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Within-Season Trends in Abundance and Distribution of Humpback Whales (Megaptera novaeangliae) in the Antarctic Peninsula Region

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Fine-Scale Spatial and Temporal Distribution of Humpback Whales (*Megaptera novaeangliae*) in the Antarctic Peninsula within an Austral Summer

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Front page: Diving humpback whale. Photo by Elling Johannessen

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Abstract

Fine-scale knowledge of cetacean abundance and distribution throughout the Antarctic Peninsula (AP) is lacking yet essential for effective ecosystem-based fisheries management (EBFM). We investigated an important area both for migratory humpback whales (*Megaptera novaeangliae*) and Antarctic krill (*Euphausia superba*) fisheries to assess potential spatio-temporal interactions, for use in adaptive EBFM and marine protected area (MPA) consideration. We collected data using tourist cruise ships as platforms of opportunity during the austral summer of 2019/2020, followed by analysis using spatial hurdle surface modeling and satellite derived oceanographic covariates. Our results indicate that small numbers of humpback whales are present in the Bransfield and Gerlache Straits at the start of the austral summer (November), becoming increasingly abundant in late December in the northern Gerlache Strait, but becoming more dispersed throughout the northern AP in late January. Using relative abundances, we estimate that whales consume approximately 0.5 – 3.3 million tons of Antarctic krill during their feeding season. Based on our results and catch data in the study area, we conclude that there is minimal spatio-temporal overlap between humpback whales and fishery activity our study period of November – January. However, there is potential for significant interaction between the two later in the feeding season, with fisheries potentially harvesting 5.9 – 11.6% of monthly humpback whale Antarctic krill consumption in highly overlapping regions in April. Research effort needs to extend later in the season to properly quantify the spatio-temporal overlap.

1 Introduction

While humans have a long history of harvesting resources from the world's oceans, only in recent decades have harvest levels increased to such a point that it has impacted several commercial stocks and even changed the structure and stability of entire ecosystems. To avoid a tragedy of the commons – a situation where several users of a system act in self-interest and collectively deplete a shared resource against the common good – several approaches to sustainable management have been developed under a common umbrella term of Ecosystem Based Fisheries Management. EBFM is not a new idea *per se,* as it has been discussed since the latter half of the 20th century (see Caldwell, 1970; McIntosh, 1986). It is, however, complex; understanding the ecosystem in its entirety and its hierarchical web of interactions – from primary production to upper-trophic predators, ocean currents and weather systems to ship traffic, fisheries and societal needs – is essential for allowing sustainable harvest while conserving living marine systems and their biodiversity (Pikitch et al., 2004). Further, implementing appropriate management that explicitly accounts for the temporal dynamics of the ecosystem can aid in counteracting overexploitation of ecosystem resources and services at a local level and promoting function and health. In the marine sector, stakeholders have generally supported the transition to EBFM. However, despite its widespread support, full implementation has been challenging (Link & Browman, 2014), and despite bottom-up and top-down effects impacting managed stocks, such theoretical strategies are unfortunately rarely implemented in management (Skern-Mauritzen et al., 2015).

Recently, in light of innumerous fish stocks being increasingly overexploited, commercial harvest has shifted focus to areas beyond national jurisdictions. In the Southern Ocean, increasingly effective harvesting equipment is being used to target Antarctic krill *Euphausia superba* (Nicol et al., 2012) for use in such things as food production, commercial supplements and aquaculture foodstuff, which in and of itself may be accompanied by broader environmental implications (Parker & Tyedmers, 2012). More importantly, the Southern Ocean has a short-chained, relatively simple food web structure compared to lower latitude ecosystems, and are therefore heavily reliant on a small number of key species, which in turn support an abundance of upper trophic predators. The Commission on the Conservation of Antarctic Marine Living Resources (CCAMLR) is the main organization responsible for managing these commercial interests in the Southern Ocean, and is moving towards increasing allowable catch. However,

before this can be done there must be an adaptive management plan in place to avoid negative localized impacts. The International Association of Antarctica Tour Operators (IAATO) is another interest organization in the region, responsible for sustainable use of popular areas by visiting tourist vessels. These two organizations share a common resource, as hotspots for fisheries and tourists often overlap. Therefore, IAATO vessels have the potential to provide nautical infrastructure in these remote areas to aid in data collection. An effective strategy to conserve an ecosystem from anthropogenic and climate pressures is establishing marine protected areas (MPA) in high interest regions (McLeod et al., 2009). This, combined with considerations of possible climate change impacts, may reduce the loss of already declining populations (Dahood et al., 2020), an advantageous means towards implementing EBFM.

The western Antarctic Peninsula (WAP) is currently where the largest volume fishery in the Southern Ocean is focused, and a key region for tourist operators to visit. Historically, this productive and diverse ecosystem has attracted high anthropogenic pressure. For over two centuries, sailors and hunters harvested furs, blubber and oils from pinnipeds and later also large cetaceans (Trathan & Reid, 2009), with some species driven to near extinction (Clapham & Baker, 2001). Surma et al. (2014) estimated that this reduction of krill-predators in the ecosystem may have resulted in the trophic release of approximately 17-25% increase of the standing krill biomass. Referred to as the Krill Surplus Hypothesis (Laws, 1977),this trophic release allowed population increases of smaller krill-predators with shorter generation times, such as penguins (such as the Gentoo (*Pygoscelis papua*), Adélie (*P. adeliae*) and chinstrap (*P. antarcticus*)) and pinnipeds (Crabeater seal (*Lobodon carcinophagus*) and Antarctic fur seal (*Arctocephalus gazella*); Surma et al., 2014). Following the moratorium set by the International Whaling Committee in 1986, whaling in the region has come to a complete halt, and now, nearly 40 years later, many cetacean populations are showing signs of recovering from their near-extinct levels (Clapham, 1999; Tulloch et al., 2018; Zerbini et al., 2019). According to Reilly et al. (2004), krill consumption by cetaceans in the CCAMLR area 48 was estimated at 1.6-2.7 million tons during the austral summer season of 1999/2000. Recovering populations of these major krill consumers may consequently significantly increase the top-down pressures on krill, potentially provoking major perturbations in the lower levels of the foodweb.

Concurrent to recovering cetacean populations, the WAP ecosystem is changing. Climate change is rapidly warming the WAP, which experiences five times the global annual mean changes in temperature since 1950 (Ducklow et al., 2013), which in turn increases ice-free habiats (Lee et al., 2017) and possibly affects krill spatial dynamics and recruitment (Atkinson,

2004; Atkinson et al., 2019). Furthermore, Adélie and Chinstrap penguin populations have been declining in the last decade (Herman et al., 2020) though these declines are not uniform throughout the region. The relative importance of the Krill Surplus Hypothesis and climate change in these declines are unclear (Trivelpiece et al., 2011; Lynch et al., 2012). In addition to the bottom-up drivers deriving from regional climate change, anthropogenic interest in commercial harvest of the WAP key species is further increasing top-down pressure. The Antarctic krill fishery is the largest by volume in the Southern Ocean (Nicol et al., 2012) and current estimates approximate the biomass to ~400 million tons in the southern ocean and ~60 million tons in CCAMLR area 48 (CCAMLR, 2019), where the vast majority of the catches take place (CCAMLR Statistical bulletin vol 31). CCAMLR uses a precautionary upper catch limit set at 9.3% of estimated biomass and serves as the maximum catch limit that despite harvest still can support krill stock maintenance and predators (Hill et al., 2016). However, regional quotas are dictated by the "trigger level", the lower operational quota created to control spatial allocation of harvest to avoid inadvertent predator effects (Constable, 2011), which is set at 620 000 tons (~1% of regional biomass). This is currently distributed by allocating regional quotas as percentages of the trigger level to the 4 sub-areas of area 48, with fishery in sub-area 48.1 (the WAP) receiving 25% of the trigger level as its regional catch limit (Hill et al., 2016) and recent hauls match the regional quota, exceeding 150 000 tons in the 2018 season (CCAMLR Statistical bulletin vol 31). In the past, Antarctic krill has mainly been harvested in the December-February period but in the 1990s, fleets redirected their focus to March-May and even so late as to the June-August period while the main fishing sectors in this era were generally around the east and west Drake Passage sectors, as well as Elephant Island (Kawaguchi & Nicol, 2006). However, in the early 2000s, increasing catches were surprisingly being made in the Bransfield Strait (Kawaguchi & Nicol, 2006), foreshadowing the next decade. By the 2008/2009 season, 65-90% of the WAP seasonal catch derived from the Bransfield Strait in increasingly smaller spatial areas (Santa Cruz et al., 2018). As fishing hotspots are currently expanding farther south, it is also entering critical zones for upper-trophic predators, increasing concern regarding potential negative effects of regional extraction of Antarctic krill in upper-trophic foraging areas.

CCAMLR is currently looking to increase EBFM effectiveness using dynamic catch limits and spatial allocations in response to monitored ecosystem indicator status (SC-CCAMLR, 2011). Furthermore, stakeholders, scientists and conservation non-governmental organizations (NGOs) mostly share the concern regarding the overall health of the ecosystem and fishery

management but have diverging views on how to achieve EBFM (Cavanagh et al., 2016). In order to properly implement EBFM, management must integrate the needs of the ecosystem, moving away from single-stock management, and including the requirements of natural krill predators such as seals, penguins, cetaceans. Penguins, and to a lesser extent, Antarctic fur seals (*Arctocephalus gazella*), are already monitored by CCAMLR, but cetaceans are not, representing an enormous knowledge gap in the EBFM approach.

The humpback whale (*Megaptera novaeangliae*) is one of the major krill consumers reliant on krill in the Southern Ocean. The majority of this species migrates annually from low-latitude breeding grounds to high-latitude feeding grounds, wherein they have been estimated to consume 83% (Lockyer, 1981) of their annual caloric intake during their summer foraging period. Abundance estimates of humpback whales in the Antarctic peninsula have been at approximately 7000 individuals in January and Februrary (Hedley et al., 2001), while Herr et al. (2016) reported ~3000 individuals in the Bransfield Strait alone. A more recent study (Pallin et al., 2018) indicates that humpback whale populations in the WAP are increasing due to relatively greater numbers of pregnant females, likely recovering from the aforementioned harvest. Furthermore, the western South Atlantic humpback whale population has recovered to approximately 93% of pre-exploitation levels (Zerbini et al., 2019). Humpback whales have been estimated to consume approximately 417 000 – 806 000 tons of krill biomass in the Antarctic peninsula (Reilly et al., 2004), the highest contributing species to the overall krill consumption by mysticetes in the region. Traditional surveys gathering cetacean count data have a broad geographic coverage, yet usually only provide a single temporal snapshot of abundances and densities, and in turn assuming temporally homogeneous distributions. Since regional consumption estimates are a function of abundance, scaling individual consumption to population levels consequently exclude fine-scale temporal variability. Regarding highly migratory animals whose regional populations fluctuate throughout the year, expressing temporally varied predatory pressure on prey organisms, dynamic spatio-temporal data are lacking and an important limitation to address for conservation and EBFM.

Cetacean abundance has traditionally been estimated using distance sampling. This method uses count data from random or systematic transects and calculates abundance by scaling the area covered to the appropriate regional area, assuming spatially homogeneous distribution. Marine line-transect surveys optimally use vessels fitted with multiple sighting platforms at different heights, following pre-determined systematic transects arranged across the study region, ensuring unbiased sampling coverage (Buckland et al., 2005). However, this requires a

dedicated research vessel and personnel, a sizeable economic prerequisite that makes such surveys costly and thus they are unlikely to be repeated often. Alternatively, the use of tourist vessels as surveying platforms are a fraction of the cost of research vessels, but also provide the considerable advantage of following highly repeatable transects multiple times throughout the season, gathering valuable temporal data. These transects, however, are neither completely systematic, nor completely random. Thus, tourist vessel transects lack the same spatial coverage obtained by dedicated research vessels. However, the increased temporal coverage obtained could provide complimentary data to traditional surveys.

Humpback whale distribution is significantly dictated by the distribution of their food (Friedlaender et al., 2006, 2009), thus assumptions of homogeneous distributions are described above as likely to be inappropriate. Recent analytical advancements (Miller et al., 2013) provide methods to overcome the assumption of homogeneous animal distribution by using Density Surface Modelling (DSM). DSM explores potential relationships between animal presence and various environmental covariates to provide potentially more ecologically reliable estimates of abundance throughout a wider area around the survey transects. Oceanographic covariates have been used as a proxy for humpback whale prey distribution in the past (Friedlander et al., 2006, 2011; Herr et al., 2016) an effective approach concerning mesozooplankton whose limited swimming ability results in that their distributions being largely driven directly by ocean currents and indirectly by the distribution of food patches, which in turn are distributed as a consequence of oceanography. Moreover, continually improving satellite technology and models provide increasingly reliable and available sea surface environmental data.

Here, we conduct a pilot study to assess whether platforms of opportunity can be used to collect data on the temporal distribution and abundance of cetaceans, which could aid in implementing effective EBFM and possible MPA design and monitoring. We aim to examine the degree to which data from platforms of opportunity can be used to develop predictive maps of humpback whale distribution, both between and more importantly within seasons, and identify potential fishery/humpback whale interactions. Our specific goals were to estimate fine-scale (within season) variation in (1) humpback whale density and distribution using spatial hurdle models, (2) abundance estimates derived from both DSMs and, comparatively, traditional distance sampling, and (3) calculate temporally discrete krill consumption estimates.

2 Materials and Methods

2.1 Field/Data Collection

In the period November 24th, 2019 to January 20th, 2020, two teams, each comprising one to two experienced Marine Mammal and Seabird Observer (MMSO) and one master's student, were placed on two IAATO tourist cruise vessels (MS Midnatsol and Fram, owned and operated by Hurtigruten A/S in Norway)), sailing in the Scotia Sea (Appendix Figure 1) and northern WAP (Figure 1).

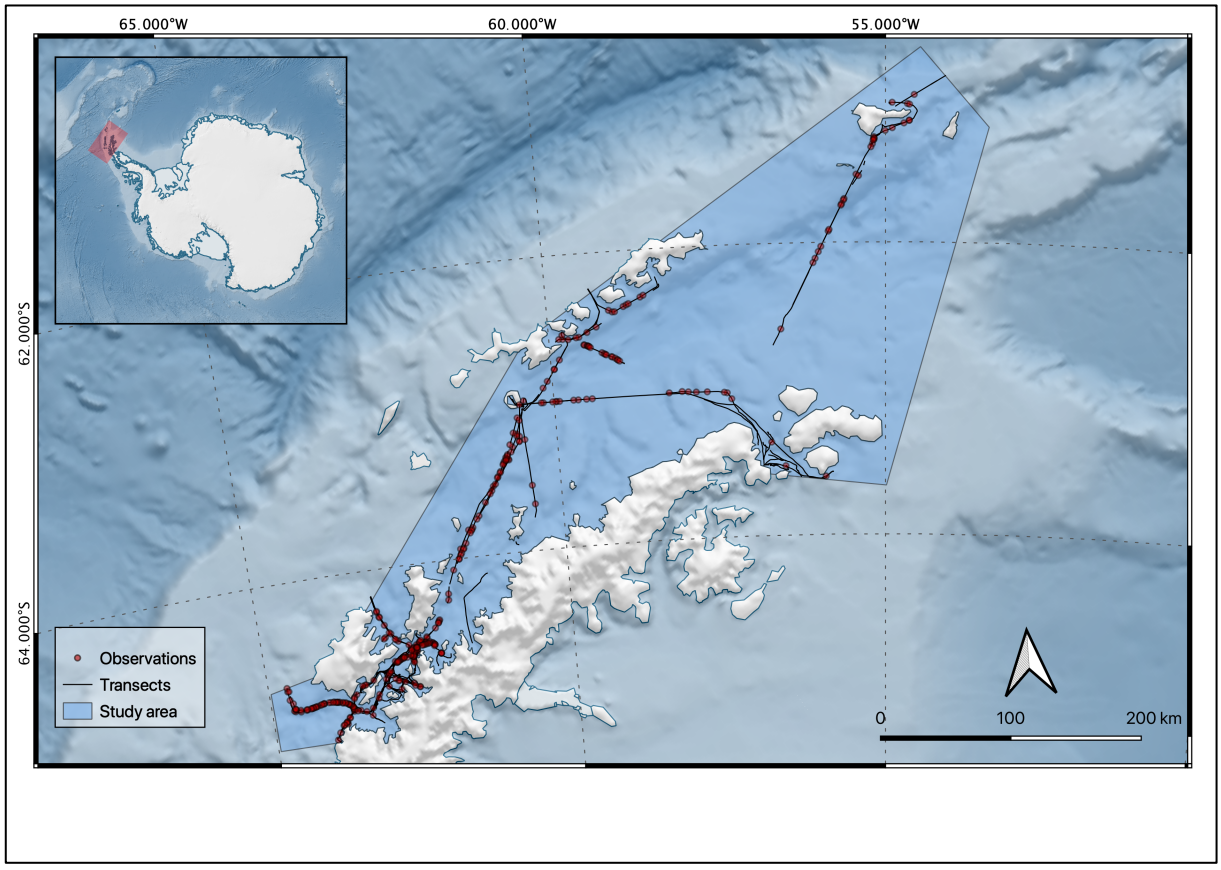


Figure 1 *- Map outlining the study area for analysis as well as transects and humpback whale observations from all cruises. Map produced using Quantarctica (Matsuoka et al., 2018).*

In total, the teams covered 7 818 nautical miles (nm) during 35 days of observational effort in the study area (Table 1). The study area polygon was defined after data collection and was

limited to the tourist vessel area of interest, as well as region with the highest recorded sightings of humpback whales. The two first trips were combined in order to ensure a sufficient sample size according to distance sampling protocols (Buckland et al., 2015). The third and fourth cruises were also combined (C2) because of a temporal overlap in the study area.

2.1.1 Effort

On-effort periods lasted from approximately 05:00 to 22:00 and consisted of two or more observers, one as the dedicated recorder and the other(s) as observer(s). Two or more team members were typically stationed on effort, each dedicated as observer or recorder, but some instances required only one member on effort serving as both observer and recorder, which could be the case in areas with low density of animals. During food breaks and necessary rests (to avoid observer fatigue and retain focus and attentiveness), effort was maintained by one observer. As much as possible, these periods were timed to coincide with periods of low-density animal sightings to minimize the potential of missed sightings. Effort was halted in difficult sighting conditions (Beaufort Sea State ≥ 8, or visibility $\lesssim 300$ m) until conditions improved.

A dedicated Dell Precision 5520 laptop computer was used for logging effort and sightings in the program Logger 2010 (Gillespie et al., 2010), and observations were stored in a Microsoft Access (Microsoft 365 MSO, version 16.0.13328.20334) database. A Globalsat USB GPS receiver was connected to the computer at all times, recording coordinates every 10 seconds, registering location, speed, heading, and time & date. Effort was manually recorded approximately every 30 minutes and during weather changes or observer rotations, including environmental conditions such as weather, general sightability, Beaufort Sea state (1-8), wind speed (m/s), glare (affecting which observational sector), sea-ice cover (%), wave height (m), *et cetera*.

2.1.2 Observations

Dedicated observations were carried out form the navigation bridge of each vessel, covering either the port or starboard by scanning for cues using the naked eye, followed by binocular confirmation. Cetaceans were mostly spotted by their blows, but sometimes also through other cues such as breaching or diving. Immediately following the sighted cue, the recorder would

measure radial distance either using a distance stick (Todd et al., 2015) or binoculars (Opticron Marine PS II 7x50 / C with integrated distance reticles). Sighting distance was similar for the two ships; bridge height was 13.5 m for MS Midnatsol and 13.2 m for MS Fram, yielding distances to the horizon of 8.25 and 8.17 nm for the two vessels, respectively, using an average eye height of 1.7 m. The radial angle was measured using an angle board. Radial distance, angle (degrees) and eye height were later used to calculate animal distance from the transect. Subsequently, additional variables were recorded, such as species, group size, swim direction, and behavior, among others. Photographs of animals were attempted if conditions allowed, but they were not prioritized. Species identifications were based on the dorsal fin, blow shape and frequency, and species-specific behavior based on relevant literature (Shirihai, 2006, 2008). In the case of species uncertainty, observations were placed in general categories, such as 'large baleen whale' or 'like Antarctic minke'.

2.2 Data preparation and analysis

We estimated relative density and abundance derived using two methods: (1) traditional, design-based distance sampling, and (2) model-based density surface hurdle modeling (DSHM). Distance sampling calculates its estimates by using average probability of detection over a given area (transect line length multiplied by perpendicular sighting distance), while DSHM explores the animal relationship to environmental covariates. We include both to compare the differences in design-based homogeneous and model-based heterogeneous distributions. Both methods use the same estimated probability of animal detection in their calculations (section 2.2.1), and the same on-effort segments in analysis.

Data were processed and handled using R Studio (R Core Team, 2020), and distance sampling abundance and density estimates were found using the 'Distance' package (Miller et al., 2019), while predicted abundance and distribution was modeled using the 'dshm' package (Franchini, 2018).

Prior to running any analyses, ship transects were divided into segments of "on-effort" periods and given a unique identification, and distances were recalculated from angular distances relative to the ship to perpendicular distances to the transect. When measuring distance using reticle binoculars (i.e., the angle from horizon or shoreline to sighting object in radians), protocols and formulae developed by Lerczak and Hobbs (1998) were used. Briefly, these

formulae use the angular drop from the reference point directly behind the animal (horizon or coastline), distance to said reference point, eye height of the observer, and distance to the center of the earth (assuming a perfectly spherical planet), to approximate surface distance to the observed object.

2.2.1 Detection function

The detection function, which describes the probability of detecting a whale as a function of perpendicular distance to the transect line, was fitted to the data using the combined observations from all cruises (C1, C2, and C3) in the study area for best representation of the overall detection probability within the study region. To find the best fitting detection function, multiple candidate models were tested. Key functions include half-normal (HN), hazard-rate (HR), and uniform (U):

$$k(y)\begin{cases}\exp\left(-\frac{y^2}{2\sigma^2}\right) & HN \\ 1-\exp\left(\left(-\frac{y}{\sigma}\right)^{-b}\right) & HR \\ 1/w & U\end{cases} \quad (1)$$

where y is the distance, σ and b are scale and shape parameters, respectively, and w is truncation distance (Buckland et al., 2015). Additionally, candidate models included cosine and Hermite polynomial series expansion to find the best fit. Lastly, these models included various covariates that relate to group size, observer bias, and environmental conditions, and truncated at an appropriate distance to improve model fit and remove observational outliers. Model selection was based on Akaike Information Criterion (AIC), a standard metric used to compare the fit of different models to the data using the number of independent parameters used and maximum likelihood, seeking the best balance between model fit and model complexity (Sakamoto et al., 1986), Goodness of fit and Cramér-von Mises test, a test statistic used when the population mean and standard deviation are unknown (Darling, 1957).

2.2.2 Abundance and density estimates

Using the fitted detection function and various data from data collection we can calculate density ($\hat{D}$; abbreviations with "^" mean relative estimates) using distance sampling. This is calculated:

$$\hat{D} = \frac{n}{2wL\hat{P}_a} \tag{2}$$

where n is the number of objects detected, w is the truncation distance, L is the total length of on-effort transect, and $\hat{P}_a$ is the proportion of animals available for detection (within w; Buckland et al., 2015). Relative abundance ($\hat{N}$) deriving from distance sampling was calculated as:

$$\hat{N} = \hat{D} \cdot A \tag{3}$$

using the same approach as density but including the total area (A) of the study area (Buckland et al., 2015). Relative abundance ($\widehat{N}$) deriving from the fitted DSHMs was found using the sum of densities ($\hat{D}$) in the modeled prediction grid.

2.2.3 Density surface hurdle modeling

We use density surface hurdle models (DSHM, Franchini et al., 2020) to predict the spatial distribution, densities and abundances of humpback whales in relation to environmental covariates throughout the study period. Hurdle models are an appropriate means for handling zero-inflated or overdispersed data common in count data (Martin et al., 2005) and in our case the product of two generalized additive models (GAMs); (1) a binomial presence-absence model (PA) and (2) a zero-inflated Poission abundance model (AB):

$$p(y|\theta,\lambda) = \begin{cases} \theta & \text{if } y_n = 0, \text{and} \\ (1-\theta)\dfrac{\text{Poisson}\,(y|\lambda)}{1-\text{PoissonCDF}\,(0|\lambda)} & \text{if } y_n > 0 \end{cases} \tag{4}$$

where PoissonCDF is the cumulative distribution function of the Poisson distribution (Stan Development Team, 2020). Both these GAMs explore the respective PA and AB response in

relation to environmental covariates (Franchini et al., 2020). This modelling approach resulted in predicted densities and distributions across an *a priori* defined prediction grid of 1 nm resolution within the defined study area (Figure 4) with the same oceanographic covariates.

2.2.4 Hurdle model calibration and selection

Both model components (PA and AB) were fitted with a shrinkage version of cubic regression splines to reduce overfitting (Franchini et al., 2020). Knots for each model were selected by trial, avoiding p-values = 0 and number of knots too close to expected degrees of freedom (EDF) and subsequently checked using the 'mgcv' package (Wood et al., 2016). To check for collinearity and concurvity (the "linear" relationship between non-linear variables, where 1 = full concurvity and 0 = no concurvity) of covariates, we ran a model that included all candidate covariates (Appendix Table 1 & 2). Two tests were used to check the GAM sub-model smoothness: (1) Un-Biased Risk Estimator (UBRE) was used to check the smoothness selection score of the binomial PA sub-model, and (2) Generalized (Approximate) Cross-Validation (GCV) was used to check the AB sub-model, in both cases lower values indicate good fit. Goodness of fit was visually assessed by Q-Q and other plots for each sub-model (Appendix Figure 1 & 2 for PA and AB, respectively), and statistically checked using the Kolmogorov-Smirnov test statistic. After GAM inspection and calibration, models were selected based on relative AIC values (ΔAIC).

2.2.5 Oceanographic covariates and prediction grid

Several environmental covariates were used to explore their relationship to humpback whales (REFS). Bathymetry data were downloaded using the 'marmap' package (Pante & Simon-Bouhet, 2013), querying the National Oceanic and Atmospheric Administration (NOAA) ETOPO1 1 arc-minute global relief model (Amante & Eakins, 2009) for the coordinates used in our analysis. The bathymetric slope was calculated using the 'terrain' function in the 'raster' package (Hijmans, 2020). Analyzed SST and sea-ice fraction data were downloaded from the Physical Oceanography Distributed Active Archive Center (UK Met Office, 2012), and is a daily sea surface temperature analysis and sea ice analysis produced using optimal interpolation on a 0.054-degree grid. The temperature gradient was found using the same 'terrain' function as bathymetry slope (Hijmans, 2020). Distance to the coast was calculated using the 'geosphere'

package (Hijmans, 2019), based on our data coordinates and coastal polygons from the Norwegian Polar Institute's Quantarctica package (Matsuoka et al., 2018), for QGIS (v 3.12.1; QGIS.org, 2020). Finite Scale Lyapunoc Exponents (FSLE; https://www.aviso.altimetry.fr/) are submesoscale oceanographic features derived from altimetry data. Values in our spatial and temporal frame varied from 0 to ~ -0.28, where lower values represent the retention of passive particles such as phytoplankton at the sea surface for days or even weeks, rather than hours, durations that may be useful to predators (Lowther et al., 2014).

All covariates were extracted for the coordinate and date associated to each observation in the observation data (i.e., data fitted to the DSHMs) while the three prediction grids' (C1, C2, C3) covariate values were rescaled to fit the grid resolution and consist of mean covariate values for each day of the respective temporal window.

2.3 Prey consumption

Daily per capita consumption estimates were derived using the relationship of ingestion to individual mass (Read & Brownstein, 2003), using a general equation developed by Kleiber (1961):

$$Y = \alpha M^{\beta} \quad (5)$$

where Y is the daily consumption, M is the average body mass of humpback whales, and α and β are species-specific parameters. Using the equation for basal metabolic rate (BMR), assuming mean krill caloric value of Antarctic krill is 1100 kcal kg^{-1} (Clarke, 1980) and a mean individual humpback whale body mass of 26 924 kg, we calculate a daily individual consumption range of 390.34 – 874.33 kg (Reilly et al., 2004). For seasonal consumption estimates, we assume a feeding season of 120 days (Lockyer, 1981).

3 Results

Cruise 1 (C1) had a total on-effort transect of 575.7 nm, 63 humpback observations consisting of 112 individuals, and an encounter rate of 0.19 individuals nm^{-1} (Table 1). Cruise 2 (C2) had a collective on-effort transect length of 1 179.5 nm, with 197 sightings containing 335 individuals, and an encounter rate of 0.28 individuals nm^{-1}. Cruise 3 (C3) had an on-effort transect covering 527 nm, with 67 observations containing 112 individuals, with an encounter rate of 0.21 individuals nm^{-1}.

Table 1 *- List of the five cruises (trip) with observer effort; M1-3 represent the three cruises on MS Midnatsol, and F1-2 represent the two cruises aboard MS Fram; Cruise is the identification of some combined cruises for analysis; along with their respective transect length in nautical miles (nm); SA (%) is the area coverage as a percentage of the survey area; Obs(ind; n) is the number of observations and number of individuals in parenthesis; encounter rate is measured in observations per nautical mile.*

Cruise	***Trip***	***Dates in the SA***	***Effort (nm)***	***SA (%)***	***Obs (ind; n)***	***Encounter rate (obs (ind; nm^{-1})***
C1	***M1***	*25–30.11.19*	*231.8*	*0.8*	*14 (18)*	*0.07*
	M2	*5–12.12.19*	*343.9*	*1.2*	*49 (94)*	*0.27*
C2	***M3***	*16–26.12.19*	*692.8*	*2.4*	*125 (203)*	*0.29*
	F1	*22–27.12.19*	*486.8*	*1.7*	*72 (132)*	*0.27*
C3	***F2***	*12–18.01.20*	*527.4*	*1.9*	*67 (112)*	*0.21*

The best detection function that fit our data was a half-normal key function with cosine adjustment terms without covariates based on 236 observations (Figure 2). Truncation distance was set to exclude 15% of the farthest observations (1 685 m) to remove observational outliers (Buckland et al., 2015).

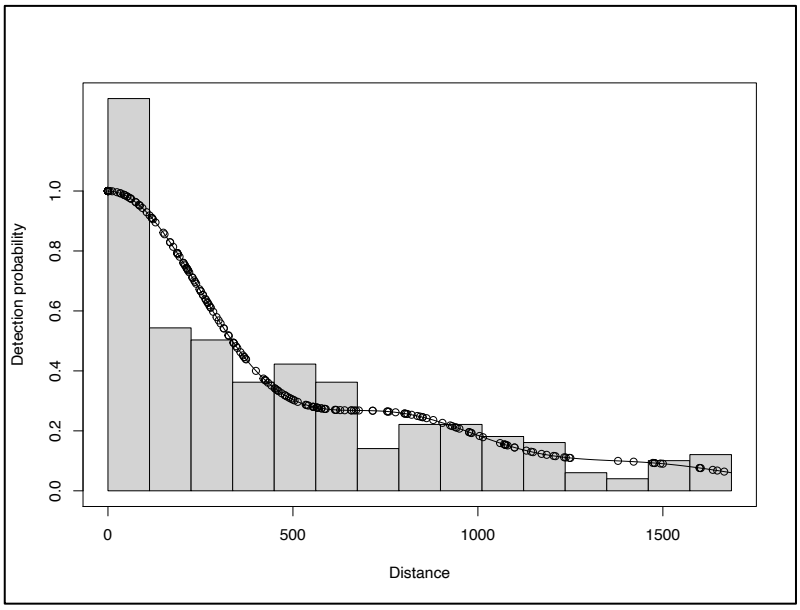


Figure 2 *- Detection function showing probability of animal detection as a function of distance (m).*

3.1 Abundance and density estimates

Densities and abundance deriving from the two methods (i.e., distance sampling (DS) and hurdle models (H); Table 3), yielded different estimates. However, they showed similar trends, as both estimates increased throughout the study period (November-January). DS had a slightly more linear increasing trend in comparison to the estimates derived from H, which had a relatively larger increase from C1 to C2. The coefficient of variation (CV) trends were inverse between the two methods, increasing and decreasing with time for DS and H, respectively. However, CVs were much higher in the H estimates.

Table 2 *–Density and abundance of humpback whales in the WAP during three periods using the distance sampling (DS) and hurdle (H) method. Estimate is total number of humpback whales in the study area; SE is standard error; CV is coefficient of variation; LCL and UCL are lower and upper 2.5 percentiles in the confidence interval; DF is degrees of freedom. As the relative abundance derived from DSHM predictions are the sum of predicted densities, 95% confidence intervals are not available.*

Estimate & method	*Cruise*	*Estimate*	*SE*	*CV*	*LCL*	*UCL*	*DF*
Relative density $\hat{D}$ (DS)	***C1***	*0.23*	*0.049*	*0.21*	*0.15*	*0.35*	*23.69*
	C2	*0.26*	*0.058*	*0.22*	*0.17*	*0.41*	*39.33*
	C3	*0.28*	*0.149*	*0.52*	*0.10*	*0.80*	*16.84*
Relative abundance $\hat{N}$ (DS)	***C1***	*5 970*	*1 252*	*0.21*	*3 890*	*9 163*	*23.69*
	C2	*6 916*	*1 505*	*0.22*	*4 477*	*10 684*	*39.33*
	C3	*7 473*	*3 855*	*0.52*	*2 679*	*20 842*	*16.84*
		Estimate	***CV***		***95% CI***		
Relative density $\hat{D}$ (H)	***C1***	*0.102*	*1.37*		*0.100 – 0.103*		
	C2	*0.534*	*0.92*		*0.527 – 0.540*		
	C3	*0.663*	*0.62*		*0.657 – 0.668*		
Relative abundance $\hat{N}$ (H)	***C1***	*2 266*	*1.37*		-		
	C2	*11 864*	*0.92*		-		
	C3	*14 729*	*0.62*		-		

3.2 Hurdle models

3.2.1 Model fit

Both final sub-models (i.e., binomial PA and zero-inflated Poisson AB) for all cruises included a combination of smooth terms of sea surface temperature (SST), temperature gradient (TG) and oceanographic coherent structures (FSLE) and corrected for cruise (C1, C2, C3) differences, giving us:

$$s(sst, bs = 'cs') + s(TG, bs = 'cs') + s(FSLE, bs = 'cs') + cruise \quad (6)$$

where SST, TG and FSLE are smooth terms using shrinkage version of cubic splines (bs = 'cs'). This model explained 30.5 and 33.7% of the overall deviance for PA and AB, respectively.

Based on the fitted components of the DSHM, all covariates had distinct effects on humpback whale probability of presence (Figure 3). Humpback whale's presence remained low, unaffected by temperature variations below 2°C, but increased with increasing temperatures above 2°C. Humpback whales showed an increasing affinity to FSLE values of -0.10 to -0.25 but showed no distinct trends in values closer to zero. Finally, our data showed a non-linear increase in the probability of presence towards higher temperature gradients. When humpbacks were present, their abundance was positively correlated to sea surface temperature, showing a rapid increase with increasing temperatures, with a peak at ~1.5°C. The species also showed a non-linear increasing affinity towards higher TG areas, while the response to changes in FSLE was weaker than for the other two covariates.

The UBRE test for the binomial PA model yielded a selection score of -0.42, while the GCV test for the zero-inflated Poisson AB model yielded a score of 8.81. Sub-model goodness of fit plots (Appendix figure 2 & 3 for PA and AB, respectively) showed a slightly better fit for the PA sub-model compared to the AB sub-model. Overall, the Kolmogorov-Smirnov (KS) test statistic yielded significant results (KS = 0.179, p-value < 0.05).

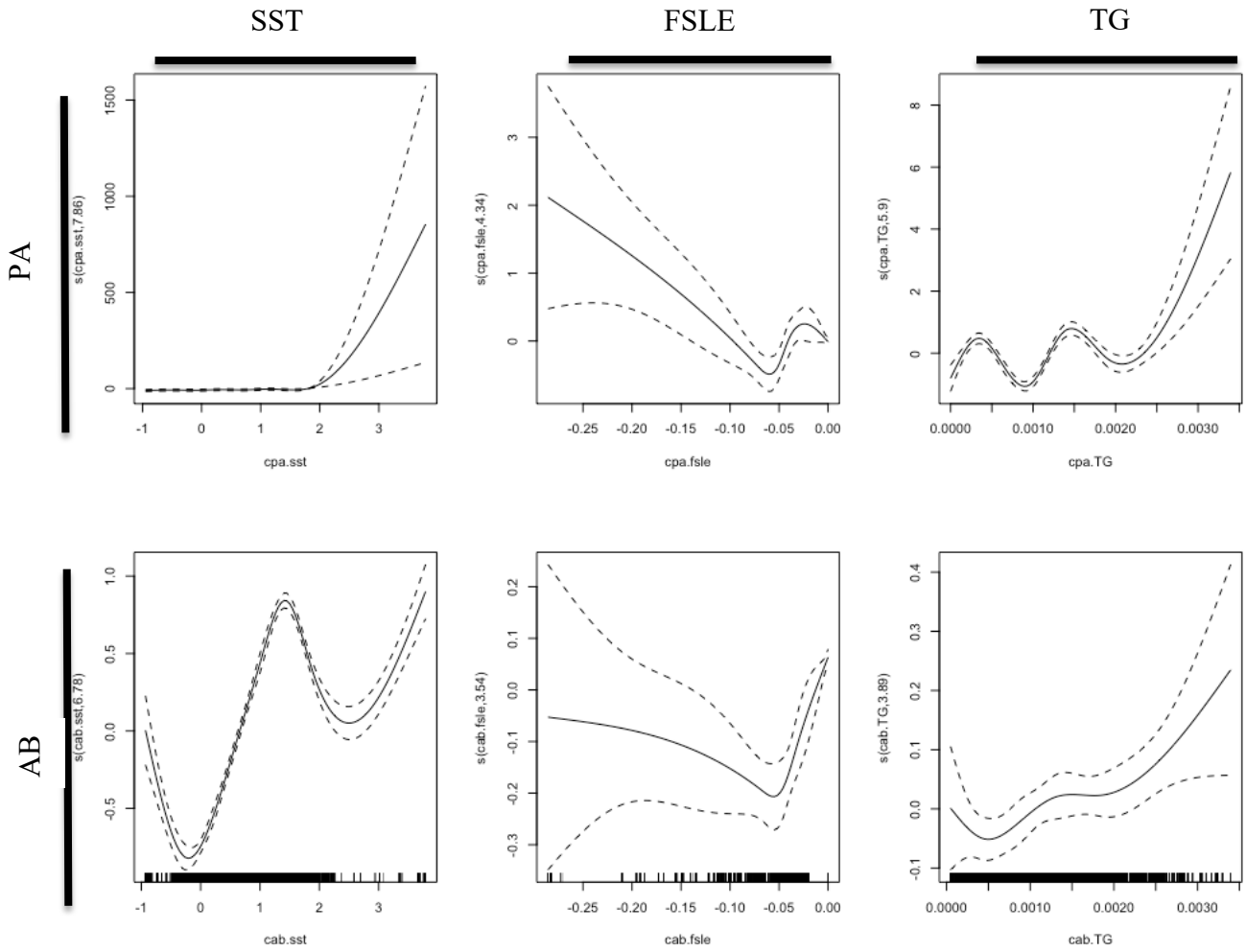
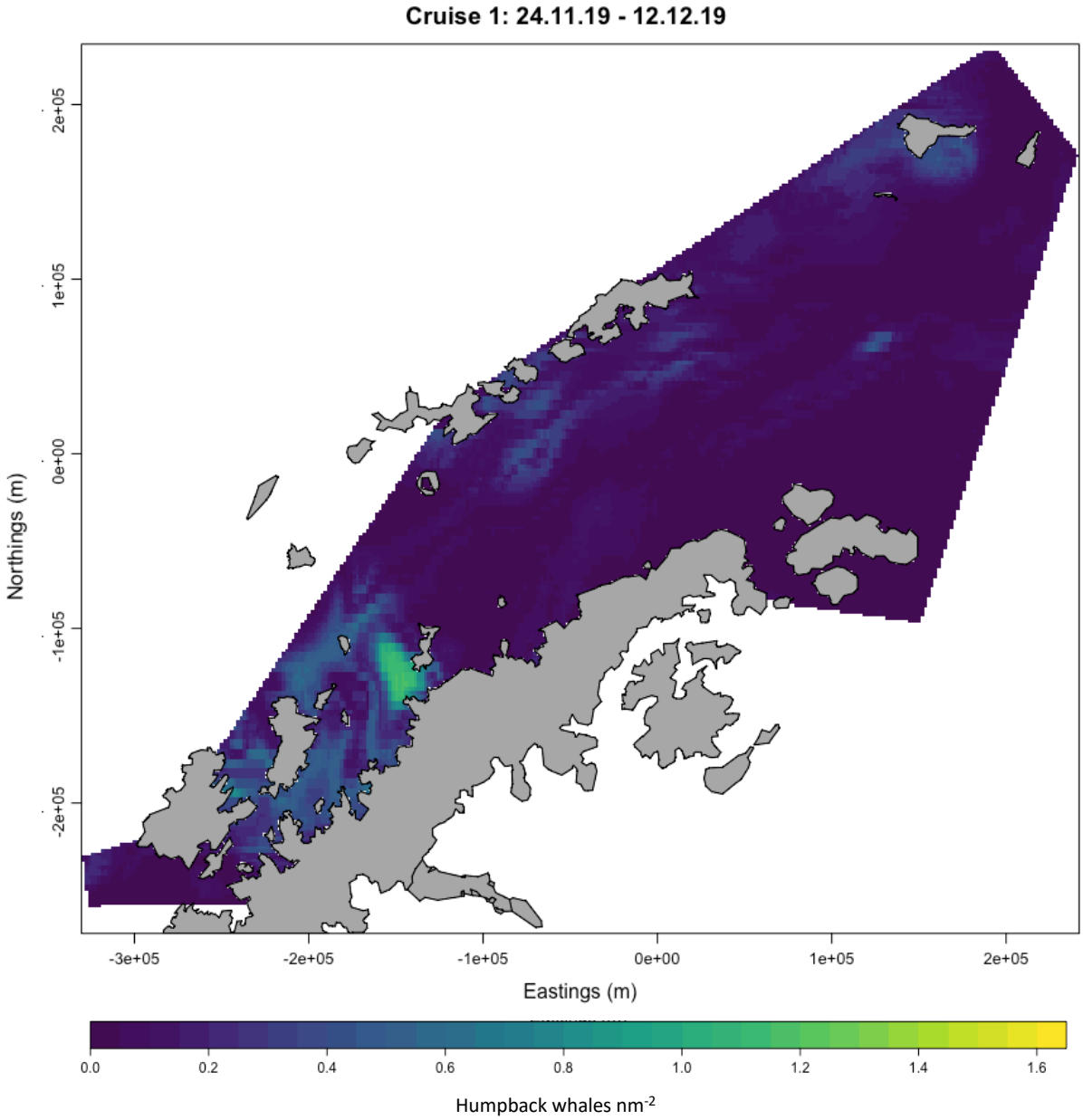


Figure 3 *- Fitted GAM model showing humpback whale presence-absence (PA) and abundance (AB) as responses to the three selected covariates: sea surface temperature (SST), finite sized lyapunov exponents (FSLE) and sst gradient (TG).*

3.2.2 Predicted distribution

Predicted humpback whale densities across the prediction grid for all three cruises, obtained from the hurdle model, are plotted in Figures 4-6. Density predictions of humpback whales from the DSHM ranged from 0.0002 to 1.161 animals nm^{-2} in C1, with highest values observed around the northern Gerlache Strait, with lower values southeast of the South Shetland Islands, and south of Elephant island (Figure 4). C2 densities ranged from 0.0001 to 1.679 animals nm^{-2}, with a broader distribution in the Gerlache Strait and central Bransfield Strait (Figure 5). C3 densities ranged from 0.0097 to 1.290 animals nm^{-2}, with a relatively more expansive, but less dense, distribution in the central and northern Bransfield Strait and the Gerlache Strait (Figure



6). See Appendix Figure 3 for plots showing the spatial covariate fields across the prediction grid for all 3 cruises.

Figure 4 *– Predicted humpback whale density and distribution in the period C1 from hurdle models fitted SST, TG and FSLE data (Appendix Figure 3). Grid cells have a resolution of 1852 (1 nm) and a total area of 88 838 km^2.*

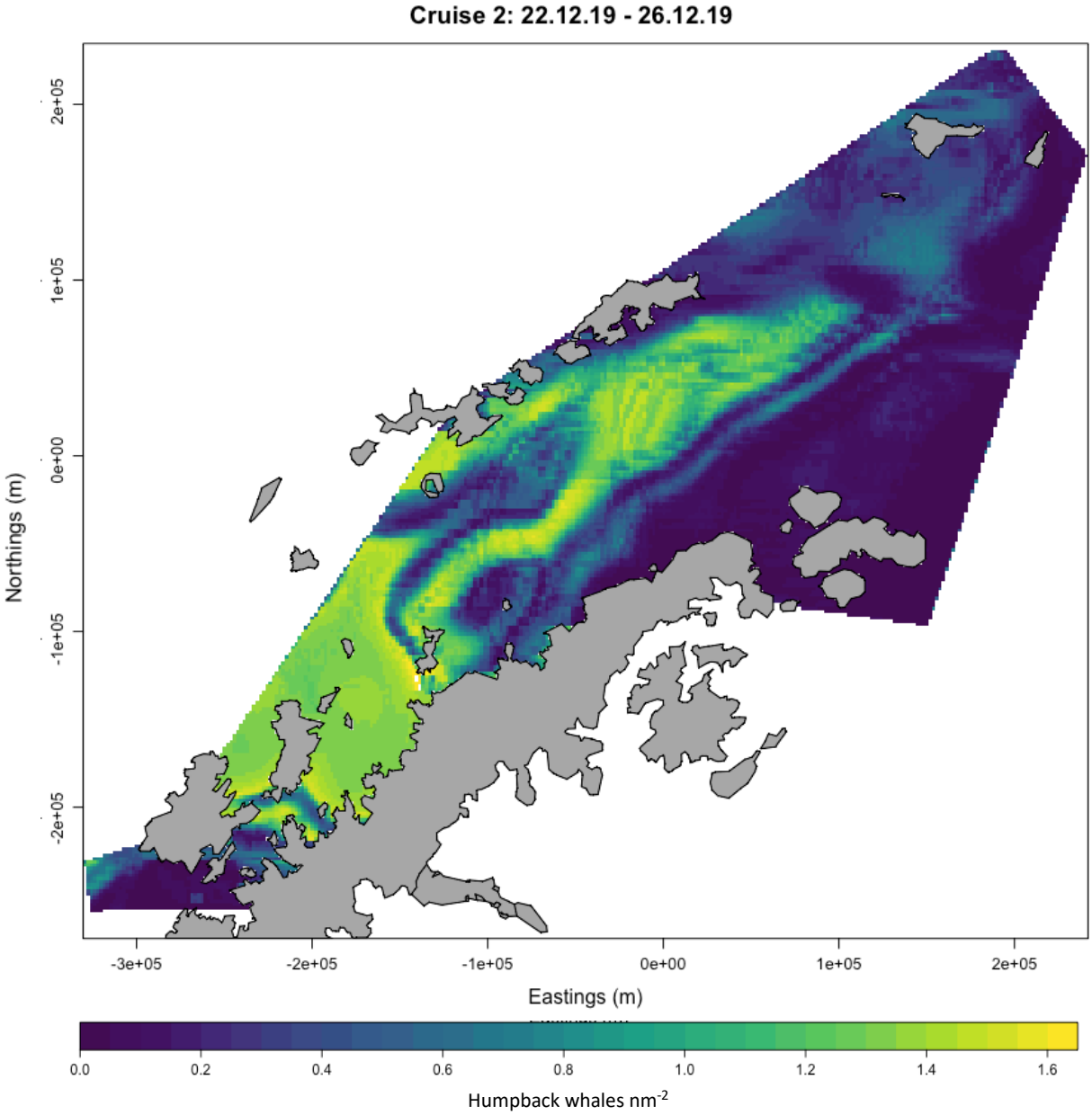


Figure 5 *- Predicted humpback whale density and distribution in the period C2 from hurdle models fitted SST, TG and FSLE data (Appendix Figure 3). Grid cells have a resolution of 1852 m (1 nm) and total area of 88 838 km2.*

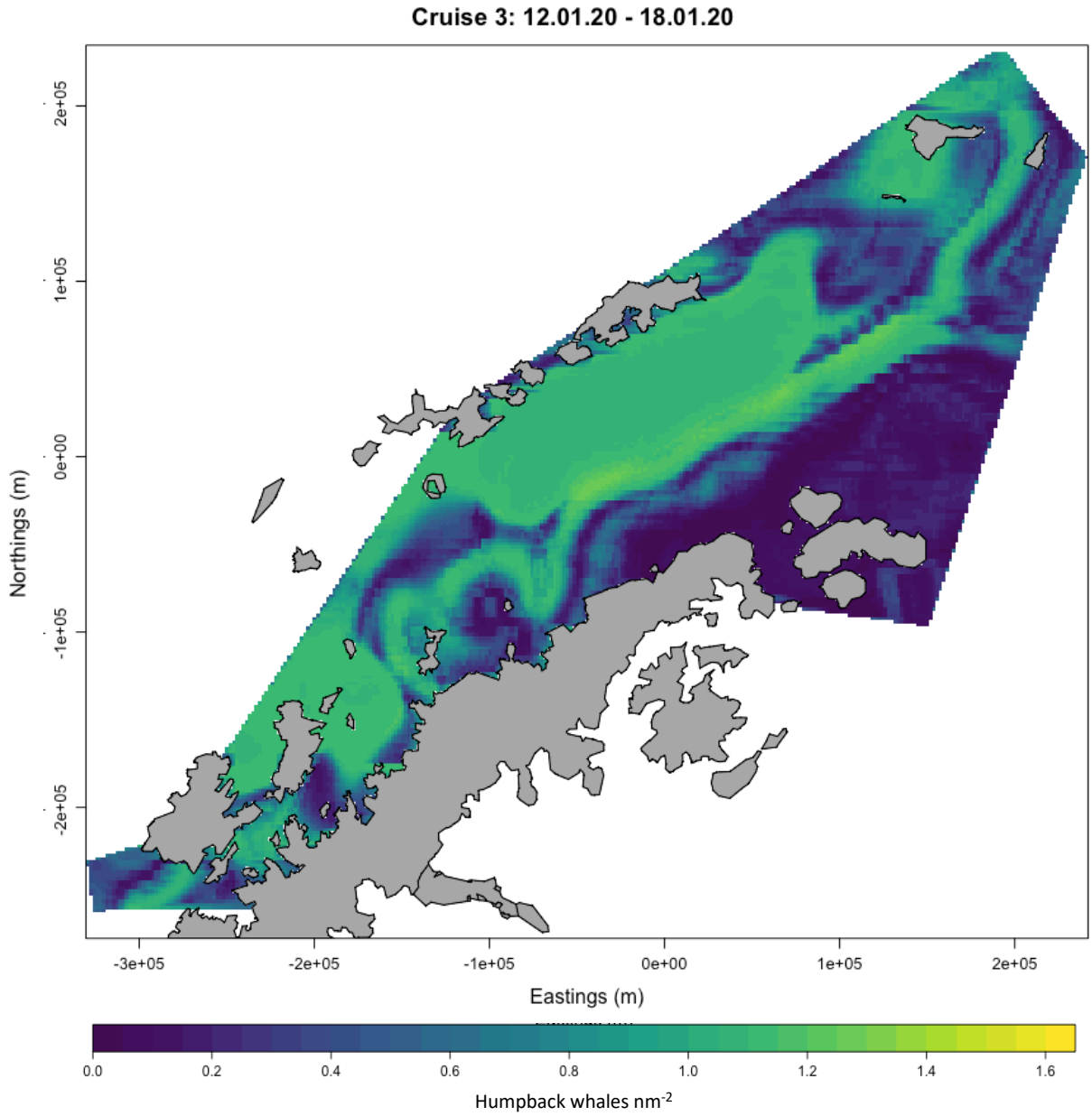


Figure 6 - *Predicted humpback whale density and distribution in the period C3 from hurdle models fitted SST, TG and FSLE data (Appendix Figure 3). Grid cells have a resolution of 1852 m (1 nm) and total area of 88 838 km^2.*

3.3 Consumption estimates

Daily consumption estimates were derived using three different functions, the first deriving from Innes et al., (1986) and yields 390.34 kg ind^{-1} day^{-1}, and second and third as 2 and 3% of mean body mass yielding daily individual consumption at 694.38 kg and 874.33 kg, respectively (Reilly et al., 2004). Daily consumption estimates ranged from 2 917 – 6 534 kg and 5 749 – 12 878 kg, using abundance estimates from distance sampling and hurdle model, respectively. Assuming that the maximum estimated abundance ($\widehat{N}$) for each method is representative for the total population in the study area, and that the feeding season lasts for 120 days, we estimate that humpback whales consume approximately 350 000 – 784 000 tons based on the distance sampling estimates and 690 000 – 1 545 000 tons based on the hurdle model estimates.

Table 3 *– Daily humpback whale consumption estimates based on abundance estimates derived from distance sampling (DS) and hurdle modeling (H), following daily consumption estimates by Innes et al., 1986, as 2% and 3% of average humpback whale body mass. Consumption estimates shown in metric tons (10^3 kg; t).*

Method	*Cruise*	*Abundance ($\widehat{N}$)*	*Innes et al. (t)*	*2% (t)*	*3% (t)*
DS	***C1***	*5 970*	*2 330*	*4 145*	*5 220*
	C2	*6 916*	*2 670*	*4 802*	*6 047*
	C3	*7 473*	*2 917*	*5 189*	*6 534*
H	***C1***	*2 266*	*885*	*1 573*	*1 981*
	C2	*11 864*	*4 631*	*8 238*	*10 373*
	C3	*14 729*	*5 749*	*10 297*	*12 878*

4 Discussion

Fine-scale understanding of upper-trophic predators is essential for successful ecosystem-based adaptive management. Historically, within-season spatial and temporal trends of humpback whales in the WAP have been somewhat unclear. We have found that the relative majority of humpback whales enter the study area in late December, still increasing through January. Early season distribution centers in the northern Gerlache Strait, and later on expands to include the Bransfield Strait. Our study offers valuable insight into the spatio-temporal dynamics of humpback whale density distribution in an area that is currently the focal point of spatial management measures to ensure sustainable krill exploitation by means of adaptive EBFM. Identifying the temporal variation and significant geographical areas critical to this species in its feeding season, as well as their estimated consumption rates, generates a spatial and temporal basis for MPA consideration, knowledge for adaptive fishery management, and contributional data for monitoring a changing ecosystem.

4.1 Spatio-temoral variation in humpback densities

Platforms of opportunity may potentially be the only logistically and financially feasible approach to gather crucial fine-scale data regarding cetacean abundance, at least until satellite-derived abundance estimates (Bamford et al., 2020) are reliable enough to be considered serviceable from a management perspective. Our results mainly indicate the importance of the highly productive Gerlache Strait and western Bransfield Strait as the feeding ground of the recovering populations of humpback whales in the southern hemisphere.

The use of oceanographic covariates as proxies for Antarctic krill has been commonly used previously to predict distribution of baleen whales such as minke (*Balaenoptera bonaerensis*; Ainley et al., 2012; Friedlaender et al., 2006), fin (*Balaenoptera physalus*; Herr et al., 2006) and humpback whales (Friedlaender et al., 2006, 2011; Herr et al., 2016; Williams et al., 2016). Nutrient-rich Circumpolar Deep Water (Prézelin et al., 2000) heavily influence the Gerlache and Bransfield Straits (Ballerini et al., 2014), entering the study area from the west and subsequently mixing with shelf water to create Transitional Zonal Waters with Bellingshausen Sea influence (TBW; Garcia et al., 2002). Our results indicate that humpback whales have a higher affinity to this warmer, fresher water mass, compared to the colder, saltier water mass entering the study area from the northeastern part of the Bransfield Strait, known as Transitional Zonal waters with Weddell Sea influence (TWW; Garcia et al., 2002). Furthermore, affinity to

sea surface temperature gradient (TG) and low Finite Size Lyapunov Exponents (FSLE) values suggest humpback whale affinity to the Bransfield (Sangrà et al., 2011), Gerlache (Anadón & Estrada, 2002) Fronts and water masses with a high degree of suspended matter created by the anticyclonic eddie system in the Bransfield Strait (Sangrà et al., 2011), respectively. These results underline the importance of western TBW influence, eddie- and frontal systems for Antarctic krill, and consequently upper-trophic predator distribution in the SA, and can subsequently be used to predict spatio-temporal variation of both trophic levels to avoid interactions between krill-dependent fauna and fishery vessels by means of adaptive EBFM.

Our results show fine-scale temporal variation in humpback whale distribution, an essential component for successful and precautionary adaptive EBFM. The predicted hurdle model plots reflect a low density early in the season, but the present animals aggregated in the southwest corner of the study area (C1; Figure 4), followed by high aggregations of humpback whales in the "mid-season" (C2; Figure 5), and subsequent dispersion of animals throughout the study area towards the end of the austral summer (C3; Figure 6). The spatial findings emphasize the relative regional importance of the northern Gerlache and western Bransfield Straits as a hotspot for foraging humpback whales and, presumably, other parts of the krill-dependent ecosystem. The reasoning behind these hotspots would be purely speculative based on our data, but align well with regional Antarctic krill spawning events taking place in the Gerlache Strait in late December (Huntley & Brinton, 1991) and humpback whales taking advantage of the local spawning hotspots and nursery areas for immature krill (Perry et al., 2019; Cleary et al., 2016), as humpback whales exhibit size-dependent predation on krill, preferring smaller size ranges (≤34 mm; Santora et al., 2010; Friedlander et al., 2008, 2009). The observed spatial trend, animals aggregating first in the Gerlache Strait, followed by higher concentrations in the Bransfield Strait later in our study period, could be a result of Pacific sub-populations arriving in the area before potential Atlantic sub-populations, as the general Scotia Sea exhibits higher concentrations of krill than the western Drake Passage. Furthermore, Our results coincide well with findings of inter-species habitat partitioning of baleen whales, where humpback whales are more likely than other baleen whales (such as fin (*Balaenoptera physalus*) and minke (*Balaenoptera bonaerensis*)) to forage in our study area and other shelf areas with relatively warmer freshwater (Herr et al., 2016). Additionally, the temporal scale of our results indicate that the majority of migratory humpback whales arrive in their summer foraging grounds in late-December, with more individuals entering the SA in late January. Identifying the temporal variation in distribution is valuable data to implement in EBFM to ensure that fishing fleets

avoid extracting this critical food source in even more critical times, ensuring ample energy particularly for susceptible immature individuals and pregnant females, demographics whose survival is imperative for population growth and well-being, in accordance with a precautionary approach.

4.2 Potential interactions between humpback whales and fisheries

Identifying spatial overlap between upper-trophic predators and regional fishing fleets is fundamental to increase EBFM effectiveness, by recognizing and safeguarding important foraging grounds for these species and consequently ensuring sufficient resources for the populations to cover not only maintenance, but also energetically expensive periods associated with reproduction in low-latitude regions with usually insufficient local prey resources. In recent decades, there has been a regional shift in fishing grounds from farther north (Drake Passage) earlier in the season (December-February), to farther south (Bransfield Strait) later in the season (March-May, June-August). This trend is concerning, as these areas are already being used as feeding grounds by penguins (Trathan et al., 2015), Antarctic fur seals (*Arctocephalus gazella;* Lowther et al., 2020) and humpback whales (Curtice et al., 2015; Weinstein et al., 2017). Reviewing the spatial distribution of the fishery fleet in the time interval 2009-2018 (Appendix Figure 4), we see that the majority of catches in sub-area 48.1 are located in the central- and southern Bransfield Strait and in the northern Gerlache Strait. Comparing that to our predicted humpback whale distribution we see that there is spatial overlap between the two, with one of the highest fishery hotspots in the being in the north-eastern Gerlache Strait along the Antarctic Peninsula coast, the areas where our analyses consistently predicted high densities of humpback whales. The second fishery hotspot and surrounding low-yield catch areas in the central- and southern Bransfield Strait, respectively, overlap somewhat with our predictions.

However, regional harvest of Antarctic krill may only serve a potential threat to surrounding upper-trophic predators if both spatial and temporal interactions overlap. Reviewing fine-scale fishery yields in the sub-area 48.1 (Appendix Table 3) we see that the fishery is minimally active in the period of our data collection, yielding 204 and 728 tons of krill in December and January 2018, respectively compared to a range of approximately 27 000 – 45 000 tons in

March-June. Regarding interactions between humpback whales and fishery activity, we can conclude that there is minimal spatio-temporal interaction in the period November-January. However, the extent of humpback whale presence in sub-area 48.1 is unknown in subsequent months, and there could be possible spatio-temporal overlap in that time. Based on our temporal data, and the assumption that the feeding period of humpback whales is 120 days (Lockyer, 1981), the feeding period can be established to be from late December to late April. If the density trends remain stable throughout this period, however, there is a substantial spatio-temporal overlap between the fisheries and humpback whales in the area. We will look further into temporal overlap while discussing consumption estimates.

4.3 Abundance and recovery

Previous studies based on the SOWER-2000 whale surveys carried out as part of the large-scale CCAMLR krill survey in 2000, indicated a population of ~7000 animals in the WAP during January and February in the same year (Hedley et al., 2001). Herr et al. (2016) used an aerial survey and density surface modeling to estimate ~3000 individuals in the Bransfield Strait alone. Considering that the Southern Ocean populations of humpback whales are increasing (Pallin et al., 2018; Tulloch et al., 2018; Zerbini et al., 2019), the abundance estimates derived from our hurdle models could be slightly overestimated and do have a higher CV than the distance sampling estimates, but they are not unrealistic, especially in light of the recent findings by Zerbini et al. (2019), indicating that the western South Atlantic population has recovered to an approximate 93% of pre-exploitation levels.

This brings us to the question of which sub-population(s) we actually observed in the study area, if the WAP home to a single or several summer foraging sub-populations. This is important to address, as the consequences of this from the management perspective is that if the austral summer population foraging in the Antarctic Peninsula are made up of multiple sub-populations that have been historically harvested, then a subsequent population recovery would possibly not only be at the rate of a single population, but rather a compounded rate based on multiple recovering sub-populations. Previous studies have indicated that the WAP is the foraging ground for Breeding Stock G (BSG) and not Breeding Stock A (BSA; IWC, 2007h) based on telemetry data (Zerbini et al., 2006) and lack of photo-identification in the WAP (Stevick et al., 2004; Dalla Rosa et al., 2008). However, Albertson et al. (2018) found through genetic analysis (n = 136) that humpback whales around the Gerlache Strait mainly contained

BSG individuals. However, there were also individuals from BSA and sub-population BSF with breeding grounds in Oceania (Albertson et al., 2018; Robbins et al., 2011). Further, during data collection, we encountered an individual with the clear markings of an Australian form humpback whale with unmistakable white markings higher up on the flank (pers obs). Although anecdotal, it does question the degree of movement the animals of different sub-populations exert within the Southern Ocean feeding ground. This variation indicates that the Bransfield and Gerlache Straits are reliable feeding grounds for multiple sub-populations of the Southern Ocean due to the consistently high density of krill and its proximity to further feeding grounds along the southern shelf and slope of the WAP (Dalla Rosa et al., 2008).

Population trajectories are not available for BSG, potentially the most abundant user of the study area, to assess the stage of recovery this population is at. However, Tulloch et al., (2018) presented modelled trajectories for Atlantic/Indian and Pacific humpback whale populations (Appendix Figure 5). Humpback whales in the Atlantic/Indian sector were depleted much earlier in comparison to the Pacific populations and have consequently recovered to a higher percentage of their estimated historic populations, reflected in the BSA population, nearing pre-exploitation population size (Zerbini et al., 2019). Considering that the Pacific humpback whale population is currently estimated to be at approximately 50% of pre-exploited levels (Tulloch et al., 2018), we can expect that use of our study area by these baleen whales are expected to significantly increase. This increases the importance of allocating feeding grounds to upper-trophic predators, to provide ample foraging opportunities to support these growing sub-populations. From a management perspective, the variation in population structure and their individual increases needs to be quantified and taken into account when managing fisheries in foraging hotspots. Disregard of this matter will potentially underestimate the rate of increase of this major krill consumer, an important factor for retaining a precautionary approach, and should be prioritized in future work.

4.4 Consumption estimates and temporal overlap

This study calculated consumption estimates for all three periods using both methods based on BMR equations and assuming a mean daily energetic requirement of approximately 2% body weight per individual. Assuming a 120-day feeding season in the study area and that abundances do not increase after C3, we estimate that humpback whales consume approximately 0.5 million (mean: 586 000 tons, range 350 000 – 784 000 tons) and 1.1 million

tons (mean: 1 157 000, range: 690 000 – 1 545 000 tons) using distance sampling and hurdle estimates, respectively, throughout their foraging season. Reilly et al. (2004) calculated in-depth krill consumption estimates for various whale species based on abundance estimates derived by Hedley et al. (2001), concluding that humpback whales in the Antarctic Peninsula consume approximately 417 000 – 806 000 tons of krill throughout their summer feeding period based on a daily bodyweight requirement, slightly less than our results, but an expected increase in line with the recovery of the populations.

These estimates can be used to compare temporal overlap between foraging humpback whales and fishery vessels. Using the average of the three consumption estimates (i.e., Innes et al., 2%, and 3%) and comparing these data to catch data from 2018 (Appendix Table 3), we see that there could be potential overlap in March and April; fisheries harvested 9.2 – 18.2% of estimated humpback whale monthly krill consumption in March and 12.4 – 24.6% in April (derived from H and DS estimates, respectively). We caution that these are estimates as no fine-scale data going into the fall season exists for the area. Thus, to minimize negative effects of regional Antarctic Krill harvest on humpback whales, the spatio-temporal extent of summer foraging needs to be quantified.

The range of humpback whale consumption in the current literature varies greatly; daily estimates range from 390 kg ind^{-1} (Innes et al., 1986) to 1 232 kg ind^{-1} (Stevick et al., 2008), Additionally, Smith et al. (2015) estimated an upper daily consumption rate of 2 110 kg ind^{-1}, representing a daily consumption of ~7% percentage body mass. If we were to use this consumption percentage for our data, we would get seasonal foraging estimates of 0.8 – 1.6 million tons and 1.6 – 3.3 million tons using abundances deriving from our distance sampling and hurdle models, respectively. These estimates agree reasonably well with more recent calculations of cetacean consumption, based on high-resolution tagging of humpback whales and in-situ hydroacoustic prey-field density estimates, both from the Antarctic (Savoca et al., 2019) and the Northeast Atlantic (Biuw, pers comm). Despite the difficulty of quantifying consumption, especially regarding highly migratory animals in foraging areas containing super-abundant prey such as the WAP, these estimates give us valuable insight in the temporal trends of humpback whale predatory pressure and potential interactions. However, the substantial variation in consumption estimates obtained depending on which approach is used, highlights the urgent need for more detailed studies of prey consumption as a function of prey availability. Further, lack of these data is detrimental, as uncertainty in the consumption of cetaceans, which

varies through both time and space, has implications with interspecific competition with land-based predators such as penguins and their utility as bioindicators for the ecosystem.

Overall, using platforms of opportunity and advanced analytical toolsets such as DSHM, we provide insight into the spatial and temporal distribution of humpback whales in the WAP during the first half of their feeding season. However, future studies should expand the temporal survey effort to include this area later in the feeding season to explore distribution in the subsequent months in order to. Additionally, quantifying krill's spatial and temporal distribution as a product of life-history traits combined with oceanographic covariates would serve as a powerful predictive tool for multiple levels of the Southern Ocean ecosystem.

4.5 Limitations of study

Despite the valuable frequency of surveying, using platforms of opportunity does, of course, include its biases and limitations. Intrinsic in the nature of tourist vessels, specifically, tours tend to stay in proximity of coastal areas, as transporting guests to determined landing locations in the area is the priority. Consequently, the observations may be biased towards these specific areas. Additionally, these vessels sail in complex coastal areas, resulting in a skewed detection function with more observations at lower perpendictular distances, but this was addressed by truncation. Regardless, the value of the relative spatio-temporal variation in data is high, and still applicable to spatial adaptive EBFM.

Running both the distance sampling and the DSHM method, we encountered a rather significant discrepancy between the respective design-based and model-based methods. Density surface modeling (DSM) has been around for a while, and Hedley et al. (2001) had higher density and abundance estimates from the basic design-based method assuming homogeneity in distribution, than from the standard DSM. However, implementing hurdle models is a relatively new method (Franchini et al., 2020), and no current literature has explored the relationship between distance sampling and DSHM. However, Potts & Elith (2006) used hurdle models to estimate abundance and found it to be the most accurate method relative to the others tested.

4.6 Overall conclusion

We have found that the northern Gerlache Strait is an important feeding area for humpback whales, with the main migration of animals to this area in late December, with more animals arriving throughout January. Comparing our results to the spatio-temporal activity of the Antarctic Krill fishery in the area, there was minimal overlap in our study period (November – January). However, if the distribution derived from our results subsides throughout the summer feeding period, there could be depletion of resources in presumed important areas for humpback whales. Our study demonstrates the utility of platforms of opportunity such as tourist vessels as a viable means to collect data in support of EBFM in the WAP area, and similar efforts should be for the subsequent months (i.e., the period of highest fishery impact). Additionally, given the progression of MPA planning in the region, the general utility of our approach in a monitoring context should also prove useful. The Southern Ocean is one of the most pristine and rich ecosystems on the planet, and effort should be made to retain that quality.

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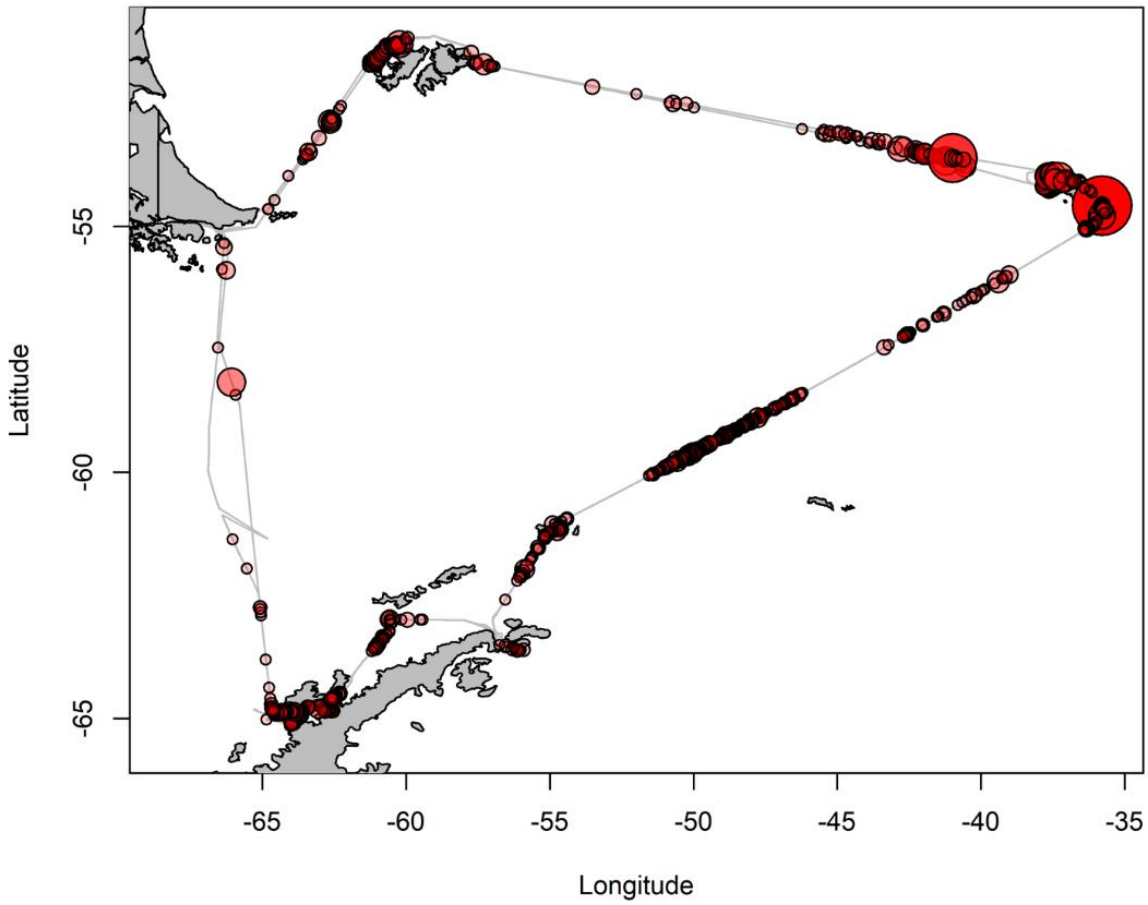
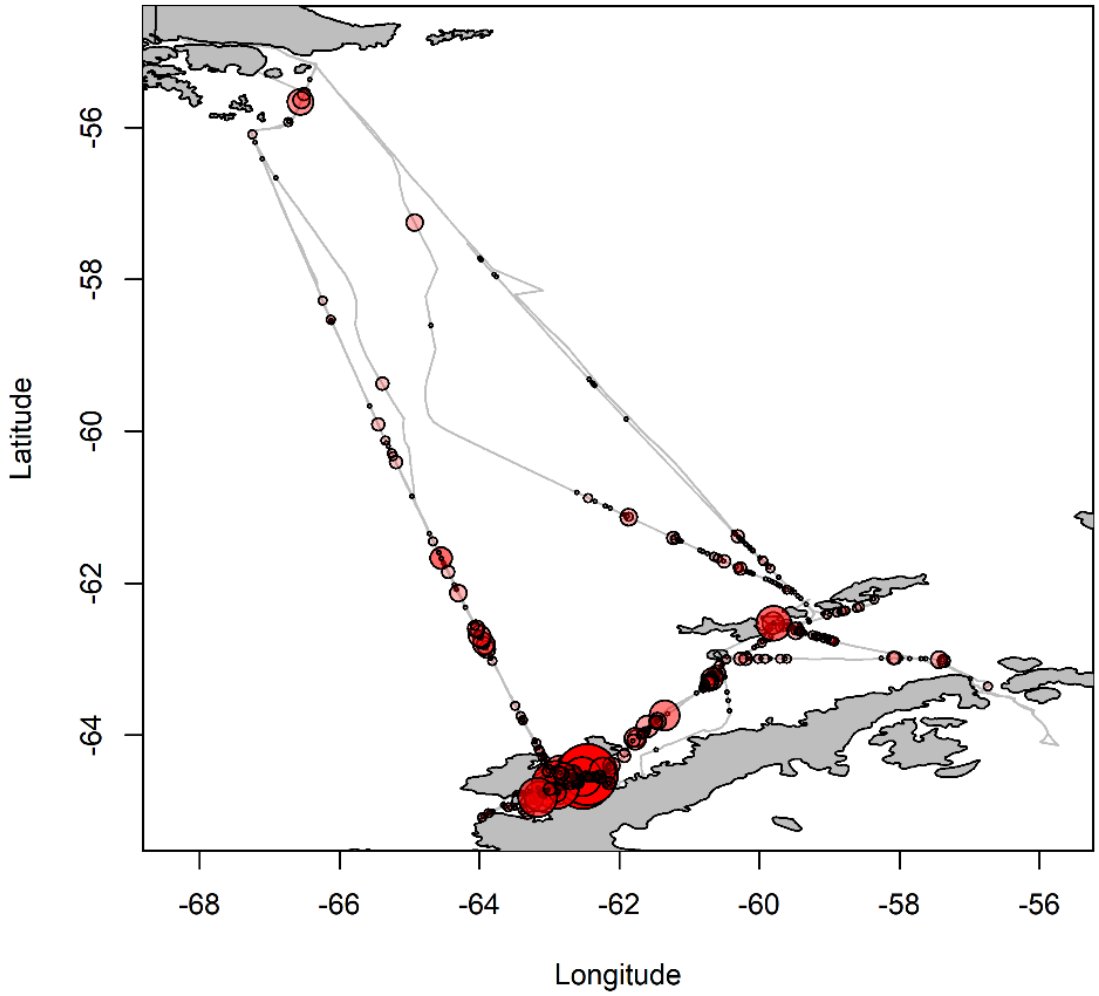
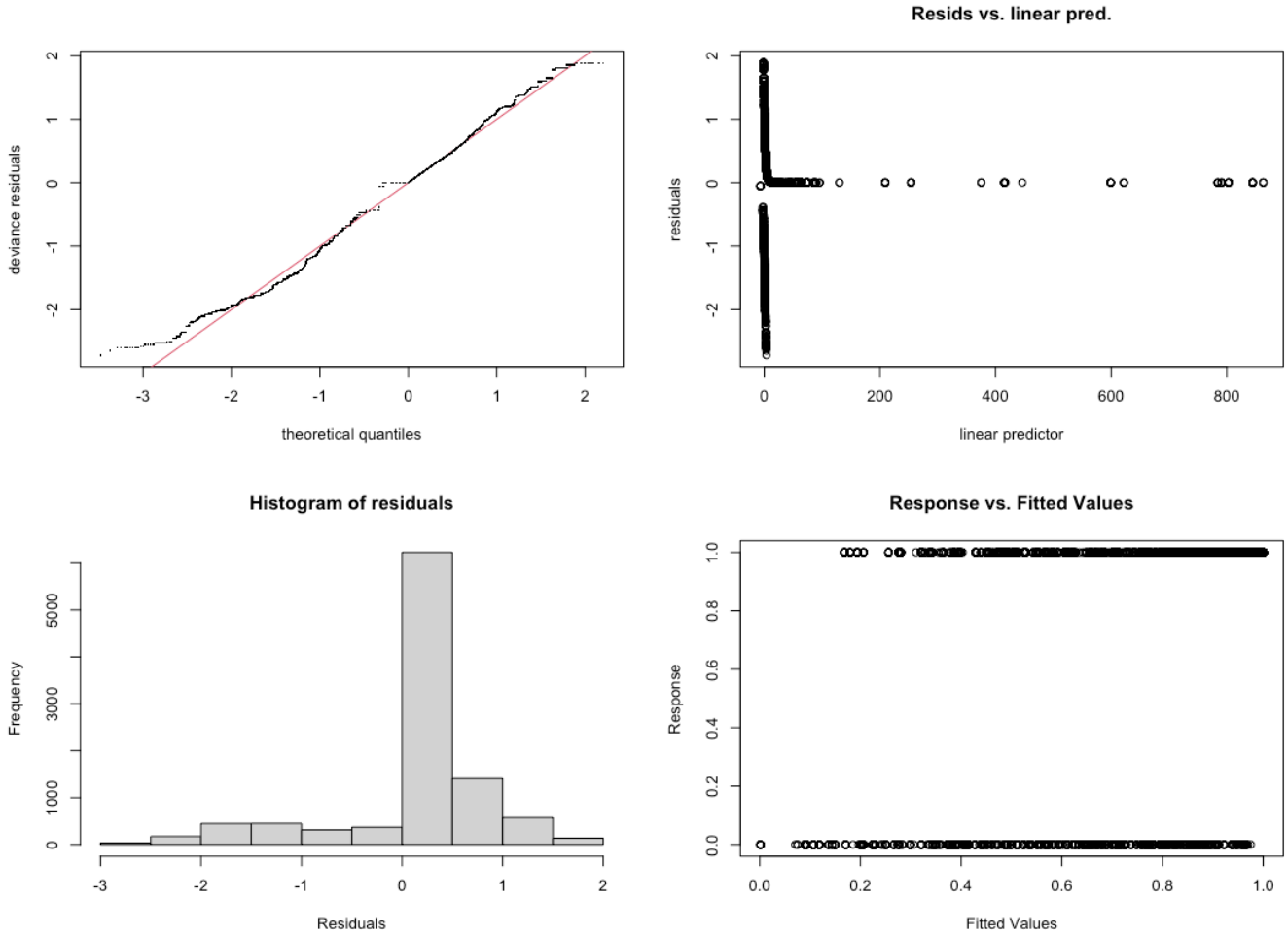
6 Appendix



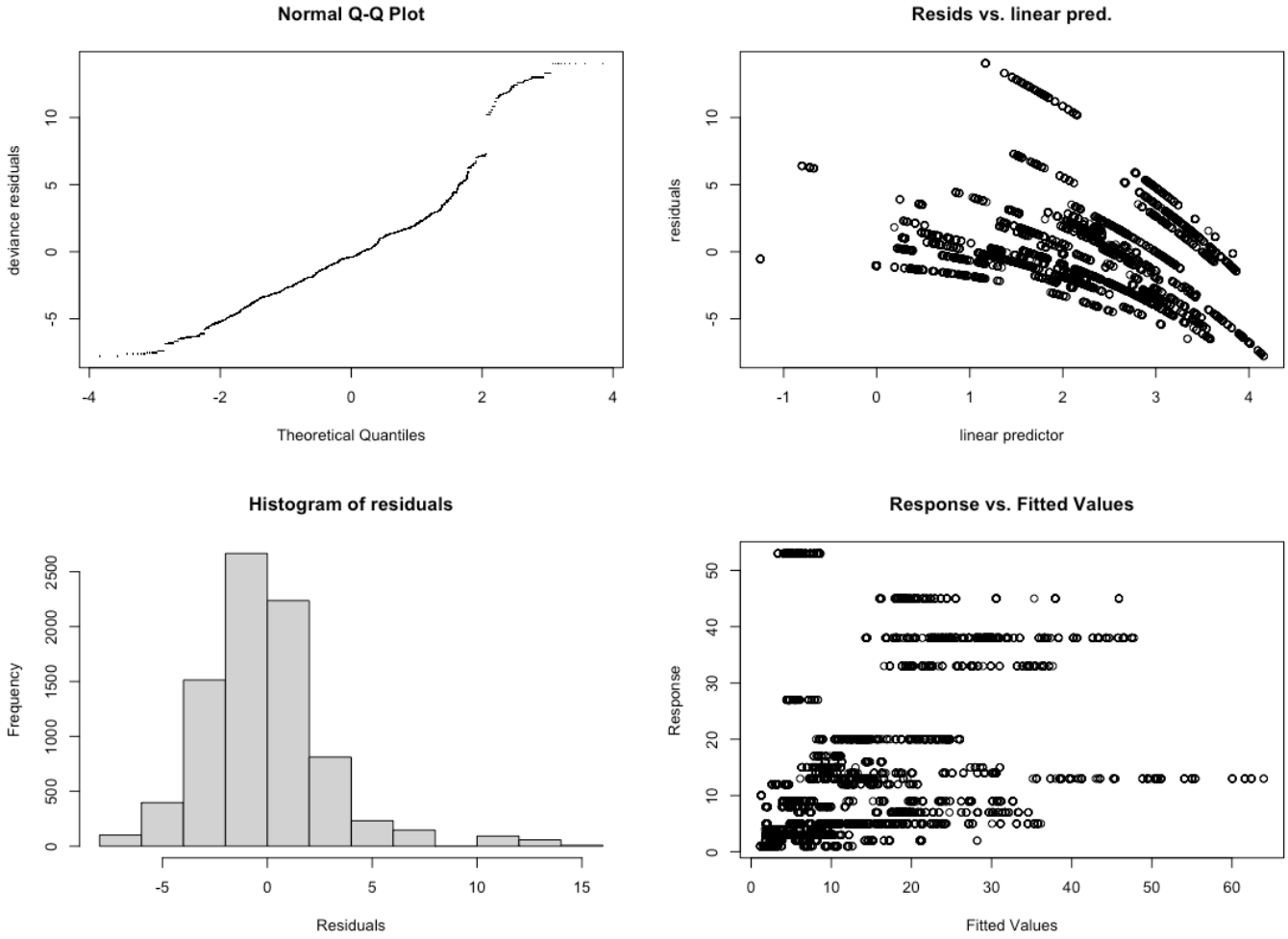
Appendix Figure 1 *- Distribution of marine mammal sightings during two MS Fram voyages (Ushuaia - Falkand islands South Georgia - Antarctic Peninsula - Ushiaua). Grey lines represent the cruise transects and red circles represent marine mammal sightings. The size of the circles is proportional to the number of animals observed.*



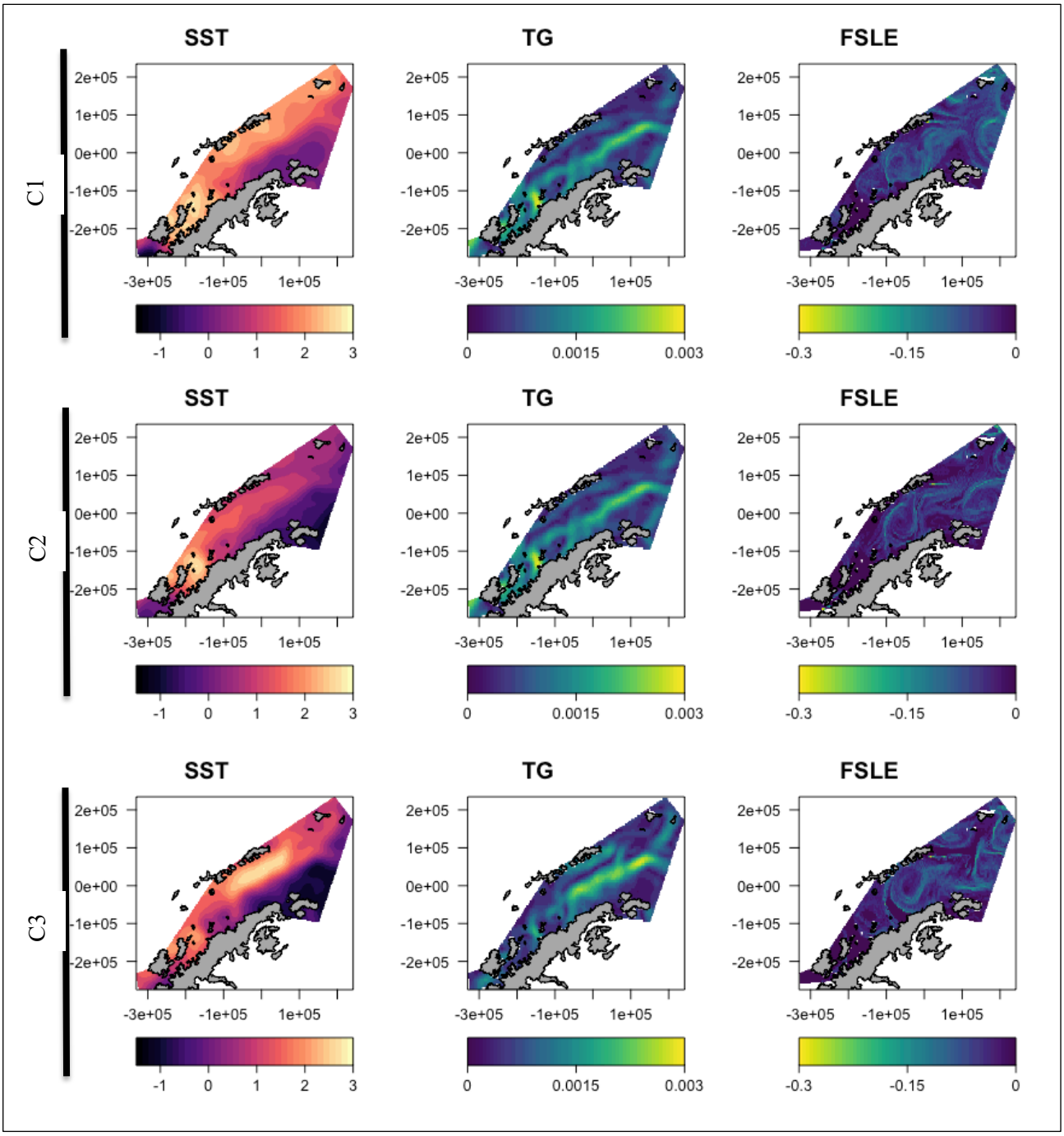
Appendix Figure 2 *- Distribution of marine mammal sightings during two MS Fram voyages (Ushuaia - Falkand islands South Georgia - Antarctic Peninsula - Ushiaua). Grey lines represent the cruise transects and red circles represent marine mammal sightings. The size of the circles is proportional to the number of animals observed.*



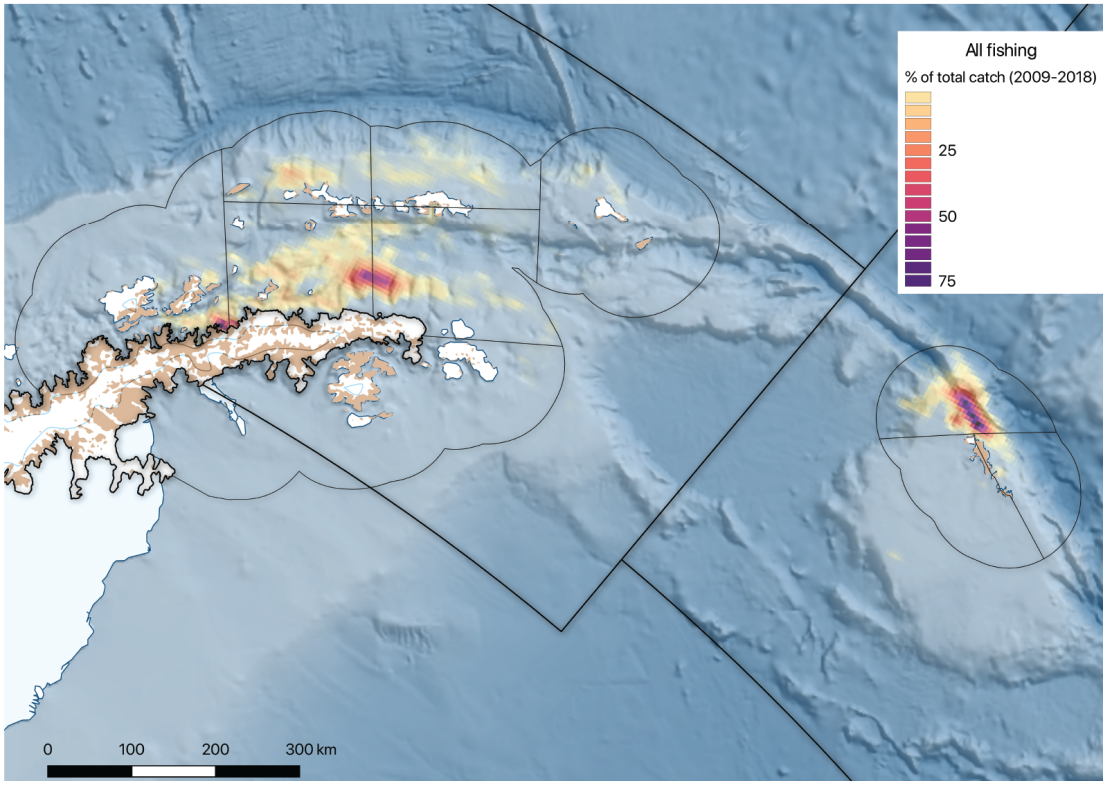
Appendix Figure 3 *– Plots showing Q-Q plots, Residuals vs Linear prediction, Histogram of Residuals, and Response vs fitted values for the fitted GAM for the binomial sub-model PA (presence-absence).*



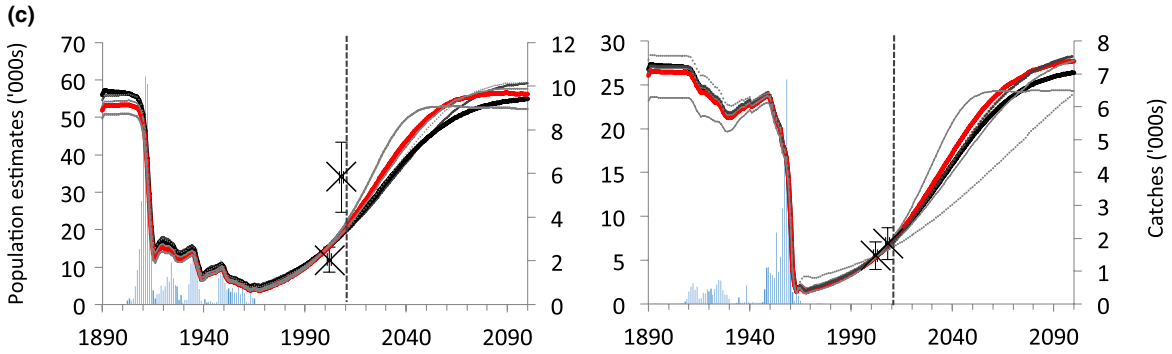
Appendix Figure 4 *- Plots showing Q-Q plots, Residuals vs Linear prediction, Histogram of Residuals, and Response vs fitted values for the fitted GAM for the zero-inflate Poisson sub-model AB (Abundance).*



Appendix Figure 5 - Oceanographic covariates in prediction grid for all 3 cruises



Appendix Figure 6 *- Map showing the spatial distribution of fishery activity in the period 2009 - 2018. Produced and borrowed from Lowther et al. (2020).*



Appendix Figure 7 *- Projected humpback whale abundances for the Atlantic/Indian (left) and Pacific (right) populations. From Tulloch et al. (2018).*

Appendix Table 1 *- table showing the concurvity indices for sub-model PA*

Concurvity check PA

	Parameter	***SST***	***TG***	***FSLE***
Worst	*3.98858e-28*	*0.3796519*	*0.37773374*	*0.13511367*
Observed	*3.98858e-28*	*0.1773197*	*0.09218982*	*0.10750031*
Estimate	*3.98858e-28*	*0.1030539*	*0.10351097*	*0.04615805*

Appendix Table 2 *- table showing the concurvity indices for sub-model AB*

Concurvity check AB

	Parameter	***SST***	***TG***	***FSLE***
Worst	*2.784855e-28*	*0.34160102*	*0.35894560*	*0.14544183*
Observed	*2.784855e-28*	*0.07976032*	*0.12155610*	*0.12072565*
Estimate	*2.784855e-28*	*0.10467141*	*0.09518244*	*0.05794214*

Appendix Table 3 *- Catch (tons) of Antarctic krill in area 48 in 2018. Data collected from CCAMLR Krill fishery Report 2018*

Month	Subarea/Division				Total
	48.1	48.2	48.3	58.4.2	
December	204	23003			23207
January	728	28911		246	29885
February	6516	31225			37741
March	27082	12971			40053
April	36602	2597			39199
May	45544	404			45948
June	35016	1767			36783
July		135	9687		9822
August		2820	11909		14729
September		28088	1577		29665
October		5957			5957
Total	151692	137878	23173	246	312989