Diving deep: Seabird foraging tactics and local prey field

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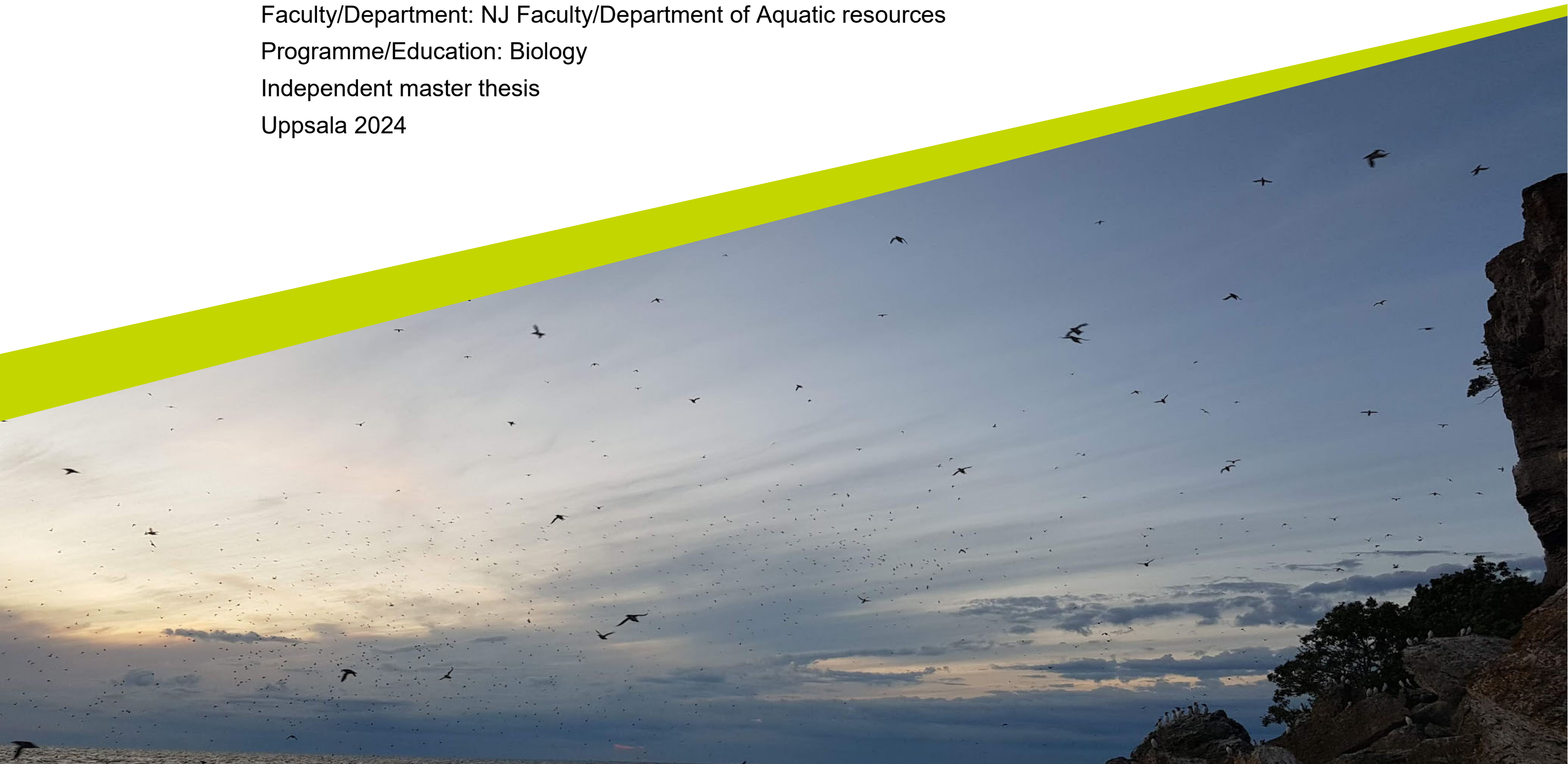

Diving Deep: Seabird foraging tactics and local prey field.

En djupdykning i sjöfåglars födosökningbeteende i relation till födotillgång.

Elin Andersson Sjöholm

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Abstract

Foragers in patchy environments need to decide what patches to use and how to allocate their time between them. Optimal foraging theory describes these choices through the relationship between energy expenditure and energy gain. Very few studies testing this have had spatiotemporally overlapping data on both predator & prey movement, but in this study an autonomous sail drone (USV) equipped with an echosounder was used to map the prey abundance with high resolution around a guillemot colony. Hydroacoustic data was combined with movement tracking data of common guillemots from the colony to determine how prey distribution and abundance affects foraging behaviour. Patch selection was investigated by comparing abundance of different patches with utilization, while GAMMs were used to describe the dive behaviour in patches with different prey abundance and depth distributions. It was found that guillemots mostly utilized patches with shallow prey and that time of day affected the depth and duration of dives, indicating that diel vertical migration patterns of prey influences dive behaviour of guillemots. The total foraging effort per trip did not decrease when dive duration increased, indicating that patches are only of acceptable quality, as total foraging effort did not decrease. It was also found that guillemots targeted patches with more available biomass further from the colony. This study increases the understanding of how guillemots are likely to be affected by further changes in prey populations and as seabirds are good indicators of overall ecosystem health this method can possibly also be used for several different species within different monitoring programmes. Mapping prey distribution with an USV is also a pioneering method that offers a time-and cost-effective method for obtaining data with high spatiotemporal resolution.

Keywords: Guillemots, Uria aalge, optimal foraging, resource selection, patchiness, hydroacoustic data

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Abbreviations

DVM	Diel Vertical Migration
GAMM	Generalized Additive Mixed Models
MVT	Marginal Value Theorem
SSB	Standing Stock Biomass
TAC	Total Available Categories in the area
USV	Unmanned surface vehicle

1. Introduction

1.1 Background

Predators foraging in patchy environments need to make choices on what patches to use and how to allocate their time between them. Optimal foraging theory aims to describe these choices through the relationship between time/energy expenditure during foraging, and the time/energy gain. Expenditure can involve distance travelled and time spent foraging, while the energetic value of food or simply increased time efficiency can represent the gain from a foraging trip (Emlen 1966). Within the optimal foraging framework there are several theories. The marginal value theorem (MVT) predicts the optimal time to spend in a patch based on prey abundance and the distance to the patch (Charnov 1976). It hypothesizes that more time should be spent in patches of high quality, as the energy intake rates are higher in these areas. This prediction has found support in studies where energy content of prey and good quality patches increased foraging effort (Mori et al. 2002; Crook & Davoren 2014). Which patch to target should also depend on how long the travel is. This is especially true for central-place foraging animals during breeding (Orians and Pearson,1979; see Houston & McNamara, 1985). As they always need to return to the central place (nest) they are limited in the distance they can travel. Different strategies are therefore thought to be deployed depending on the distance from the colony, where higher quality patches should be targeted in longer travels to compensate time/energy expenditure (Burke & Montevecchi 2009). The theory of central-place foraging can also be applied to diving animals, as they always need to return to the surface. While a longer dive duration may increase the chance of prey capture, it also increases the time at the surfaces needed for dive preparation or recovery (Carlsen et al. 2021), and increased time spent at the surface decreases the amount of time available for foraging. As dive depth and duration is strongly correlated, deeper dives should indicate targeting of higher quality prey patches. However, as predators encounter prey, interactions between the two occur, that also affects foraging behaviour. When less fish is available locating prey should be more difficult, and dive duration should be long. However, if predators instead give up dive duration should be short. Fish also have defence behaviours, such as e.g.

schooling (Magurran 1990). Predators can therefore have difficulties identifying and pursuing individual prey when a lot of fish is available. Predators should seek out an optimal amount of available prey between these two extremes, where the capture rate is the highest. However, there is currently no established way to define boundaries of aquatic foraging patches in a natural system, and the predictability of prey distribution is still a field under development.

Aquatic resources are highly dynamic and typically heterogeneously distributed. Only with high spatiotemporal resolution can the environment be divided into patches that can be defined at different scales (White & Pickett 1985). While optimal foraging has been tested through indirect measures such as overall time/effort cost versus gain in fecundity (Cohen et al. 2014), with paired bird observations & trawling (Erikstad et al. 1990; Burke & Montevecchi 2009) and with data-based models (Mori et al. 2002; Thaxter et al. 2013; Boyd et al. 2014), very few studies have had spatiotemporally overlapping data on both predator movement and prey abundance/distribution in a natural environment. Studies performed on the relationship between spatial scales and predator aggregation have found that correlation decreases for smaller scales (Schneider & Piatt 1986; Erikstad et al. 1990), possibly due to the difficulties with obtaining data with high enough spatiotemporal resolution. The reason might also be that the patchiness of environments often has a hierarchical structure, where different organisms experience this at different scales (Kotliar & Wiens 1990). As the purpose of describing foraging patches often is to draw conclusions for entire populations, based on data from few individuals, decisions need to be made on how to best capture the patchiness from an organismal point of view. To do so one needs to understand the basic dynamics that affects the prey distributions in the study area.

Many factors affect fish distribution, e.g. abiotic factors such as salinity, temperature and oxygen have effects on survival, growth, spawning success, distribution and food availability (Tomkiewicz et al. 1998; Orlowski 1999). Importantly, food availability also affects distribution and abundance, e.g. planktivorous fish often display diel vertical migration (DVM) (Cardinale et al. 2003; Solberg & Kaartvedt 2017) and fish are more abundant in areas where preferred prey is present (Rajasilta et al. 2014). DVM is the daily movement of fish and zooplankton from deep layers to the surface. Small pelagic fish constitute the main diet of guillemots, and in the Baltic Sea, sprat (*Sprattus* sprattus), herring (*Clupea harengus*) and possibly three-spined sticklebacks (*Gasterosteus aculeatus)* are key prey species for common guillemots (*Uria aalge*, “guillemots” from now on) (Lyngs & Durinck 1998; Kadin et al. 2016). While sprat and herring often reside at depths deeper than 40m during the day, and then surface at dusk to feed (Cardinale et al. 2003; Ferreira et al. 2012; Solberg & Kaartvedt 2017), sticklebacks stay close to the surface throughout all hours, usually staying within 0-20m (Jurvelius et al. 1996; Mustamäki et al. 2016). The Baltic Sea spawning stock biomass (SSB) in 2020 was estimated to be 977 000 tonnes of sprat (ICES 2021c) and 365 448 tonnes of herring (ICES 2021b). However, both species are important for commercial fisheries in the area and human activity has had large effects on these populations. Herring have decreased in stock and body size in the Baltic Sea over the last decades, and while sprat had a population peak in the 90s, it has since then stabilized and in addition decreased in size (ICES 2021a). Three-spined stickleback have on the other hand increased in the Baltic (Olin et al. 2022). As these fish species make up the majority of guillemot diets, these changes are likely to affect guillemot foraging behaviour.

Guillemots have small wings in comparison to their body weight, leading to high wing loading that is energetically expensive. This makes them inefficient flyers, but highly efficient, wing-propelled, divers (Thaxter et al. 2010) and they have been observed diving to depths of up to 250m (Chimienti et al. 2017). The largest colony in the Baltic Sea is located on Stora Karlsö, west of Gotland (57°17´1N, 17°58´2E). The population on the island was estimated to 26 000 breeding pairs in 2023 with a stabile annual breeding success of ~70-75% (Hentati-Sundberg et al. 2021). Extensive research has also been conducted on this colony, and a lot of knowledge regarding feeding preferences and areas utilized for foraging is therefore available (Evans et al. 2013; Hentati-Sundberg et al. 2018). The availability of such a large, well-studied, colony with existing research facilities coupled with the good diving abilities of guillemots makes this population optimal to study.

For this study I had the unique opportunity to combine high resolution prey distribution data, collected by an autonomous sail drone (hereafter *Unmanned Surface Vehicle* (USV), with movement and diving telemetry data of guillemots, collected within the same time frame. The data was used to determine how prey abundance and vertical distribution affects diving behaviour, focusing on biomass and depth of prey, as the quality of the patch and the cost of reaching it are the main drivers in foraging theory. An increased understanding of these interactions can aid in predicting how guillemots are likely to be affected by climate change, fisheries and/or other anthropogenic factors that affects prey distribution patterns. Further, the method can also possibly be applied to other species and as seabirds are good indicators of overall ecosystem health (Piatt & Sydeman 2007) increased understanding of their foraging response to prey conditions is highly important for ecosystem management and monitoring.

1.2 Aim and hypotheses

This thesis aims to explain how seabirds select and utilize spatiotemporal variation in prey distribution, divided into two main parts. The first part focus on foraging patch selection and the second on dive behaviour in relation to prey distribution and abundance.

1.2.1 Part 1: Foraging patch selection

I hypothesize that patch types selected by Guillemots are non-random compared to proportion of patch types available in the general area. As more foraging effort should be put into patches with favourable foraging conditions the distribution should be biased towards preferred patch types.

I also hypothesize that patches of higher quality should be targeted further from the colony, to compensate for the high energetic cost of longer travels.

1.2.2 Part 2: Dive behaviour as a response to prey distribution

I hypothesize that the distribution of prey, in depth and distance from the colony, along with the available prey biomass affect guillemot foraging and dive behaviours, in the following ways:

H1: Depth of dives should reflect depth of prey, and deeper dives should only be performed in areas with higher amounts of prey biomass at deeper depths.

H2: Foraging effort within dives and bouts should increase with patch quality, leading to an overall decrease in total foraging effort per trip.

H3: In relation to this, there should be an optimal biomass to target where prey capture rate is the highest. More, or longer, dives should be performed here and total foraging effort per trip should be low.

H4: Patches of higher quality should be targeted further from the colony to compensate for the energy cost of the travel.

2. Method

2.1 Data collection

2.1.1 Local prey field

The local prey field was assessed using echosounder data on prey distribution collected in 2019, 2020 and 2022 by an USV (*fig. 1*) equipped with a Simrad Wide Band Transceiver WBT-mini scientific echosounder with an ES-200CDK transducer (frequency sweep 185-255 kHz). All missions were designed in Simrad EK Mission Planner 3.3x with a ping rate of 1/1.4 seconds and was calibrated using a 38.1 mm tungsten sphere each season.

The USV was steered via an Iridium Satellite Communications system, where movement was wind driven and electronics were powered by solar energy. It followed a semi-random track, which was dependent on wind directions, with the aim to evenly cover the entire foraging area several times (*fig. 2*). It was deployed in April and operated until late July each season.

Figure 1: Unmanned surface vehicle (USV) used to collect prey distribution data around the guillemot colony (photo: Elin Sjöholm).

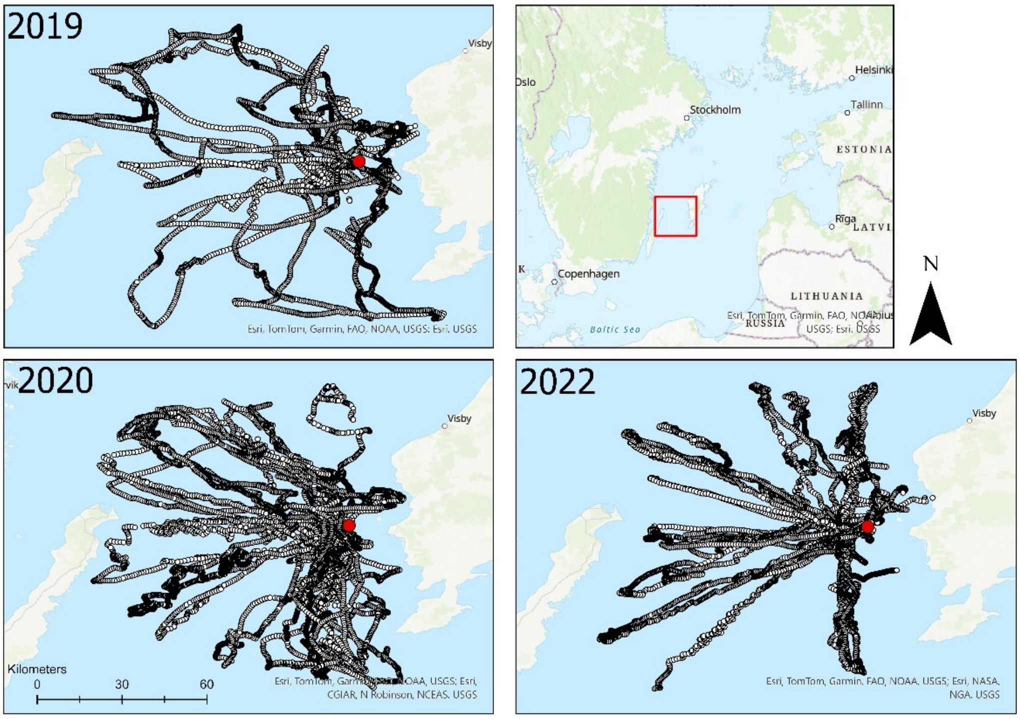

Figure 2: USV track around the Guillemot colony for the three study years 2019, 2020 & 2022. Each white point represents a USV interval, and the red point indicates the location of the Guillemot colony (Stora Karlsö, Sweden).

2.1.2 Guillemot dive data

Guillemot diving data was collected at Stora Karlsö, Gotland, Sweden. Data collection primarily occurred between the end of June and beginning of July all seasons. Breeding guillemots were captured with a noose-pole from the artificial breeding cliff, Auklab (Hentati-Sundberg et al. 2012; *AukLab – BSP*). Time-depth recorders (TDR, CEFAS G5 DST, interval 1-5s, mass ≈ 3g), which were covered with self-fusing tape for better friction, were attached with cable ties to colour identification rings on the bird's leg. GPS loggers (Igot-U 120, 3 min interval, mass after modification ≈ 18g) were deployed at the same time. They were modified to reduce weight and buoyancy (i.e. removal of hard casing and change of battery) and were covered in heat-shrinking tube. They were attached to some back feathers on the guillemots so that if recollection was not possible it would fall off at the latest by next moult. After 24-48h loggers were retrieved and data collected. Birds were weighed once, usually at retrieval. The total weight of both TDR (3g) and GPS (18g) added up to ~2.2% of mean body mass (based on collected data from 2021 & 2022). Total handling time was between 9 and 15 minutes, with a mean of 11.8 min.

2.2 Data processing

2.2.1 Local prey field

Hydroacoustic raw data was calibrated, cleaned and analysed in Echoview v. 13 (Echoview Software Pty Ltd n.d.). Nautical Area Scatter Coefficient (NASC) values were transformed into biomass (kg/km^2) following the ICES standardized procedure for abundance calculations based on NASC, species and size composition (Doray et al. 2021). This was done by assuming prey species based on depth and time of day. During daytime (04-21h) fish located < 30m were assumed to be sticklebacks and fish >30m 50% herring and sprat respectively. At night (21-04) it was assumed to be equal proportions of all three species. The mean size per species was then used for calculations (Sticklebacks: 5.5cm, sprat: 9.2cm & herring: 13.3cm (Nilsson et al. 2022)).

From the three years (2019, 2020 & 2022) around 36 000 sampling points (here after "intervals") were available (*fig. 2*). The data was filtered in time so that only hydroacoustic data sampled within the dates of the first and last dive per season (of tracked birds) +- 14 days was kept. However, in 2019 the first dive occurred on the 2nd of June but there was no hydroacoustic data until the 28th. This is summarized in table 1. A total of 8836 intervals remained after this filtering.

Table 1: Dates of the first and last dive of tracked birds (+- 14 days) per season and dates of available USV data.

Year	Date of first dive (-14 days)	Date of last dive (+ 14 days)	Hydroacoustic data
2019	2nd of June	8th of July	28/6 - 8/7
2020	10th of June	11th of July	10/6 - 11/7
2022	19th of May	26th of June	19/5 – 26/6

For each interval (*fig. 3:* vertical lines) the water column was divided into 4 layers (*fig. 3:* horizontal lines) and biomass was summarized per layer, to be able to classify different vertical prey distribution categories. Vertical prey distribution was then classified by looking at the proportion of the total biomass in each interval per layer. If a layer contained >20% of total biomass it was marked as containing a significant proportion, which resulted in 15 different prey distribution categories (appendix, *fig. A1*). However, the frequencies were very uneven and in 80% of intervals prey was located in the first 50m and in 15% in both deep and shallow layers. After further visual inspection of echograms it was determined that 2 layers should capture the most frequently observed depth distributions of prey. As the echosounder was set to only record down to 100m each layer was 50m. The vertical prey distribution categories based on the 4 layers were therefore merged into 3 vertical prey distribution categories. Category A: Prey mostly located in top layer

(0-50m), Category B: Prey mostly located in bottom layer (50m+) & Category C: Prey in both layers (*fig. 4*). This should also capture the two different types of dives observed, shallow (<50m) and deep (>50m), dives (*fig. 5*).

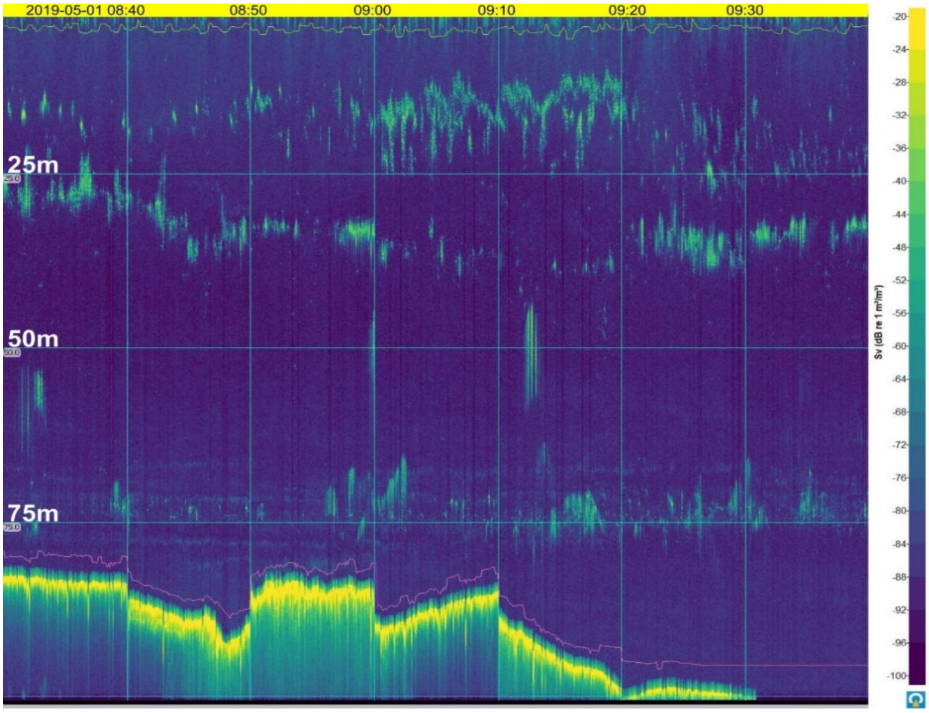

Figure 3: Echogram sampled by USV on the 1st of May 2019 between 8:30 and 9:40. Vertical lines represent intervals and horizontal lines defined layers. Each interval was divided into 2 layers, 0-50m and 50m+.

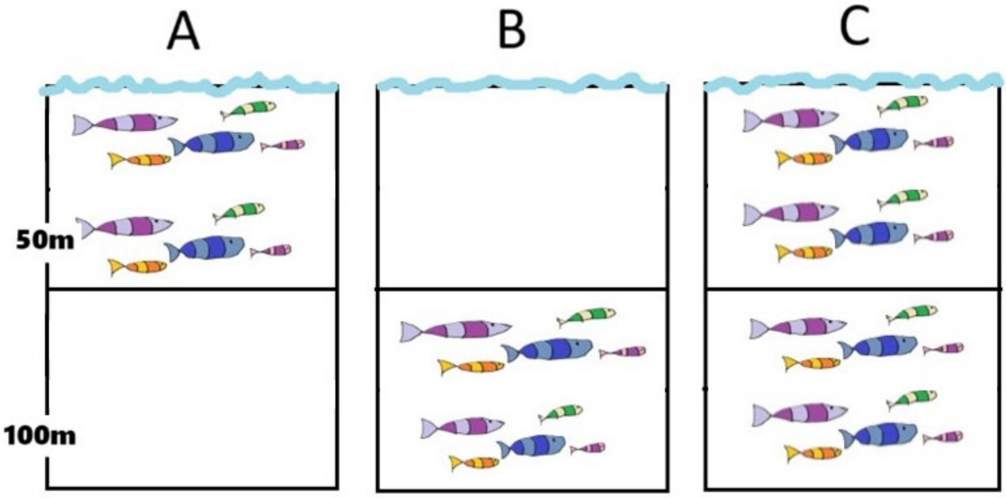

Figure 4: The different prey distribution categories. In category A, prey is mostly located in the first 50m, in Category B most prey is located >50m. In category C prey is located within both top and bottom layers.

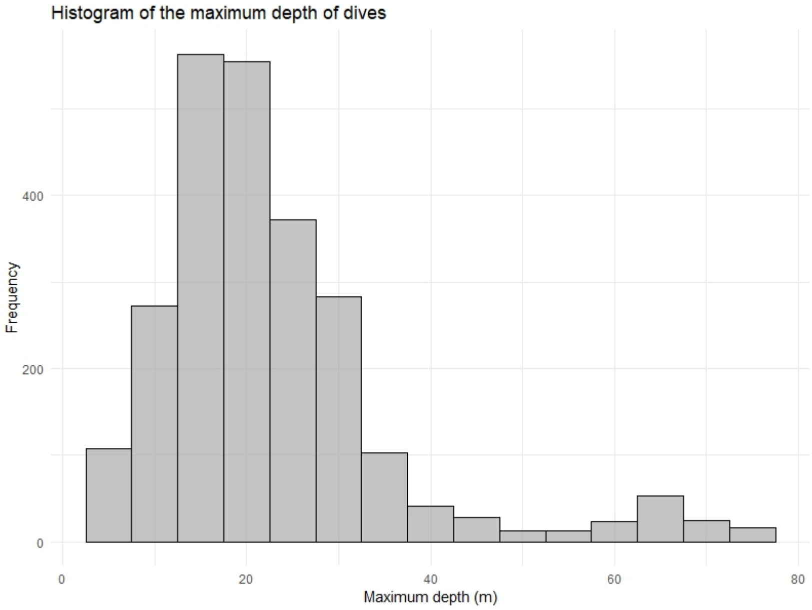

Figure 5: Histogram of the distribution of the maximum depth of tracked dives. A bimodal distribution is visible, with the first peak around 15-25m and the second around 65m.

The ABC categories only contain information about where prey is located, and a biomass classification was therefore added to describe the quantity of prey. The 25, 50 and 75 and 100th quantiles of the total biomass per interval were used to create 4 biomass categories, where each quantile represents the upper limit of a category (1=221, 2= 462, 3=911, 4=16279 kg/km^2). This resulted in 12 categories (A:1-A:4, B:1-B:4 & C:1-C:4), which describe vertical prey distribution and total amount.

Each interval was then classified as occurring during the day, at dawn or at dusk, depending on when it was sampled. The Suncalc package from R was used to obtain the time of sunrise, dusk and nadir. Dusk and dawn occur when the sun is 6° below the horizon and nadir is the sun's lowest point (90° below the horizon) (*Astronomy Answers: Position of the Sun* n.d.; *suncalc package - RDocumentation* n.d.). In this study dawn was classified as occurring from nadir to sunrise, day from sunrise to dusk, and dusk from dusk to nadir. No intervals were classified as occurring during "night", as dawn and dusk were estimated as continuous in the monitored area at the time of sampling.

2.2.2 Guillemot dive data

To be able to determine the prey distribution at the time of a dive, dives performed within 5km & 14 days of a USV sampling point were selected. However, some dives were included that lay outside these boundaries, to get complete trips of birds (437 dives distance >5km, 994 dives time >14 days). By deciding on these limits circles with a radius of 5km, around each dive, were essentially categorized as patches. The mean distance from the colony per trip was 20km with a minimum and maximum of 0.6 and 69km respectively and the chosen limits (5km and 14 days) were based on visual inspections and statistical models of the dynamics of fish distribution in the area (In prep. Carlsen, et.al.). Dives that overlapped were identified in ArcGIS (ESRI 2023), with the tool "Point Distance", and resulting dataset was then filtered to remove dives where difference in days >14 days. This resulted in 14 suitable birds (12 unique individuals), and 3206 dives (*table 2*). Dives shallower than 2m were also excluded, as the TDR has an uncertainty of +-2m. Trips were defined as beginning and ending with geopoints at the colony. Trips can also be divided into bouts, in which several dives occur with a shorter pause in-between. This is referred to as post-dive duration, and in this study a post-dive duration >=600s (10min) was used to distinguish bouts from each other.

Dives were classified as dusk, dawn or day with the same method as USV intervals. One dive usually overlapped with several sampling points (*fig. 5*) and only overlaps where USV interval and dive occurred within the same dawn/day/dusk period were kept, as that hydroacoustic data is more likely to accurately describe the foraging conditions at the time of the dive. This resulted in some dives being removed and a total of 2467 dives remained (*table 2*). However, for model 3 in part 2, all dives were kept for analysis, where total dive duration per bout and trip were used as factors. This is explained more in detail under Data analysis.

The mean biomass and depth of prey were calculated per unique bout for all overlaps. The mean biomass was calculated per bout by calculating the mean biomass of all USV interval overlaps. The depth of prey was calculated with a weighted mean. In the original USV data each interval was divided into vertical 4m layers, with summarized biomass per layer. The mean depth of prey was therefore obtained by calculating the mean layer where the weight was the biomass within each layer. These parameters were estimated per bout and not per dive as the scale of the data does not allow for such detailed assumptions. Each dive was also assigned a vertical prey distribution category based on its overlaps with sailor sampling points. This was done by calculating a weighed mode, where the weight of each overlap was equal to the inversed distance between dive and USV sampling.

In summary, a patch was defined for each bout, where the biomass, mean depth of prey and vertical prey distribution category was estimated, based on the dives overlaps in time and space with USV sampling.

Table 2: Summary of number of dives per bird and year. To the left, all overlaps and to the right, number of overlaps left after taking out those who occurred at the same time of day as USV sampling.

Bird individual /Year	2019	2020	2022
AAH388	596 / 383	-	-
AAK970	200 / 135	233 / 199	-
AAK999	548 / 400	-	22 / 22
AAL016	618 / 421	-	-
AAT927	88 / 65	-	-
AAZ988	68 / 62	-	-
ABH817	12 / 1	-	-
ADK088	69 / 69	-	-
AAZ969	-	255 / 230	-
ACF535	-	-	97 / 97
ADE087	-	-	80 / 76
ADR258	-	-	320 / 307
Total n. dives	**2199 / 1536**	**488 / 429**	**519 / 502**
Total n. birds	**8**	**2**	**4**

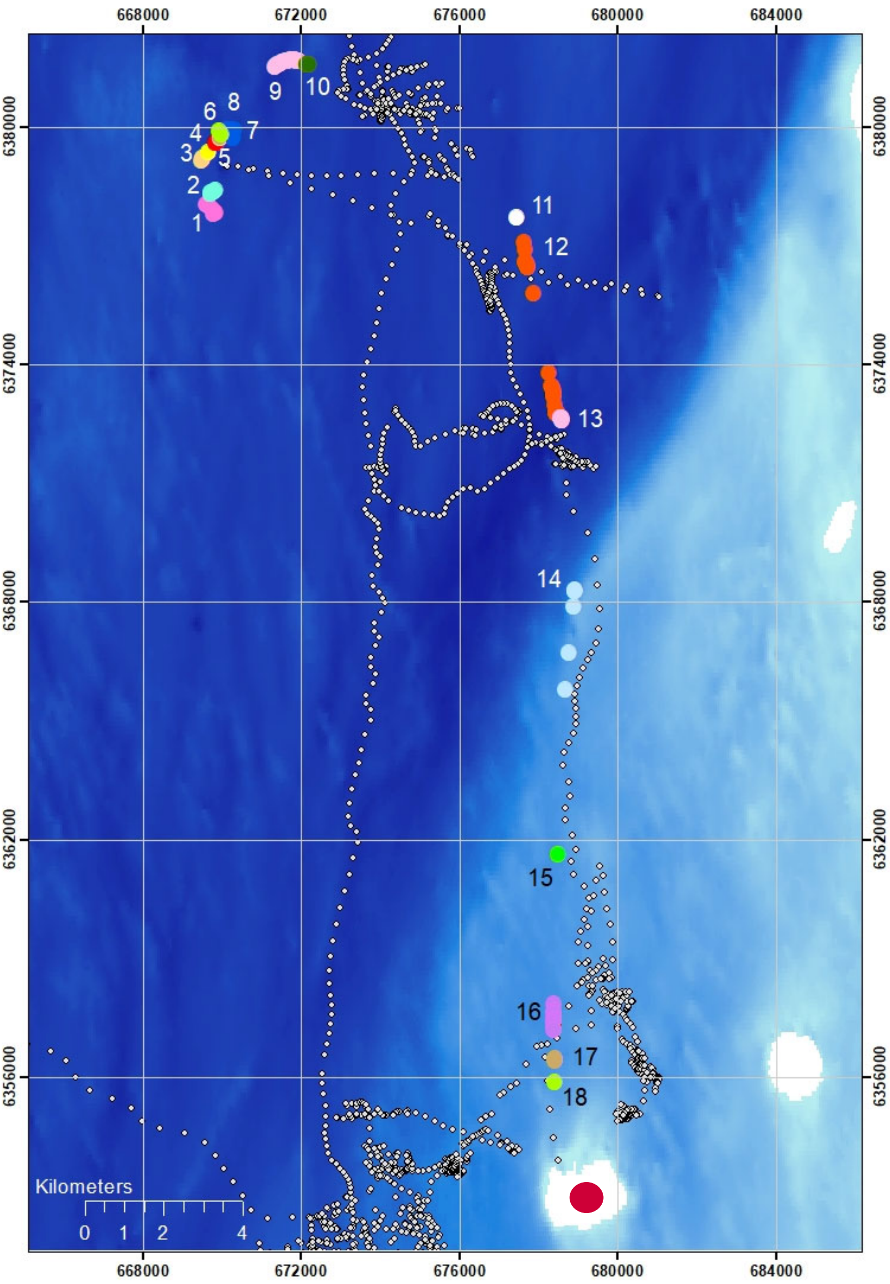

Figure 6: Example map of how overlaps between dives and USV intervals were identified in ArcGIS. Colourful points indicate bird dives, which are color-coded to visualize bouts. Numbers indicate bout number, white smaller points are USV intervals and the large red point is the location of the colony. This is bird ACF535 from 2022. One grid cell is approx. 6km high and 4km wide.

2.3 Data analysis

2.3.1 Part 1: Selection of foraging patches

Barplots with the proportion of each vertical prey distribution category per dusk, dawn and day were constructed in R with ggplot2 v3.3.4 (Wickham et al. 2023). This was done to compare differences between which categories that were the most common in the area and which that were mostly utilized by guillemots.

Maps of the spatial distribution of different categories were constructed in ArcGIS pro (ESRI 2023). Grids were constructed with the tool Fishnet, and grid size was set to 0.04, which with the WGS 84 coordinate system equals approx. 4-5km. Dives were then plotted over the grid and each cell was categorized based on the most common category for all dives within that cell with the summary statistics tool. The map is based on what the dives were categorized as (the weighted mode) and not the USV dataset.

2.3.2 Part 2: Dive behaviour in relation to prey distribution

Autocorrelation between dive number and post-dive duration as well as pre-dive duration was investigated, as these have been found to correlate in other seabird species (Carlsen et al. 2021). Two linear mixed-effects models were constructed in R with nlme v. 3.1-162 (Pinheiro et al. 2023), where either pre-dive or post dive duration was set as the dependent variable, and dive duration as the fixed effect. Dive number was set as a correlation factor. Autocorrelation plots were then created with the R base function acf(), and visually inspected. Neither pre-dive nor post dive duration was autocorrelated with dive number (appendix, *fig.A2*) and no correlation factor was therefore included in the final models.

Generalized additive mixed models (GAMMs) were used to investigate the relationships between dive behaviour and prey distribution & availability with the R package mgcv v1.9-0 (Wood 2011) with restricted maximum likelihood (REML). Plots were created using the two R packages itsadug v. 2.4.1 and ggplot2 (Rij et al. 2022; Wickham et al. 2023). Generalized additive models (GAM) allows for non-linear relationships, while GAMMs also include random effects, which is ideal for non-independent nested data (Aarts et al. 2008). Seven models were constructed to test the different variables and the Akaike information criterion (AIC) was used to compare models to identify the best fitting ones (appendix, table A1-7). Q-Q plots were used to assess normality of residuals (appendix, *fig. A3*) and histograms to assess normality of dependent variables (appendix, *fig. A4*). Random intercepts, not random slopes, were used for random effects to reduce complexity of the models and a significance level of 0.05 was used.

Model 1: Depth of dives in relation to prey distribution

In model 1 it was tested how the max depth of dives (m) was affected by biomass, depth of prey and distance from colony (H1). Max depth was set as the dependent variable and log-transformed total biomass in patch, depth of prey (m) and distance from colony (km) as fixed effects, with an interaction between biomass and depth of prey. All fixed effects were set with cubic polynomial smoothers. Random effects were set as year, bird, bout, depth of ocean (m) and time of dive (h) (appendix, table A1). Only dives ≤ 50m were included in the model (297 dives removed), due to the bimodal distribution of depth of dives (*fig.* 2). Dives with log(biomass) > 7.25 and log(biomass) < 5.5 were also removed (26 dives) due to data scarcity, to better improve predictability (n=2144 remained). Residuals were normally distributed (appendix A1, *fig. 3*).

$$\begin{aligned} Depth\ of\ dive \sim\ & poly(Depth\ of\ prey, 2) * poly(Biomass(\log), 3) \\ & + poly(distance\ colony, 3) + (1|Year) + (1|Bird\ ID) \\ & + (1|Bout) + (1|Ocean\ depth) + (1|Time\ of\ dive) \end{aligned}$$

Model 2: Foraging effort per dive in relation to patch quality

In model 2 it was tested how dive duration (s) was affected by biomass, depth of prey and distance from the colony (H2-H4). Dive duration was set as the dependent variable, with the same fixed effects as in model 1, but the best smoother selected for depth of prey was squared. Random effects were year, bird, breeding status (incubating/chick rearing), bout and time of dive (h) (appendix, table A2). Both shallow and deep dives were used in this model as dive duration was normally distributed (appendix 1, *fig. A4*). Residuals were normally distributed (appendix 1, *fig. A3*). Dives with log(biomass) > 7.25 and log(biomass) < 5.75 were removed due to data scarcity, to better improve predictability. This resulted in 2432 dives.

$$\begin{aligned} Dive\ duration \sim\ & poly(Depth\ of\ prey, 2) * poly(Biomass(\log), 3) \\ & + poly(distance\ colony, 3) + (1|Year) + (1|Bird\ ID) \\ & + (1|Breeding\ status) + (1|Bout) + (1|Time\ of\ dive) \end{aligned}$$

Model 3: Total foraging effort per bout in relation to patch quality

In model 3 it was tested how the total foraging effort per bout was affected by biomass and distance from colony (H2-H4). The sum of dive duration for all dives in a bout (s) was set as the dependent variable and it was log transformed as that improved the normality of the residuals (appendix. *fig A3.*). Log-transformed biomass and distance from colony (km) were set as fixed effects with cubic polynomial smoothers. As biomass values already were calculated per bout, and not per dive, the same biomass values were used in this model as in previous ones. The maximum distance from the colony per bout was used as the distance value. The random effects were set as year, bird, time of dive (h) and number of dives in bout (appendix, table A3).

The dataset with all dives, not only does that occurred on the same dawn/day/dusk as USV sampling was used, to get entire trips and bouts. The data was summarized to one row per bout, which resulted in 299 data points. Bouts with log(biomass) >7.5 and log(biomass) < 5.75 were removed due to data scarcity, which resulted in 291 bouts.

$$\begin{aligned}&Tot.dive\ d.bout\ (\text{log}) \sim poly(Biomass\ (\text{log}), 3)\\&* poly(Max\ distance\ colony, 3 + (1|Year)\ +\ (1|Bird\ ID)\\&+ (1|Time\ of\ dive) +\ +(1|Number\ of\ dives\ in\ bout)\end{aligned}$$

Model 4: Total foraging effort per trip in relation to patch quality

In model 4 it was tested how total foraging effort per trip was affected by biomass and distance from colony (H2-H4). Total dive duration per trip (s) was set as dependent variable and it was log transformed as that improved the normality of the residuals (appendix. *fig A3.*). The fixed effects were the same as in model 3 but random effects were only year and time of dive (h) (appendix, table A4).

The dataset with all dives, not only does that occurred on the same dawn/day/dusk as USV sampling was used, to get entire trips and bouts. The data was summarized to one row per trip which resulted in 33 data points.

$$\begin{aligned}&Tot.\ dive\ d.trip\ (s)(\text{log}) \sim poly(Biomass\ (\text{log}), 2)\\&+ poly(Max\ distance\ colony, 3) +\ (1|Year)\\&+\ (1|Time\ of\ dive)\end{aligned}$$

Model 5: Mean foraging effort per dive per bout in relation to patch quality

In model 5 it was tested how the mean dive duration per bout was affected by biomass and distance from colony (H2-H4). Total dive duration per bout was divided by the number of dives in the bout to get mean dive duration per dive per bout (s). It was used as the dependent variable, and log-transformed biomass & maximum distance from colony (km) as fixed effects, biomass with a polynomial squared smoother and distance with a cubic. Random effects were set as year, breeding status, bird, time of dive (h) and number of dives in bout (appendix, table A5).

The same dataset as for model 3 was used, with one row per bout.

$$\begin{aligned}&Mean\ dive\ dur.bout\ \sim poly(Biomass\ (\mathrm{log}), 2)\\&+ poly(Max\ distance\ colony, 3) + (1|Year)\\&+ (1|Breeding\ status) + (1|Bird\ ID) \quad + (1|Time\ of\ dive)\\&+ (1|Number\ of\ dives\ in\ bout)\end{aligned}$$

Model 6: Mean foraging effort per dive per trip in relation to patch quality

In model 6 it was tested how the mean dive duration per trip was affected by biomass and distance from colony (H2-H4). Total dive duration per trip was divided by the number of dives in the trip to get mean dive duration per dive per trip (s). It was used as the dependent variable, and log-transformed biomass and maximum distance from colony (km) as fixed effects. The only random effect was number of dives in trip (appendix, table A6).

The same dataset as for model 4 was used, with one row per trip.

$$\begin{aligned}Mean\ dive\ dur.trip \sim\ & poly(Biomass\ (\mathrm{log}), 3)\\&+ poly(Max\ distance\ colony, 3)\\&+ (1|Number\ of\ dives\ in\ trip)\end{aligned}$$

Model 7: Patch quality in relation to distance from colony

In model 7 it was tested how biomass in targeted patch was affected by distance from the colony (H4). Log-transformed biomass in targeted patch was set as the dependent variable and distance from colony as the fixed effect, with a polynomial cubic smoother. Random effects were year, bird individual, bout, and time of dive (h) (appendix, table A7).

The same dataset as in model 2 was used, with one row per dive.

$$\begin{aligned}Biomass\ (\mathrm{log}) \sim\ & poly(Distance\ colony, 3) + (1|Year) + (1|Bird\ ID)\\&+ (1|Bout) + (1|Time\ of\ dive)\end{aligned}$$

3. Results

3.1 Part 1: Foraging patch selection

Looking at the total available categories in the area (TAC) at dawn, prey in shallow layers (Category A) was most common (*fig. 7*). Categories with more available biomass were most common, and category A:2, A:3 and A:4 each made up about 20% of all samples, while category A:1 was less frequent, at around 10%. Less than 3% of TAC were category B:1-4. Category C:1-4, in total, made up about 25%, each with a frequency less than 10%. Most dives at dawn were performed in category A:1-4 (~90%), the rest in C:2 (10%). Category A:3 was the most utilized with 70% of dives and then A:2 with 17%. Less than 3% of dives were performed in either category A:1 or A:4.

During the day, each A category made up about 20% of TAC, categories B:1-4 less than 1.5% and categories C:1-4 about 18% (*fig. 7*). Out of the C categories, C:1 was the most common (7.5%) and then C:2 (4.3%). Dives were mostly performed in category A:1-4 (90%), where A:4 was the most utilized (~35%), then A:3 (~30%) and A:2 (~20%).

At dusk, Category A:1-4 made up 90% of TAC. The proportion of different A categories varied more here, then during dawn or day (*fig. 7*). A:4 was the most common (40%), both category A:3 and A:2 laid around 20% and A:1 was the least frequent at approx. 10%. Category B:1-4 made up less than 1% of TAC and category C:1-4 less than 10%. Dives were only performed in category A:3 (35%) and A:4 (65%).

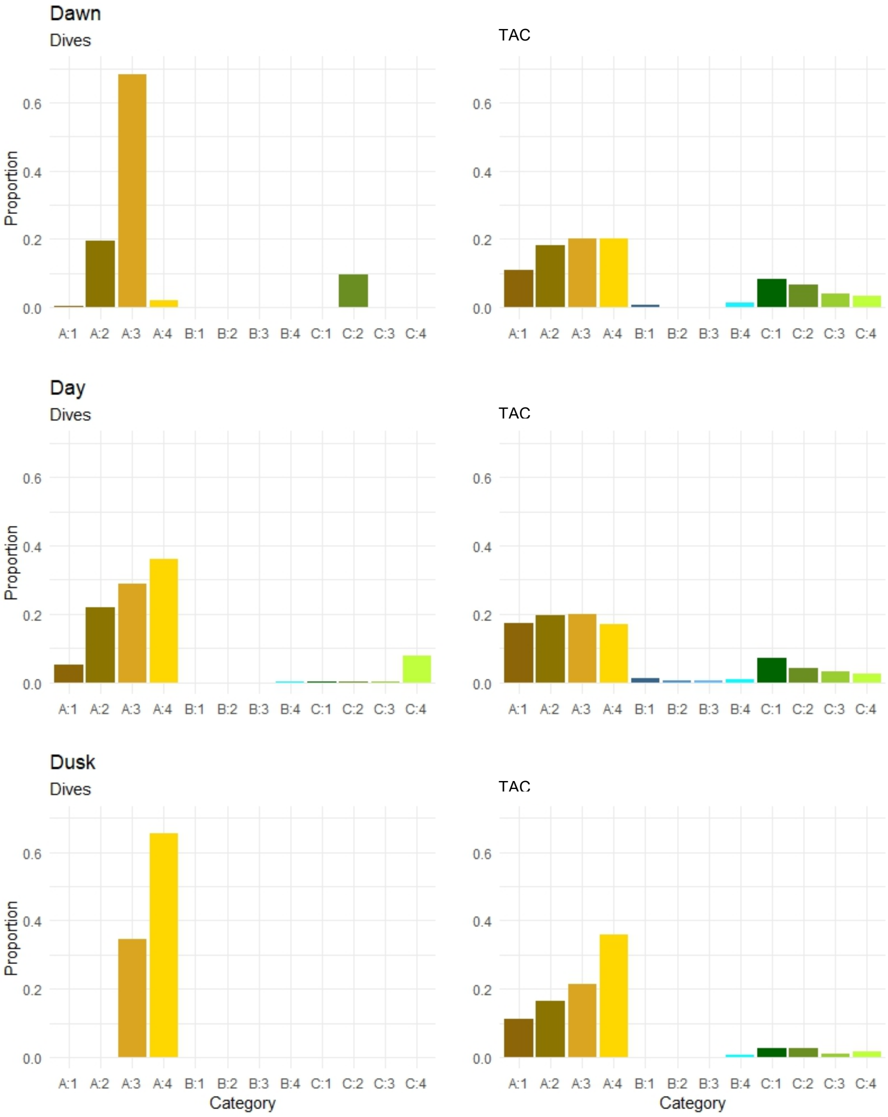

Figure 7: The proportion of each category based on TAC and guillemot dives at dawn, day and dusk. Category A is when prey was located within the first 50m, Category B deeper than 50m and category C when prey was distributed in two layers (shallow & deep). The numbers indicate biomass, where 1 represents less and 4 more. n= TAC: dawn= 744, day= 6894, dusk= 1198, Dives: dawn=190, day= 2135, dusk= 142.

In 2019 dives performed closer to the colony targeted categories A:1 and A:2, while dives performed further from the colony mainly targeted categories A:3 and A:4 (*fig. 8*).

In 2020 dives performed closer to the colony mainly targeted categories A:2, A:3 and A:4, while dives performed further from the colony mainly targeted categories A:2 and A:3 (*fig. 8*).

In 2022 dives performed closer to the colony mainly targeted categories A:1 and A:2, while dives performed further from the colony mainly targeted categories A:4, C:3 and C:4 (*fig. 8*).

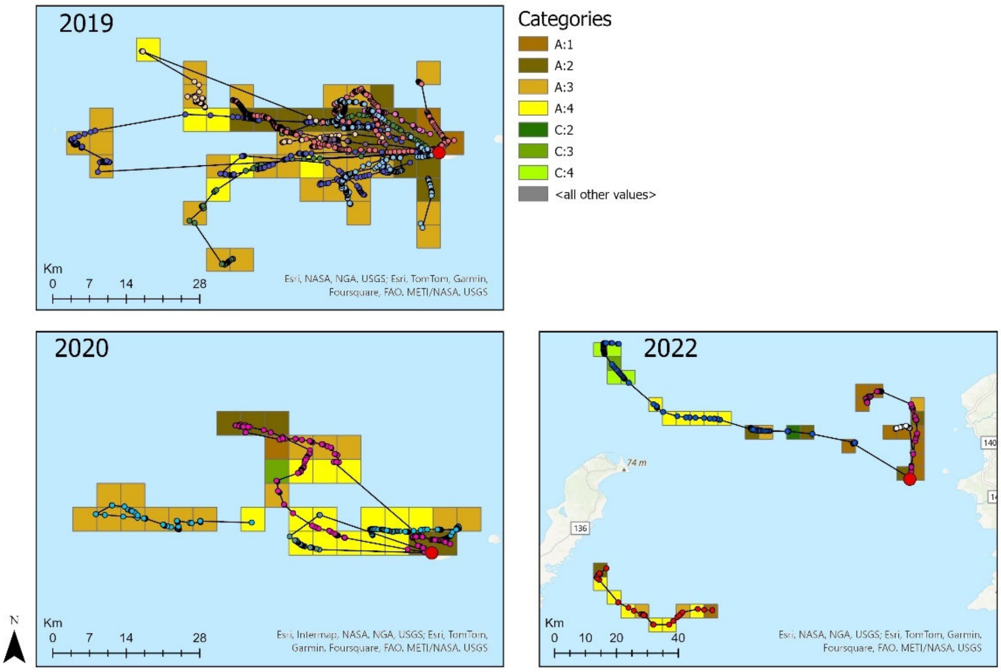

Figure 8: Guillemot trips with dives and prey distribution. Points indicate dives and are colour coded for different individuals, the coloured squares indicate vertical prey distribution category. Large red point marks the colony. n: 2019=1532, 2020=407, 2022=502.

3.2 Part 2: Dive behaviour and prey distribution

Model 1: Depth of dives in relation to prey distribution

To determine how prey distribution and travel distance affected the depth of dives it was tested how max depth per dive was related to available biomass, depth of prey and distance from colony (H1). Distance from colony had a significant effect on dive depth (p: 3.1e^{-8}) but neither biomass (p: 0.50), depth of prey (p:0.06), nor the interaction between the two did (p:0.07).

The relationship between distance from colony and max depth had a sinusoidal shape. Max depth first increased with distance from colony and peaked around 25m at approx. 10km. Then it decreased to about 12m at 50km, and then it increased again (*fig. 9*). Few data points were available for distances between 40 and 60km.

According to the model estimates, the max depth of dives increased with biomass and peaked at around 27m when biomass was approx. 735 kg/km^2. Then the max depth of dives decreased to about 25m at 1100 kg/km^2 (*fig. 9*).

The max depth of dives was around 33m when depth of prey was approx. 10m. Then it decreased to 25m when depth of prey was around 20m. Max depth of dives then increased back to approx. 33m when depth of prey was around 30m. Then depth of dive decreased with prey depth, but the uncertainty was high due to data scarcity (*fig. 9*).

The interaction between biomass and depth of prey showed that dives were deepest when biomass was high (545-900kg/km^2) at shallow depths (<20m) (*fig. 9*). The model had an R^2 value of 0.12.

Out of the six random effects, the proportion of variance explained by bout was the largest (0.40), then year (0.14), time of dive (h) (0.13), ocean depth (0.11), bird individual (0.02). The proportion of unexplained variance was 0.20.

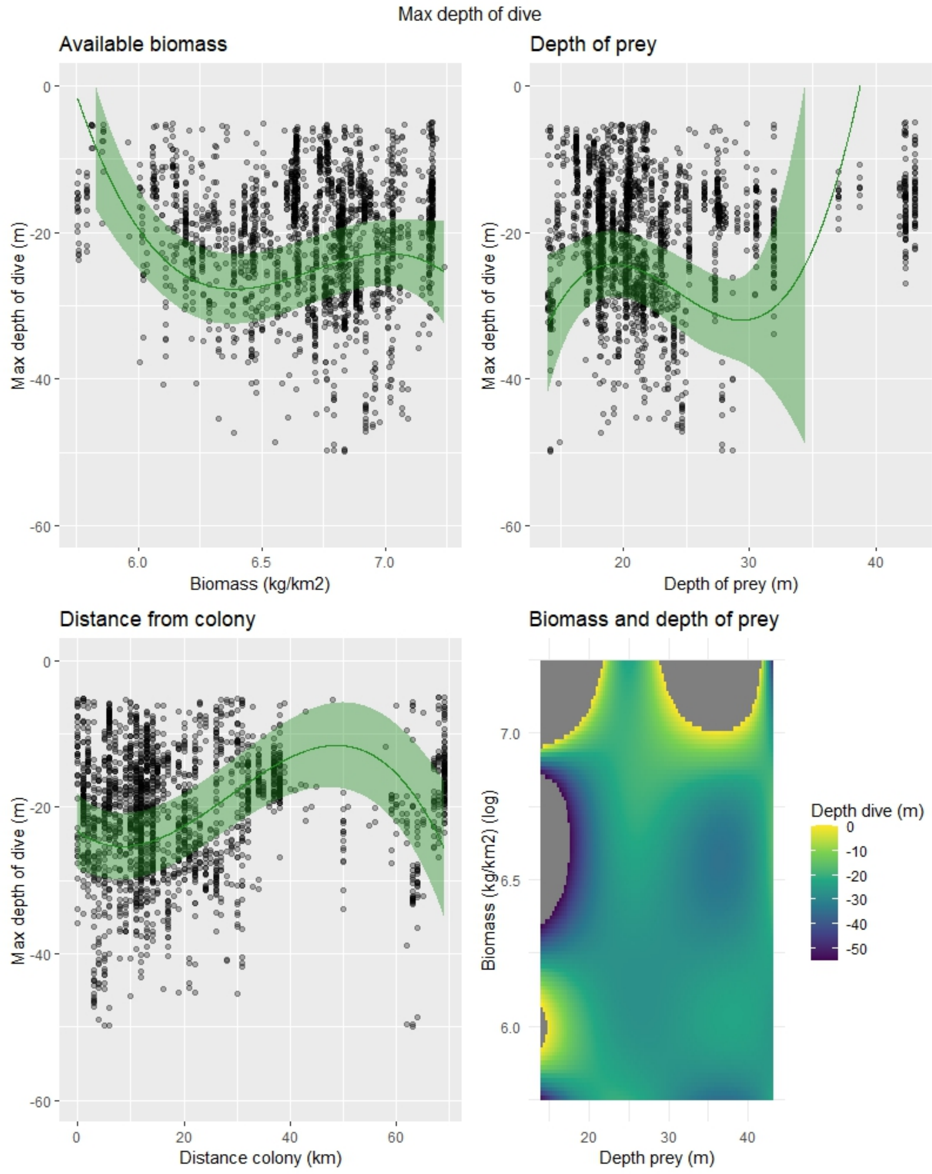

Figure 9: GAMM plots for the relationship between max depth of dive and biomass, depth of prey and distance from colony. The interaction between biomass and depth of prey is also visualised by a contour plot, where biomass is represented on the y-axis and depth of prey on the x-axis. The depth of dives is represented as a colour gradient where blue indicates deeper dives, and yellow shallower.

3.2.1 Duration of dive

Model 2: Foraging effort per dive in relation to patch quality

To determine how patch quality affected foraging effort per dive it was tested how dive duration per dive was related to available biomass, depth of prey and distance from colony (H2-H4). Biomass (p: 0.003), depth of prey (p: $3.4e^{-6}$) and distance from colony (p: $2.6e^{-4}$), all had significant effects on dive duration, including the interaction between depth of prey and biomass (p: 0.003).

Dive duration increased with biomass until approx. 665 kg/km^2 where it reached a maximum of approx. 90s. Then it decreased and stabilized at around 1400 kg/km^2 at a dive duration of approx. 80s (*fig. 9*).

Dive duration increased with depth of prey, to approx. 90s at 24m. Then it decreased rapidly. Few data points were available for when depth of prey was > 30m (*fig. 9*).

Dive duration decreased with distance from colony, from approx. 90s at 0km to 70s at around 45km distance. Then it increased again to about 110s at 70km. Few data points were available between 40 and 60km (*fig. 9*).

For the interaction between biomass and depth of prey, dive duration peaked (150-200s) when biomass was high (850-1400 kg/km^2) and depth of prey low (<20m). Dive duration was also high when prey was located deeper than 25m and biomass was <850 kg/km^2 (*fig. 9*). The model had a R^2 value of 0.10.

Out of the five random effects, the proportion of variance explained by time of dive (h) was the largest (0.34), then year (0.24), bout (0.05), breeding status and bird (both 0.02). The proportion of unexplained variance was 0.33.

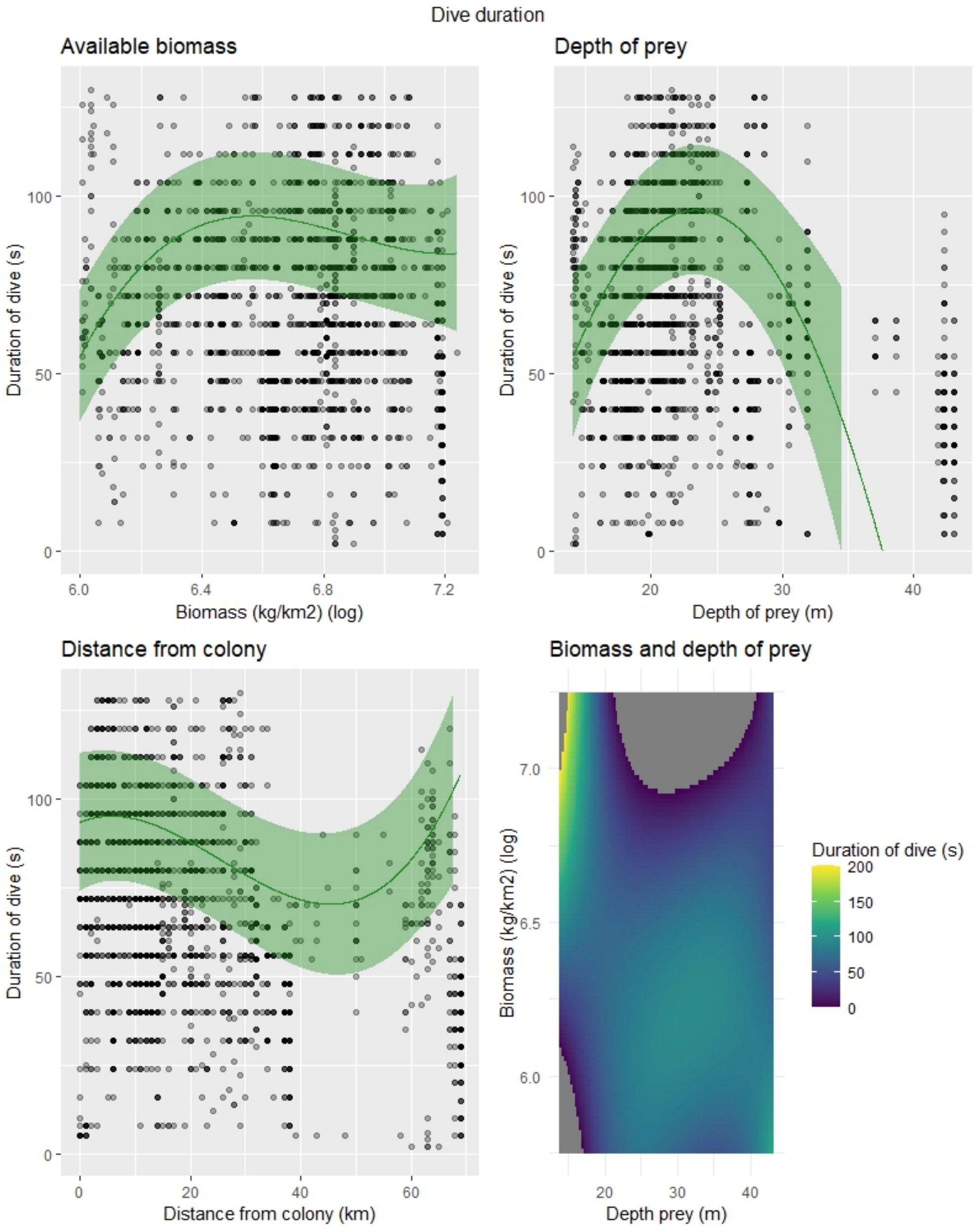

Figure 10: GAMM plots for the relationship between dive duration per dive, biomass, depth of prey and distance from colony. The interaction between biomass and depth of prey is also visualised by a contour plot, where biomass is represented on the y-axis and depth of prey on the x-axis. Dive duration is represented as a colour gradient where blue indicates shorter dives, and yellow longer.

Model 3: Total foraging effort per bout in relation to patch quality

To determine how patch quality affected foraging effort, it was tested how total dive duration per bout was related to available biomass & distance from colony (H2-H4). Both biomass (p: 0.005), distance from colony (p: 0.002) and the interaction between the two (p: 0.009) had significant effects.

Total dive duration per bout first decreased with biomass, from approx. 490s (8min) at 300kg/km^2 to 245s (4min) at 400kg/km^2. Total dive duration then increased to about 670s (11min) at 850kg/km^2, to the decrease to about 90s (1.5min) at 1400kg/km^2 (*fig. 10*).

Total dive duration per bout first increased with distance from colony from approx. 250s (4min) at 0km to around 600s (10min) at 15km. Then it decreased to approx. 165s (3min) at 55km. Total dive duration then seemed to increase, but uncertainty was high for distances > 40km due to data scarcity (*fig. 10*).

Total dive duration seemed to be the highest when biomass was high (660-1400kg/km^2) and distance from colony <40km. Total dive duration was also high when biomass vas very high (1200-1400kg/km^2) and distance from colony was >55km (*fig. 10*). The model had an R^2 value of 0.23.

Out of the four random effects, the proportion of variance explained by the number of dives in the bout was the largest (0.83) then the time of dive (h) (0.11), year (0.007) and bird (5.6e^{-9}). The proportion of unexplained variance was 0.05.

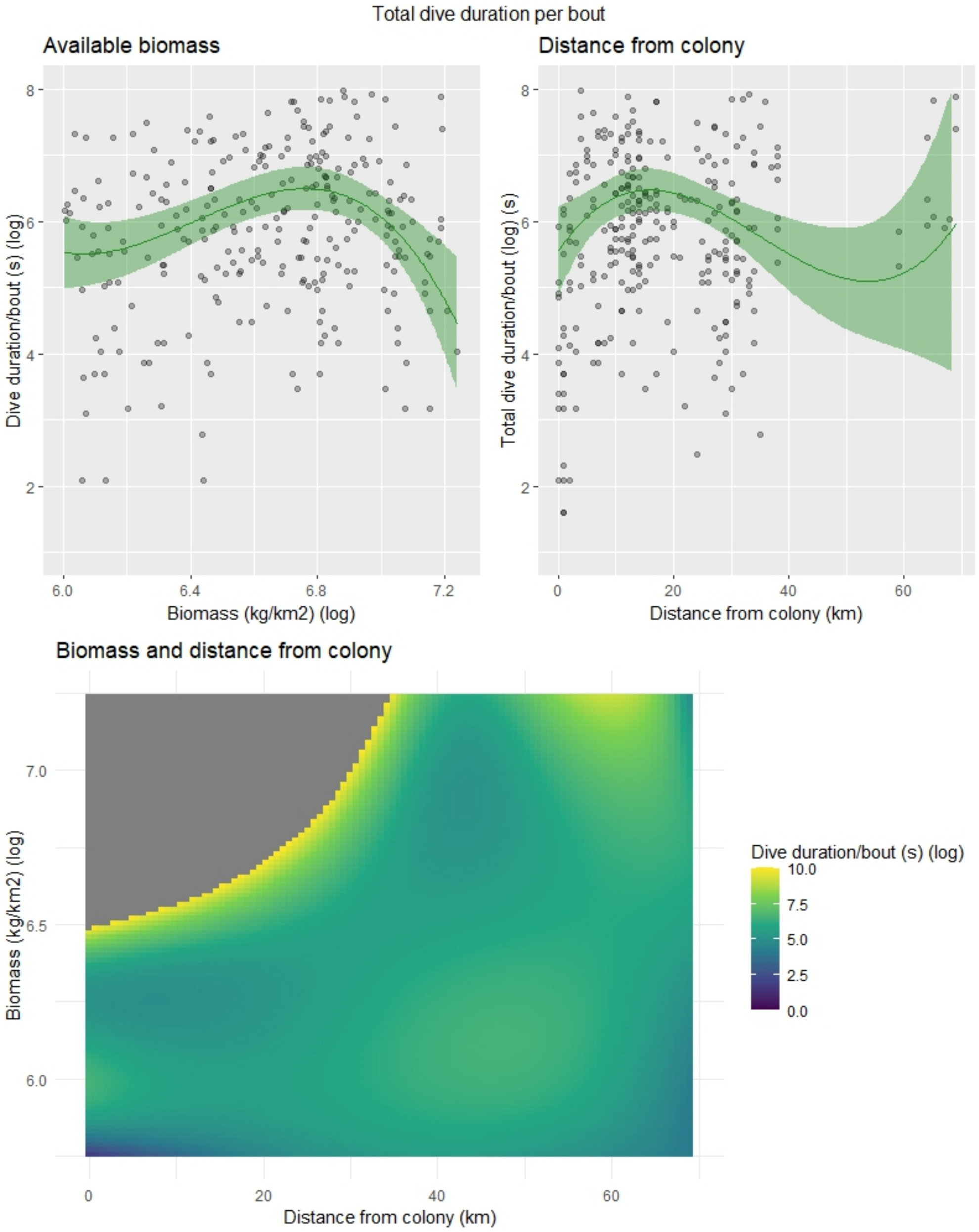

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Figure 11: GAMM plots of the relationship between total dive duration per bout and biomass and distance from colony. The interaction between biomass and distance from colony is also visualised by a contour plot, where biomass is represented on the y-axis and distance on the x-axis. Dive duration is represented as a colour gradient where blue indicates shorter dives, and yellow longer.

Model 4: Total foraging effort per trip in relation to patch quality

To determine how patch quality affected foraging effort, it was also tested how total dive duration per trip was related to available biomass & distance from colony (H2-H4). Both biomass (p: $7.8e^{-4}$) and distance from colony (p: 0.004) had significant effects on dive duration.

Dive duration increased with biomass from approx. 850s (14min) at 400 kg/km^2, to about 17000s (4.7h) at 820 kg/km^2. Then it decreased to approx. 3800s (1h) at 1200 kg/km^2 (*fig. 11*).

Dive duration increased with distance from colony from approx. 900s at 0km to 22000s (6h) at 20km. Then total dive duration decreased to about 3300s (55min) at 55km. Dive duration then seemed to increase again but the uncertainty was high when distance was >40km, due to data scarcity (*fig. 11*). The model had an R^2 value of 0.43.

Out of the two random effects, the proportion of variance explained by year was the largest (0.48) then time of dive (h) (0.23). The proportion of unexplained variance was 0.29.

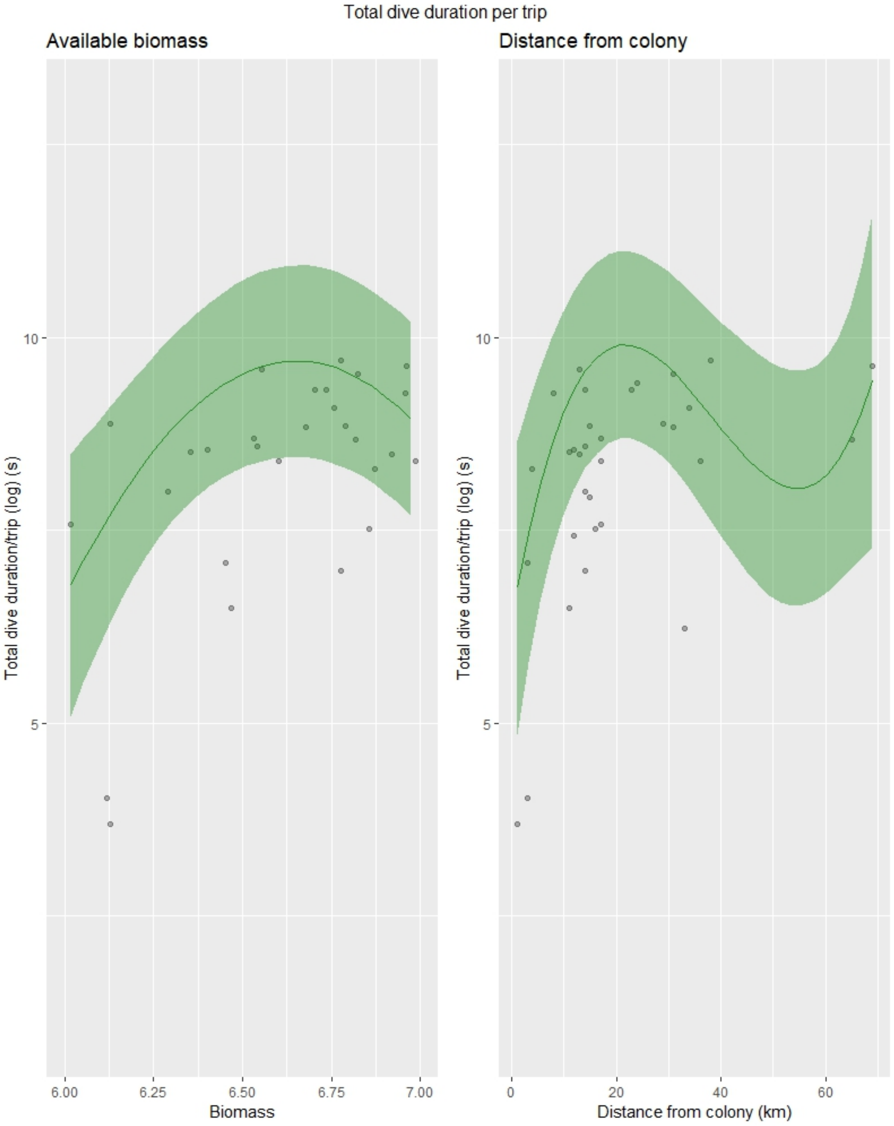

Figure 12: GAMM plots for the relationship between total dive duration per trip and biomass and distance from colony.

Model 5: Mean foraging effort per dive per bout in relation to patch quality

To determine how patch quality affected foraging effort it was also tested how mean dive duration per dive per bout was related to available biomass and distance from colony (H2-H4). Both biomass (p: $8.4e^{-4}$) and distance from colony (p: $9.6e^{-8}$) had significant effects on mean dive duration.

Mean dive duration increased with biomass, from about 60s at 315 kg/km^2 to around 85s at 735kg/km^2. Then dive duration decreased to about 65s at 1400kg/km^2.

Mean dive duration initially increased with distance from colony, from about 60s at 0km to around 70s at 15km. Dive duration then decreased to about 45s at 50km, and then increased to 85s again at 69km. Uncertainty was hight for distance <40km due to data scarcity. The model had an R^2 value of 0.12.

Out of the three random effects, the proportion of variance explained by time of dive (h) was the largest (0.23), then bird (0.13), year (0.12), breeding status (0.12) and number of dives (0.008). The proportion of unexplained variance was 0.57.

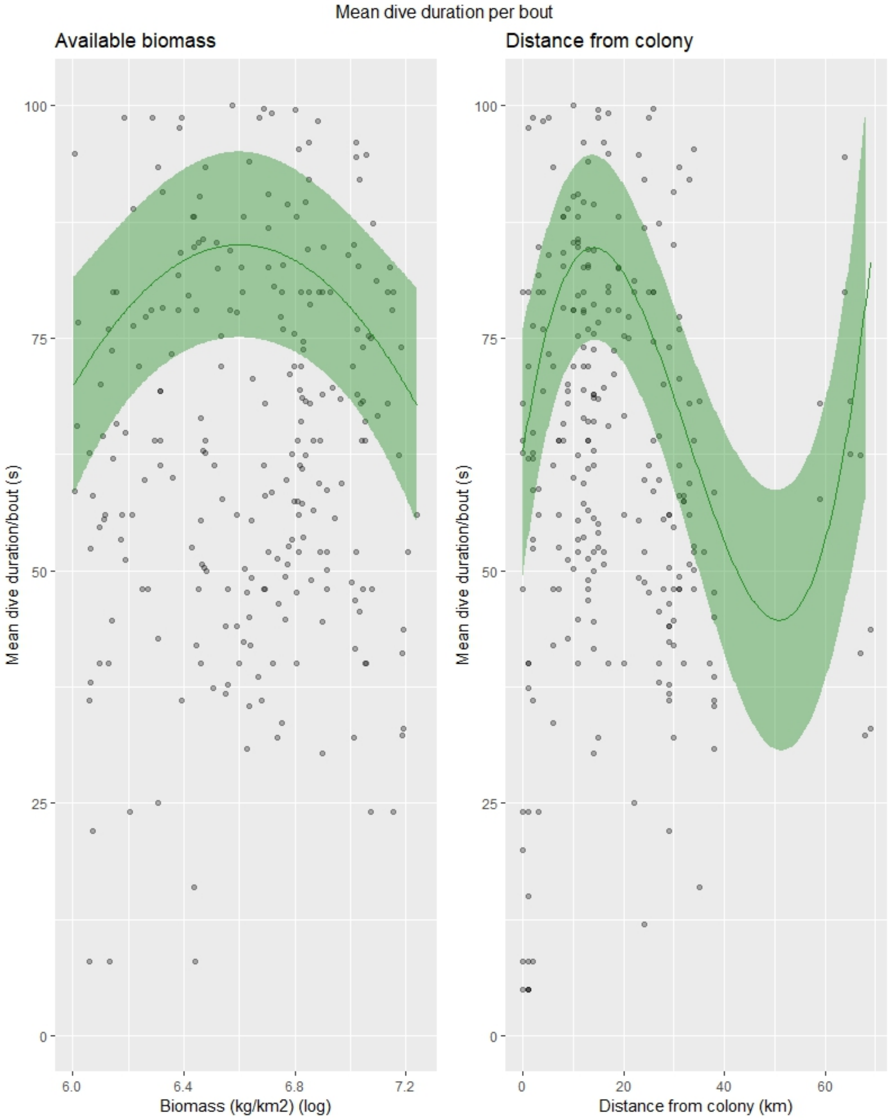

Figure 13: GAMM plots for the relationship between mean dive duration per dive per bout and biomass and distance from colony.

Model 6: Mean foraging effort per dive per trip in relation to patch quality

To determine how patch quality affected foraging effort it was also tested how mean dive duration per dive per trip was related to available biomass and distance from colony (H2-H4). Neither biomass (p: 0.13) nor distance from colony (p: 0.19) had significant effects on mean dive duration per trip.

Mean dive duration decreased with biomass from about 85s at 400kg/km^2 to approx. 70s at 545kg/km^2. Dive duration then increased to about 80s at 990kg/km^2, and then decreased again to 75s at 1200kg/km^2.

Mean dive duration first increased with distance from colony, from around 65s at 0km distance to about 80s at 15km. Then dive duration decreased to about 50s at 60km distance. Then dive duration seemed to increase again. The uncertainty was high when distance was >40km due to data scarcity. The model had an R^2 value of 0.0.

The random effect number of dives in trip explained a proportion of 0.42 of observed variance and the unexplained variance was 0.58.

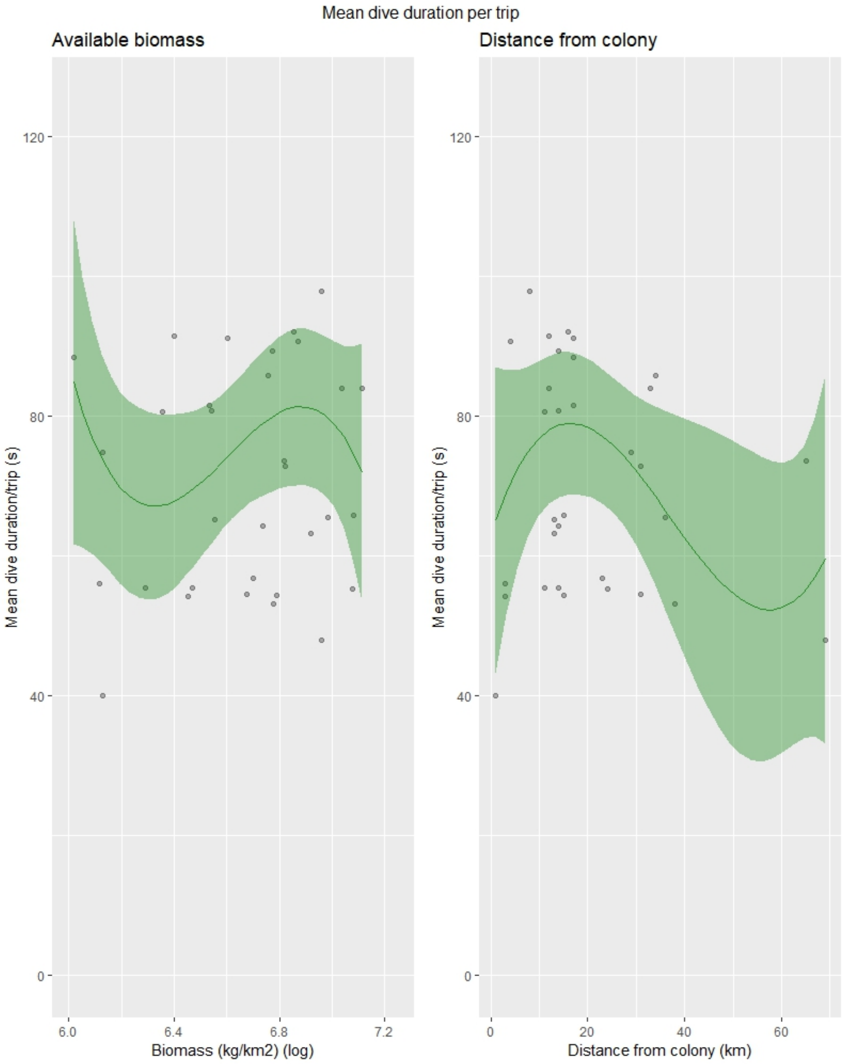

Figure 14: GAMM plots for the relationship between mean dive duration per dive per trip and biomass and distance from colony.

3.2.2 Targeted biomass and distance from colony

Model 7: Patch quality in relation to distance from colony

To determine how distance from colony affected quality of patch targeted, it was tested how biomass of targeted patch was related to distance (H4). The effect of distance on biomass was significant (p: $<2e^{-16}$).

Biomass increased with distance from colony, from approx. 520kg/km^2 at 0km to 900kg/km^2 at 69km. The model had an R^2 value of 0.12.

Out of the four random effects, the proportion of variance explained by year (0.46) was the largest, then time of dive (h) (0.22), bout (0.18) and bird (0.13). The proportion of unexplained variance was 0.006.

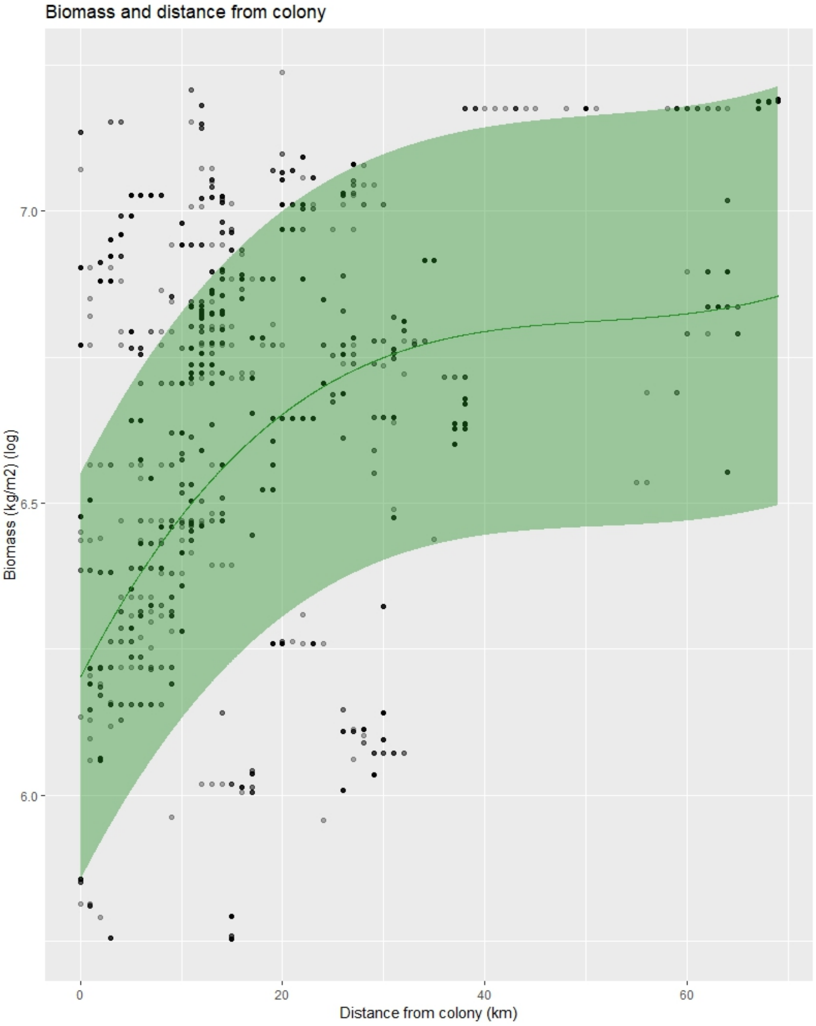

Figure 15: GAMM plot for the relationship between biomass in targeted patch and distance from the colony.

4. Discussion

Dive behaviour and time allocation was investigated within the optimal theory framework based on hydroacoustic data on prey distribution collected by an USV. I hypothesized that the distribution of prey in depth and space and available biomass would determine diving behaviour of common guillemots. This was tested by comparing patch availability with utilization by birds and by using GAMMs to test the relationship between dive behaviour and prey distribution and availability.

According to the MVT more foraging effort should be put into patches of higher quality. This was used as the basis for part 1, where patch availability vs. utilization was investigated. The results showed that birds mostly utilized patches with shallow prey (category A, which also made up the majority of TAC). More dives were also performed in patches with more available biomass (A:3 & A:4). However, as no statistical test was conducted on the differences between availability and utilization it is difficult to investigate significance. This decision was made as the data was not independent, and therefore did not meet the assumptions of eg. a chi-square goodness of fit test. While many studies have been conducted on habitat use in relation to availability, with the use of methods such as resource selection functions, doing so in an aquatic environment is more difficult, as habitats and prey availability are highly dynamic (Boyd et al. 2015). To be able to predict foraging conditions one must predict prey distribution patterns in the area, which are largely driven by environmental factors such as temperature, salinity, algal blooms, wind patterns etc. Constructing an accurate enough model of this was too time consuming for this master thesis but will be addressed in future research (in prep. Carlsen et. al.). Petrides (1975) and White & Garrott (1990) (in Manly et al. 1993) also states that resources might be used out of necessity not favouring and that these two cannot always be distinguished from one another. Aarts et al. (2008) also mentions this, and I can therefore not state *how* important patches with prey in shallow layers are to guillemots, or if they're preferred (Manly et al. 1993) by only testing dive duration and depth. However, I here show that these patches are utilized more often than what would be expected if chosen at random, and that they sustain the population, as the annual breeding success has remained stable and high (~70% success, with a drop in 2020 due to other factors (Hentati-Sundberg et al. 2023)). However previous studies from the same colony, have found that Guillemots mostly forage at dusk and dawn, and that dives performed then are shallower than during daytime (Evans et al. 2013; Menestrina 2021). As fish migrate closer to the surface at night (DVM), more biomass is available in shallow layers. This study, combined with previous findings, identifies that DVM of prey is likely to have significant impact on the foraging behaviour of common guillemots on Stora Karlsö. By modelling the prey abundance and distribution in the area, more foraging trips and dives could be utilized, and this relationship could be further investigated.

Foraging effort was also investigated in part 2, where I hypothesized that dive duration should increase in high quality patches while total dive duration per trip should decrease, due to high foraging efficiency. Dive duration & mean dive duration/bout did increase with biomass, indicating that birds are not only targeting patches with more available biomass, but also perform longer dives there (the model that tested mean dive duration per trip had an R^2 value of 0, probably due to very few available data points (n=31), and is therefore not considered here). This could indicate that birds are capturing several prey items per dive, which would result in longer, but fewer, dives, and that the patches are of high quality. However, total dive duration per trip did not decrease when dive duration per dive increased. Total dive duration per trip seems to have been the lowest when biomass was lower and higher than average, following the same pattern as dive duration per dive. This indicates that the quality of the patches might not be very high, but only acceptable, as the total foraging effort per trip did not decrease. Dive duration (total & per dive) did decrease when biomass continued to increase. Further investigation of the hydroacoustic data indicates that in intervals with more available biomass, prey was located deeper. However, the max depth of dives was found to decrease with biomass, indicating that guillemots are not targeting these layers with more biomass. However, in model 1, only dives < 50m were analysed (this is discussed further later on), and to better understand the drivers behind deep dives more data would be needed. The time between trips could also be an indicator of how successful the previous trip was and would be interesting for future studies. Time of dive (hour of the day) explained quite a lot of the observed variance in dive duration between dives, which means that *when* a dive was performed affected its duration. This might be related to the DVM of prey, as discussed previously.

An optimal amount of biomass was not identified though certain biomass levels seemed to be sought out. Foraging effort in part 1 was found to be the highest in biomass categories 3-4 and dive duration peaked in biomasses that corresponds to biomass categories 3-4. I therefore identify a preferred biomass range, that the guillemots seek out and spend more time diving in.

The depth of dives was hypothesized to be determined by the depth of prey. In this study a sinusoidal-like relationship was observed between depth of dives and prey. When depth of prey increased from 15 to 30m the depth of dives increased as well. However, when depth of prey was < 15m bird dives where deeper and when depth of prey was > 30m dives were shallower. This could potentially reflect ecological variations (e.g. prey species compositions at different depths), but few data points were also available for depth of prey >35m and out of all intervals 75% had a depth of prey < 30m. This might be an indication of that most prey in the area was located in shallow layers, or an implication of using a weighted mean (which is discussed more later). The random effects “bout” and “year” explained the most observed variance. These contains *all* differences between bouts and years, e.g. environmental differences such as temperature, currents, algal blooms etc. and prey composition, and therefore acts as bins to contain all eventual differences between bouts and years that were not considered. Time of dive (h) explained about the same prop. Of observed variance between dives as year. This could further indicate that the DVM of prey affects the diving behaviour of guillemots. The interaction between biomass and depth of prey showed that dives were deepest when biomass was intermediate and depth of prey shallow, not following the hypothesized trend of deeper dives only being performed when more biomass is available. In this study I did not have the possibility to differentiate fish species, but assumptions can be made based on knowledge of the behaviour of different fishes. During the day, mostly sticklebacks and very few (<1% of catch), larger herring and sprat individuals reside closer to the surface, while most individuals hide at deeper depths (pers. Comm. Olavi Kaljuste). Different behaviours might therefore be needed at different times of the day, to target the same prey species. However, the weighted mean used to calculate mean depth of prey also does not capture the vertical spread of the prey patch (size), neither does it capture if prey is located in several layers. This also complicates the discussion around prey selectivity, as *only* the layer with the most available prey is used for analysis. Also, in model 1, only dives < 50m were included, due to the bimodal distribution of the data. Deeper dives (15% of dives) were therefore not investigated further. The range of mean depth of prey was 14-43m and looking into the relationship between dives deeper than 50m and mean depth of prey would however not have been useful. While the results could indicate that the depth of prey isn’t a driver of dive depth, the unclear relationship is more likely due to problems with using the weighted mean as the only factor of prey depth. However, as 75% of dives in this study were < 28m and ~90% were performed in category A patches, indicates that patches with shallow prey are most utilized. Out of the deep dives (>50m), 94% were performed during the day, remaining 6% at dusk. This also indicates the previously mentioned theory, that DVM of prey highly impacts guillemot foraging behaviour. However, further analysis is needed to understand why and when deep dives are conducted.

It was also hypothesized that higher quality patches should be targeted further from the colony. In part 1, birds in 2019 and 2022 targeted patches with more biomass further from the colony, while in 2020 high biomass patches were available closer to the colony. However, in 2019 and 2020 only data from chick rearing birds was available, while in 2022 it was only from incubating birds. This is also reflected in the mean distance travelled from the colony, which was much longer in 2022 (2019: 14.6, 2020: 15.3 & 2022: 44.9km). Dive duration and mean, as well as total, dive duration per bout and trip all decreased with distance from colony. However, all models also showed an increase in dive duration when distance was >60km, but this was based on very few data points. Models of prey distribution patterns in the area (in prep. Carlsen et. al.) have found that more biomass is available closer to the colony and further away, while in between there seems to be less available prey. The sinusoidal like relationship between dive duration and distance from colony could therefore reflect this pattern, that more time is spent foraging where more prey is available. This pattern is also seen in model 3, where total dive duration per bout was longer when biomass was high and distance from colony was either <40km or >55km. However, the range in distance for chick rearing birds was only 0-38km (mean: 15km), while for incubating birds it was 0-69km (mean 45km), which indicates that this patterns probably only reflects differences between chick rearing and incubating birds. While this affects the per year results, the general trend was that biomass in targeted patches did increase with distance from colony, with almost a doubling in targeted biomass between 0 and 69km distance. Higher quality patches are hypothesized to be targeted further away to maximize prey capture rate, as energy expenditure increases with distance. In this study, only 4 birds were incubating (12 chick rearing) and they performed about 25% of all dives and 4 (out of 32) trips. In future studies, where more data is available, these two groups should be investigated separately.

Horizontal and vertical patches were defined in this study by selecting dives that were performed within 5km of USV sampling and by dividing the water column into two layers. As organisms perceive the environment at different scales (Kotliar & Wiens 1990) an initial goal was to try and capture what the guillemots experience during a dive. However, to do so it is crucial to, as accurately as possible, capture the movement and distribution of prey. By visual inspection of echograms from the area three main distribution types were identified. Prey close to the surface, prey closer to the bottom or two layers of prey at different depths. Dividing the water column into 3 or 4 layers quite often resulted in division of prey aggregations, as the limits didn't really capture these general prey distribution patterns (*fig. 2*). Also, in ~80% of all USV sampling points prey was located within the first 50m and in ~15% the first 50m and bottom 50m (two layers of prey). A division of the water column into 2 layers should therefore have captured both these main distributions of prey. The bimodal distribution of depth of dives also showed two main types of dives, deep (>50m) and shallow (<50m), which should also be captured by two 50m layers. As these categories only were used in part 1, while the relationship between Guillemot dive behaviour and depth of prey was investigated further in part 2, it was decided to be an acceptable balance between complexity and accuracy.

When investigating patch selection there is also a question of what is ecologically relevant. For this study the patchiness that the birds are experiencing within their foraging extent during breeding is of interest, and patches should therefore be defined within this range. The dives in this study were performed between 0-69km from the colony, and the patches should therefore be defined within this range. Five kilometres and 14 days were used as the limits to classify an overlap between dives and USV sampling, based on visual inspections and statistical models of the dynamics of fish distribution in the area (In prep. Carlsen et. al.). However, at what scale the seabirds experience the patchiness of the environment is probably highly influenced by how predictable the environment is (Weimerskirch 2007). This could be further investigated with modelling of prey distribution in the area at a high spatiotemporal scale.

In this study, models explained a small amount of observed variance (range R^2: 0 - 0.43, mean R^2: 0.16). This thesis was a first trial of this method, and many factors were highly based on assumptions (such as patch size etc.). Prey distribution and abundance was calculated per bout, while distance between dives, within the same bout, could be several kilometres. Foraging conditions could therefore have varied within bouts, while this variation was not captured. This decision was made as it was not believed that the spatial resolution of the hydroacoustic data in reference to dive position was high enough to describe the foraging conditions for each dive. Additionally, as USV intervals and dives could've occurred several days and kilometres from each other, it was thought that a general assumption of the foraging conditions experienced within a bout would be most accurate. The mean depth of prey, as mentioned, was also calculated with a weighted mean, while a more advanced measurement might be needed to accurately test the relationship between prey depth and dive depth. However, if DVM patterns are strong, hour might be the best indicator of prey depth (In prep. Carlsen et. al.). There are also issues with the method used for calculating biomass from NASC values. It was assumed that at daytime all prey located < 30m were sticklebacks, and prey > 30m were 50% herring and sprat (respectively), while at night equal proportions were assumed. This is an overestimation of herring, as sprat is much more abundant, leading to an overestimation in overall biomass during the night (as herring is generally larger than sprat), and in depths during the day. The mean size per species was also used to calculate the biomass, while it would be more accurate to use the actual proportions of different size classes per species. Problematically, the USV cannot make biological samples and the acoustic data was collected 1-2 months after the nearest trawl survey, and so available size distributions (and perhaps even species compositions) are unlikely to be accurate. This will be addressed in future studies. Prey has also been found to hide close to the sea bottom at day (in prep. Carlsen et.

al.), which might result in misrepresentative biomass values as they can't be distinguished from the bottom strata. The heterogeneity of prey (eg. size and species) could also not be captured in this analysis, but it likely impacts the diving behaviour of guillemots, as discussed. By constructing an extensive prey prediction model of the area higher spatial resolution could be estimated and more dives could be analysed, as it would not be as dependent on spatial overlap between the USV and the tracked guillemots. In this study, only dives from 12 unique individuals were available, with very unbalanced sample sizes (table 2). Studies have found that different individuals often vary in their dive style (Patrick et al. 2017; Jeffries et al. 2021), and this could better be captured if more dives per bird were available, as birds in this study only had, on average, 2 trips each. It could also be interesting to look into when the next trip occurred, as this could be an indicator of how successful the previous trip was (i.e. longer between-trip durations should reflect higher success, and revisits to the same area may reflect individual versus population level preferences). Due to telemetry data not being available, it could not be done in this study. Studies also show that adults may feed chicks different prey than what they themselves consume (Wilson et al. 2005). As the Guillemots return a single prey to the colony, the last dives per trip could possibly differ from previous dives. With more trips per bird this could be investigated further. Possible differences in time allocation in relation to prey availability between chick rearing vs. incubating birds could then also be investigated. It becomes clear that, as per usual within ecology (Breckling 1992), a lot of factors influence dive behaviour of common guillemots. Predictions will never be perfect, but the findings of this thesis has increased the understanding of the effects of local prey field on guillemot foraging behaviour and findings will be used to further develop the use of USV collected hydroacoustic data.

This is a pioneering method that combines high resolution prey distribution data with dive telemetric data of guillemots to better understand the effects of local prey conditions on foraging behaviour. The guillemot colony on Stora Karlsö is of high interest to continue study as seabirds are seen as indicators of overall ecosystem health (Piatt & Sydeman 2007) and long-term data is available, which is highly important to identify population trends in response to e.g. climate change and other anthropogenic effects (Orgeret et al. 2022). The guillemots on Stora Karlsö are also currently the only species assessed by HELCOM for breeding success of waterbirds in the Baltic Sea (*Breeding success of waterbirds* n.d.). This method can possibly also be scaled up to be used for different species and monitoring programmes to further increase the understanding of top predators in aquatic environments and to predict effects of changing prey populations.

5. Conclusions

H1: In conclusion it was found that, the depth of dives was somewhat related to depth of prey, but the method used for determining prey depth needs to be revised. Due to this and that deep dives (>50m) couldn't be analysed in this study it was difficult to assess if deeper dives only occurred when a lot of biomass was available at deeper depths.

H2 & H3: In conclusion, it was found that foraging effort was higher in patches where prey was located in shallower layers and biomass was high. More dives were performed there, and dive duration also increased with biomass. The total foraging effort per trip did however not decrease which indicated that patches were only of acceptable quality, but enough to sustain the population. An optimal amount of biomass was therefore not identified, but a preferred range. To identify if conditions were optimal, or just acceptable, number of dives in trips and the duration between trips would need to be analysed.

H4: Foraging effort was higher closer to the colony, and further than 60km from it, probably only reflecting differences between incubating and chick rearing birds. The general trend was that patches with more available biomass were targeted further from the colony. In future studies incubating and chick rearing birds should be considered separately.

Diel vertical migration (DVM) was also found to possibly affect guillemot dive behaviour, due to the high utilisation of patches with shallow prey, deep dives being performed almost exclusively during the day and time of day (h) explaining a lot of the observed variation in dive duration and max depth between dives.

This thesis was the first trial of this method, and future studies will build on these findings to increase the understanding of this highly important population of guillemots in the Baltic Sea. Findings can also possibly be utilized in e.g. HELCOM monitoring programs and this method can probably be scaled up and utilized for different species within different programs.

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Popular science summary

Resources aren’t evenly distributed in the environment, and predators need to use different strategies to maximize their gain. Optimal foraging theory is a framework that entails several theories that describes how predators should behave to do so. The Marginal Value Theorem (MVT) predicts the optimal time to spend in different patches depending on quality and travel distance and hypothesizes that more time should be spent in patches of high quality. Central-place foraging is another theory, which is applicable to organisms that need to return to a central-place during foraging. This can also be applied to diving animals, as they always need to return to the surface. As a result, these organisms are limited in the distance they can travel, both vertically & horizontally. However, to test these theories high resolution spatial temporal data on both predator and prey distributions is needed, which is often both costly and time consuming to obtain.

Different organisms react to the patchiness of environments at different scales, and patches need to be defined in a way that is ecologically relevant for the target species. However, doing so in aquatic environments is especially difficult due to their highly dynamic nature. Fish distribution is highly affected by abiotic factors, but many fish populations have also been affected by commercial fisheries. Small pelagic fish is the main food source for guillemots, and in the Baltic Sea these are mainly sprat, herring and sticklebacks, whose populations have all changed significantly.

Guillemots are inefficient flyers, but highly efficient, wing-propelled divers that have been observed diving to depths up to 250m. The largest colony in The Baltic Sea is located on the island of Stora Karlsö, outside of Gotland, Sweden. In this study I had the opportunity to use high-resolution data on prey distribution collected by an autonomous sail drone, operated around the colony. Using an autonomous sail drone is a pioneering method that offers a time-and cost-effective method for obtaining high resolution data on prey distribution and by combining it with telemetric dive data from guillemots it allows for in-depth analysis of foraging behaviour in relation to prey availability and distribution.

Several effects of prey distribution on foraging behaviour were observed. It was found that foraging effort was the highest in patches where more prey was available and located in shallow layers. This in combination with that when a dive was performed (time of day (h)) effected the duration and depth and that deep dives almost exclusively occurred during the day indicated that diel vertical migration of prey highly impacts guillemot dive behaviour. The total foraging effort per trip did not decrease with dive duration, which indicated that patches were only of acceptable quality. A preferred range of biomass was identified, and guillemots also targeted higher quality patches further from the colony. Seabirds are seen as good indicators of overall ecosystem health, and an increased understanding of their foraging behaviour in response to prey availability can aid us in predicting potential effects of changing fish populations. This method also offers new possibilities to study predator-prey interactions and can possibly be applied to different species and within different monitoring programmes.

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Lastly, I want to thank my partner and friends, for continuously encouraging me and also reminding to take breaks!

Appendix 1

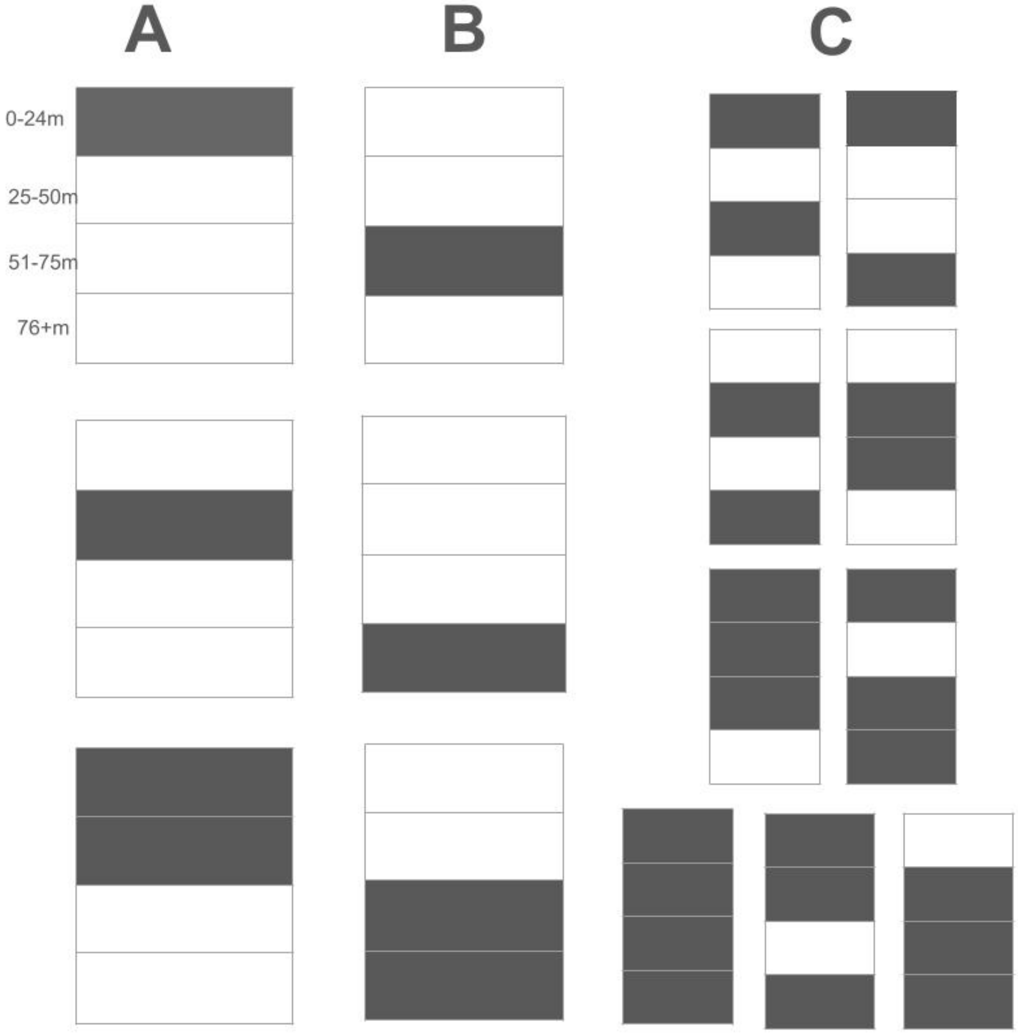


Figure A1: The 15 vertical prey distribution types that USV intervals were originally classified as, and how they were merged into category A, B and C.

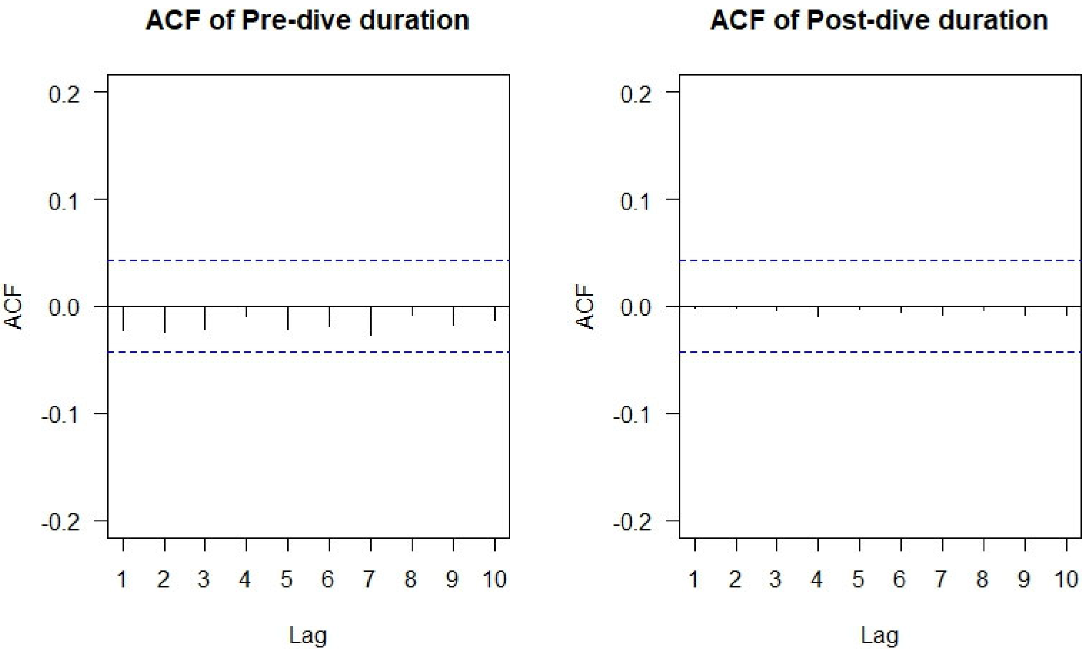
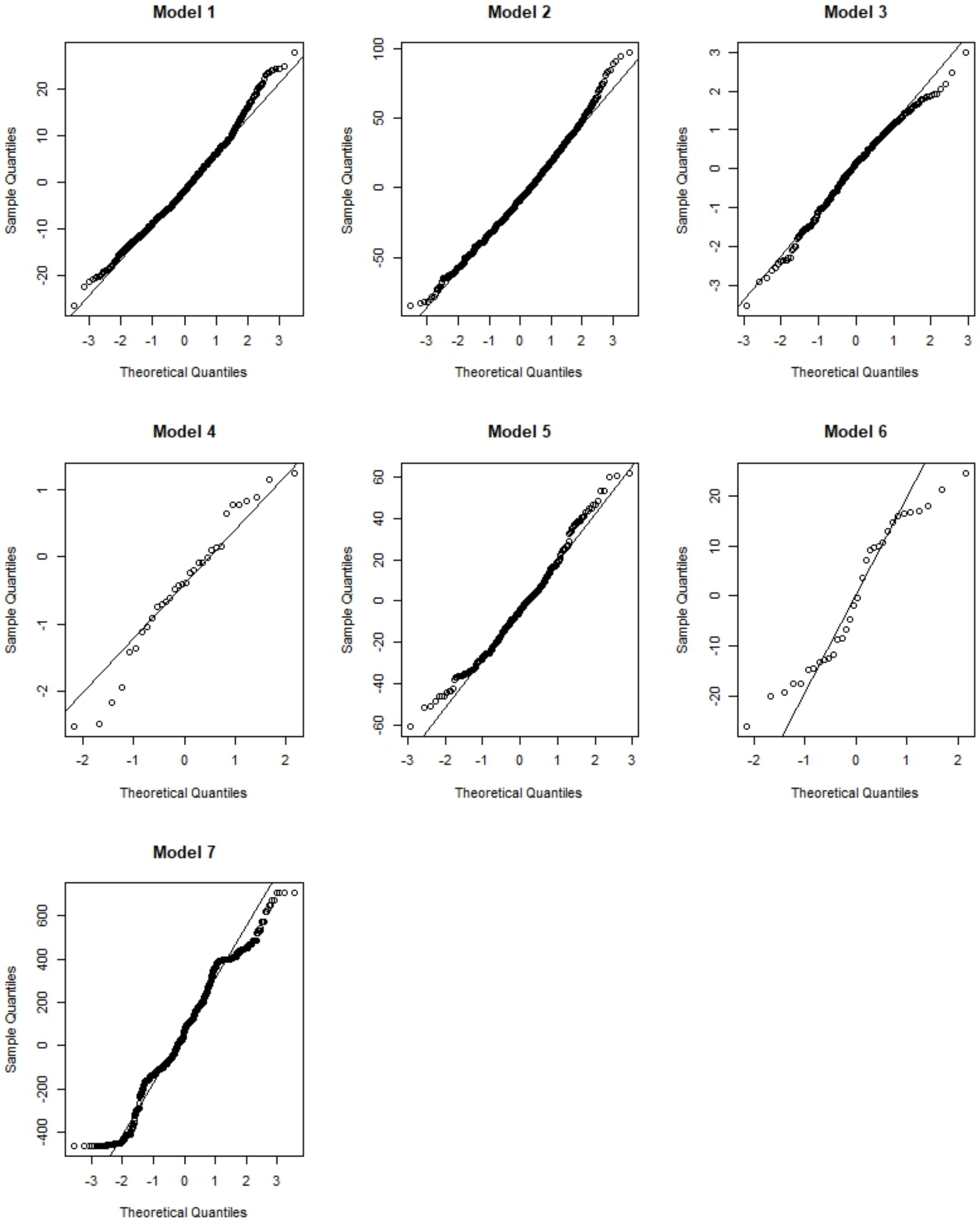


Figure A2: Autocorrelation between dive number and pre-and post-dive duration. No Autocorrelation was observed between either.



Model 1

Model 2

Model 3

Model 4

Model 5

Model 6

Model 7

Figure A3: Q-Q plots of residuals for all GAMM models. All models show a normal distribution of residuals.

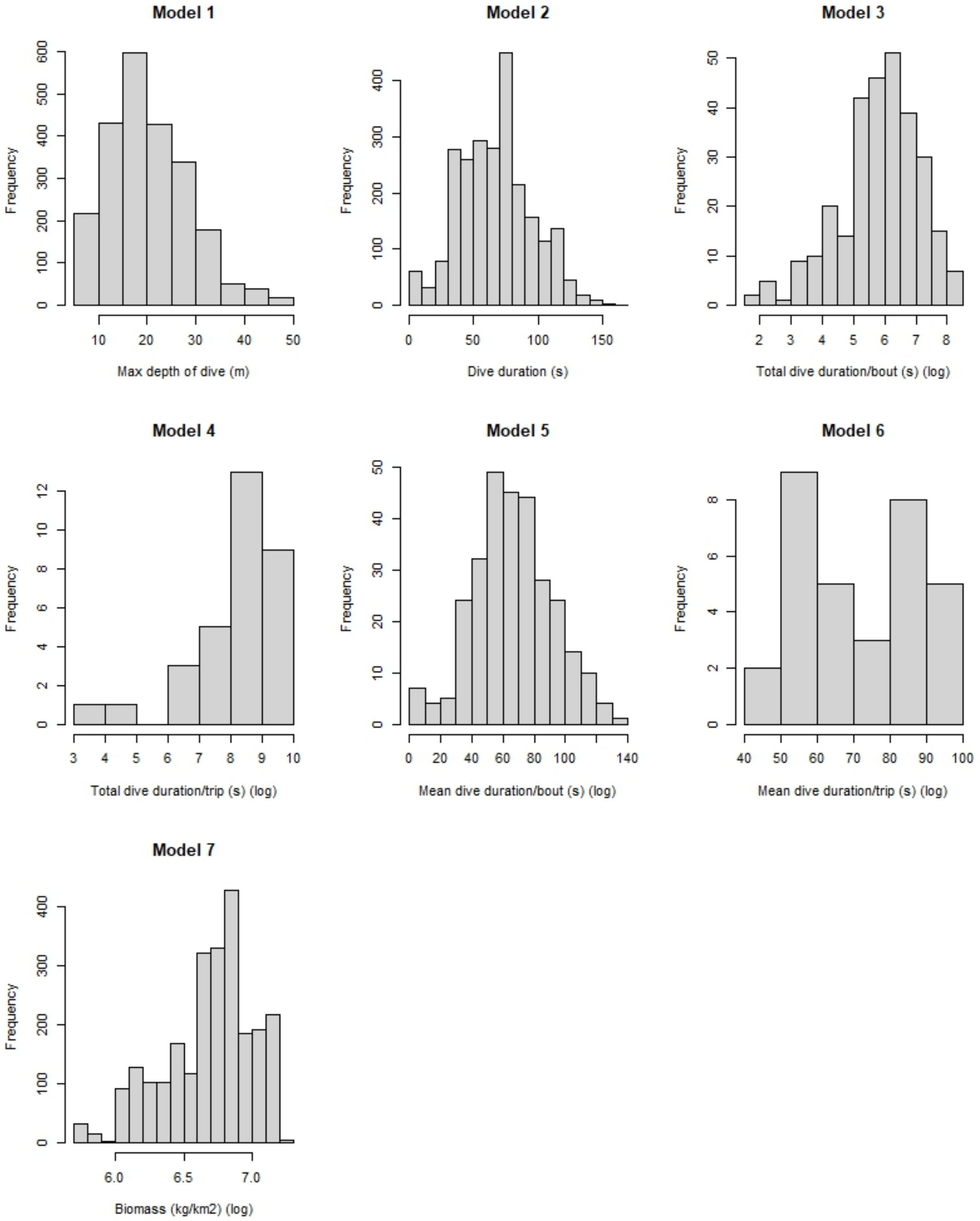


Figure A4: Histogram of all response variables. Models 4 and 7 are dive duration per trip, and only have 31 datapoints.

Table A1: Model selection process and AIC values for model 1.

Level	**Model**	**AIC**
Simplest	Max depth~	11226
Most complex	Max depth ~ poly(depth prey , 2) * poly(biomass(log), 3) + poly(distance colony, 3) + (1|Year) + (1|BirdID) + (1|Breeding status) + (1|Ocean depth) + (1|Bout) + (1|Time of dive (h))	10944
Selected	Max depth ~ poly(depth prey , 2) * poly(biomass(log), 3) + poly(distance colony, 3) + (1|Year) + (1|BirdID) + ~~(1|Breeding status)~~ + (1|Ocean depth) + (1|Bout) + (1|Time of dive (h))	10942

Table A2: Model selection process and AIC values for model 2.

Level	**Model**	**AIC**
Simplest	Dive duration~	22320
Most complex	Dive duration ~ poly(depth prey , 2) * poly(biomass (log), 3) + poly(distance colony, 3) + (1|Year) + (1|BirdID) + (1|Breeding status) + (1|Bout) + (1|Time of dive (h))	21809
Selected	Dive duration ~ poly(depth prey , 2) * poly(biomass (log), 3) + poly(distance colony, 3) + (1|Year) + (1|BirdID) + (1|Breeding status) + (1|Bout) + (1|Time of dive (h))	21809

Table A3: Model selection process and AIC values for model 3. Neither breeding status nor trip could be added to model as it led to singular fit.

Level	**Model**	**AIC**
Simplest	Tot. Dive d. bout ~	508
Most complex	Tot Dive d. bout ~ poly(biomass(log), 3) * poly(distance colony(log), 3) + (1|Year) + (1|BirdID) + (1|Time of dive (h)) + (1|number of dives in bout)	394

Selected	Tot Dive d. bout ~ poly(biomass(log), 3) * poly(distance colony, 3) + (1|Year) + (1|BirdID) + (1|Time of dive (h)) + (1|number of dives in bout)	394

Table A4: Model selection process and AIC values for model 4.

Level	**Model**	**AIC**
Simplest	Tot. Dive d. trip ~	122
Most complex	Tot dive d. trip ~ poly(distance colony, 3) + poly(biomass(log),2) + (1|Year_dive) + (1|BirdID) + (1|Breeding status) + (1|Hour_dive)	94
Selected	Tot dive d. trip ~ poly(distance colony, 3) + poly(biomass(log),2) + (1|Year_dive) + ~~(1|BirdID)~~ + ~~(1|Breeding status)~~ + (1|Hour_dive)	90

Table A5: Model selection process and AIC values for model 5.

Level	**Model**	**AIC**
Simplest	Mean dive d. bout ~	508
Most complex	Mean dive d. bout ~ poly(distance colony, 3) + poly(biomass(log),3) + (1|Year_dive) + (1|Trip) + (1|Breeding status) + (1|BirdID) + (1|Hour_dive) + (1|Nmbr_dives)	2570
Selected	Mean dive d. bout ~ poly(distance colony, 3) + poly(biomass(log),3) + (1|Year_dive) + ~~(1|Trip)~~ + (1|BreedStatu) + (1|BirdID) + (1|Hour_dive) + (1|Nmbr_dives)	2569

Table A6: Model selection process and AIC values for model 6.

Level	**Model**	**AIC**
Simplest	Mean dive d. trip ~	269
Most complex	Mean dive d. bout ~ poly(biomass(log), 3) + poly(distance colony(log), 3) + (1|Year) + (1|Time of dive (h)) + (1|number of dives in trip)	259

Selected	Mean dive d. bout ~ poly(biomass(log), 3) + poly(distance colony(log), 3) + ~~(1|Year)~~ + ~~(1|Time of dive (h))~~ + (1|number of dives in trip)	231

Table A7: Model selection process and AIC values for model 7.

Level	**Model**	**AIC**
Simplest	Biomass(log)~	320
Most complex	Biomass(log) ~ poly(distance colony ,3) + (1|Year) + (1|BirdID) + (1|Bout) + (1|Time of dive (h))	-1410
Selected	Biomass(log) ~ poly(distance colony ,3) + (1|Year) + (1|BirdID) + (1|Bout) + (1|Time of dive (h))	-1410

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