in SG, and the association between high species richness and overall abundance with specific values of predictor variables were in many cases explained by their location around SG. The SG area is considerably more productive than most of the Southern Ocean and holds a high abundance of krill (Atkinson *et al.* 2001), making it an attractive site for breeding seabirds (Clarke *et al.* 2012). The grey-headed albatross is currently listed as endangered by IUCN (IUCN 2021), while the white-chinned petrel is listed as vulnerable, and for both species, SG is the most important breeding site (Clarke *et al.* 2012). This study was conducted in the breeding season, and the results underline the importance of SG as a breeding area for a variety of seabirds, including endangered species. Further our observations showed an increased overall density of seabirds close to the mean positions of sACCf and sbACC, as well as South Shetland Islands and Elephant Island (Figure 7), agreeing with the findings of Santora and Veit (2013), who identified persistently important areas for top predators in the northern Antarctic Peninsula by comparing data collected over several years in the months January to March. They found that sACCf and sbACC were important both for pelagic species breeding further north, and for AP breeders, while the Bransfield Strait hosted hotspots of more coastal species. In this study, we encountered high overall densities also in the Gerlache Strait, which could be a consequence of elevated effort spent in the area, or due to elevated prey abundance. Because the Scotia Sea and AP region is an ecologically important area with predicted changes in species distributions and predator hotspots (e.g., Hindell *et al.* 2020), it deserves special attention in management and in the consideration of future Marine Protected Areas (MPAs).

Data on seabirds distributions is important in risk assessment, and for conservation efforts like the establishment of MPAs and spatial and temporal management of fisheries. Studies like ours can reveal previously unknown areas of importance to seabirds, and thereby point out areas where research efforts should be increased, as well as identify Important Bird Areas (IBAs, Donald *et al.* 2019) and areas to be considered for conservation. They also provide distributional data on seabirds for future comparisons assessing ecosystem change, for which community-level data are particularly useful. Models that incorporate multiple species and predictors, can be effective in revealing complex relationships, since they consider multiple responses inside the same community (Reid *et al.* 2005, Piatt, Sydeman & Wiese 2007, Hindell *et al.* 2020). Considering community-level responses is important in making meaningful management decisions, and networks of MPAs should be designed in a way that they consider the diversity of communities as well as future change in species distributions (Hindell *et al.* 2020).

## 4.3 Conclusions

Seabirds associate with specific oceanographic habitats, reflecting the distribution of their prey. Differences in diets and adaptations between species of seabirds create differing species assemblages between distinct oceanographic zones. Aggregations occur in areas of assumed high biological productivity, such as oceanographic fronts and coastal areas. The results from this study reflect the association of species with specific water masses and underline the importance of distance to colonies for seabird distributions in the breeding season. The results further captured seabirds' ability to track biological productivity and can be used to describe areas of relatively higher seabird abundance and species richness.

This study shows that community-level data collected on seabirds using the strip-transect method onboard vessels of opportunity are useful in describing seabird distributions. This type of opportunistically collected data can be a valuable addition to structured surveys. Large data sets are needed to cover the spatial and temporal scales relevant to seabirds on a fine-enough resolution to detect change. Apart from the economic advantages allowing considerably more data to be collected, reducing the number of vessels on the sea is smart from an environmental perspective. Regularly conducted multi-species seabird surveys are paramount in detecting distributional changes and fine-scale species distribution data are a prerequisite for distributions modelling. Ultimately effective management and conservation rely on knowledge of species distributions and habitat use. The results from this study can serve as a background for future studies aiming to assess year-to-year variation and long-term changes in seabird distributions throughout the Antarctic Peninsula and Scotia Sea.

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# Appendix

***Table S1.*** *Taxonomic groups observed, with abbreviations, species included in the groups (based on Shirihai 2007), total number of individuals observed per group, conservation status (IUCN 2021), and principal food-type (based on Griffiths et al. 1982, Barrera-Oro 2002, Xavier 2003, Shirihai 2007, and Moreno et al. 2016). Conservation status abbreviations are EN (endangered), VU (vulnerable), NT (near threatened), and LC (least concern) following IUCN (2021).*

| **Taxonomic group** | **Abbreviation** | **Species included** | **Number of individuals observed** | **Conservation status** | **Principal food-type** |
|---|---|---|---|---|---|
| **Great albatrosses** | GreatAlb | Wandering (*Diomedea exulans*) and Royal (*D. epomophora*) albatrosses | 102 | VU (*D. exulans* and *D. epomophora epomophora*), EN (*D. epomophora sanfordi*) | Cephalopods |
| **Grey-headed albatross** | GheadAlb | Gray-headed albatross (*Thalassarche chrysostoma)* | 70 | EN | Cephalopoda |
| **Black-browed albatross** | BbrowAlb | Black-browed albatross (*Thalassarche melanophrys melanophrys*) | 743 | LC | Cephalopods |
| **Light-mantled sooty albatross** | LmsAlb | Light-mantled sooty albatross (*Phoebetria palpebrata*) | 33 | NT | Cephalopods |
| **Southern fulmar** | SFulmar | Southern fulmar (*Fulmarus glacialoides*) | 734 | LC | Cephalopods |
| **Giant petrels** | GiantPt | Southern (*Macronectes giganteus*) and Northern (*M. halli*) giant petrels | 490 | LC | Mixed |
| **Cape petrel** | CapePt | Cape petrel (*Daption capense*) | 2007 | LC | Cephalopods |
| **Antarctic petrel** | AntarcticPt | Antarctic petrel (*Thalassoica antarctica*) | 61 | LC | Mixed |

| | | | | | |
|---|---|---|---|---|---|
| **Snow petrel** | SnowPt | Snow petrel (*Pagodroma nivea*) | 13 | LC | Mixed |
| **Storm petrels** | StormPt | All species of storm petrels (*Oceanites spp.* and *Fregetta spp.*) | 519 | LC (*O. oceanicus*, *F. tropica*, and *F. grallaria*) | Plankton |
| **Diving petrels** | DivingPt | All species of diving petrels (*Pelecanoides spp.*) | 41 | LC (*P. magellani*, *P. urinatrix*, and *P. georgicus*) | Plankton |
| **White-chinned petrel** | WchinPt | White-chinned petrel (*Procellaria aequinoctialis*) | 243 | VU | Cephalopods |
| **Atlantic petrel** | AtlanticPt | Atlantic petrel (*Pterodroma incerta*) | 12 | EN | Cephalopods |
| **Soft-plumaged petrel** | SplumPt | Soft-plumaged petrel (*Pterodroma mollis*) | 3 | LC | Mixed |
| **Skuas** | Skuas | All species of skuas (*Catharacta spp.*) | 217 | LC (*C. antarctica* and *C. maccormicki*) | Mixed |
| **Kelp gull** | KelpGull | Kelp gull (*Larus dominicanus*) | 12 | LC | Mixed |
| **Shags** | Shags | All species of shags (*Phalocrocorax spp.*) | 268 | LC (*P. articeps* and *P. magellanicus*) | Mixed |
| **Terns** | Terns | All species of terns (*Sterna spp.*) | 123 | LC (*S. paradisaea* and *S. vittata*) | Fish |
| **Prions** | Prions | All species of prions (*Pachyptila spp.*) | 6166 | LC (*P. desolata*, *P. belcheri*, and *P. turtur*) | Plankton |
| **Blue petrel** | BluePt | Blue petrel (*Halobaena caerulea*) | 723 | LC | Plankton |
| **Shearwaters** | Shearwaters | Sooty shearwater (*Puffinus griseus*) and great shearwater (*P. gravis*) | 510 | NT (*P.griseus*), LC (*P.gravis*) | Fish (*P.griseus*), cephalopods (*P.gravis*) |

| | | | | | |
|---|---|---|---|---|---|
| **King penguin** | KingPg | King penguin (*Aptenodytes patagonicus*) | 13 | LC | Fish |
| **Adélie penguin** | AdeliePg | Adélie penguin (*Pygoscelis adeliae*) | 166 | LC | Plankton |
| **Gentoo penguin** | GentooPg | Gentoo penguin (*Pygoscelis papua*) | 495 | LC | Mixed |
| **Chinstrap penguin** | ChinPg | Chinstrap penguin (*Pygoscelis antarcticus*) | 218 | LC | Plankton |
| **Macaroni penguin** | MacPg | Macaroni penguin (*Eudyptes chrysolophus*) | 25 | VU | Mixed |
| **Magellanic penguin** | MagPg | Magellanic penguin (*Spheniscus magellanicus*) | 50 | LC | Mixed |
| **Rockhopper penguin** | RockPg | Rockhopper penguin (*Eudyptes chrysocome*) | 18 | VU | Mixed |

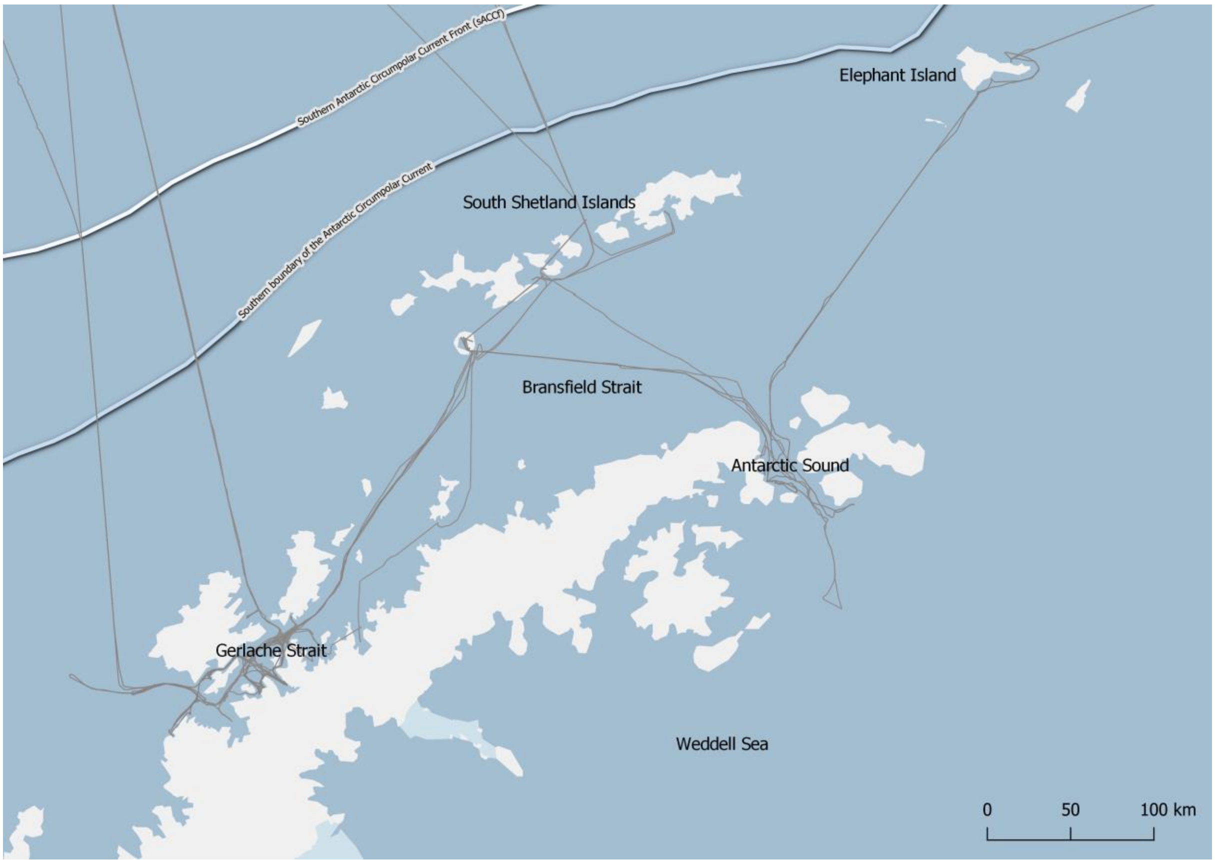

***Figure S1**. Map of the northern Antarctic Peninsula with oceanographic fronts and places names. Track lines of the vessels are indicated as grey lines. The map was created using Quantarctica (Matsuoka et al. 2018) in QGIS (QGIS.org 2019).*

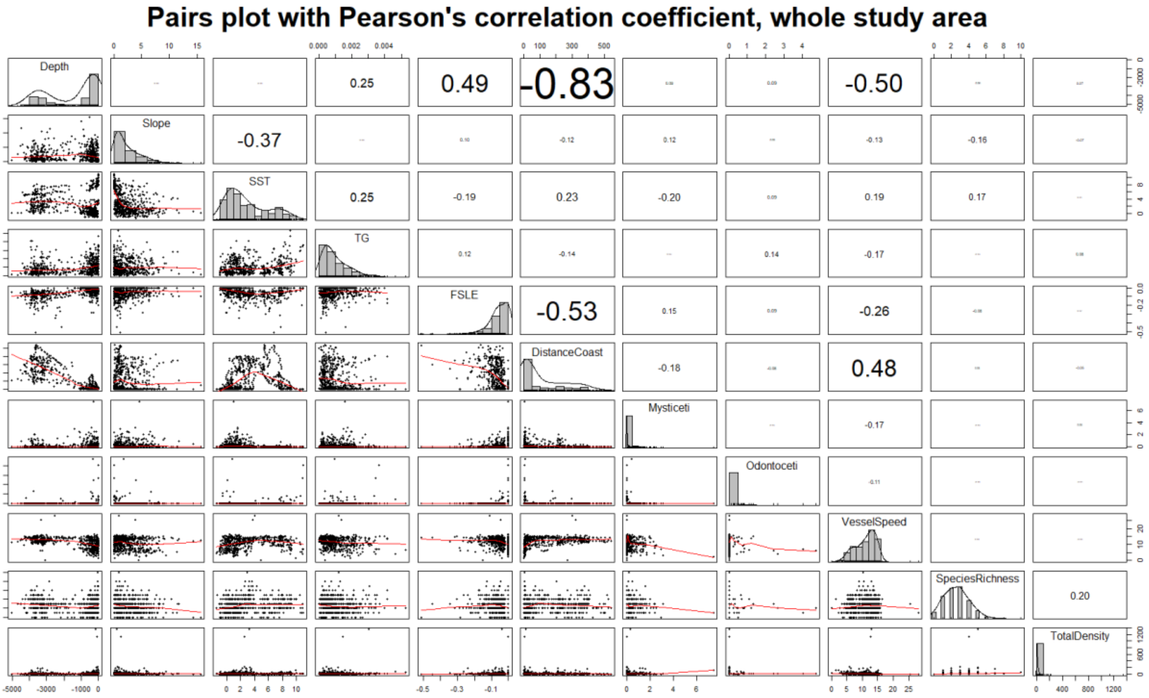

***Figure S2.*** *Pairs plot with Pearson's correlation coefficients between depth, bathymetric slope, sea surface temperature (SST), the SST gradient (TG), Finite Scale Lyapunov Exponents (FSLE), distance to coast, baleen whale abundance (Mysticeti), toothed whale abundance (Odontoceti), vessel speed, species richness and total seabird density. Data from the whole study area is included.*

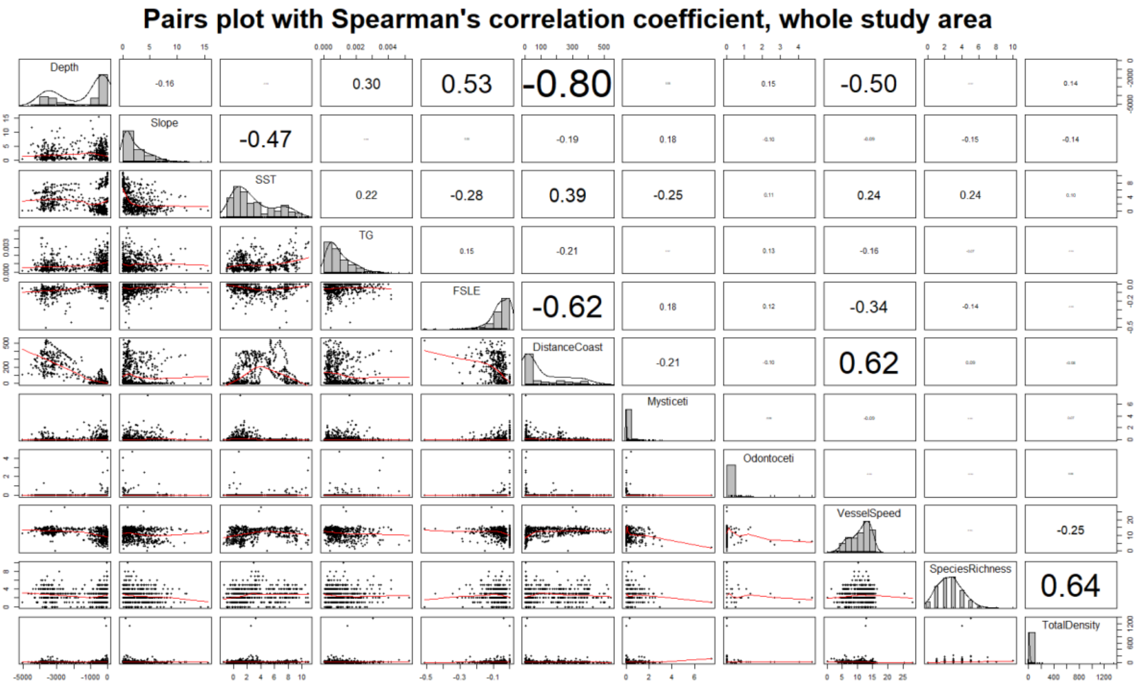

***Figure S3.*** *Pairs plot with Spearman's correlation coefficients between depth, bathymetric slope, sea surface temperature (SST), the SST gradient (TG), Finite Scale Lyapunov Exponents (FSLE), distance to coast, baleen whale abundance (Mysticeti), toothed whale abundance (Odontoceti), vessel speed, species richness and total seabird density. Data from the whole study area is included.*

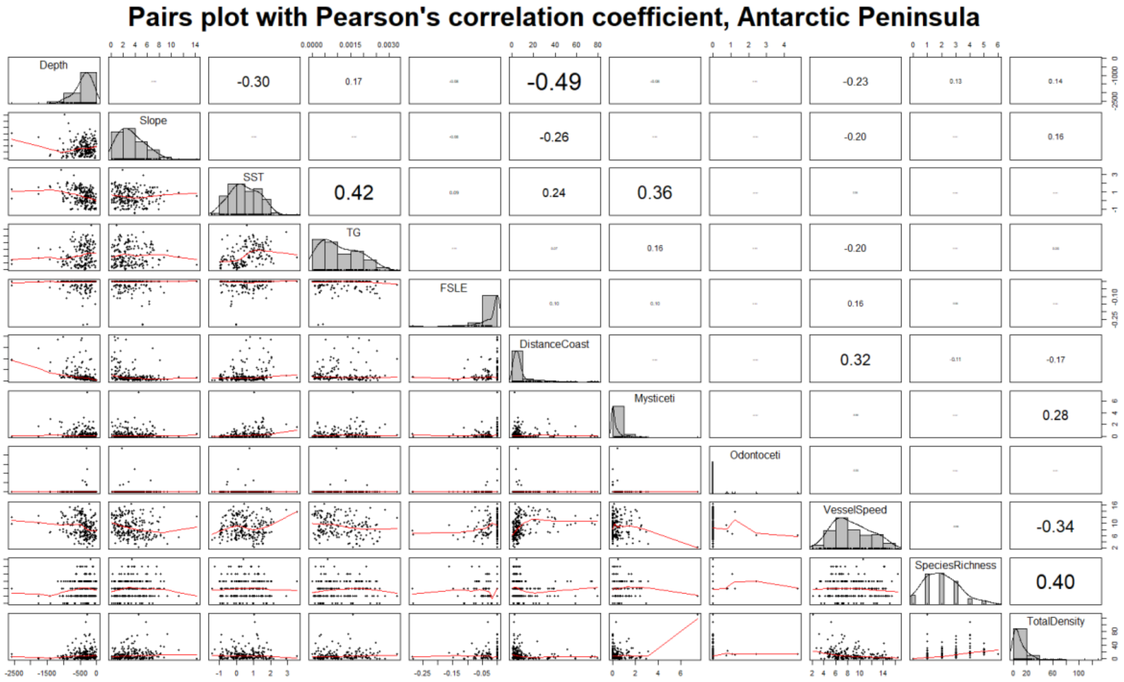

*__Figure S4.__ Pairs plot with Pearson's correlation coefficients between depth, bathymetric slope, sea surface temperature (SST), the SST gradient (TG), Finite Scale Lyapunov Exponents (FSLE), distance to coast, baleen whale abundance (Mysticeti), toothed whale abundance (Odontoceti), vessel speed, species richness and total seabird density. Only data from the Antarctic Peninsula region is included.*

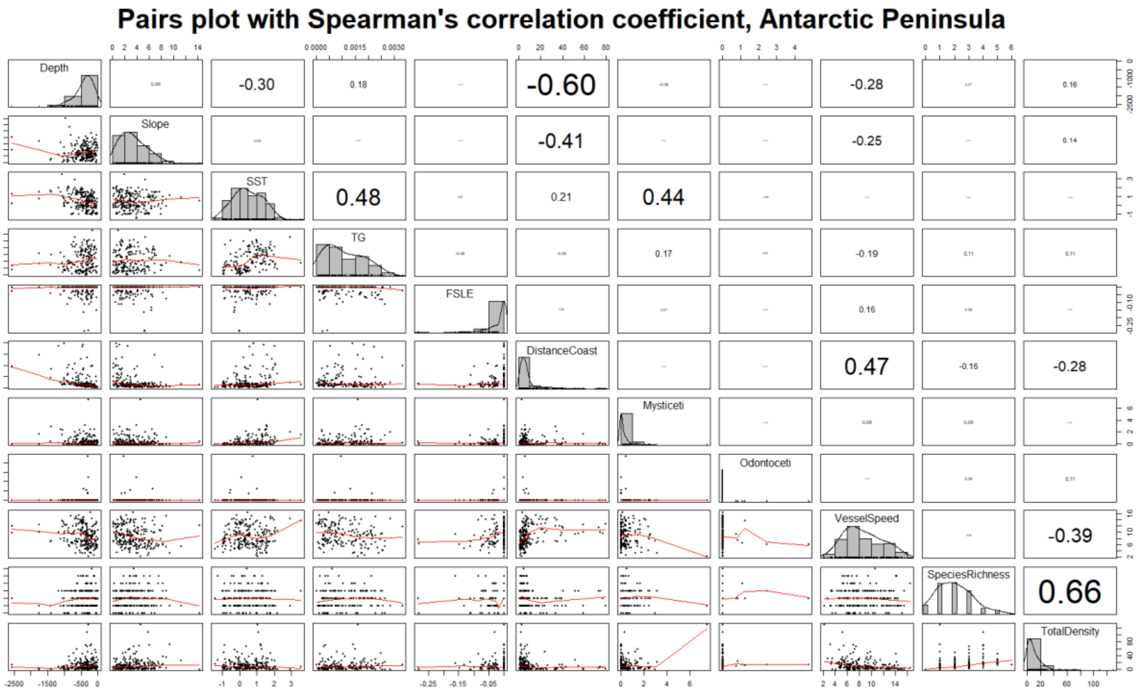

***Figure S5.*** *Pairs plot with Spearman's correlation coefficients between depth, bathymetric slope, sea surface temperature (SST), the SST gradient (TG), Finite Scale Lyapunov Exponents (FSLE), distance to coast, baleen whale abundance (Mysticeti), toothed whale abundance (Odontoceti), vessel speed, species richness and total seabird density. Only data from the Antarctic Peninsula region is included.*

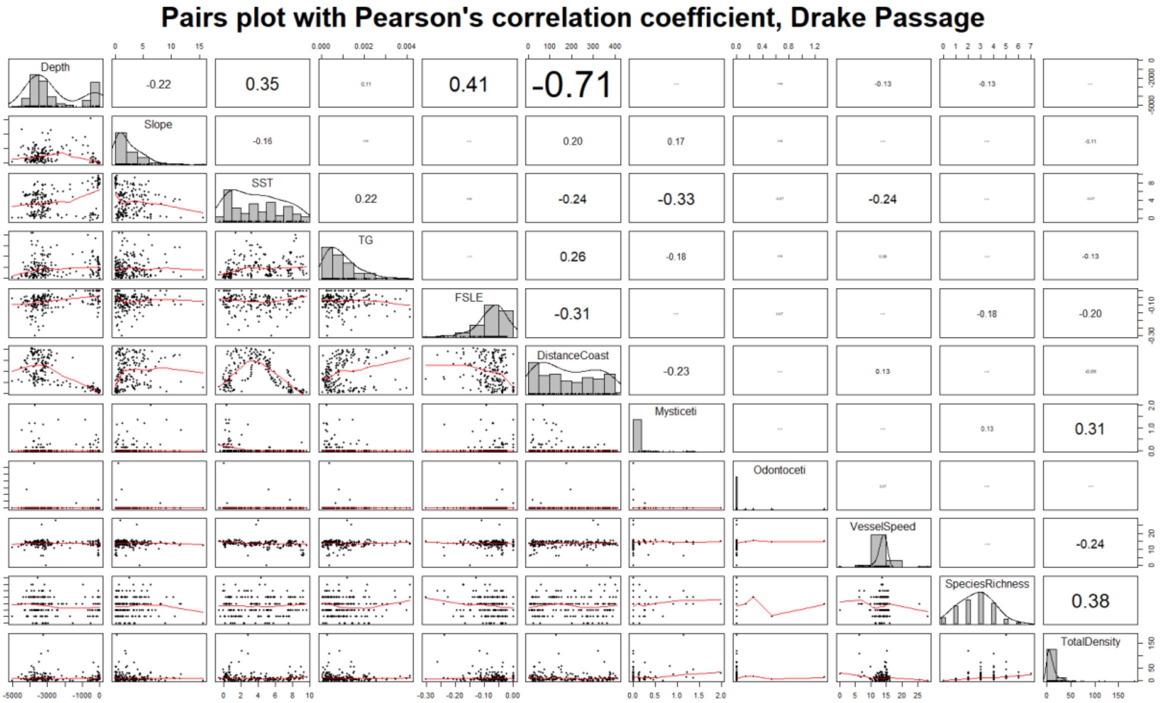

***Figure S6.*** *Pairs plot with Pearson's correlation coefficients between depth, bathymetric slope, sea surface temperature (SST), the SST gradient (TG), Finite Scale Lyapunov Exponents (FSLE), distance to coast, baleen whale abundance (Mysticeti), toothed whale abundance (Odontoceti), vessel speed, species richness and total seabird density. Only data from the Drake Passage region is included.*

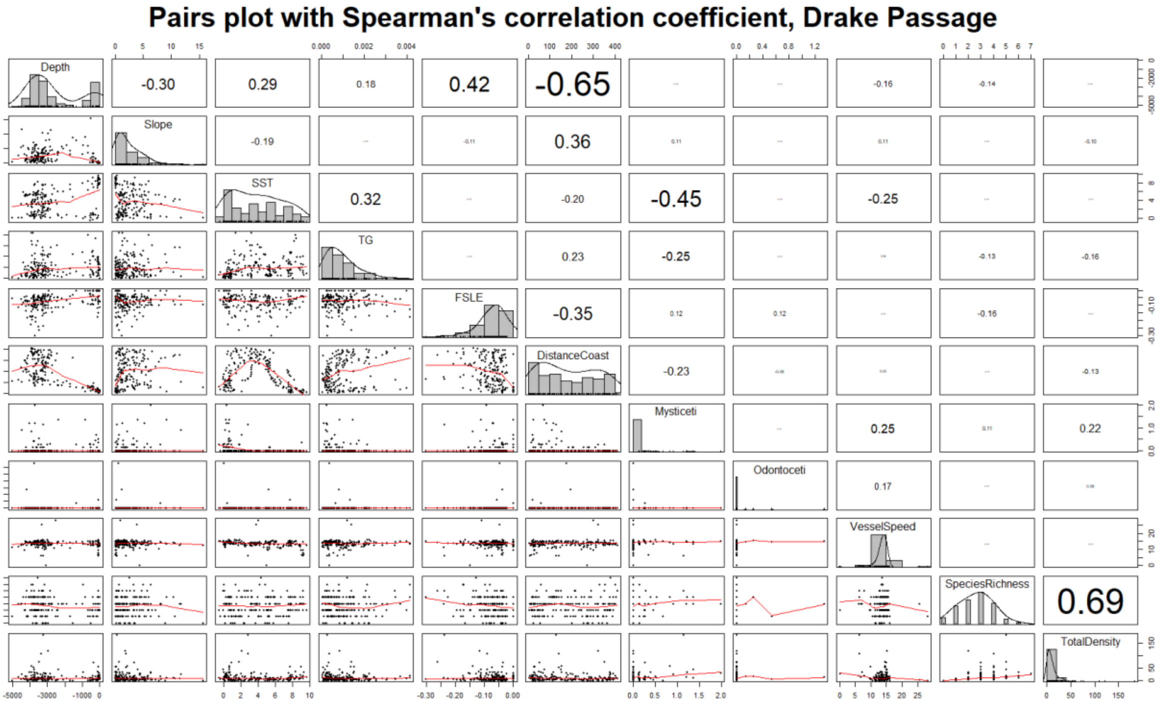

***Figure S7.*** *Pairs plot with Spearman's correlation coefficients between depth, bathymetric slope, sea surface temperature (SST), the SST gradient (TG), Finite Scale Lyapunov Exponents (FSLE), distance to coast, baleen whale abundance (Mysticeti), toothed whale abundance (Odontoceti), vessel speed, species richness and total seabird density. Only data from the Drake Passage region is included.*

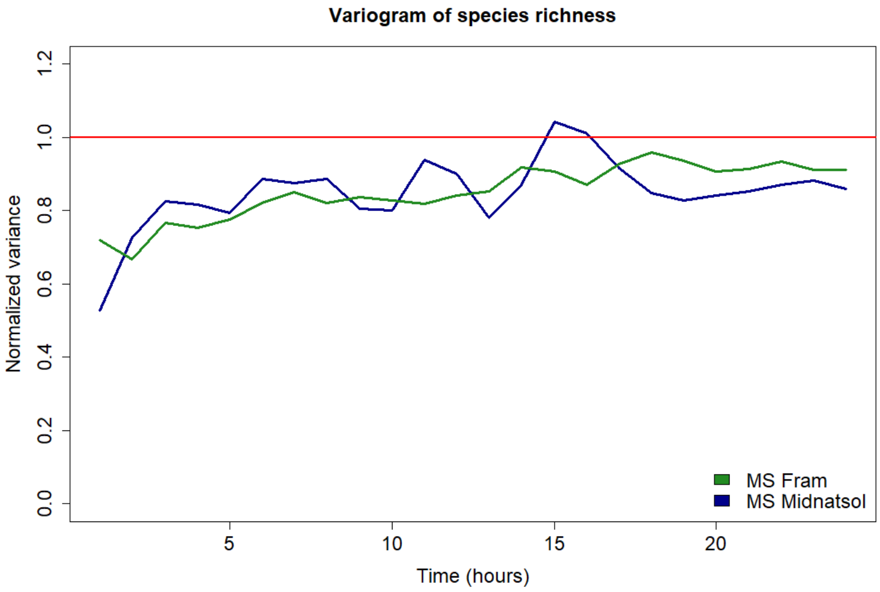

***Figure S8.*** *Variogram showing temporal autocorrelation in species richness between observations.*

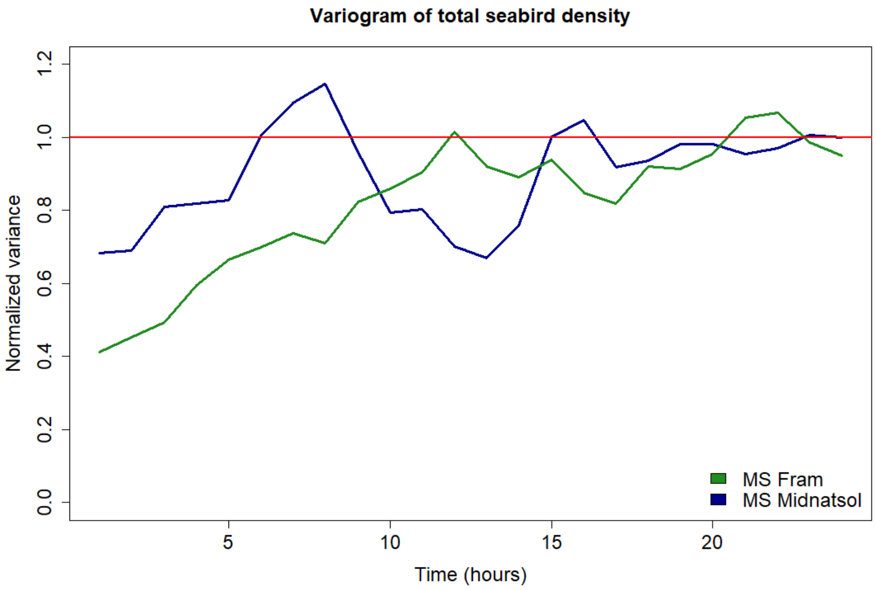

***Figure S9.*** *Variogram showing temporal autocorrelation in total seabird density between observations.*

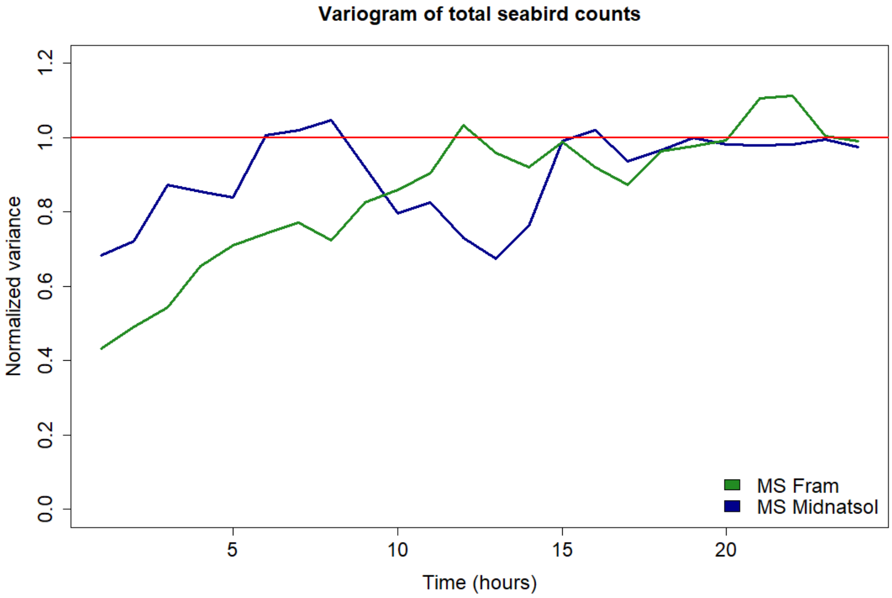

***Figure S10.*** *Variogram showing temporal autocorrelation in total seabird counts between observations.*

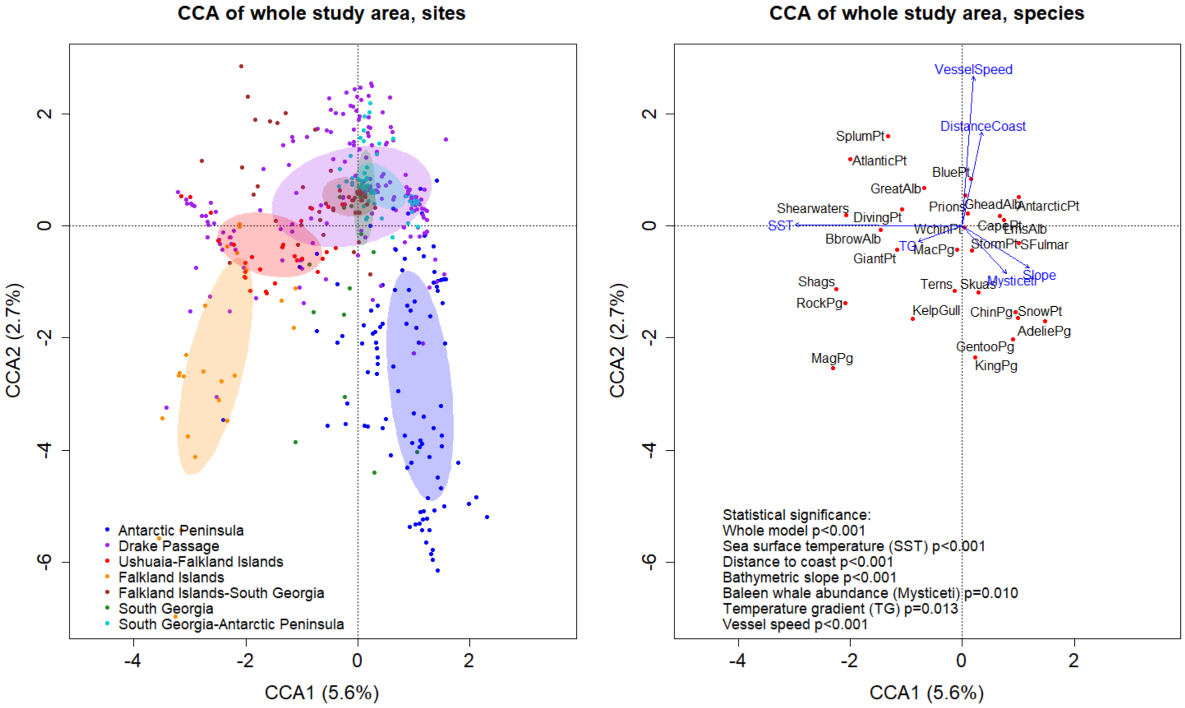

***Figure S11.*** *CCA ordination biplot of axes 1 and 2 for CCA of seabird communities in the whole study area, performed on untransformed data and divided into two plots. The left hand side plot shows sites (strip-transects) as dots with colour indicating region, and ellipses representing standard deviations of observations inside each region. The right hand side plot shows species (red dots) and significant predictors (blue arrows). The significant predictors, which are sea surface temperature (SST), distance to coast (DistanceCoast), the bathymetric slope (Slope), baleen whale abundance (Mysticeti), the SST gradient (TG), and vessel speed (VesselSpeed), explained 11.8% of the total variation in community composition.*

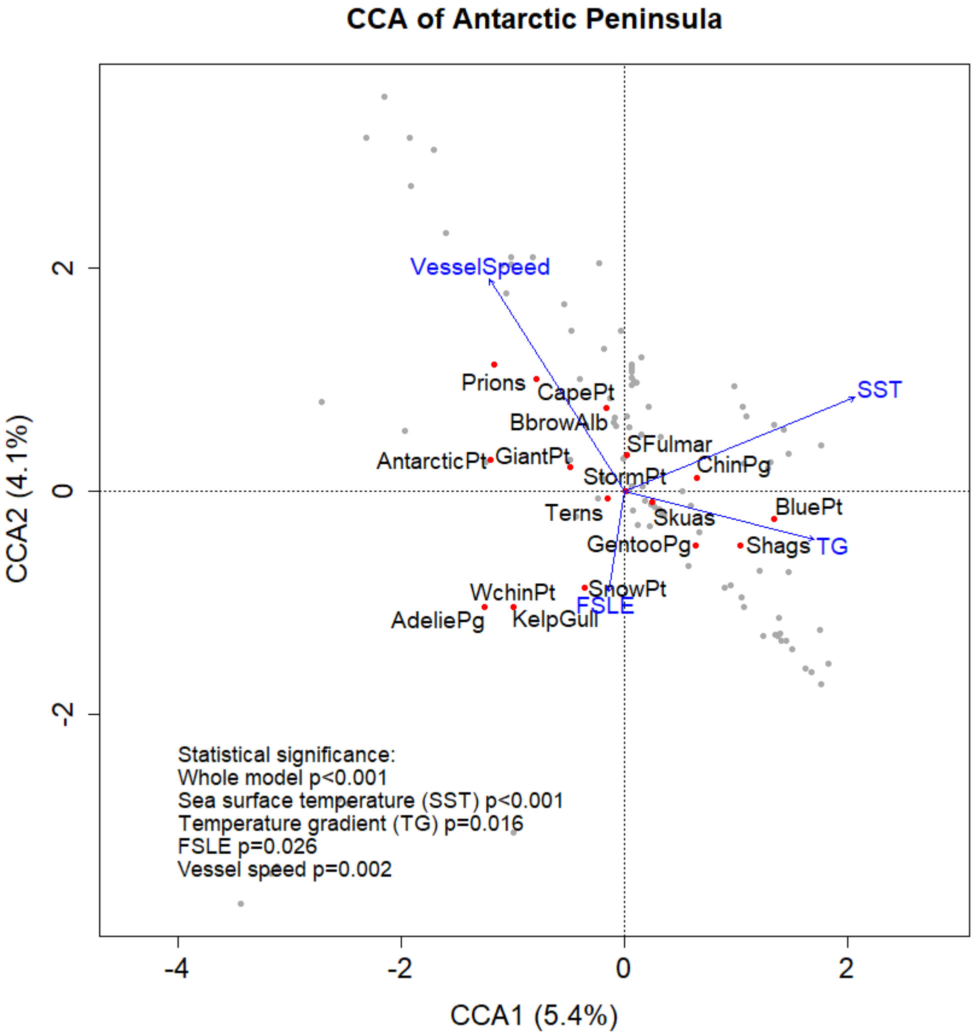

***Figure S12.*** *CCA ordination biplot of axes 1 and 2 for CCA of seabird communities in the Antarctic Peninsula region, performed on untransformed data. Sites (strip-transects) are shown as grey dots, species as red dots, and significant predictors as blue arrows. The significant predictors, which are sea surface temperature (SST), the SST gradient (TG), Finite Scale Lyapunov Exponents (FSLE), and vessel speed (VesselSpeed), explained 11.6% of the total variation in community composition.*

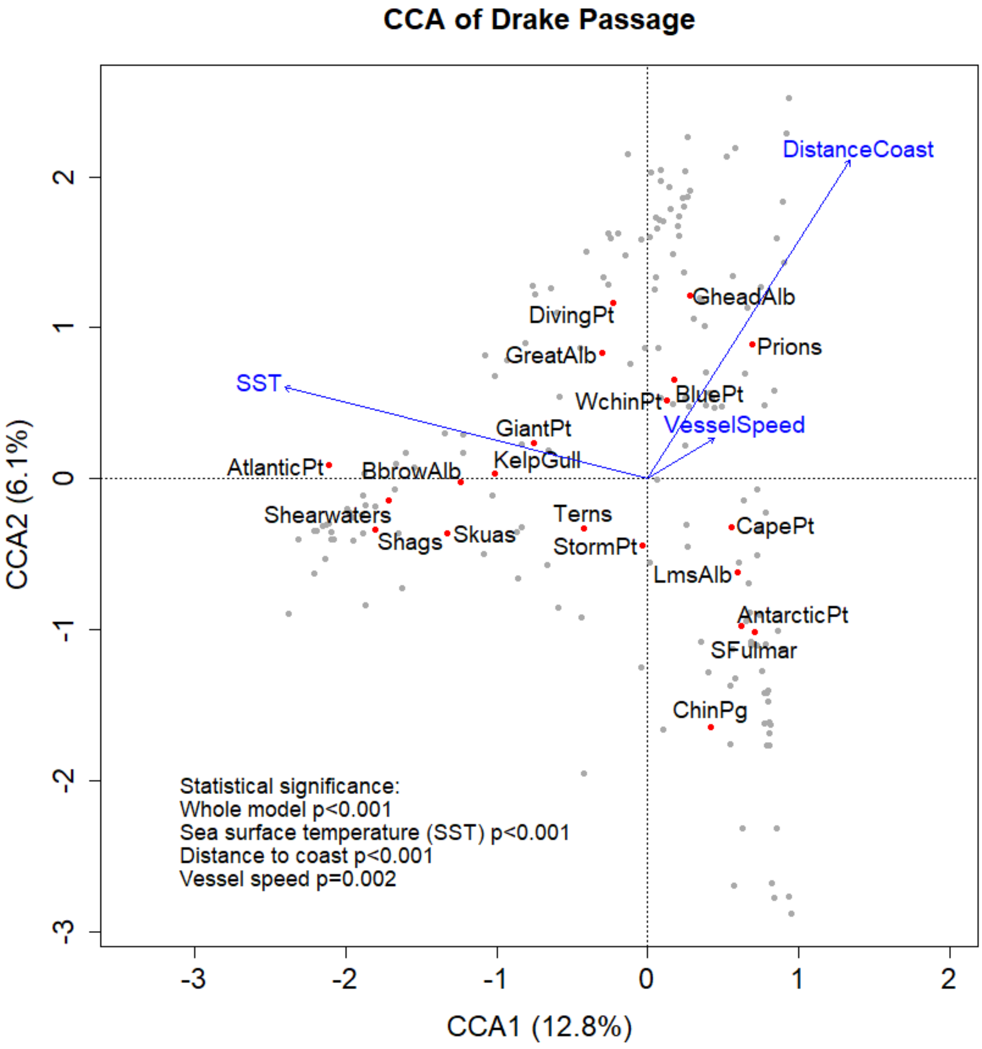

***Figure S13.*** *CCA ordination biplot of axes 1 and 2 for CCA of seabird communities in the Drake Passage, performed on untransformed data. Sites (strip-transects) are shown as grey dots, species as red dots, and significant predictors as blue arrows. The significant predictors, which are sea surface temperature (SST), distance to coast (DistanceCoast), and vessel speed (VesselSpeed), explained 20.1% of the total variation in community composition.*

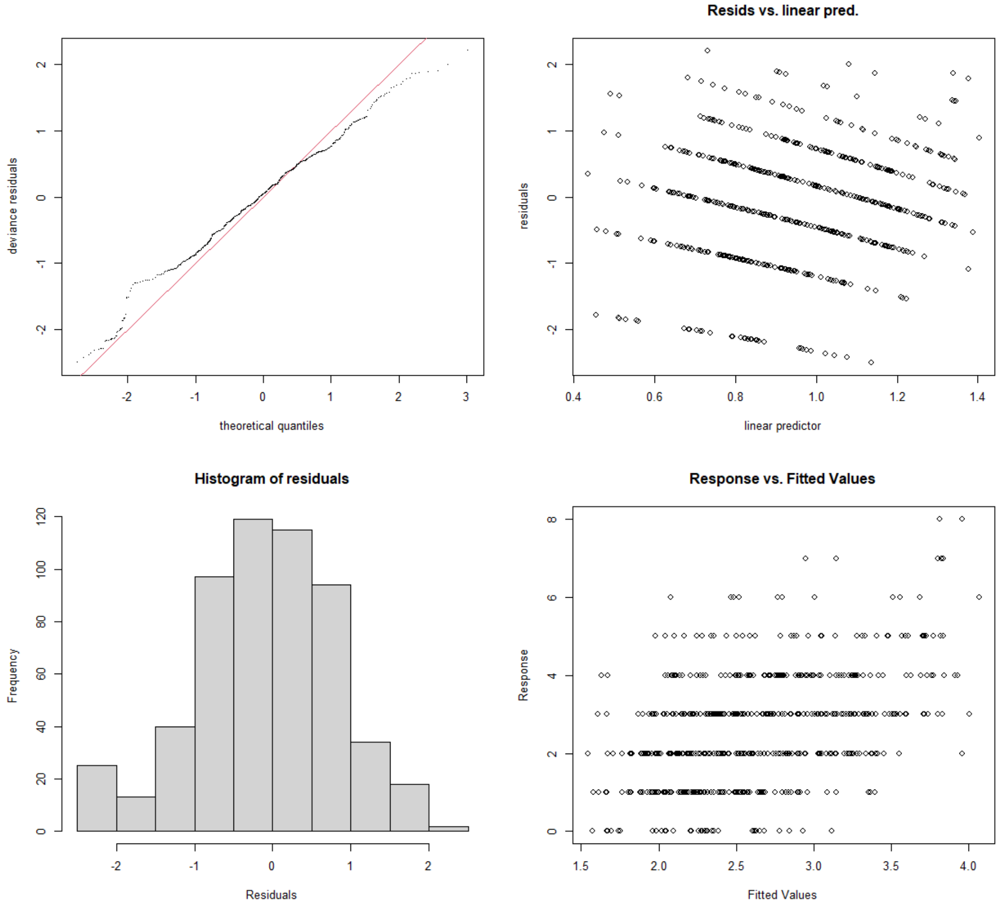

***Figure S114.*** *Diagnostic plots for the fitted GAM for species richness: Q-Q residual plot (topleft panel), residuals vs linear predictor (topright panel), residual distribution (bottomleft panel), and response vs fitted values (bottomright panel).*

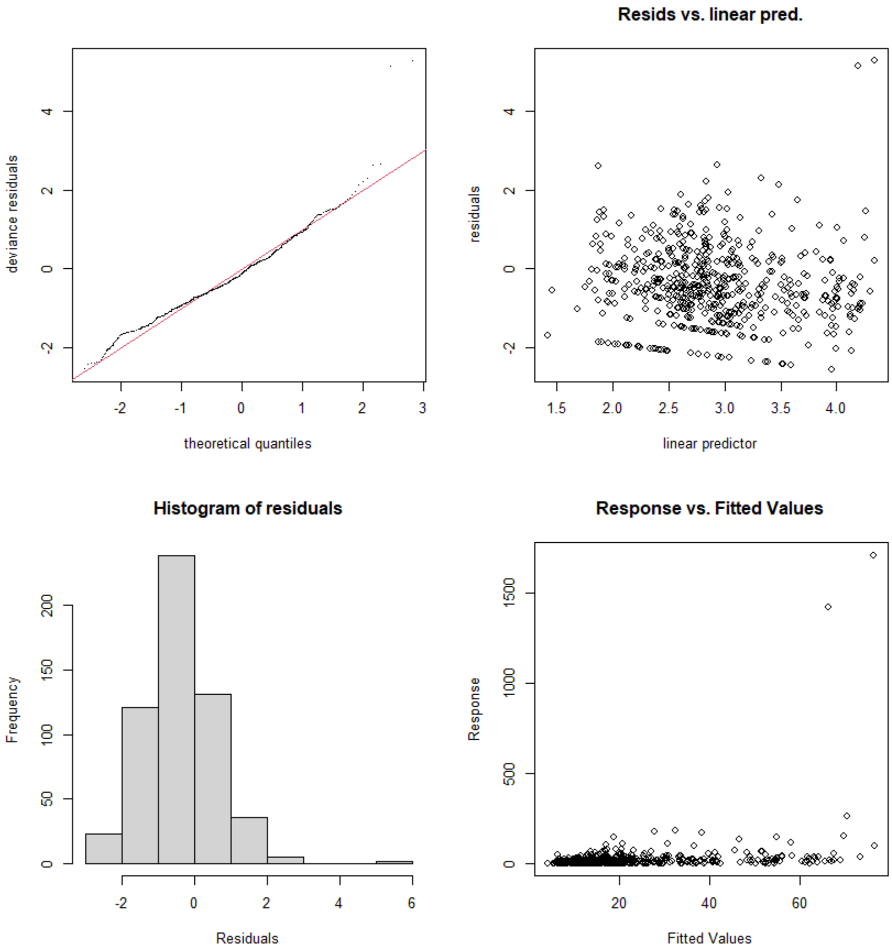

***Figure S15.*** *Diagnostic plots for the fitted GAM for total seabird counts: Q-Q residual plot (topleft panel), residuals vs linear predictor (topright panel), residual distribution (bottomleft panel), and response vs fitted values (bottomright panel).*

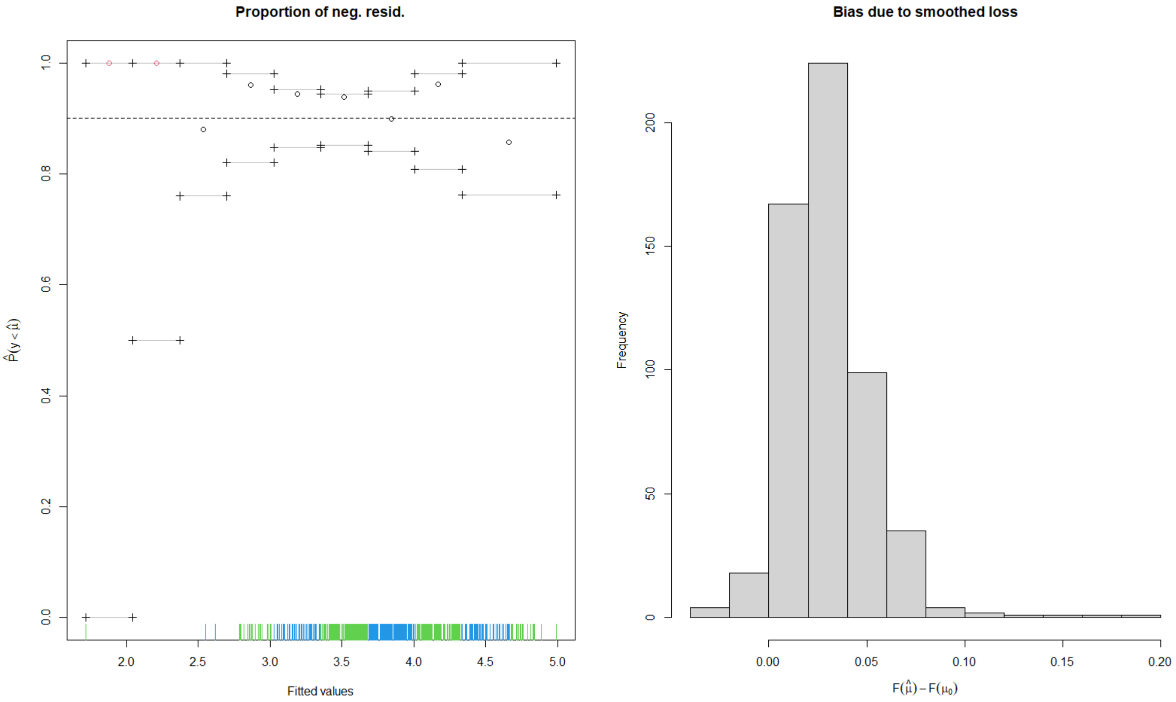

***Figure S16.*** *Diagnostic plots for the fitted QGAM (qu=0.9) for total seabird counts: Proportion of negative residuals (left hand side panel) and bias due to smoothed loss (right hand side panel).*

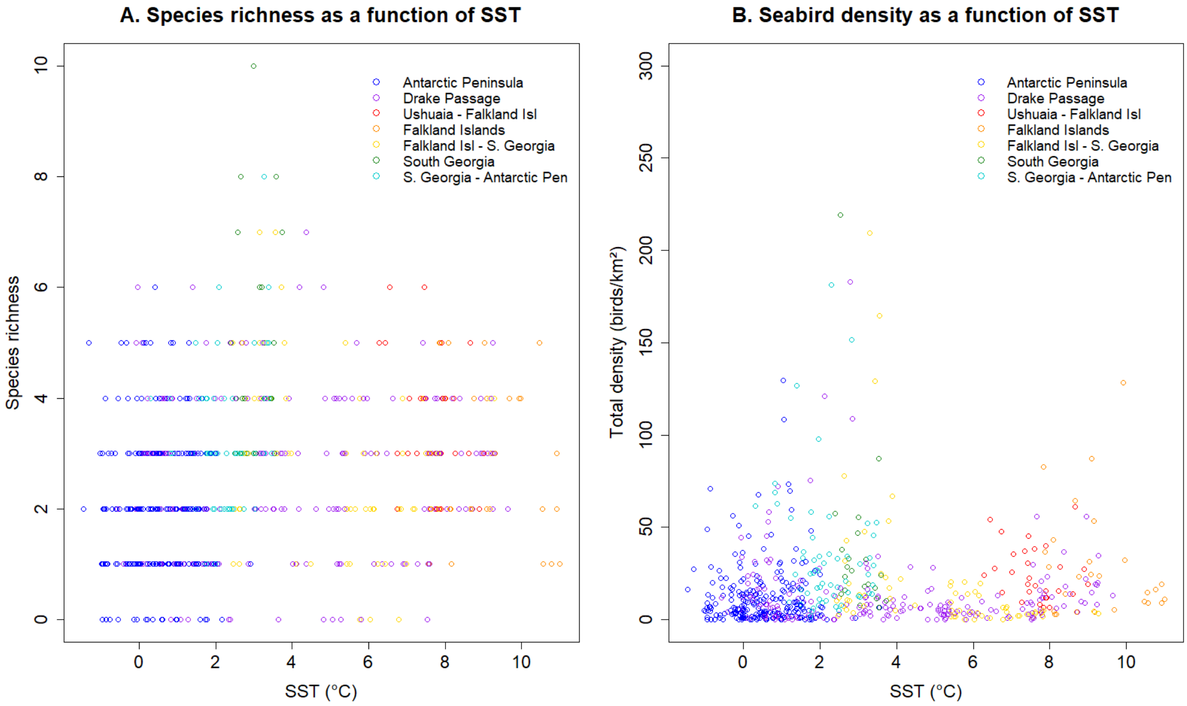

***Figure S17.*** *Species richness (A) and total seabird density as birds/km² (B) plotted against sea surface temperature (SST). In B, two observations with more than 1000 birds/km² in South Georgia have been removed. Both species richness and densities are affected by higher flux in lower speeds (not corrected for in the plots).*

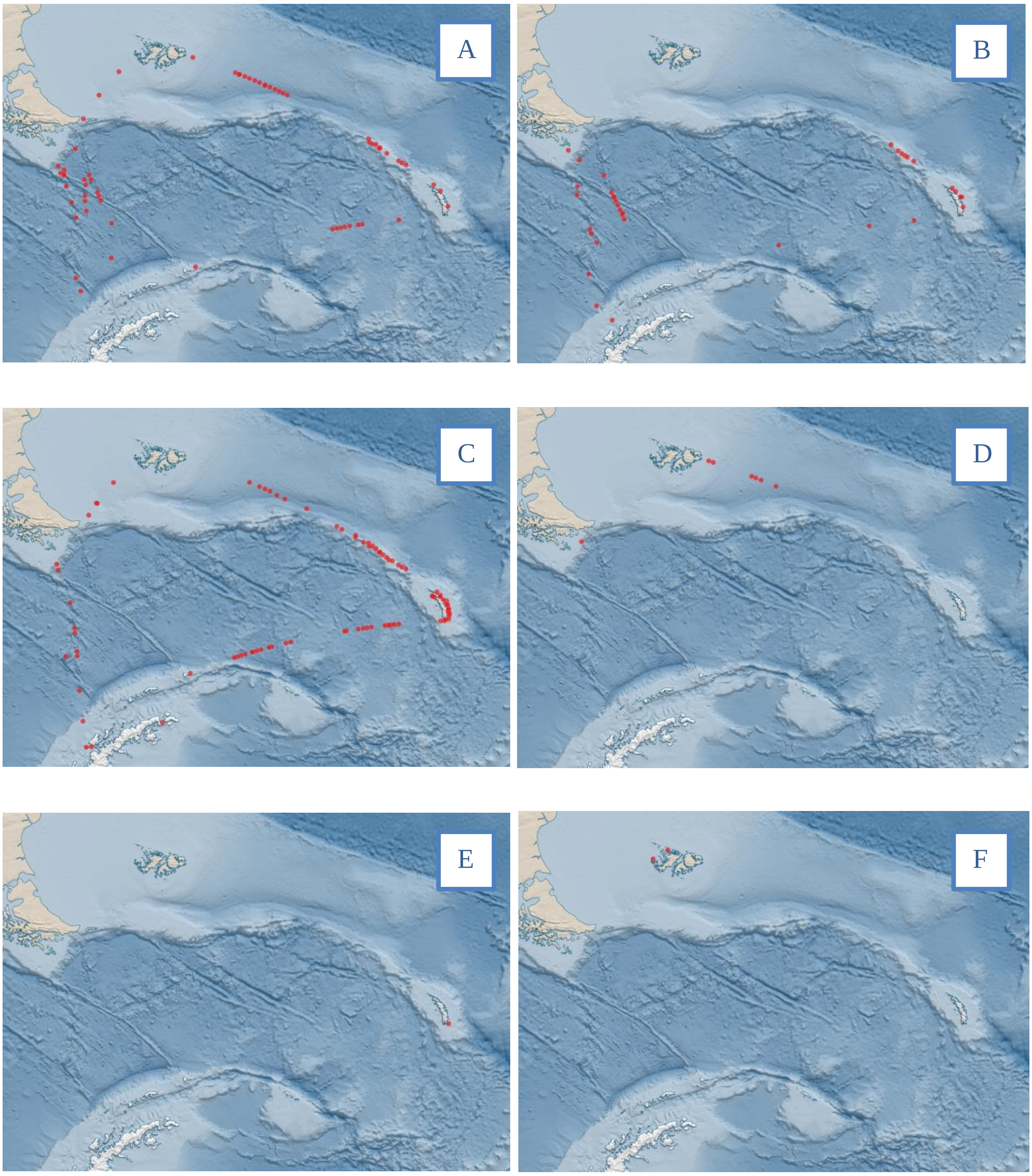

***Figure S18.*** *Observations of threatened species (IUCN 2021) with red dots indicating presence. (A) Wandering (Diomedea exulans) and Royal (Diomedea epomophora) albatrosses, (B) Gray-headed albatross (Thalassarche chrysostoma), (C) White-chinned petrel (Procellaria aequinoctialis), (D) Atlantic petrel (Pterodroma incerta), (E) Macaroni penguin (Eudyptes chrysolophus), and (F) Rockhopper penguin (Eudyptes chrysocome).*