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Department of Arctic and Marine Biology

## **Foraging Behavior of Chinstrap Penguins (*Pygoscelis antarctica*) at the South Orkney Islands (Antarctica) during their Breeding Season**

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# Table of Contents

Abstract .....	4
1 Introduction .....	5
2 Methods.....	9
2.1 Study site & species .....	9
2.2 Data processing .....	10
2.2.1 Definition of trips and homeranges .....	10
2.2.2 Dive classification .....	11
2.2.3 Interpolating dive locations .....	14
2.2.4 Prey availability.....	14
2.2.5 Linking predator and prey .....	15
3 Results .....	17
3.1 Foraging trips & homerange .....	17
3.2 Identified dive types & their properties.....	18
3.3 Diel foraging pattern of chinstrap penguins .....	20
3.4 Krill density and distribution.....	23
4 Discussion .....	25
5 Conclusion.....	32
6 References .....	33
7 Appendix .....	40

## List of Tables

Table 1. Overview of sampling, homerange estimates and trips of the chinstrap penguins from Monroe and Powell Island. The homerange estimates are based on the values for a 95% confidence interval showing minimum and maximum, mean and standard deviation as well as total area (all in km<sup>2</sup>) estimated. The trip summary includes of the total and mean number of trips, distance and duration, minimum and maximum distance and duration as well as the trip

direction of the trips done by the chinstrap penguins from Monroe and Powell Island. \*The number in the brackets indicates the number of tagged individuals used for the analysis due to cropping of the sampling duration. .... 17

Table 2. Summary (given as mean  $\pm$  standard deviation) of the dive properties namely maximum depth (in m), dive duration (in s), bottom time (s), bottom distance (in m), post dive duration (in s) and dive frequency (in dives/hour) for each type of dive of the chinstrap penguins in the South Orkney Islands. Colours indicate lowest (white) to highest (blue) value for each variable. See Table Appendix 1 for additional properties..... 18

Table 3. Summary of the number of dives categorized in regard to the type of dive (foraging, exploratory or travelling) and the time of day (Daytime, Civil Twilight or Nautical Twilight) in total and for each penguin colony. .... 20

## List of Figures

Figure 1. Inlet map of the South Orkney Islands and the surrounding seas. The two tagging sites on Powell and Monroe Island are marked with a red point. Map data was obtained from Dorschel et al. (2022). .... 9

Figure 2. Overview of the methodology of the dive classification based on Lesage et al. (2011) and Krafft et al. (2011). .... 11

Figure 3. Overview of the transects of the acoustic krill monitoring survey in 2022 and 2023. The five main transects and the denser sampling grid in the main fishing area northwest of the South Orkneys are shown. Cumulative NASC values detected at each station indicated by the size and colour. The outline of the occurrence distribution of the penguins from each colony are shown in red. .... 15

Figure 4. Schematic depiction of the different dive shapes found for the chinstrap penguins in the South Orkney Islands based on the properties of the cluster results. Increasing dive duration is indicated by the horizontal axis. Dive depth is based on the clustering results. Foraging dives (shallow, medium and deep u-dives) are additionally marked by the krill pictograms in the bottom phase of the dives. Pictograms obtained from Freepik. .... 19

Figure 5. Histogram of the number of dives summed up by hours of the day for each type of dive indicating the daily patterns of the chinstrap penguins in the South Orkney Islands. The colour scale indicates the amount of light during the hours of the day (from low (blue) to high (yellow)). .... 21

Figure 6. Selection of the dive types that make up for more than 15% of the dives during the time of day they occurred (Daytime, Civil Twilight and Nautical Twilight) visualizing their

locations. Density can be seen as a relative measure of the probability of a dive occurring in a certain place (the higher the more likely it is). Bathymetric contours are in 500m depth intervals except the first thicker contour marking 100m depth. See also Figure Appendix 2, Figure Appendix 3 and Figure Appendix 4 for a complete overview of all the dives during all times of the day. .... 22

Figure 7. The average distribution of krill in 2022 for the whole water column is shown by the bubbles (zero values removed for clarity). The boxplots summarize the diving depth of all foraging dives for the respective hour of the day. Maximum diving depth of the penguins is indicated by the dashed line and the number of dives for each hour of the day is shown above the respective boxplot. (See also Figure Appendix 5 for a zoomed in version of the plot focusing on the subset of the maximum diving depth of the penguins). The boxplots are showing the 25% (upper line), 50% or median (middle line) and 75% quantiles of the data; the whiskers show the minimum (upper) and maximum (lower) values, respectively, and outliers, if occurring, are shown as single dots beyond that. .... 23

Figure 8. Boxplots showing the depth distribution of the krill maxima for 2022 and 2023 within and outside the homerange of Monroe Island for the whole water column and the subset according to the maximum diving depth of the penguins. The boxplots are showing the 25% (upper line), 50% or median (middle line) and 75% quantiles of the data; the whiskers show the minimum (upper) and maximum (lower) values, respectively, and outliers, if occurring, are shown as single dots beyond that. Red dashed line indicating the maximum diving depth of the chinstraps. .... 24

Figure 9. Figure (left) showing the NASC values of the krill in 2022 that match up with the foraging dive depth and the hour of the day, meaning these are the krill densities that could be a potential foraging target (orange). The values of the hourly averaged maximum krill values are shown in comparison (violet). Figure on the right shows the depth distribution of the NASC values shown in the left figure (maximum diving depth of the penguins shown as red dashed line). For both plots the first (dashed), second (solid) and third quantile (dashed) of the 95% confidence interval are shown in the respective colour of the curve they belong to; if a quantile is not visible it is due to its overlap with the plot border. .... 24

## Abstract

Chinstrap penguins (*Pygoscelis antarctica*) are central place foragers during their breeding season in the austral summer, which restricts the distance and duration they can forage away from their chicks. Recent studies indicate a regional decline in chinstrap penguin populations across their distribution range. During breeding, they almost exclusively feed on Antarctic krill (*Euphausia superba*), a prey resource that is unevenly distributed and undergoes diel vertical migration to evade predators like penguins. Using acoustic krill survey data from the South Orkney Islands and four-dimensional tracking data from 35 individuals across Monroe and Powell Islands from the austral summer seasons of 2022 and 2023, this study links predator and prey dynamics. I demonstrate that chinstrap penguins exhibit a pronounced diel foraging pattern, utilizing different areas and dive types. The findings suggest that chinstrap penguins target shallowly distributed krill at the shelf areas north on the South Orkneys – an area known for high krill concentrations – at nighttime, where the reduced energy expenditure from shallow diving offsets the increased travel distance. In contrast, when krill is located deeper during the daytime, chinstrap penguins tend to remain closer to their colonies and dive deeper. Furthermore, the results indicate that chinstrap penguins target lower krill densities than those found at peak concentrations, suggesting that suitable prey is determined more by encounter rates than sheer density. The presence of a large multispecies aggregation, including whales, seals, and seabirds, within the penguins' home range in 2022 likely influenced the observed krill depth distribution, reflecting varying top-down pressures from different krill predators. However, due to the lack of synoptic data, the latter observations should be viewed as broad patterns that warrant further investigation through studies with temporally overlapping and appropriately scaled data. In the face of climate change, understanding the intricate biotic interactions among recovering krill predators, such as baleen whales, and penguins alongside the effects of krill fisheries, is essential for gaining a comprehensive insight into the dynamics of Southern Ocean ecosystems.

# 1 Introduction

Globally, human-driven modification of the climate has rapidly changed our atmosphere, cryosphere, oceans and biosphere in a manner unprecedented in the last 420 million years (Foster et al., 2017; IPCC, 2023), with these changes becoming increasingly pronounced toward the poles—a phenomenon known as polar amplification (Xie et al., 2022). In the Southern Ocean, climate change is causing alterations to sea ice extent, impacting global ocean circulation and contributing to rising sea levels (Cavanagh et al., 2021; IPCC, 2019). Increased glacial melt from Antarctica is altering ocean salinity and temperature patterns, which in turn can influence weather systems and marine conditions globally (Cavanagh et al., 2021; IPCC, 2019). These changes are also affecting the global carbon cycle, as the Southern Ocean plays a crucial role in absorbing atmospheric carbon dioxide (IPCC, 2019; Long et al., 2021).

Biota in the Southern Ocean have evolved to thrive in polar conditions and their associated seasonal cycles over long evolutionary periods (Barnes & Peck, 2008; Cavanagh et al., 2021). Climate warming is expected to impose thermal stress on many polar species (Gutt et al., 2021), depending on their temperature tolerance and life history traits (Nogués-Bravo et al., 2018). Declining sea ice and retreating glaciers (Cavanagh et al., 2021; IPCC, 2019) may reduce physical barriers for some species, while for others, this represents significant habitat loss (Gutt et al., 2021). The Southern Ocean's increased CO<sub>2</sub> absorption is altering seawater biochemistry, leading to acidification that can be harmful to calcium carbonate shell-producing organisms (Cavanagh et al., 2021; Long et al., 2021). Changes in wind patterns affect ocean circulation, stratification, nutrient upwelling, and sea ice dynamics, which have been linked to shifts in primary production in the Southern Ocean (Cavanagh et al., 2021; IPCC, 2019). Biota have few ways to respond to this rapid change: they can adapt to the new environment, migrate to more suitable environments, or go extinct. The choice of which response is exhibited is highly dependent on the species life history and mobility (Nogués-Bravo et al., 2018). With projected future impacts being anticipated to surpass the existing ones (Gutt et al., 2015), the urgency of scientific advancement in order to mitigate the impacts of climate change on these regions increases.

Antarctic krill (*Euphausia superba*, hereafter referred to as krill) is a key species in Antarctic ecosystems supporting numerous predator populations and a commercial fishery in the Southern Ocean (Atkinson et al., 2008; Lowther et al., 2018). Present climatic changes such as sea ice decline, increasing air and water temperatures, increased stratification and changing

wind patterns are affecting the abundance, distribution, and life cycle of krill (Flores et al., 2012; McBride et al., 2021), having a bottom-up effect on the ecosystem. The resulting changes in krill availability, composition and distribution have various implications for krill-dependent predator populations such as whales, seals, fishes and penguins in the Southern Ocean (Klein et al., 2018).

Among krill dependent predators, penguins in particular are vulnerable to changes in krill availability (Gutt et al., 2021; Klein et al., 2018; Trivelpiece et al., 2011). This is partially due to the fact that penguins are central place foragers (CPF's) during their austral summer breeding seasons with their at-sea distribution limited in both time and distance from their colony due to the need to return to land at regular intervals to feed their offspring (Salmerón et al., 2023). Thus, only a limited area around colonies is accessible to breeding animals, limiting the amount of prey available to them. Previous studies have shown that during the guard phase, when seabird parents must regularly provide food for their chicks, food availability is crucial for chick survival (Clarke et al., 2002). As the chicks grow and their food demands increase, parents' foraging ranges tend to become more restricted (Phillips et al., 2021) and any changes in the availability of krill might have serious impacts on their breeding success (Salmerón et al., 2023).

Chinstrap penguins (*Pygoscelis antarcticus*) are part of the *Pygoscelis* genus, which also includes adélie (*P. adeliae*) and gentoo penguins (*P. papua*). They can be found on the Antarctic continent as well as on sub-Antarctic islands (Black, 2016). However, the chinstrap penguins' breeding colonies are primarily located throughout the western Antarctic Peninsula and the South Sandwich, South Orkney, and South Georgia Islands (Strycker et al., 2020). The global population of chinstrap penguins is estimated to be around 3.42 million breeding pairs, or approximately 8 million individuals in total (IUCN: The Red List of Threatened Species, 2020; Strycker et al., 2020). Despite being listed as a species of 'least concern,' recent trends indicate a decline in their numbers (IUCN: The Red List of Threatened Species, 2020; Lynch et al., 2012). During the austral breeding season, the chinstrap penguins' diet consists almost exclusively of krill (Kokubun et al., 2010; Rombolá et al., 2010; Wawrzynek et al., 2022), making them particularly vulnerable to environmentally-driven changes to krill abundance and distribution (Polito et al., 2015; Trivelpiece et al., 2011). Chinstraps were initially thought to benefit from sea ice decline due to their ice-avoidant foraging behaviour, but several studies have shown that this is an oversimplification, with widespread regional declines emphasizing

the need for a deeper understanding of their ecology and the impacts of climate change (Lynch et al., 2012; Strycker et al., 2020; Trivelpiece et al., 2011).

The chinstraps main prey, krill, can grow to a total body length of 6 cm and can live for 5+ years (Atkinson et al., 2008). They have a circumpolar distribution, but the density of krill is regarded to be the highest in the Atlantic sector of the Southern Ocean especially associated with shelves and some open ocean areas (Atkinson et al., 2008; Skaret et al., 2023). Krill is further known to be one of the most aggregating marine invertebrates (Krafft et al., 2012). They form swarms with varying properties which fluctuate due to numerous reasons such as the season, food concentrations, sexual developmental stages, light level, bathymetry and predation in addition to regional differences (Krafft et al., 2012). In addition, krill perform diel vertical migration (DVM), feeding on surface production at night and residing in deeper waters during the day to avoid visual predators, including penguins (Bahlburg et al., 2023). However, this behaviour is highly variable and can be influenced by factors such as food availability, predator presence, and latitude. Instances of no vertical migration or inverse vertical migration are also observed (Bahlburg et al., 2023).

The negative impacts of climate change on krill are believed to outweigh the positive ones (Flores et al., 2012; McBride et al., 2021), raising concerns for the future of the krill populations in the Southern Ocean as well as the predator populations it supports. Krill are sea-ice associated throughout all the stages of their life cycle, providing food, a habitat and protection especially during the early life stages, and changes in extent, duration and distribution are likely to have negative impacts on the survival and recruitment of krill (Flores et al., 2012; McBride et al., 2021). Krill is furthermore a cold-water adapted species and are normally found in areas with a narrow water temperature range (Flores et al., 2012). While adult krill might profit from a higher production in warmer waters, thermal stress by ocean warming is most likely to affect their growth and recruitment negatively (Flores et al., 2012). Ocean warming might furthermore lead to a southward shift in the distribution of krill or a shift towards deeper waters in order to avoid warmer surface waters (Flores et al., 2012). Both of these possibilities could have potentially detrimental impacts on krill predators. Whether one can already proof that such an effect of climate change is demonstrable is an ongoing discussion (Atkinson et al., 2019; Cox et al., 2018).

The South Orkney Islands are located in the Atlantic sector of the Southern Ocean at the southern edge of the Scotia Sea and are situated south of the southern boundary of the Antarctic



Circumpolar Current (Warwick - Evans et al., 2018). Several regions of the Atlantic sector are found to be some of the places where climate warming is currently the most pronounced for the Antarctic (Flores et al., 2012; Klein et al., 2018; Trivelpiece et al., 2011), marking the South Orkney Islands as a frontier of climate change. The island group is furthermore one of the locations where all three pygoscelid penguin species are known to breed sympatrically (Forcada et al., 2006), making it a desirable location to study chinstrap penguins.

During the past decades krill has become the most intensely harvested resource in the Southern Ocean, with fishery efforts during the last three decades mainly concentrating in the West Atlantic sector (Krafft et al., 2018; Skaret et al., 2023). The Convention for the Conservation of Marine Living Resources (CCAMLR) was established to conserve the Antarctic marine ecosystems while also mediate commercial interests. There are four management subareas established by CCAMLR in the West Antarctic Sector (South Shetland Islands; Subarea 48.1; South Orkney Islands, Subarea 48.2; South Georgia, Subarea 48.3 and the South Sandwich Islands, Subarea 48.4 (CCAMLR, 2017)). Both Skaret et al. (2023) and Krafft et al. (2018) identified that, out of the four subareas, the fishery at the South Orkney Islands has developed into a high-intensity krill fishery area and this could potentially be adding pressures locally to krill-dependent predators (CCAMLR, 2023a; Skaret et al., 2023). The extensive harvesting of cetaceans during the 20th century likely reduced competition for krill, leading to a period in which penguin populations, including those of pygoscelid penguins, may have benefited from increased krill availability due to the diminished presence of their primary competitors (Trivelpiece et al., 2011).

As climate change impacts both predators and prey, and as competition for krill increases with the recovery of cetacean populations (Biuw et al., 2024; Zerbini et al., 2019) alongside ongoing fishery activities in the Southern Ocean, it is essential to understand how krill-dependent predators like chinstrap penguins utilize their resources and interact with their habitat and other predators. Gaining this understanding is crucial for unravelling the complex relationships between predators and prey, identifying potential behavioural adaptations to cope with environmental changes, establishing critical conservation areas, and informing management decisions in the krill fishery.

The aim of this study is to relate the three-dimensional foraging patterns of chinstrap penguins to the distribution of krill on a diel timescale and to identify the preferred krill densities targeted by the penguins. I do this using two data streams: krill survey data collected acoustically

throughout the region, and four-dimensional tracking data of the penguins' vertical and horizontal movements during this critical period of their life cycle.

## 2 Methods

### 2.1 Study site & species

A total of 80 breeding chinstrap penguins in two colonies (Monroe and Powell Islands) were equipped with Axy-Trek Marine Loggers (TechnoSmArt); 66 penguins were tagged at Monroe Island between 5 January and 2 February in 2022 and 14 penguins were tagged at Powell Island between January 16 and January 26 in 2023 (Table 1, Figure 1). To ensure comparable datasets, the sampling duration for Monroe Island was adjusted to align with the shorter sampling period at Powell Island, resulting in usable data from 31 individuals at Monroe Island in 2022 and 14 individuals at Powell Island in 2023. All tagged individuals were confirmed to be breeding adults (both partners present with at least one chick), but no additional information (e.g. sex,

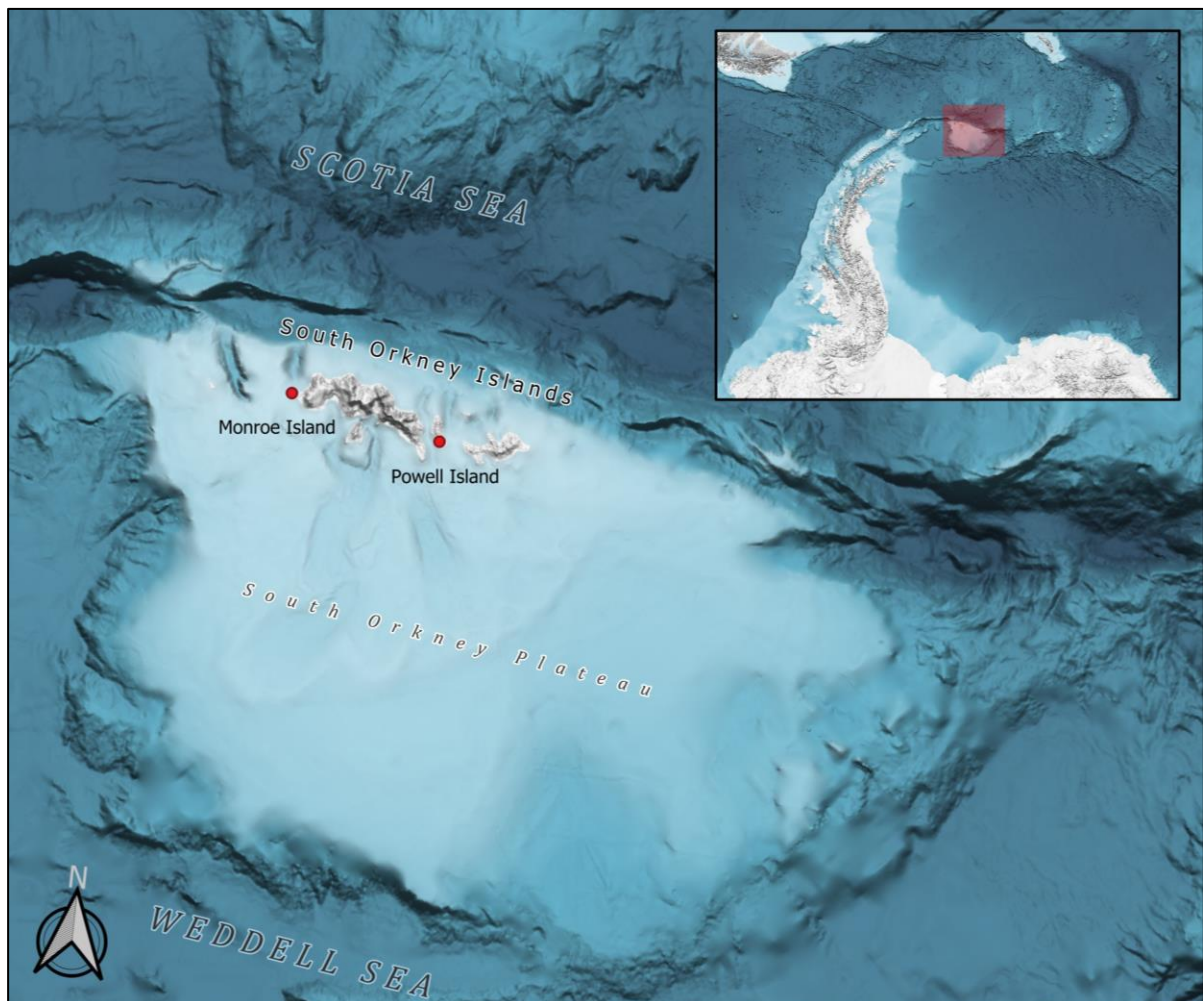


Figure 1. Inlet map of the South Orkney Islands and the surrounding seas. The two tagging sites on Powell and Monroe Island are marked with a red point. Map data was obtained from Dorschel et al. (2022).

weight, or breeding success) was recorded. Penguins were caught by hand and briefly restrained during the attachment and retrieval of the instruments. The data loggers were securely attached to the dorsal feathers in the middle of the back using Loctite glue and Tesa tape. The loggers recorded GPS positions and Time-Depth Recordings (TDRs) for each individual. The instruments were retrieved after a minimum of one trip, with some loggers collecting data over multiple trips.

## 2.2 Data processing

The analysis was done in R (R version 4.3.2, R Core Team (2023)) using R studio (RStudio version 2023.12.1.402, Posit team (2024)). The dive statistics were calculated using the *diveMove* package (Luque, 2007).

### 2.2.1 Definition of trips and homeranges

Trips were defined using the colony coordinates (Monroe colony is located at 60°35'46.0"S 46°1'45.8"W and Powell at 60°44'03.0"S 45°01'18.7"W) as start location. A threshold distance of 1000 meters from the colony was established to define a trip for each individual. A trip started when this threshold is crossed and ended when the individual penguin entered it again; trips shorter than 1 hour were removed to exclude activities like bathing etc. near the colony in order to only identify actual foraging trips. The trip direction, which was determined by using the GPS position that was furthest away from the colony, was divided into 45° bins: 337.5-22.5° (north), 22.5-67.5° (northwest) etc.).

The GPS positions from the trips were then used to calculate homeranges based on the Brownian bridge approach which in comparison to a classic kernel homerange takes into account the trajectory between the relocations of an animal. This was done with the *adehabitatHR* package (Calenge, 2023). To avoid the inclusion of erroneous GPS locations, the relocations were checked for speed outliers using 10m/s as the threshold according to (Phillips et al., 2021). Afterwards the Brownian bridge homerange was calculated using the *kernelbb()* function from the *adehabitatHR* package (Calenge, 2023). *kernelbb()* utilizes two smoothing parameters, sig1 and sig2, with sig2 being the imprecision of the relocations (10 meters for the used GPS tags). Sig1 on the other hand was estimated by the *liker()* function for each individual. The homerange of each tagged penguin was calculated with their unique sig1 values to portray the individual variation. Lastly, due to the discrepancy in sampling size between the two years/islands, no comparison between the homeranges of the two colonies was done and the homeranges itself were mostly used to identify relevant krill stations.

## 2.2.2 Dive classification

The methodology outlined by Lesage et al. (2011) and Krafft et al. (2011) was used to classify the dives in this study (overview given in Figure 2). To avoid the problem of collinearity the dive variables were first introduced to a Principal Component Analysis (PCA) to reduce collinearity in their data before a combination of hierarchical and non-hierarchical clustering was used to sort the dives into distinct clusters based on their properties, utilizing the strength of each clustering algorithm. The dive properties were obtained from the TDRs which after inspection were zero-offset corrected to account for the instrument drift and calculated using the *diveMove* package (Luque, 2007). The dive statistics included descend time, bottom time, ascend time, dive duration, descend distance, bottom distance (defined as the cumulative depth difference in the bottom phase of the dive), ascend distance, mean bottom depth, maximum depth and post dive duration. Additional dive parameters were calculated in order to describe the dives in more detail which included dive efficiency, dive frequency, bottom-time-per-depth ratio, and average ascend and descend rates. Dive efficiency was calculated based on Kokubun et al. (2010) which use the common formular of ‘bottom time / (dive duration + post dive duration)’ (Ydenberg, 1988; Zimmer et al., 2010) with a cutoff of 200s for the post dive

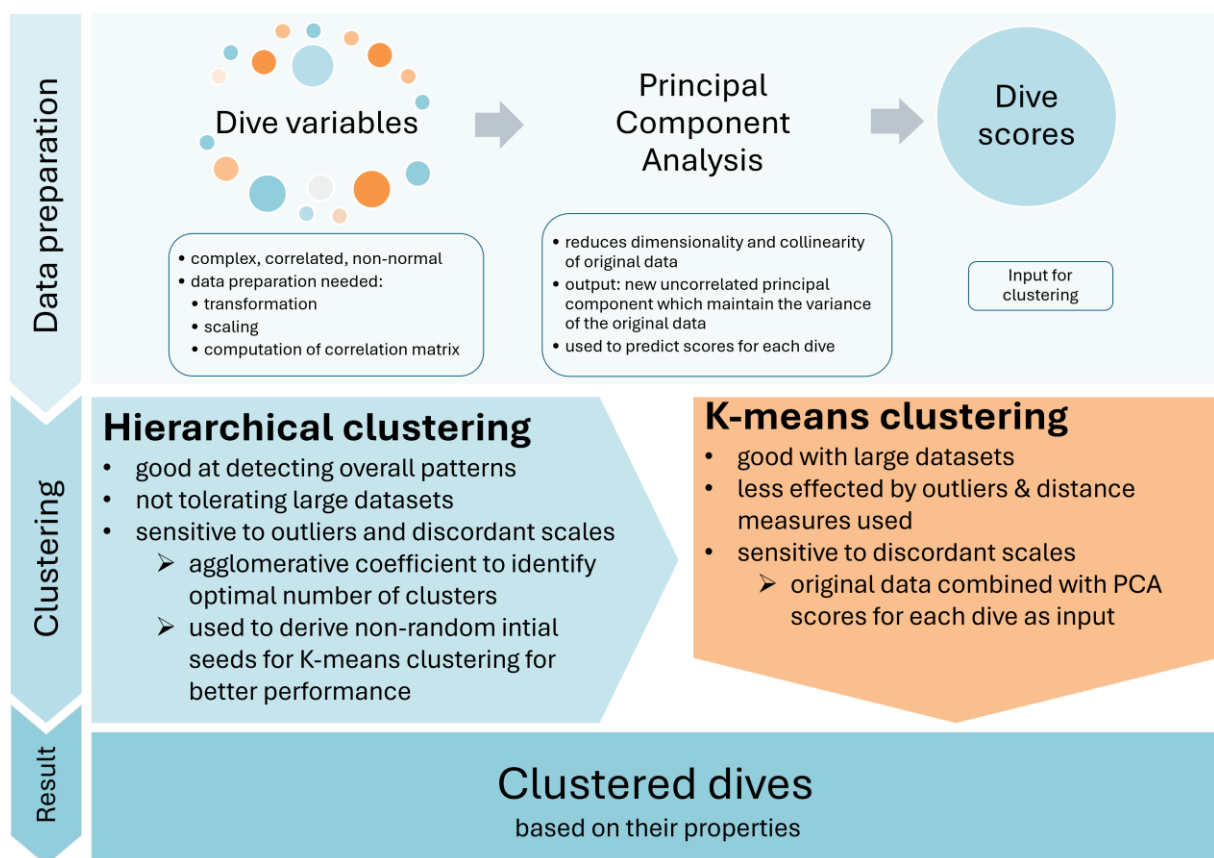


Figure 2. Overview of the methodology of the dive classification based on Lesage et al. (2011) and Krafft et al. (2011).

duration. Dive frequency was defined as the number of dives per hour of each individual (Kokubun et al., 2010). Bottom-time-per-depth ratio calculated as 'bottom time/maximum depth' gives an insights into the duration an individual spent in the bottom phase of a dive relative to the depth reached (Lesage et al., 2011). Average ascend rate (ascend distance/ascend time) as well as the average descend rate (descend distance/descend time) can give indication of the skewedness of a dive, possibly hinting at foraging as opposed to simply diving during these phases.

A multicollinearity test on all the variables was performed using *multicollinearity()* function from the *performance* package (Lüdecke et al., 2021) to ensure none of the variables were highly collinear, ensuring easier interpretability of the PCA results. The dive variables were tested for normality using the Kolmogorov-Smirnov test and none of the variables showed normal distribution. A PCA does not necessarily require normal distributed data, however according to Lesage et al. (2011), it might provide more clarity in the results. Therefore, the data was square root or natural log transformed based on which of the transformations was able to achieve a higher similarity to a normal distribution. Since both the PCA and clustering methods are sensitive to discordant scales, the variables were standardized using the *scale()* function in R. A correlation matrix was computed using the *cor()* function which then serves as the input for the PCA. A first PCA was done using the *princomp()* function from the *stats* package (R Core Team, 2023). According to the latent root criterion, which suggests retaining only factors with an eigenvalue greater than 1 or those explaining more than 5% of the variance, only the first three factors of the PCA were retained. The number of factors that should be retained should be known before doing the PCA again with the *principal()* function from the *psych* package since that function does essentially the same as the *princomp()* function but requires a specified number of factors, which in my case is three. This function was used to apply the varimax rotation to the matrix ensuring easier interpretability of the results, following the methods of Lesage et al. (2011) closely. Using the loadings of the PCA, one score per factor for each dive was predicted. The resulting scores and uncorrelated factors are used further in the cluster analysis ensuring that these methods are not impacted by multicollinearity. The PCA itself was cross validated using data partitioning and inspecting the consistency of the results, which showed high consistency in the proportion of variance explained, the cumulative variance explained varied from 98-100% and the Root Mean Square of the Residuals (RMSR) stayed low across all results (0.1).

Hierarchical clustering is good at detecting the general patterns and provides a quick visual inspection of your data but at the same time does not well with large datasets and tends to be sensitive to outliers. It is therefore used to determine the optimal number of clusters and provide non-random seed points for the k-means clustering, which in contrast to the former can handle large datasets well, is less perceptible to outliers and performs slightly better with non-random seed points.

*kNNdist()* from the *dbscan* package (Hahsler & Piekenbrock, 2023) was used to determine the 10<sup>th</sup> neighbor distance and all datapoints, whose 10<sup>th</sup> nearest neighbor distance was below the threshold of the 10<sup>th</sup> percentile distance, were removed. This was done to remove outliers and get a more precise result with the hierarchical clustering. Since hierarchical clustering cannot handle large datasets, five random subsamples of 1000 dives and introduced to the complete-linkage hierarchical clustering. Complete linkage clustering is an agglomerative approach to clustering where at each level the two clusters with the smallest maximum distance between them are merged resulting in tightly linked and distinct clusters. The maximum change in the agglomerative coefficient (defined as the squared Euclidean distance between two clusters merging, with a large coefficient indicating bigger differences in the two clusters) was calculated for 2-10 clusters to identify the optimal number of clusters. These two steps were repeated for 1000 iterations until the estimate for the optimal number of clusters stabilized around 7.51. In order to decide if 7 or 8 clusters should be used further on, both clustering results were inspected. Since the 8<sup>th</sup> cluster seemed to only add a subcategory of an existing cluster which would not necessarily add more meaning to the analysis, it was decided to use 7 clusters further on for better interpretability.

The cluster centroids were extracted from the complete-linkage clustering and used as the nonrandom, initial seeds in the non-hierarchical K-means clustering. K-means clustering using the *kmeans()* function from the *stats* package (R Core Team, 2023) was performed on the complete dataset of dives scores and factors. The function itself automatically iterates and adjust the cluster centroids until convergence or the maximum number of iterations (by default 10) is reached. The properties of each cluster (achieved by linking the dive scores and factors with original, untransformed dive data) gave insight into the dive shapes and distinct ranges of each cluster in regard to my input variables allowing for ecological interpretation. Due to non-normality and uneven dispersion of the data for each dive cluster, a non-parametric Kruskal-Wallis test was used to test for the difference between dive clusters for each variable. This was followed up with a pairwise Wilcoxon test to identify where the dive clusters might or might

not differ. A PERMANOVA was done to test for differences between the years for each dive shape.

The package *suncalc* (Thieurmél & Elmarhraoui, 2022) was used to determine the sun's position for each time and location of a given dive and categorize them into 'Nautical Twilight' (sun elevation  $> -12^\circ$  below horizon), 'Civil Twilight' (sun elevation  $> -6^\circ$  below horizon) and 'Daytime' (sun elevation  $> 0^\circ$  above horizon); astronomical twilight and night are not occurring during the sampling period.

### 2.2.3 Interpolating dive locations

GPS and TDR recordings are mutually exclusive methods: the GPS only records when penguins are at the sea surface or on land, able to connect to a satellite, while TDRs only record when the penguin is underwater. The *move* package (Kranstauber et al., 2023) provides a function called *interpolateTime()* that allows the user to interpolate trajectories and obtain the positions of given timestamps. In order to do that the GPS locations are essentially connected by linear trajectories (Euclidean distance as a space interpolation function was used) in chronological order for each individual. The dive timestamps, along with their IDs and dive type classifications, were extracted from the clustered dive dataset. The *interpolateTime()* function then estimated the dive locations based on the provided GPS positions, timestamps, and IDs. This method was applied to all seven types of dives identified in the clustering analysis, yielding the original timestamps and interpolated locations for each dive. These locations were visualized with the *stat\_density\_2d()* function from *ggplot2* (Wickham, 2016). The centers of these estimates were extracted for each colony and dive shape and the distance between colony and 'hotspot' was calculated using the *distHaversine()* function from *geosphere* (Hijmans, 2023).

### 2.2.4 Prey availability

The krill density data used in this study was obtained from the annual acoustic-trawl krill survey conducted by the Norwegian Institute of Marine Research (IMR) in collaboration with the krill fishing industry (Skaret et al., 2023). The surveys in 2022 and 2023 were conducted by the cargo vessel "Antarctic Provider", which was equipped with Simrad EK80 (18 kHz) and EK60 (38, 70, 120 and 200 kHz) echo sounders (Krafft et al., 2023) in the periods 9<sup>th</sup> – 17<sup>th</sup> of February



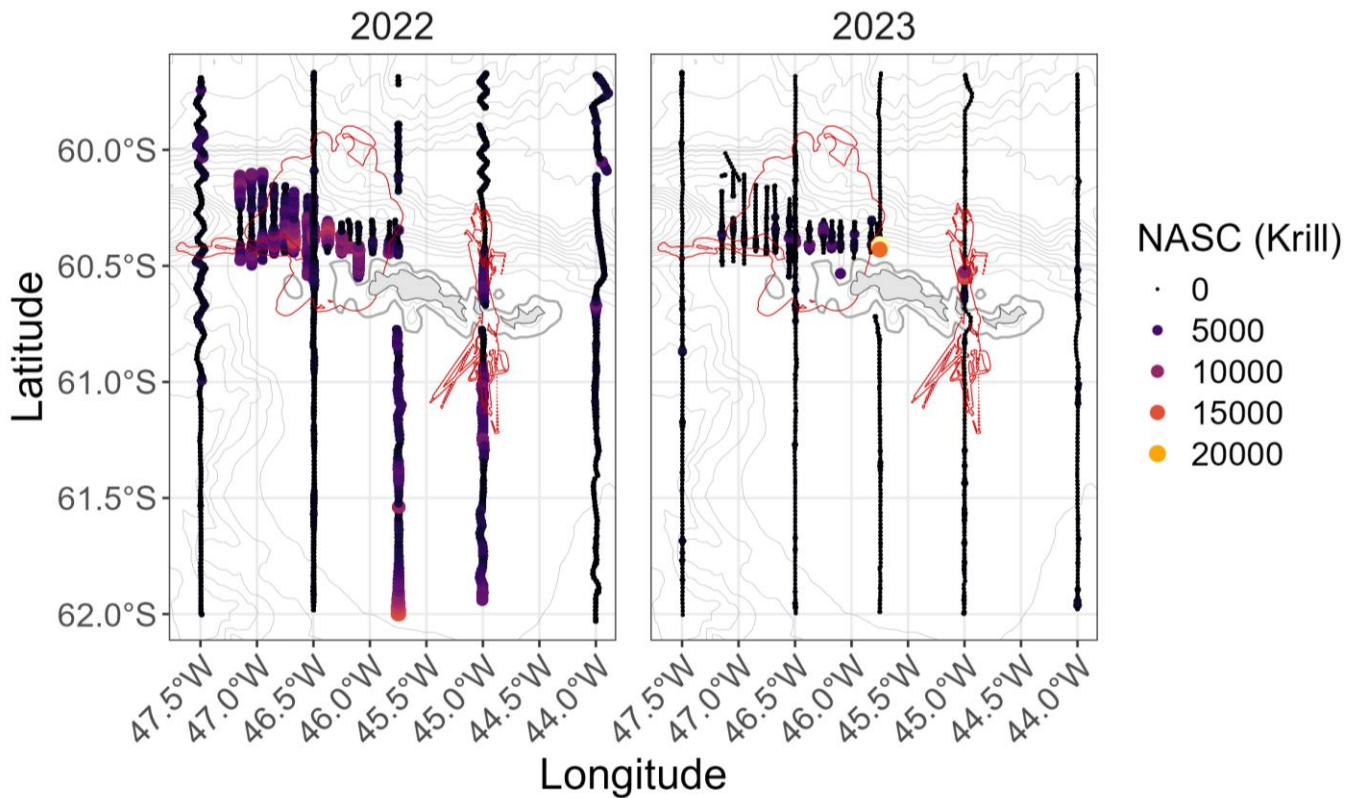


Figure 3. Overview of the transects of the acoustic krill monitoring survey in 2022 and 2023. The five main transects and the denser sampling grid in the main fishing area northwest of the South Orkneys are shown. Cumulative NASC values detected at each station indicated by the size and colour. The outline of the occurrence distribution of the penguins from each colony are shown in red.

and 28<sup>th</sup> of January – 2<sup>nd</sup> of February 2023, respectively. The acoustic data (Nautical Area Scattering Coefficient; NASC) was integrated over one nautical mile and 10-meter depth segments. The deepest NASC of krill was detected up to 360 meters depth within the homerange and 440 meters depth outside the homerange. The survey area covers the shelf area in the south of the South Orkney Islands as well as the shelf edge and submarine canyons in the north (Figure 3), surveying a total area of > 60000 km<sup>2</sup> (Skaret et al., 2023). This particular shelf edge has historically been the location with the highest krill catches which led to the establishment of an additional more dense sampling grid in this subarea (Skaret et al., 2023). The data was scrutinized using an Echoview work template for a standard swarm-based technique for krill discrimination on 120 kHz and was implemented using the Large Scale Survey System (LSSS) (Krafft et al., 2023).

### 2.2.5 Linking predator and prey

The krill surveys were conducted ca. 14-21 days and 2-14 days after the penguin tagging in 2022 and 2023, respectively. This lack of temporal overlap between krill surveys and penguin data did not allow for fine-scale analysis of predator-prey interactions. The krill data was therefore aggregated at a coarser scale and was pooled into ‘within’ and ‘outside’ the



homerange of the colonies for each year. The homeranges were then used to identify the krill sampling stations inside and outside the areas accessible to breeding penguins. Krill sampling around Powell Island did not capture the diel variation that is needed for my analysis since the transect that overlaps with the homerange of the Powell colony can be completed in a few hours. Consequently, the analysis of predator-prey interactions focuses mostly on the Monroe colony and krill distribution within the homerange of the penguins in 2022. Two assumptions were made in that regard: First, that the depth distribution of the krill does not change significantly in the time lag between the tagging of the penguins and the krill survey. Second, all the detected NASC values in 2022 within the homerange of the Monroe penguins that match up with the depth and hour of the respective dives are theoretically potential foraging targets.

The link of predator and prey was analyzed in two ways: (1) comparing the foraging dives to the mean distribution of krill during each hour of the day (Figure 7) and (2) comparing the krill densities that match up with the depth of each dive (referred to later on as potential foraging target, Figure 9) with the highest krill densities of that hour in order to find out which krill densities chinstraps tend to exploit.

The mean distribution of krill was calculated by taking the average of all stations for each depth segment within each hour of the day. The foraging dives (this includes all u-dives) were also averaged for each hour of the day. The krill densities that fell within the horizontal and vertical ranges of penguins were identified by matching up the maximum depths of each dive with the NASC values at that specific depth for that specific hour (Figure 9). The highest krill densities were aggregated by filtering for the highest densities for each station and taking an hourly average of these maximum values (referred to as average krill maxima, Figure 9). In order to find out the average depth distribution of these highest krill densities a weighted mean was used, giving higher NASC values more weight in order to achieve a more accurate estimate of where the krill maxima's might be distributed for each hour.

Lastly, the difference of the depth distribution of the highest krill densities for each station within and outside the homerange for 2022 and 2023 was tested (Figure 8, the underlying data is visualized in Figure Appendix 6 and Figure Appendix 7). The krill data from within the homerange is from the Monroe homerange for both years. The highest krill densities are aggregated for two depth subsets, the first one is the whole water column, and the second one is the 'penguin subset' which provides a closer look of the NASC values that are within diving depth of the penguins. For each of the depth subsets the highest krill densities for each station

within each hour of the respective year were filtered out. Due to non-normality of the data a Mann-Whitney U test was used to test for if the depth distribution of the highest krill densities differed within vs. outside the homerange for the respective year. The level of significance ( $\alpha$ ) was set at 0.05 for all statistical analyses.

### 3 Results

#### 3.1 Foraging trips & homerange

		Monroe Island	Powell Island
<b>Sampling overview</b>	<i>Sampling duration</i>	05.01. – 02.02.2022	16.01. – 26.01.2023
	<i>Colony coordinates</i>	60°35'46.0"S 46°1'45.8"W	60°44'03.0"S 45°01'18.7"W
	<i>Individuals tagged</i>	66 (31)*	14
<b>Homerange</b>	<i>Mean area</i>	922.2 ± 426.5 km <sup>2</sup>	96.9 ± 64.3 km <sup>2</sup>
	<i>Minimum – maximum area</i>	88.6 – 1637.3 km <sup>2</sup>	1.1 – 204.0 km <sup>2</sup>
	<i>Total area</i>	4425.0 km <sup>2</sup>	842.5 km <sup>2</sup>
<b>Trip summary</b>	<i>Total number of trips</i>	84	44
	<i>Mean number of trips by individual</i>	2.7 ± 1.3	3.1 ± 1.4
	<i>Mean distance</i>	44.5 ± 16.7 km	23.5 ± 16.4 km
	<i>Minimum – maximum distance</i>	4.1 – 93.2 km	1.3 – 56.0 km
	<i>Mean duration</i>	12.8 ± 8.2 h	11.0 ± 14.8 h
	<i>Minimum – maximum duration</i>	1.2 – 41.4 h	1.2 – 93.3 h
	<i>Trip direction</i>	136 N, 43 NW, 2 SW, 12 W	19 N, 8 NE, 1 E, 4 SE, 10 S, 2 SW

Table 1. Overview of sampling, homerange estimates and trips of the chinstrap penguins from Monroe and Powell Island. The homerange estimates are based on the values for a 95% confidence interval showing minimum and maximum, mean and standard deviation as well as total area (all in km<sup>2</sup>) estimated. The trip summary includes of the total and mean number of trips, distance and duration, minimum and maximum distance and duration as well as the trip direction of the trips done by the chinstrap penguins from Monroe and Powell Island. \*The number in the brackets indicates the number of tagged individuals used for the analysis due to cropping of the sampling duration.

The 31 chinstrap penguins from Monroe Island took a total of 84 trips during the sampling period, while the 14 individuals from Powell Island made 44 trips, averaging in  $2.7 \pm 1.3$  trips per individual for Monroe and  $3.1 \pm 1.4$  trips per individual for Powell (Table 1). There was a high individual variation in trip distance and duration for both colonies. However, the chinstraps from Powell tended to undertake shorter trips on average ( $23.5 \pm 16.4$  km) than the chinstraps from Monroe ( $44.5 \pm 16.7$  km, Table 1). Chinstrap penguins from Monroe Island travelled predominantly north, while those from Powell Island primarily undertook trips northwards, with a notable proportion traveling southwards (Table 1).

The homerange (95% confidence interval) of the 31 and 14 penguins on Monroe and Powell Islands was estimated  $4425 \text{ km}^2$  and  $842.5 \text{ km}^2$ , respectively (Table 1). There was major range in both the minimum and maximum estimates, as well as in the mean area estimates, between the two locations (see Figure Appendix 1 for more details).

### 3.2 Identified dive types & their properties

The combined clustering method resulted in seven clusters, categorized into distinct shapes based on dive properties. These include u-shaped and v-shaped dives (hereafter referred to as u- and v-dives). All dives have a descend and ascend phase, but they differ in their bottom phases. U-dives are dives with a prolonged bottom phase which is typically associated with foraging behavior (Schoombie et al., 2024), resulting in a u-shaped dive profile. V-dives are dives without a bottom phase or a very short bottom phase, resulting in a v-shaped dive profile (Halsey et al., 2007). They are often considered exploratory dives, but they may involve lower

<i>Dive shape</i>	<i>Maximum depth (m)</i>	<i>Dive duration (s)</i>	<i>Bottom time (s)</i>	<i>Bottom distance (m)</i>	<i>Post dive duration (s)</i>	<i>Dive frequency (dives/h)</i>
deep U-dive	$71.6 \pm 30.0$	$108.4 \pm 33.8$	$18.6 \pm 9.7$	$12.0 \pm 9.3$	$66.0 \pm 37.0$	$53.5 \pm 28.9$
deep V-dive	$79.0 \pm 30.5$	$116.6 \pm 28.1$	$1.0 \pm 0.2$	$0.4 \pm 0.4$	$79.0 \pm 45.2$	$49.4 \pm 27.9$
medium u-dive	$31.9 \pm 18.6$	$80.2 \pm 28.4$	$28.2 \pm 14.0$	$15.6 \pm 12.4$	$39.7 \pm 22.9$	$80.4 \pm 41.2$
medium v-dive	$23.6 \pm 15.5$	$56.2 \pm 24.4$	$1.2 \pm 0.7$	$0.3 \pm 0.3$	$45.8 \pm 33.1$	$82.2 \pm 49.0$
shallow u-dive	$17.7 \pm 11.7$	$42.2 \pm 18.1$	$18.4 \pm 9.3$	$10.6 \pm 8.0$	$29.6 \pm 16.6$	$123.3 \pm 56.9$
shallow v-dive	$7.9 \pm 5.1$	$13.9 \pm 9.3$	$2.1 \pm 1.4$	$0.5 \pm 0.6$	$44.3 \pm 35.8$	$103.1 \pm 64.0$
travelling dive	$5.2 \pm 4.2$	$3.8 \pm 2.9$	$1.5 \pm 1.1$	$0.5 \pm 1.8$	$38.4 \pm 40.0$	$102.2 \pm 58.3$

Table 2. Summary (given as mean  $\pm$  standard deviation) of the dive properties namely maximum depth (in m), dive duration (in s), bottom time (s), bottom distance (in m), post dive duration (in s) and dive frequency (in dives/hour) for each type of dive of the chinstrap penguins in the South Orkney Islands. Colours indicate lowest (white) to highest (blue) value for each variable. See Table Appendix 1 for additional properties.

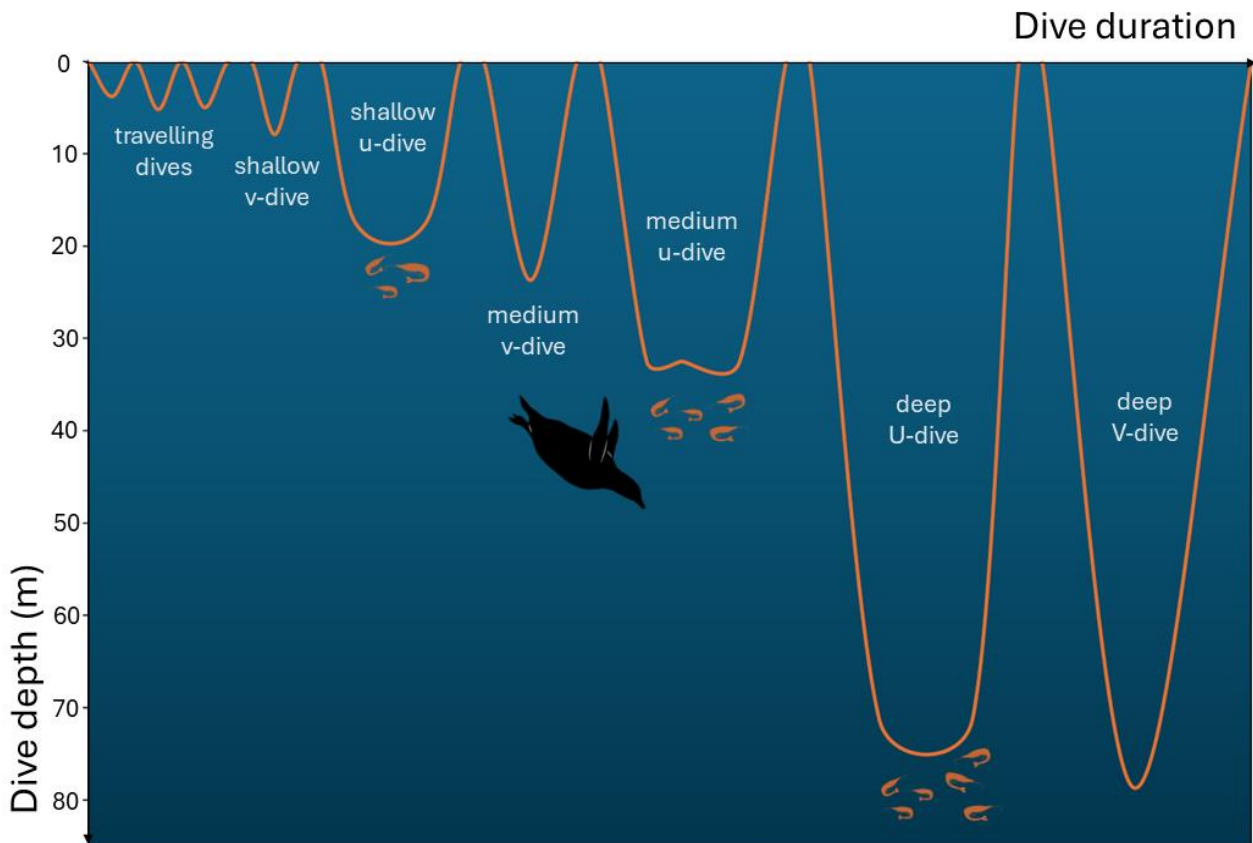


Figure 4. Schematic depiction of the different dive shapes found for the chinstrap penguins in the South Orkney Islands based on the properties of the cluster results. Increasing dive duration is indicated by the horizontal axis. Dive depth is based on the clustering results. Foraging dives (shallow, medium and deep u-dives) are additionally marked by the krill pictograms in the bottom phase of the dives. Pictograms obtained from Freepik.

rates of prey consumption and serve as predator avoidance behavior, too (Halsey et al., 2007; Schoombie et al., 2024). Travelling dives are a type of v-dive but serve different purpose. They are characterized by being frequent, shallow and short dives used for travelling (Phillips et al., 2021). Both u- and v-dives occurred in three different depth categories: shallow, medium, and deep (Figure 4).

Deep V-dives tended to be the deepest dives ( $79.0 \pm 30.5$  m) with the longest dive duration ( $116.6 \pm 28.1$  s), closely followed by the deep U-dives ( $71.6 \pm 30.0$  m deep and  $108.4 \pm 33.8$  s long, Table 2). All types of v-dives including travelling dives were characterized by their short bottom time and bottom distance, rarely exceeding  $2.1 \pm 1.4$  s or  $0.5 \pm 1.8$  m (Table 2), leading to their V-shape. Deep V-dives also had the longest post dive duration ( $79.0 \pm 45.2$  s) and lowest dive frequency ( $49.4 \pm 27.9$  dives/h), closely followed by the deep U-dives (post dive duration of  $66.0 \pm 37.0$  s and a dive frequency of  $53.5 \pm 28.9$  dives/h, Table 2). Medium u-dives had the longest bottom time ( $28.2 \pm 14.0$  s), furthest bottom distance ( $15.6 \pm 12.4$  m) and second highest dive efficiency of all dives ( $0.2 \pm 0.1$ , Table Appendix 1). Out of the three types of u-

dives, shallow u-dives had the shortest bottom time ( $18.4 \pm 9.3$  s) and bottom distance ( $10.5 \pm 8.0$  m), but also the shortest post dive duration ( $29.6 \pm 17.0$  s), highest dive frequency ( $123.3 \pm 56.9$  dives/h) and highest dive efficiency of all dives ( $0.3 \pm 0.1$ , Table Appendix 1). Shallow v-dives had the second highest dive frequency with  $103.1 \pm 64.0$  dives/h (Table 2).

Overall, the dive shapes were shown to significantly differ in their properties (Kruskal-Wallis test with a  $p < 0.001$  for all variables summarized in Table 2). However, the pairwise Wilcoxon test showed that there is no significant difference between the bottom time of a deep U-dive and a shallow u-dive. No significant difference was found between the post dive duration of shallow v-dives and medium u-dives as well as between shallow u-dives and travelling dives. Furthermore, no significant difference between the dive frequency of travelling and shallow v-dives as well as for medium u- and v-dives was found. The PERMANOVA revealed a significant difference between the years ( $p < 0.001$ ), but 49.1% of the variance in the data was explained by the dive types and only 0.4% was explained by the year.

### 3.3 Diel foraging pattern of chinstrap penguins

The dives exhibited a daily pattern, with shallow and medium dives dominating during the crepuscular hours, particularly the u-dives (Figure 5). Deep U-dives tended to occur at low rates during the crepuscular hours (used as a summary term for the duration of civil and nautical twilight), peaking at the end of dawn with a second peak at the beginning of dusk. During the daytime, the number of deep U-dives showed no clear pattern and occurred on average rates

	<i>Monroe Island</i>	<i>Powell Island</i>	<i>Total</i>
<b>Number of dives, n</b>	22406	9681	32087
<b>Type of dives</b>	-	-	-
foraging	12793 (57 %)	5426 (56 %)	18219 (57 %)
exploratory	8414 (38 %)	3769 (39 %)	12183 (38 %)
travelling	1199 (5 %)	486 (5 %)	1685 (5 %)
<b>Time of day</b>	-	-	-
Daytime	11796 (53 %)	6238 (64 %)	18034 (56 %)
Civil Twilight	4109 (18 %)	1403 (15 %)	5512 (17 %)
Nautical Twilight	6501 (29 %)	2040 (21 %)	8541 (27 %)

Table 3. Summary of the number of dives categorized in regard to the type of dive (foraging, exploratory or travelling) and the time of day (Daytime, Civil Twilight or Nautical Twilight) in total and for each penguin colony.

(Figure 5). Similarly, deep V-dives peaked at the beginning of dusk, occurred at low rates during the crepuscular hours, and at a medium rate during the daytime (Figure 5).

For both years, the majority of the dives (57%) were spent foraging (this includes all u-shaped dives), while 38% percent of the dives were categorized as exploratory (this includes all v-shaped dives, Table 3). Even though civil twilight occurs for approximately 10% of the day during the austral summer in the South Orkney Islands, the dives during civil twilight made up 17% of the total number of dives. Similarly, nautical twilight occurs for approximately 16% of the day, but the dives during that period made up for 27% of the total dives. Daytime, which makes up approximately 74% of the day during austral summer, only accounted for 56% of the

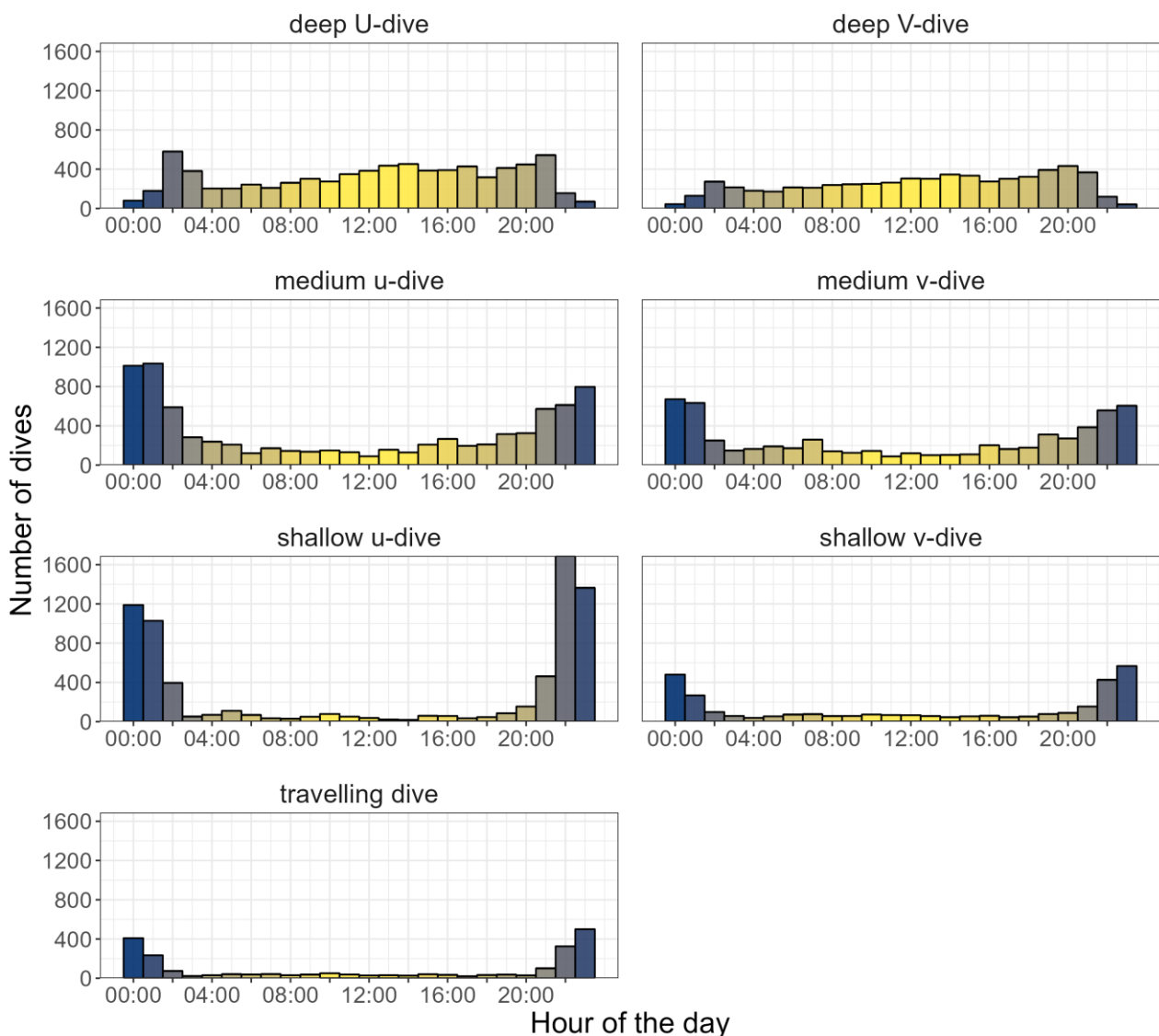


Figure 5. Histogram of the number of dives summed up by hours of the day for each type of dive indicating the daily patterns of the chinstrap penguins in the South Orkney Islands. The colour scale indicates the amount of light during the hours of the day (from low (blue) to high (yellow)).

total dives (Table 3). Note that due to the high latitude and the sampling duration overlapping with austral summer, no astronomical twilight or night occurred.

The dive locations varied throughout the day: Chinstrap penguins for both Monroe and Powell Islands tended to forage further offshore during the crepuscular hours than during the day. The interpolation of the dive locations revealed more pronounced sometimes multiple ‘hotspots’ during civil and nautical twilight while daytime dive locations were mainly situated just outside the colony, extending slightly in the predominant trip directions for each colony (Figure 6).

Analyzing dive types that constituted more than 15% of the dives during each respective time of day revealed that deep dives were most predominant during the daytime (Figure 6). Meanwhile medium dives seemed to be more influential during the civil twilight. Nautical twilight was the only time of the day where all three types of u-dives seemed to be occurring

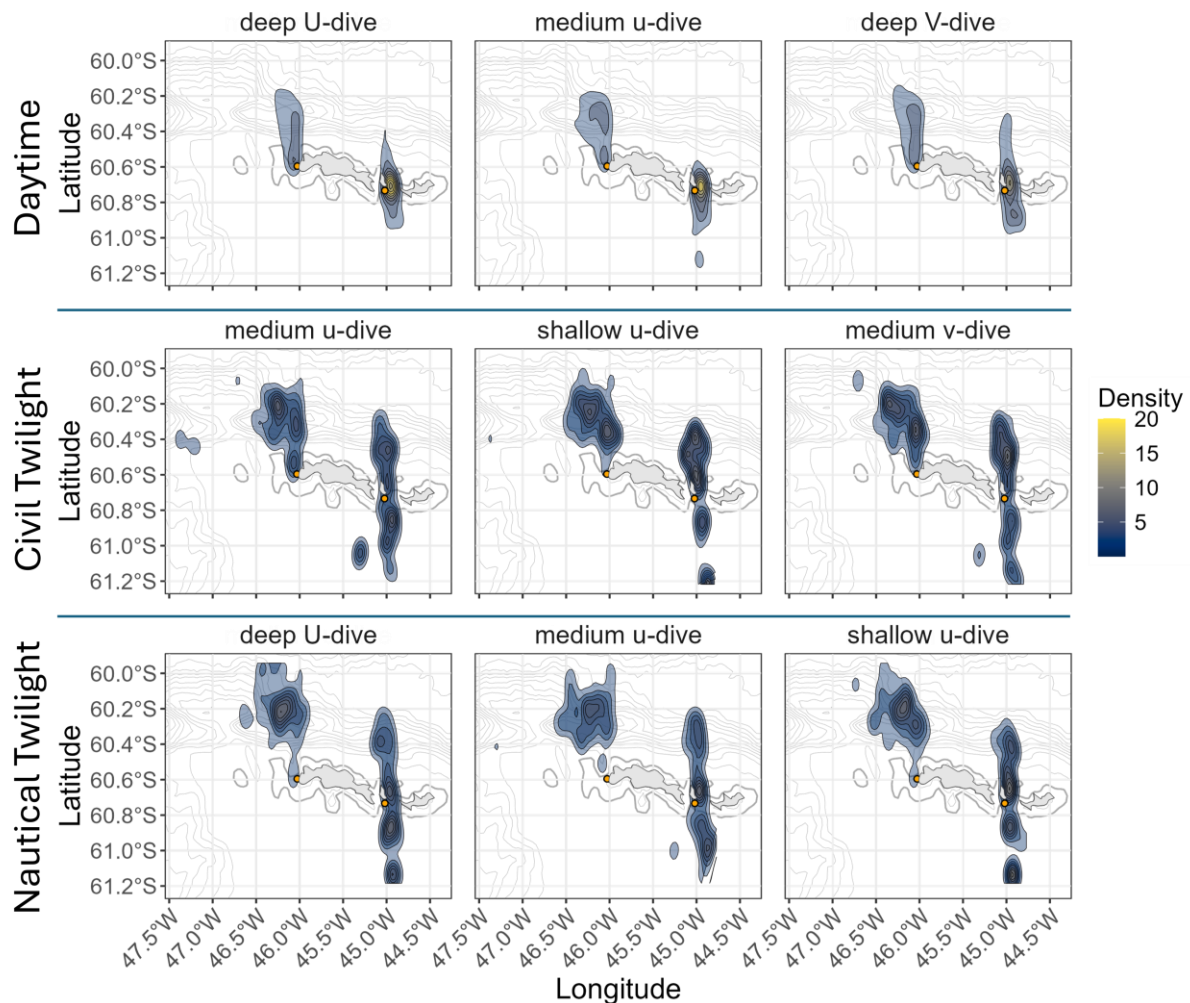


Figure 6. Selection of the dive types that make up for more than 15% of the dives during the time of day they occurred (Daytime, Civil Twilight and Nautical Twilight) visualizing their locations. Density can be seen as a relative measure of the probability of a dive occurring in a certain place (the higher the more likely it is). Bathymetric contours are in 500m depth intervals except the first thicker contour marking 100m depth. See also Figure Appendix 2, Figure Appendix 3 and Figure Appendix 4 for a complete overview of all the dives during all times of the day.



the most (Figure 6). The penguins diving ‘hotspot’ during daytime was  $12.8 \pm 15.1$  km away from the colony for the individuals from Monroe Island and  $6.1 \pm 1.0$  km away from the colony for penguins from Powell Island. During civil twilight, the ‘hotspots’ for Monroe Island penguins were on average  $39.4 \pm 11.8$  km from the colony, while for Powell Island penguins, the average distance was  $19.1 \pm 4.8$  km. During nautical twilight the center of the ‘hotspots’ were  $43.9 \pm 1.2$  km from Monroe Island and  $33.1 \pm 20.4$  km away from Powell Island.

### 3.4 Krill density and distribution

There was a high overlap between the denser survey transect, which marks the major fishing areas northwest of the South Orkneys, and the homerange of the penguins from Monroe Island, which extends further north- and southwards (Figure 3).

The depth distribution of the highest krill values for each station in 2022 was significantly different between inside and outside the homerange for both the entire water column ( $p < 0.001$ ) and for the subset of the maximum diving depth of the penguins ( $p < 0.001$ , Figure 8). However, in 2023, there was no significant difference in the krill distribution within and outside the homerange for either the whole water column or the subset (Figure 8).

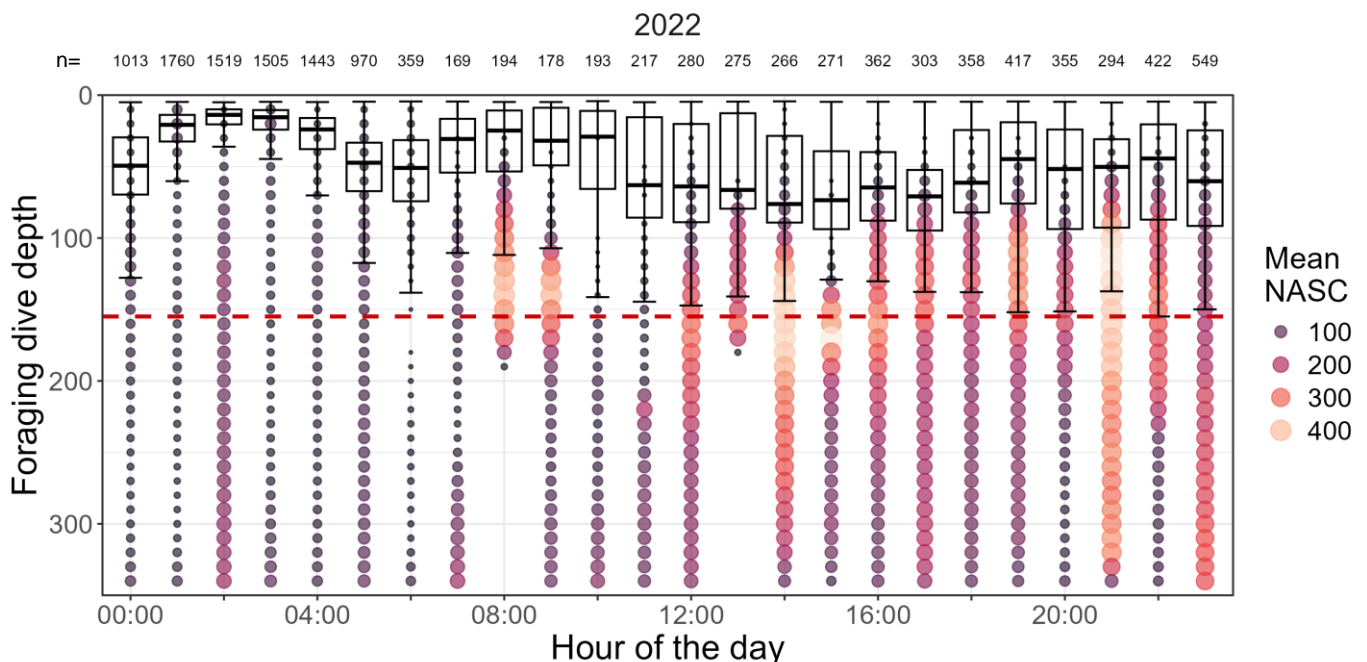


Figure 7. The average distribution of krill in 2022 for the whole water column is shown by the bubbles (zero values removed for clarity). The boxplots summarize the diving depth of all foraging dives for the respective hour of the day. Maximum diving depth of the penguins is indicated by the dashed line and the number of dives for each hour of the day is shown above the respective boxplot. (See also Figure Appendix 5 for a zoomed in version of the plot focusing on the subset of the maximum diving depth of the penguins). The boxplots are showing the 25% (upper line), 50% or median (middle line) and 75% quantiles of the data; the whiskers show the minimum (upper) and maximum (lower) values, respectively, and outliers, if occurring, are shown as single dots beyond that.



The upper values of the mean NASC distribution regularly overlapped with the dive depths of the foraging dives (Figure 7). However, higher NASC values of the krill were often situated deeper than the penguins dive depths, as observed in the distribution of both the maximum and mean NASC values (Figure 9, Figure Appendix 5, Figure Appendix 6).

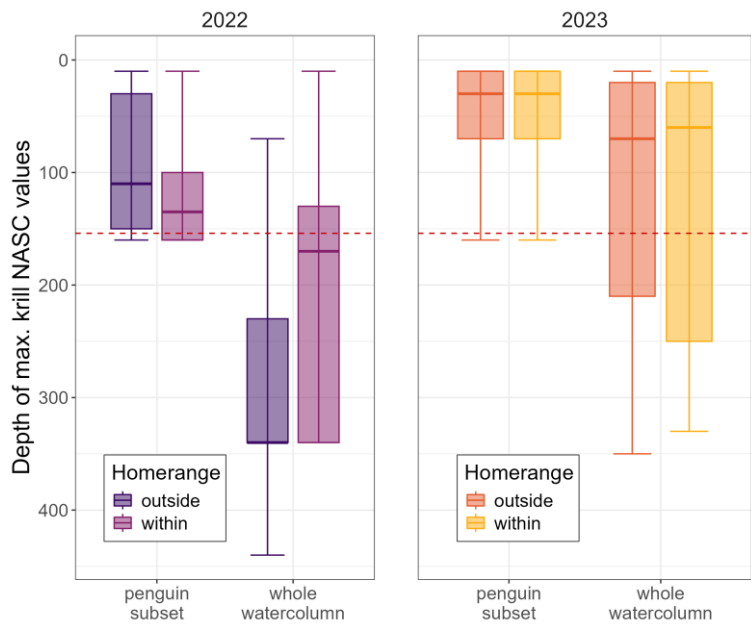


Figure 8. Boxplots showing the depth distribution of the krill maxima for 2022 and 2023 within and outside the homerange of Monroe Island for the whole water column and the subset according to the maximum diving depth of the penguins. The boxplots are showing the 25% (upper line), 50% or median (middle line) and 75% quantiles of the data; the whiskers show the minimum (upper) and maximum (lower) values, respectively, and outliers, if occurring, are shown as single dots beyond that. Red dashed line indicating the maximum diving depth of the chinstraps.

In 2022, matching the individual dive depths with the potential average NASC values at those depths within the homerange showed

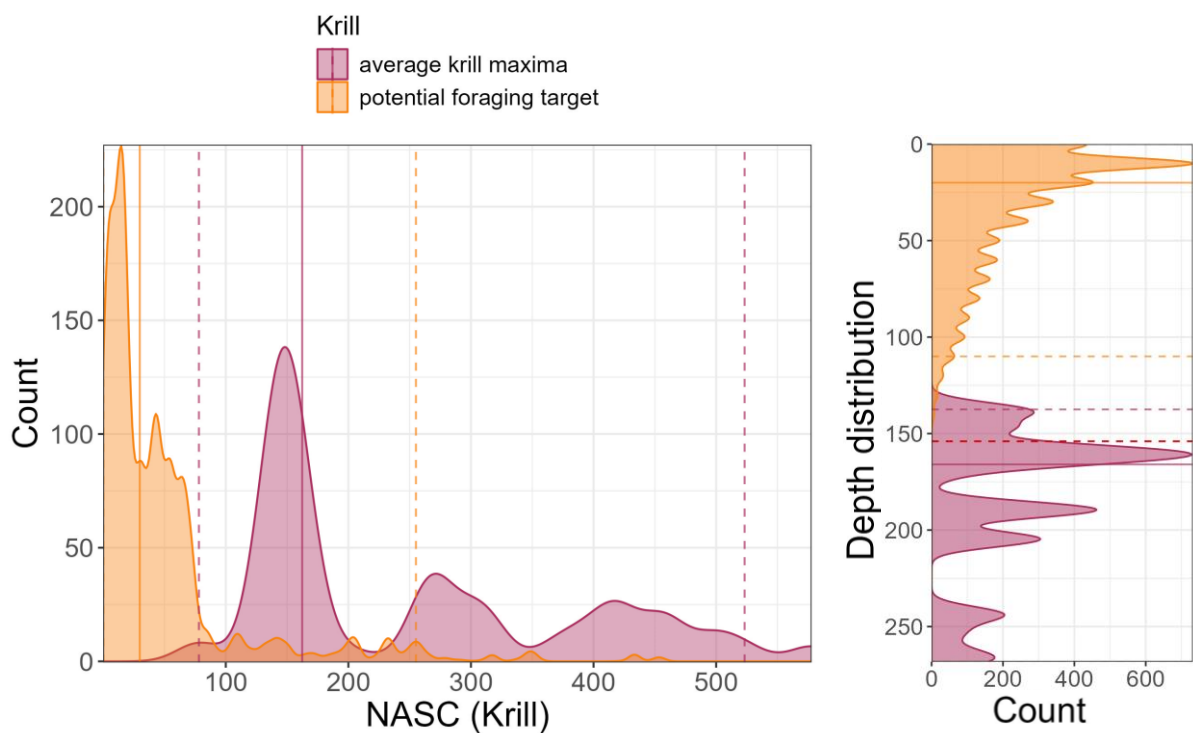


Figure 9. Figure (left) showing the NASC values of the krill in 2022 that match up with the foraging dive depth and the hour of the day, meaning these are the krill densities that could be a potential foraging target (orange). The values of the hourly averaged maximum krill values are shown in comparison (violet). Figure on the right shows the depth distribution of the NASC values shown in the left figure (maximum diving depth of the penguins shown as red dashed line). For both plots the first (dashed), second (solid) and third quantile (dashed) of the 95% confidence interval are shown in the respective colour of the curve they belong to; if a quantile is not visible it is due to its overlap with the plot border.

that the NASC values of krill available to the penguins were not only visibly lower (median NASC of 30 m<sup>2</sup> per nautical mile<sup>2</sup> for potential krill targets) but also showed little overlap with the average NASC values that make up the krill maxima (median of 162 m<sup>2</sup> per nautical mile<sup>2</sup> for the highest krill densities, Figure 9). The depth distribution of these NASC values indicated minimal overlap between the depths that the penguins exploit and the depths where the highest krill values were typically found (Figure 9). Only a small proportion of the highest krill densities was theoretically within reach of the penguins (as indicated by red dashed line in Figure 9).

## 4 Discussion

The results of this study revealed a pronounced diel foraging pattern in both the horizontal and vertical at-sea distribution of chinstrap penguins from the South Orkney Islands during 2022 and 2023. These findings provide detailed insights into the temporal dynamics of their foraging trips, dive locations, and dive types, highlighting the crepuscular hours as a previously overlooked ecological niche for chinstrap penguins to avoid competition with sympatrically breeding penguins. Additionally, the data suggests that chinstrap penguins frequently forage at depths with lower krill densities than those at peak concentrations in the water column, indicating that encounter rates, rather than density, may be the key factor in determining suitable prey.

The pronounced and expected diel foraging pattern in chinstrap penguins suggests distinct foraging strategies that are likely influenced by prey availability, particularly the DVM of krill. The penguins tend to intensify their dive efforts and forage further offshore during crepuscular hours (used as a summary term for the duration of civil and nautical twilight from here on), likely taking advantage of prey that becomes accessible at shallower depths due to DVM. During these hours, medium and shallow u-dives dominate, likely enabling the penguins to maximize their food intake. These dives are characterized by long bottom phases, where most prey ingestion theoretically occurs (Schoombie et al., 2024). However, medium u-dives involve a trade-off, as they require slightly longer recovery times, resulting in a lower dive frequency. The high occurrence of deep U-dives during nautical twilight, despite krill theoretically being situated higher in the water column at night, might be a response to increased predation pressure near the surface. Krill may descend to safer depths after feeding (Bahlburg et al., 2023), and the penguins likely follow this downward migration as long as it remains energetically advantageous.

Previous studies have suggested that prey availability generally improves with increasing distance from shore at the South Orkney Islands, supporting the concept of 'Ashmole's halo'—the idea of prey depletion around the central area of distribution of a central foraging species, although environmental variation and natural flux in an area must be considered (Ashmole, 1963; Phillips et al., 2021). Thus, foraging further offshore during night could allow penguins to exploit less depleted prey patches at shallower depths, potentially offsetting the increased travel distance and optimizing their foraging success during nighttime. Although penguins are visual predators, the extent to which they see in low light conditions is still uncertain (Hadden & Zhang, 2023), but the occurrence of nighttime foraging dives suggests that chinstraps are not only capable of navigating but also hunting prey at depth during low-light conditions. Miller and Trivelpiece (2008) demonstrated that chinstrap penguins can forage on myctophid fish at night, likely by detecting their bioluminescence (Hadden & Zhang, 2023). Similarly, euphausiids like krill exhibit bioluminescence (Herring & Locket, 2009; Krafft & Krag, 2021), suggesting that chinstraps can detect krill despite natural light being almost absent. Thus, prey detection at nighttime during the austral summer where the South Orkney Islands only experience civil and nautical twilight may not pose a significant challenge for chinstraps and light conditions may not be a limiting factor in their foraging behavior.

During the daytime, chinstrap penguins tended to forage closer to their colonies but engaged in deeper dives, likely reflecting the diel vertical migration of krill. The frequent occurrence of these deep exploratory and foraging dives suggests lower prey availability in the upper water column during daylight hours. The extended recovery periods and reduced dive frequency following these deep dives indicate their high energetic cost. This overall lower search and foraging frequency, driven by the deeper distribution of krill during the day, may suggest that traveling to the shelf break is too energetically demanding compared to foraging closer to their colonies. However, chinstrap penguins may engage in deep benthic foraging dives during the day, especially over the shelf area, where the depth distribution of krill is limited by the seafloor (Takahashi et al. (2003). This predictable krill depth in certain shelf areas could make these energy-intensive deep dives worthwhile. Although benthic diving was not the focus of this study, it could contribute to foraging success, suggesting that daytime foraging does not necessarily result in lower success due to deeper krill availability. According to Optimal Foraging Theory (OFT), animals aim to maximize energy gain or minimize the time spent obtaining a fixed amount of energy (Stephens & Krebs, 1987). Watanabe et al. (2014) demonstrated that chinstrap penguins forage optimally; the observed diel patterns might

therefore reflect a trade-off between travel time, energy requirements based on krill's diel vertical migration, and food intake optimization. Consequently, chinstrap penguins may adopt different foraging strategies during the day and night to enhance efficiency.

These findings align with previous studies (Ichii et al., 2007; Takahashi et al., 2003), which suggested that chinstrap penguins engage in different types of foraging trips: shorter daytime trips closer to the colonies, with diving occurring over the shelf area, and longer overnight trips farther from the colony, over the shelf break. The diel pattern in dive locations is notable because many studies have already established the diel pattern in dive depth for chinstrap penguins as well as analyzed the competition between the sympatrically breeding pygoscelid species in regard to their homerange and diet composition (Ainley et al., 2015; Kokubun et al., 2010; Lee et al., 2021; Miller & Trivelpiece, 2008; Wawrzynek et al., 2022). These studies established the diet overlap in these three congeneric species, but showed the greater diet flexibility of both gentoo and adélie penguins compared to chinstrap penguins, as well as the tendency of adélie penguins to forage further from the shore (Pickett et al., 2018; Wienecke et al., 2000) and of gentoo penguins to forage over the shelf (Kokubun et al., 2010). Fewer studies however address that the diurnal pattern in chinstrap foraging might help to mitigate competition with adélie and gentoo penguins, which are predominantly foraging during the daytime (Jansen et al., 1998; Miller et al., 2010), and point it out as a potential niche for the species.

The described diel pattern reflects population-level trends, but the wide range in trip duration, distance, and direction suggests significant individual differences in foraging behaviour among chinstrap penguins. Nonetheless, the results are consistent with previous studies (Ichii et al., 2007; Kokubun et al., 2010; Lynnes et al., 2002; Miller & Trivelpiece, 2008). There is no evidence of sex differences influencing foraging behaviour in chinstrap penguins (Lynnes et al., 2002; Miller et al., 2010), reinforcing the idea that this variation is likely driven by individual factors. Several factors could contribute to this variability, including fluctuations in prey availability and distribution, environmental conditions, breeding progress, and individual foraging behaviour. Variations in trip parameters might reflect changes in krill availability throughout the day, influenced by DVM, and across the sampling period, potentially due to the contraction of foraging ranges as chicks grow or improved foraging conditions with increased distance from the colony (Miller & Trivelpiece, 2008; Phillips et al., 2021). Environmental variability, such as changes in wind patterns leading to downwelling and deeper krill aggregations, could also impact chinstrap penguins' foraging behaviour (Lowther et al., 2018;

Salmerón et al., 2023). Both sampling periods in this study occurred during La Niña conditions, with Antarctic summer sea ice extent reaching unprecedented lows in both years (Copernicus, 2023; NOAA). These similar climatic conditions likely minimized behavioural differences between the two years, as supported by PERMANOVA analysis, which attributed only 0.4% of the variance in diving data to the year, suggesting minimal interannual climatic differences. Moreover, individual differences may play a crucial role, as studies on other predator species have emphasized the importance of factors such as individual physiology, age, experience, and sex in determining foraging success. These factors remain subjects of ongoing debate and are likely species-specific (Freeman et al., 2022; Lescroel et al., 2020; Michelot et al., 2021; Patrick & Weimerskirch, 2014). Given the theoretical link between foraging success and the frequency of feeding offspring – critical for their growth and survival (Clarke et al., 2002; Lescroel et al., 2020) – understanding individual foraging behaviour could provide valuable insights into breeding success. Exploring the relationship between individual foraging strategies and reproductive outcomes in chinstrap penguins could be a compelling focus for future research, potentially offering insights into how behavioural plasticity might enhance an individual's climate resilience. This highlights that while population-based trends in diel foraging provide valuable insights, a larger sample size would enhance the robustness of these conclusions, especially considering the potential for high individual variability in foraging behaviour. Furthermore, the uneven sampling size between colonies suggests that the presented patterns should be interpreted with caution.

In examining the horizontal distribution of krill around the South Orkney Islands, it becomes evident that the foraging trips of chinstrap penguins predominantly extend toward or along the northern shelf edge, with only a few individuals from Powell Island venturing south to feed above the plateau, essentially mostly towards areas with high krill abundance. Previous studies have identified the northern and northwestern shelf edge of the South Orkneys as areas of high krill advection and retention due to the region's bathymetric features (Krafft et al., 2018; Young et al., 2024). These conditions are favourable to maintaining high krill densities, as the retention and upwelling processes prevent krill from being carried away by local fronts or currents and simultaneously enhance local primary production. This combination leads to increased food availability for krill aggregations, making the northern shelf edge a reliable foraging spot for penguins (Santora & Reiss, 2011; Skaret et al., 2023). However, the main foraging trip directions may be restricted to certain areas due to the presence of other penguin colonies on the islands, which leads to intra- and interspecific competition (Lee et al., 2021), thereby

partitioning forage areas (Kokubun et al., 2010). Alternatively, penguins may simply choose the fastest routes to the nearest foraging hotspots, minimizing travelling time according to the OFT (Stephens & Krebs, 1987). In this study, krill aggregations were also observed along the northern shelf, reinforcing the idea that this area offers predictable and suitable foraging opportunities for penguins. In contrast, historic snapshots of krill distribution on the southern plateau show that high krill densities appeared in only two of the eleven years within the home range of chinstrap penguins from Powell Island (Skaret et al., 2023). This suggests that the southern plateau may be a less reliable foraging area compared to the northern shelf edge. However, the dynamic nature of krill flux in this region (Young et al., 2024) is not considered, and the available krill data for Powell Island, especially in the south, may be insufficient to accurately determine the specific krill densities that penguins are targeting. Furthermore, Skaret et al. (2023) highlighted that krill biomass estimates can vary depending on sampling effort and location, implying that areas of high krill abundance outside the sampling transect might go undetected. This underscores the need for comprehensive and synoptic data in predator-prey studies to fully understand the factors driving penguin foraging behavior.

Analyzing the vertical distribution of predators and prey reveals that the krill densities available for chinstrap penguins to forage on are, on average, significantly lower than the highest krill densities found within the water column of their homerange. Reaching the daytime depths where krill reside, which is around 100 m – 150 m around the South Orkney Islands on average (Bahlburg et al., 2023), is theoretically possible for chinstrap penguins but highly energy-intensive, as indicated by their dive types. Consequently, it is unsurprising that peak krill concentrations are generally beyond their reach, especially during daytime, leading chinstrap penguins to forage at depths with lower krill densities most of the time. Similar to adélie penguins, chinstrap penguins may concentrate their foraging efforts in areas with numerous krill swarms rather than high overall krill biomass (Riaz et al., 2023). In the context of their foraging mode, chinstrap penguins may even not require high krill densities to be successful, as they target and capture individual krill rather than engulfing large swarms like baleen whales, achieving this with a relatively high success rate (Riaz et al., 2023; Schoombie et al., 2024). For a penguin, a suitable prey patch might therefore be characterized by a high encounter rate with krill swarms rather than a high krill density (Riaz et al., 2023). By selecting these areas with a high swarm encounter rate, penguins can theoretically optimize their food intake while minimizing travel times (Riaz et al., 2023). Future research, utilizing appropriate synoptic and

fine-scale data, could explore whether chinstrap penguins, like adélie penguins, prioritize areas with frequent krill swarms over regions with higher overall krill density.

This analysis has several limitations. The acoustic krill surveys were conducted 2–3 weeks and 2–14 days after tagging the penguins in 2022 and 2023, respectively, which creates a significant challenge in linking predators to their prey. The lack of temporal overlap between tagging and acoustic monitoring, combined with the differing spatial scales of these surveys, limits the ability to make precise connections. While the large-scale krill surveys primarily inform krill fisheries, linking specific krill aggregations to the penguins' foraging dives would necessitate much finer-scale data focused around the colonies. The krill analysis assumes that the depth distribution of krill remains stable during the two sampling periods. However, krill are known to exhibit seasonal variations in depth distribution, abundance, and behavior on a broader scale (Bahlburg et al., 2023), but the timeframe of this study is significantly shorter than those variations. In the absence of significant climate changes affecting depth distribution during the sampling period, as observed in Lowther et al. (2018), I argue that diel patterns are likely to play a predominant role in influencing krill's depth distribution. It is also important to note that krill swarm behavior is highly complex and exhibits significant plasticity, with neighboring swarms often displaying contrasting behaviors (Bahlburg et al., 2023). Their behavior is theorized to be influenced not only by environmental factors but also by life stage, physiology, and the presence of predators (Bahlburg et al., 2023). During the austral summer, increased surface productivity can lead to multiple ascent-descent cycles per day for krill (Bahlburg et al., 2023). Averaging krill distribution may obscure this heterogeneity, potentially removing critical details about how chinstrap penguins exploit krill aggregations that differ from the average. Thus, the findings presented should be regarded as preliminary indications of a pattern that warrants further investigation. Due to the limitation addressed above the exact krill density thresholds targeted by chinstraps could not be identified. This highlights the need for synoptic predator and prey data that captures daily variations and appropriate spatial resolutions. Future research should focus on identifying target krill thresholds for chinstrap penguins to understand their ecological niche, interactions, and competition with other krill predators, ultimately aiding in the improvement of krill fishery management and species conservation. The methods outlined in Schoombie et al. (2024), which employ video recorders and TDRs to estimate prey capture events, represent a significant advancement toward this goal.

Focusing on the impact of fisheries on local penguin populations, it is important to note that penguin bycatch in the krill fisheries is relatively rare—largely because penguins can outswim

the slow trawling speeds and marine mammal mitigation systems on the trawls also aid penguins to escape (CCAMLR, 2023b; Crawford et al., 2017). Illegal and unreported catches may therefore pose a greater threat to penguin populations than regulated fisheries in the area (Crawford et al., 2017). Acoustic monitoring data of krill around the South Orkney Islands from 2011 to 2020 showed no significant trends in krill abundance, suggesting that, from a fisheries management perspective, regional fisheries have not had any noticeable impact on the krill biomass in the past decade (Skaret et al., 2023). However, this assessment focuses solely on the krill population itself and does not account for the potential effects of krill fisheries on local predator populations, such as penguins (Skaret et al., 2023). Several studies have pointed that many predators tend to forage very localized and have warned about the potential impacts of fisheries on this local scale (Warwick - Evans et al., 2022; Warwick - Evans et al., 2018; Watters et al., 2020). However, when considering the overall scale of fishery operations, the annual krill consumption of fin whales alone was estimated to be 20 times higher than the total krill catch by fisheries in CCAMLR Area 48 during the 2019/2020 season (Biuw et al., 2024). This comparison with just one species suggests that the overall impact of recovering baleen whale populations in the Southern Ocean may significantly exceed that of krill fisheries, indicating that the fisheries' effect on krill abundance could be relatively minor.

Historically, some studies have suggested that penguins might have benefited from the commercial harvest of cetacean populations, which reduced competition for krill (Lynch et al., 2012; Trathan et al., 2012; Trivelpiece et al., 2011). However, viewing whales merely as competitors for krill may oversimplify the complex interactions among krill predators. Baleen whales, by engulfing swarms of krill either at the surface or during deep dives (Friedlaender et al., 2020), may break up dense aggregations, making krill more accessible to penguins. Krill swarming behaviour, a defence mechanism against visual predators (Tarling & Fielding, 2016), can be disrupted by whales, leading to patchy krill distributions that penguins can more easily exploit. Additionally, the deep foraging dives of whales (Friedlaender et al., 2020) may push krill closer to the surface, benefiting shallower-diving predators like penguins. The observation in 2022 of thousands of seabirds, including penguins, feeding alongside a "supergroup" of about 1,000 fin whales, two humpback whales, a blue whale, and numerous Antarctic fur seals within the homerange of the Monroe colony supports the idea of a facilitative effect in this multispecies aggregation (Ryan et al., 2023). This supergroup likely caused the contrasting depth distribution patterns observed within the homerange compared to outside of it that year. This further highlights how predators can exert top-down pressures on prey populations, influencing each



other's behaviour and distribution (Annasawmy et al., 2023), though not all predators exert the same type or level of pressure on krill populations.

Most of the scientific research conducted in the Southern Ocean since the mid-1970s, which now serves as the baseline for contemporary studies, coincides with the period following the end of industrial whaling in the 1980s (Zerbini et al., 2019) and the peak of intense fisheries (Ainley et al., 2007). These activities had devastating effects, depleting many top- and mid-trophic predators from the Antarctic marine food web (Ainley et al., 2007). Ainley et al. (2007) argue that there is a bias in current scientific interpretations, where population changes are predominantly viewed through the lens of climate change, with an emphasis on bottom-up physical forces such as temperature and sea ice extent affecting predator populations. They suggest that a fuller understanding of population trends would benefit from integrating the historical depletion of predators into these assessments. Similarly, in the context of this study, while climate change remains a significant threat—primarily through warming temperatures, sea ice decline, and altered weather patterns that affect prey abundance and availability, thereby influencing predator foraging behaviour (Flores et al., 2012; Lowther et al., 2018; McBride et al., 2021; Salmerón et al., 2023; Trivelpiece et al., 2011)—considering the biotic interactions of recovering whale populations (Biuw et al., 2024; Zerbini et al., 2019) and other predators in our analyses could offer a more comprehensive perspective. This approach, as demonstrated in studies like Warwick - Evans et al. (2022), may help disentangle the effects of climate change from those of competition, facilitating the development of informed management strategies that more effectively mitigate impacts on chinstrap penguin populations and advance ecosystem-based management.

## 5 Conclusion

In conclusion, this study revealed a pronounced diel pattern in the foraging behaviour of chinstrap penguins, characterized by distinct differences in dive locations and types between day- and nighttime. My findings underscore the significance of crepuscular hours as critical foraging periods, during which penguins increase their diving efforts, particularly employing medium- and shallow u-dives to exploit krill that ascend to shallower depths due to diel vertical migration. This suggests that foraging during these twilight hours represents a previously overlooked ecological niche, potentially allowing chinstrap penguins to minimize competition with sympatrically breeding gentoo and adélie penguins. Moreover, the considerable individual variability observed in the data indicates that foraging behaviour may be influenced by

individual quality, presenting an intriguing avenue for future research on how individual behavioural plasticity might aid the resilience of chinstrap penguins in the face of climate change and shifting ecosystem dynamics. Notably, my findings suggest that chinstrap penguins target lower krill densities than those found at peak concentrations in the water column, indicating that suitable prey may be determined more by encounter rates than sheer density. However, these results necessitate further investigation through finer-scale predator-prey data, which could help identify specific krill density thresholds targeted by chinstrap penguins. Additionally, the interactions between penguins and other krill predators, such as whales, warrant attention, as these relationships may influence krill distribution and the dynamics of competition and facilitation among predators. In light of climate change, a comprehensive understanding of these predator-prey interactions, including the potential impacts of krill fisheries and the recovery of previously depleted krill predators like baleen whales, is essential for informing effective conservation and management strategies.

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## 7 Appendix

Table Appendix 1 Additional properties summarized for the different types of dives of the chinstrap penguins in the South Orkney Islands.

Dive shape	Bottom-time-per-depth ratio	Average ascend rate	Average descend rate	Dive efficiency
<b>deep U-dive</b>	$0.3 \pm 0.2$	$1.5 \pm 0.5$	$1.7 \pm 0.4$	$0.1 \pm 0.05$
<b>deep V-dive</b>	$0.02 \pm 0.01$	$1.3 \pm 0.4$	$1.5 \pm 0.4$	$0.01 \pm 0$
<b>medium u-dive</b>	$1.1 \pm 0.7$	$1.0 \pm 0.4$	$1.3 \pm 0.5$	$0.2 \pm 0.1$
<b>medium v-dive</b>	$0.1 \pm 0.1$	$0.7 \pm 0.3$	$1.1 \pm 0.5$	$0.01 \pm 0.01$
<b>shallow u-dive</b>	$1.3 \pm 0.8$	$1.2 \pm 0.5$	$1.7 \pm 0.6$	$0.3 \pm 0.1$
<b>shallow v-dive</b>	$0.3 \pm 0.3$	$1.5 \pm 0.8$	$2.1 \pm 1.0$	$0.04 \pm 0.03$
<b>travelling dive</b>	$0.3 \pm 0.1$	$6.4 \pm 3.5$	$6.7 \pm 3.1$	$0.1 \pm 0.1$

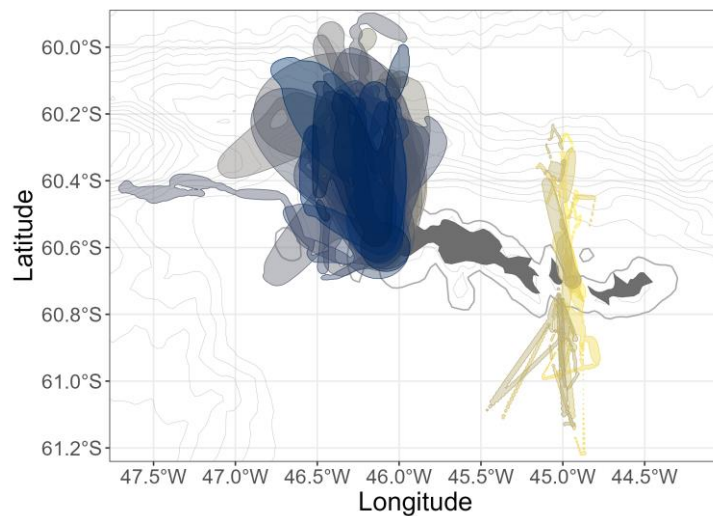


Figure Appendix 1 Overview of the homerange (95% confidence interval) for each individual from Monroe and Powell Island calculated with kernelbb(). Colour gradient is indicating different individuals.

# Daytime

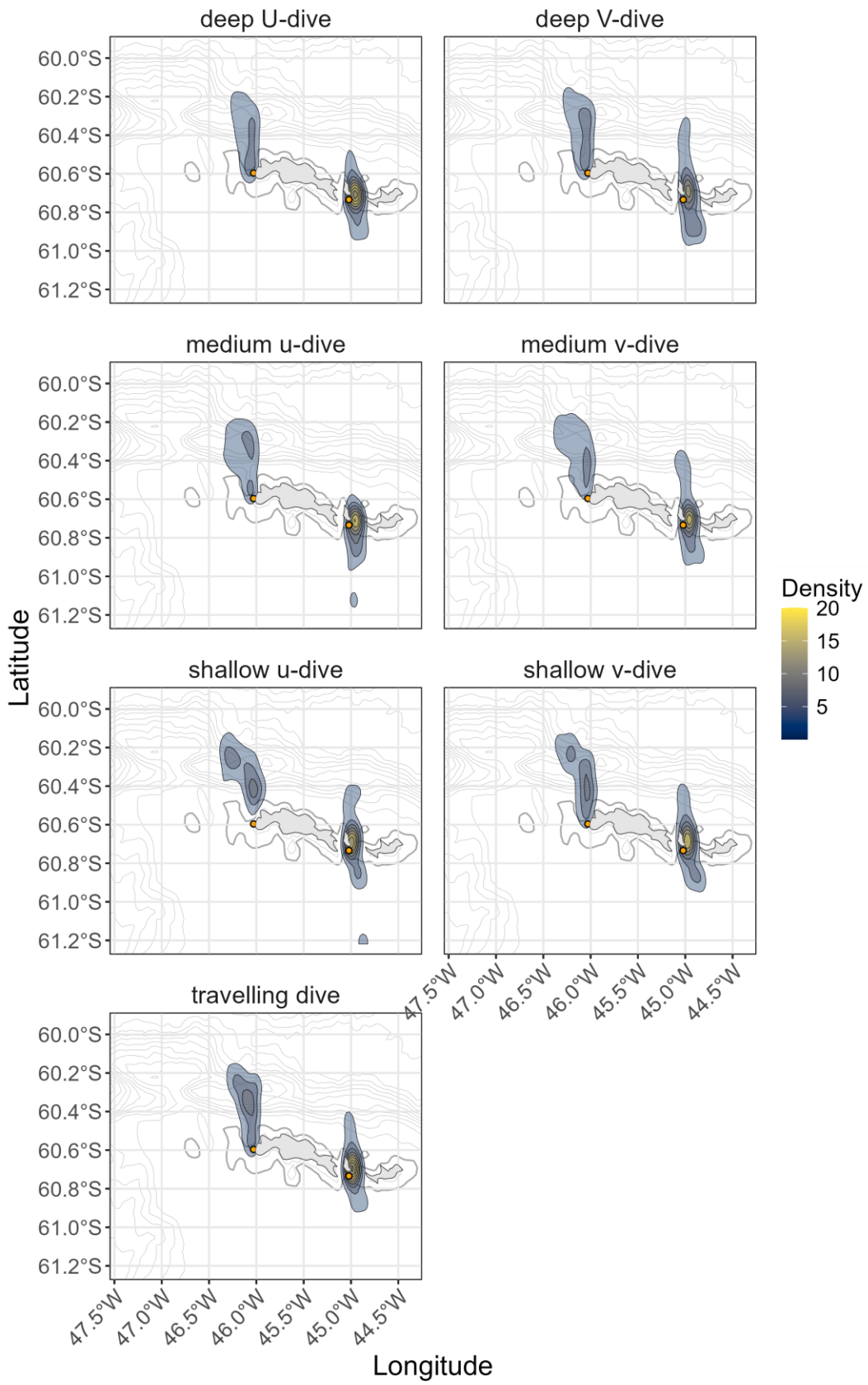


Figure Appendix 2. Visualization of dive spots for all seven dive types during daytime.

# Civil Twilight

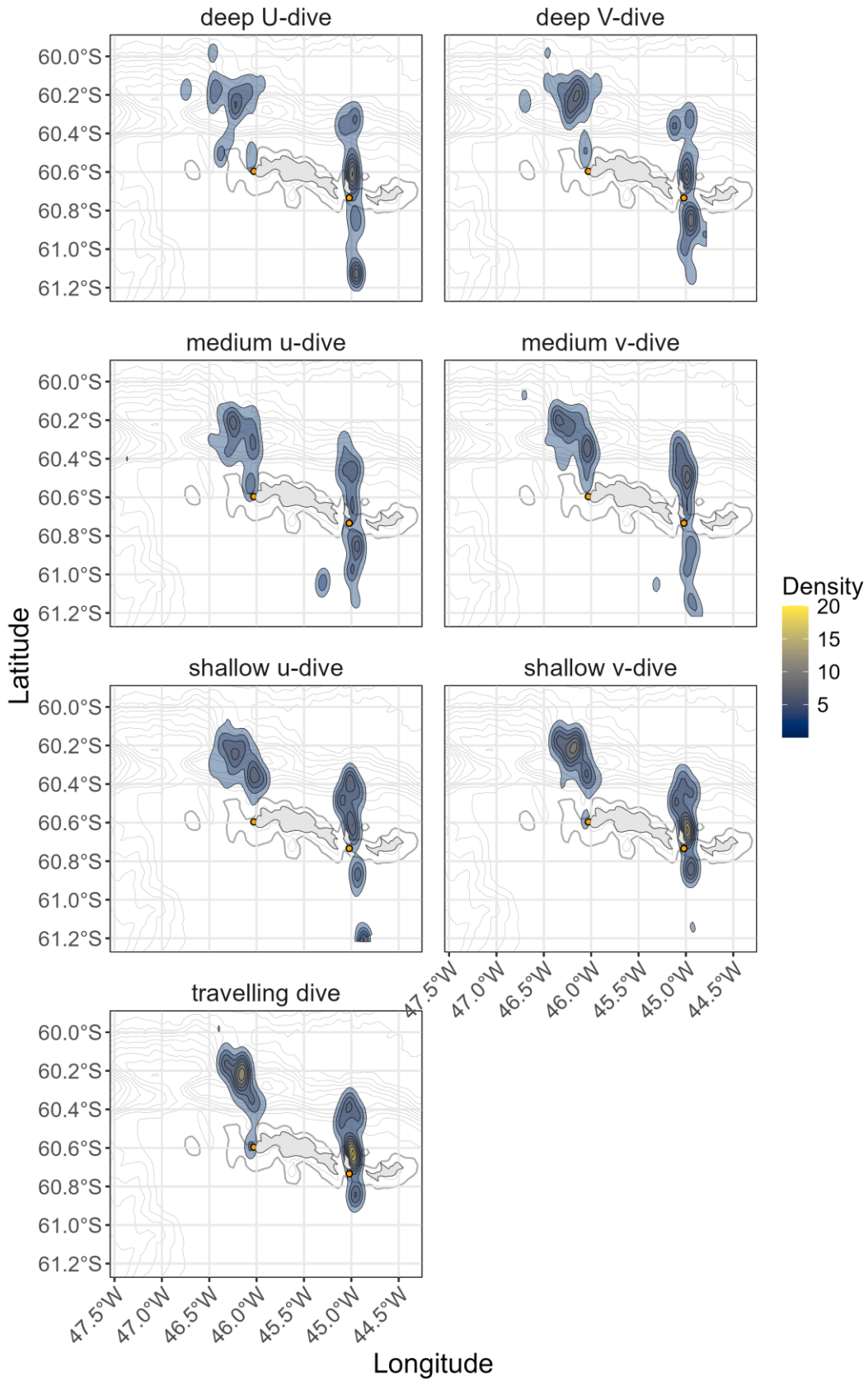


Figure Appendix 3. Visualization of dive spots for all seven dive types during civil twilight.

# Nautical Twilight

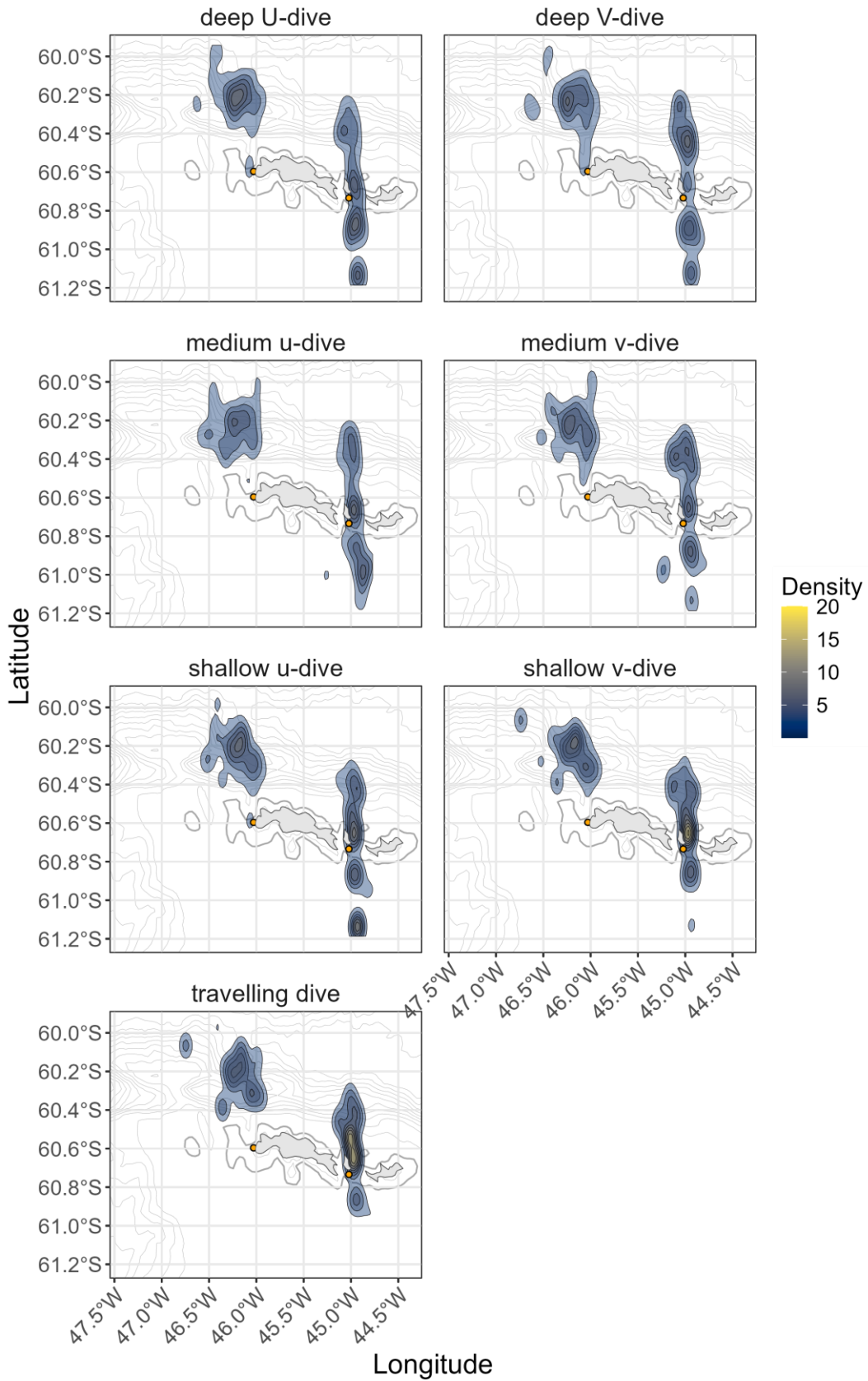


Figure Appendix 4. Visualization of dive spots for all seven dive types during nautical twilight.

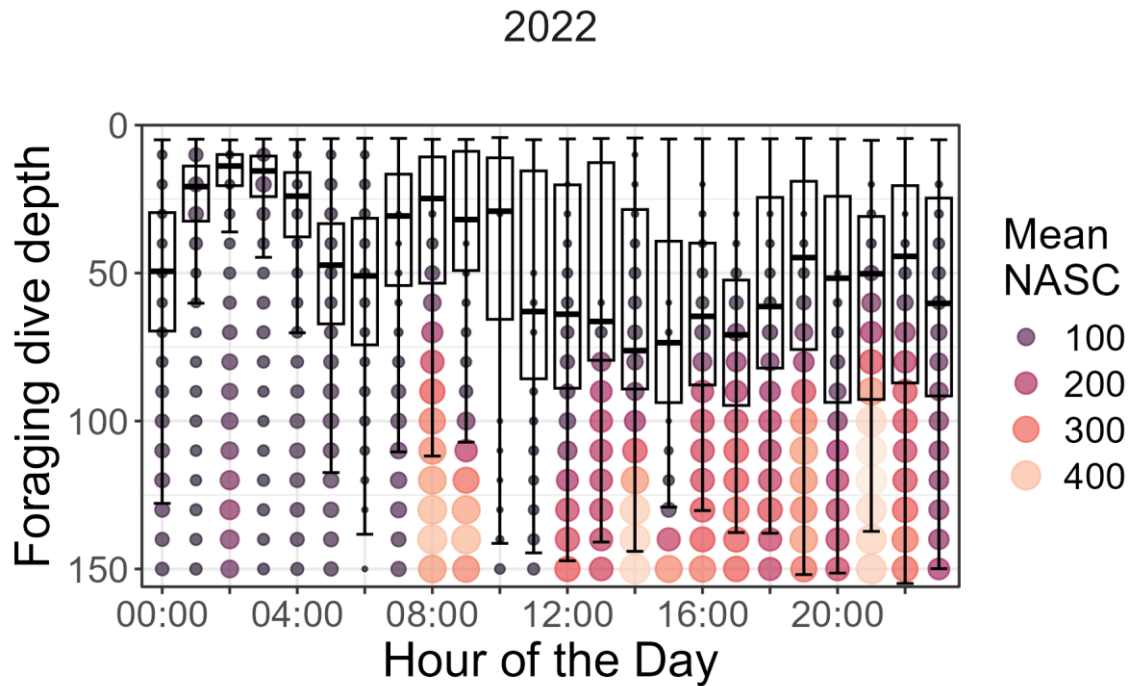


Figure Appendix 5. Zoomed in version of **Error! Reference source not found.** showing the average krill distribution in 2022 up to the maximum diving depth of the penguins.

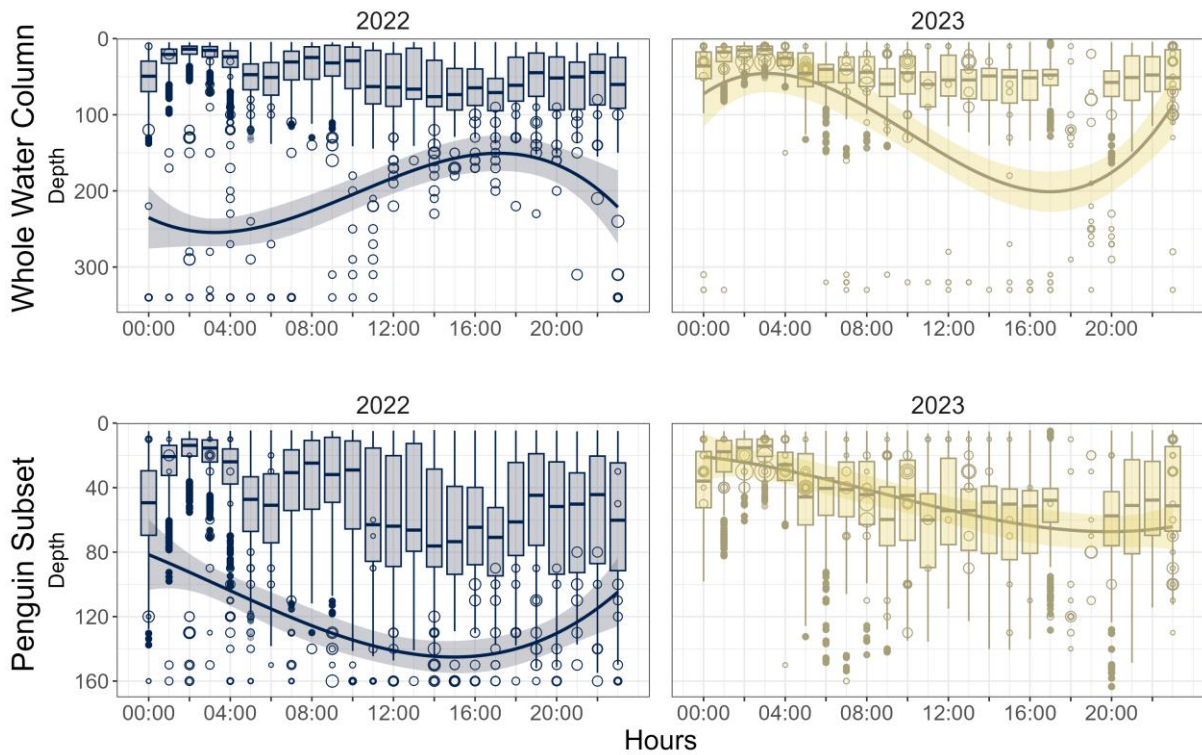


Figure Appendix 6. Figure showing the depth distribution of the maximum krill values in 2022 and 2023 within the homerange. Each bubble corresponds to a station and bubble size increases with higher values (zero values removed for clarity). A b-spline is fitted through the depth distribution of the krill maxima. The boxplots summarize the depth of the foraging dives per hour. The krill maxima filtered out for the whole water column and filtered out for the penguin subset (up the maximum diving depths of the chinstraps) are shown.



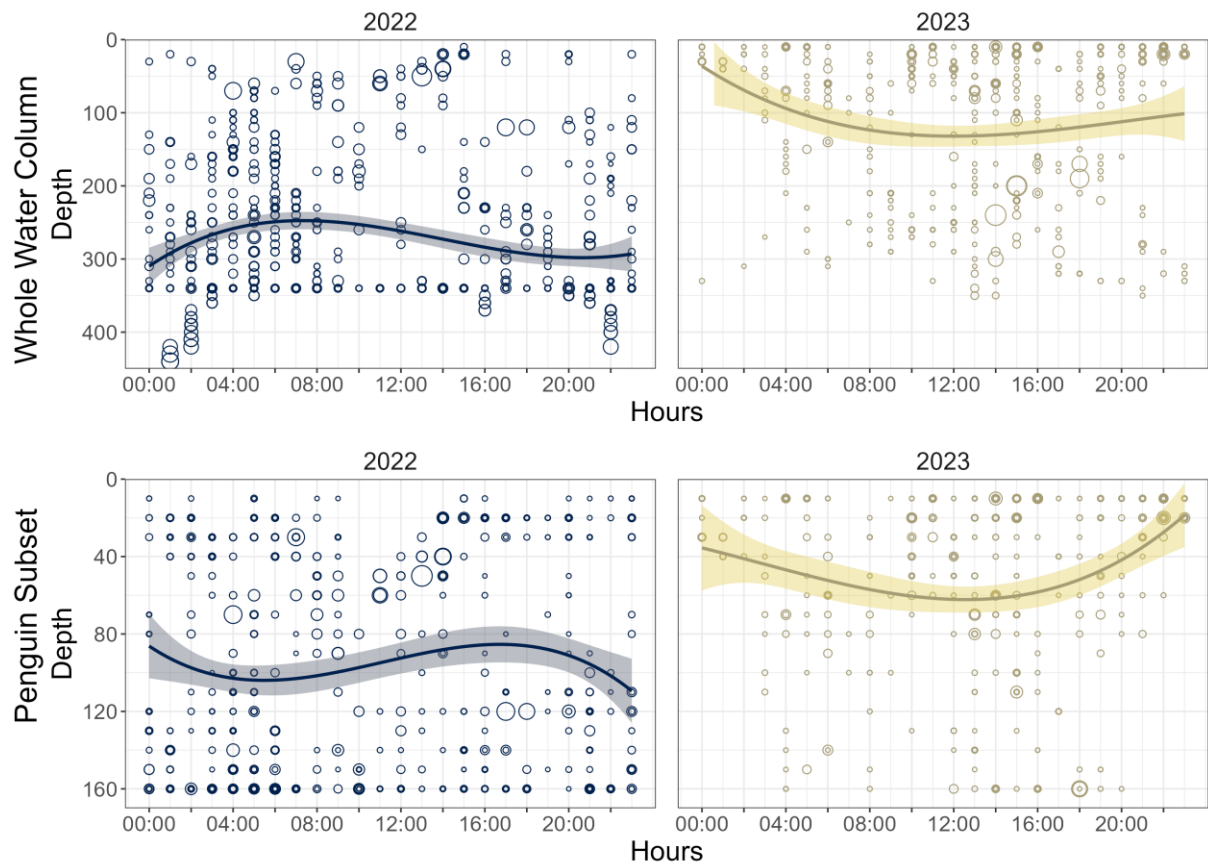


Figure Appendix 7. Figure showing the depth distribution of the maximum krill values in 2022 and 2023 outside the homerange. Each bubble corresponds to a station and bubble size increases with higher values (zero values removed for clarity). A b-spline is fitted through the depth distribution of the krill maxima. The krill maxima filtered out for the whole water column and filtered out for the penguin subset (up the maximum diving depths of the chinstraps) are shown.

