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Movements and diving behavior of humpback whales in relation to the capelin distribution in the Barents Sea

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Cover photo: Two humpback whales (*Megaptera Novaeangliae*) showing their fluke as they dive down, outside of Skjervøy. November 2020. Photo: Stine Skalmerud.

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1 Abstract

Humpback whales (*Megaptera novaeangliae*) are a cosmopolitan species, migrating between their mid- and high latitude foraging- and low latitude breeding grounds. Of these, the Northeast Atlantic (NEA-) population cover the longest migration distance of all mammals that last up to half a year. On the foraging grounds they feed extensively throughout the summer until early winter to gain enough energy for their migration. To date, not much is known about their movement and dive behavior in relation to prey, individual variation in humpback whale feeding and how dive behavior differs in 'feeding dives' and 'migration dives'. Therefore, in this study we satellite tagged 10 NEA-humpback whales during autumn in the northern Barents Sea. Their behavior was classified using a behavioral index and diving information was compared with capelin biomass, which was estimated using acoustic and trawl data that overlapped both spatially and temporally with the whales. Capelin has a known diurnal vertical migration; therefore, we use sun angle as a proxy for light availability, which in turn is representative of capelin distribution in the water column. Although with some individual variation, we found that humpback whale behavioral movement was influenced by both the horizontal and vertical distribution of capelin. The diving depth of humpback whales followed the diurnal migration of capelin early in the fall when we had data of capelin distribution. Towards the polar night period (shorter days) the differences in depth use of the whales were more even during day and night, this corresponds to reduced diurnal vertical migration in the capelin distribution as a result of decreasing light intensity. Our results also showed that the whales conducted significantly shorter and shallower dives, after leaving the Barents Sea and initiating their southward breeding migration. We conclude that the energy rich and abundant capelin is an important food source that shape the feeding behavior of for the NEA-humpback whales at their main polar feeding ground. Capelin therefore may be their main energy source for the long migration and thus shape humpback whale population dynamics.

Keywords: biotelemetry, diving, foraging, spatial ecology, humpback whale, capelin

2 Introduction

The humpback whale (*Megaptera novaeangliae*) is a cosmopolitan species, with different sub-populations in separate parts of the world, that do not necessarily mix with each other (Baker et al., 1993; Gulland, 1966; Rasmussen et al., 2007; Stone et al., 1990). All populations of humpback whales habituate warm, low latitude waters during breeding time in the spring and summer and migrate towards mid- or high latitude waters to feed in the fall or early winter (Clapham, 2009). Humpback whales conduct the longest migration of any mammal between these two areas (Rasmussen et al., 2007), and the Northeast Atlantic (NEA-) humpback whale population conduct the longest migrations of all (Kettemer et al., in press).

The North Atlantic humpback whale population have their most common breeding ground in the West Indies (also called Caribbean), where they mate and calve (Katona & Beard, 1990; A. H. Larsen et al., 1996; Smith et al., 1999; Stevick et al., 1999). A second, but smaller breeding ground is found off the Cape Verde Islands (Clapham, 2009; Wenzel et al., 2009). However, the number of individuals in this area has decreased in recent years (Clapham, 2009). The known North Atlantic feeding grounds range from the Gulf of Maine to the Barents Sea, including areas off the west coast of Greenland and off Newfoundland-Labrador and around Iceland and Ireland (Katona & Beard, 1990; A. H. Larsen et al., 1996; Ryan et al., 2016; Smith et al., 1999; Stevick et al., 1999). In the Barents Sea and adjacent feeding areas, they gain energy needed for their long breeding migration (Kettemer et al., in press). The reason why they travel all this distance to breed is not known, but might be related to (1) warm water that help thermoregulate newborn calves as blubber layers are thin right after birth (Brodie, 1975), (2) a safe space from calf-predation by killer whales (Naessig & Lanyon, 2004; Steiger et al., 2008), which do not inhabit such warm waters and or (3) warm waters facilitate shedding of skin, helping the humpback whales to get rid of algae growing on their skin in arctic waters (Pitman et al., 2020). During their migration, humpback whales might use stop-over areas to refuel if prey is available (Danilewicz et al., 2008; Kettemer et al., in press; Ramm, 2020; Stockin & Burgess, 2005).

Humpback whales main feeding grounds are usually in mid- or high latitude waters and their diet has been found to consist of a variety of prey: fish, krill, copepods, and squid (Baker et al., 1985; Clapham, 2009; Clapham & Palsbøll, 1997; Meynecke et al., 2021). Previous studies from the North Atlantic have compared spatial and temporal overlap and or indirect proxies to suggest specific prey species for the humpback whales in the area. Among these are sand lance (*Ammodytes* spp), capelin (*Mallotus villosus*), euphasiids (*Meganyctiphanes norvegica*, *Thysanoessa longicaudata*, and *Thysanoessa inermis*), herring (*Clupea harengus*), sandeels and sprat (*Sprattus sprattus*) (Friedlaender et al., 2009; F. Larsen & Hammond, 2004; Løviknes et al., 2021; Meynecke et al., 2021; Ochoa Zubiri, 2017; Piatt & Methven, 1992; Ryan et al., 2014; Smith & Pike, 2009; Víkingsson et al., 2015).

The Northeast Atlantic is regarded as a highly productive area, in particular the Barents Sea (Carmack & Wassmann, 2006; Sakshaug, 1997; Sakshaug & Slagstad, 1991). This area houses some of the world's most productive pelagic fish species, like polar cod (*Boreogadus saida*), Norwegian spring spawning herring and capelin, often regarded as key species in the North Atlantic ecosystem (Hansen et al., 2019; Hop & Gjøsæter, 2013). Therefore, in the same area we also find high densities of different predators that feed on these fish resources, including several marine mammals (Gjøsæter et al., 2009; Hamilton et al., 2021; van der Meeren & Prozorkevich, 2019). Humpback whales have been assumed to feed mainly on herring, capelin and krill (Løviknes et al., 2021). In the last decades, an increase of humpback whales and other baleen whales have been observed in the northern Barents Sea (Leonard & Øien, 2020). These marine mammal hotspot areas seem to overlap with the main feeding ground for adult capelin feeding on krill (Hamilton et al., 2021; van der Meeren & Prozorkevich, 2019)

Capelin is an energy rich fish that grows up to 21 cm in length and has a life span up to 5 years (Jourdain et al., 2021). It is a semelparous species where both male and females die after spawning at the banks of Northern Norway and Russia, which has its peak in March-April (Gjøsæter, 1998; Hop & Gjøsæter, 2013). After the eggs hatch in early summer, the larvae drift with ocean currents into the central and southern parts of the Barents Sea. During the summer months capelin migrates to central and northern areas of the Barents Sea to feed. The youngsters prefer feeding on copepod species (*Calanus spp*.), and the adults on amphipods and euphausiid species (*Meganyctiphanes norvegica* and *Thysanoessa inermis*)(Dalpadado et al., 2002; Gjøsæter, 1998). Capelin conduct diel vertical migration, and they are known to aggregate in schools (Gjøsæter, 1998; Hop & Gjøsæter, 2013). For upper trophic levels capelin represent a high energy prey, because of their lipid stores and also because they form large aggregations (Hop & Gjøsæter, 2013). Capelin is therefore possibly an important prey species for NEA-humpback whales in the Barents Sea.

In the last 50 years there have been large fluctuations in the capelin stock, with at least four known capelin stock collapses for the Barents Sea population (Gjøsæter et al., 2009; Prozorkevich & Sunnanå, 2017). Counting surveys of humpback whales within the Barents Sea increased from 1358 sightings between 2002-2007 to 3220 sightings between 2008 and 2013 (Leonard & Øien, 2020), whereas they were largely abundant between 1995-2001 (Øien, 2009). As one capelin collapse was between 1993 and 1997, and another from 2003-2006 (Gjøsæter et al., 2009), Leonard & Øien (2020) hypothesized that the increase in humpback whale sightings is related to ecosystem changes that affect the distribution of their important prey species. In addition, the Norwegian spring spawning herring has increased significantly since the collapse in the 1960s, which could also have had a positive effect on the NEA-humpback whale population (Huse et al., 2010; Rikardsen, 2019). Furthermore, several hundred humpback whales have also conducted a feeding stop-over in some specific fjord areas of Northern Norway there they feed on overwintering herring before they continue their southward breeding migration (Kettemer et al., in press; Ramm, 2020).

Schooling fish are a typical prey of humpback whales, as their feeding techniques are more efficient when fish aggregations are dense (Ware et al., 2011). Two feeding modes are observed for humpback whales: ram feeding and lunge feeding (Goldbogen et al., 2013). Ram feeding is when the whales at constant, slow speeds swim through groups of prey with their mouths open, and in that way force water through the exposed baleen plates (Goldbogen et al., 2013). Lunging, on the other hand, is when the whale engulfs a large body of prey-filled water at high speed, thereafter filtering the water out with a closed mouth (Goldbogen et al., 2013). Furthermore, whales have been observed doing lateral-, vertical-, and inverted lunges (Jurasz & Jurasz, 1979). Feeding occurs both by individuals alone and in groups, either at the surface, in shallow waters, at depth and at the bottom (Jurasz & Jurasz, 1979; Mastick et al., 2022; Ware et al., 2011, 2014). Humpback whales use a variety of feeding and trapping techniques, including bubble-net feeding and side roll bottom feeding to successfully catch their highly mobile prey (Mastick et al., 2022; Ware et al., 2014). Feeding behavior of humpback whales has been inferred to vary diurnally, possibly depending on prey availability (Friedlaender et al., 2009, 2013).

In August 2018 10 NEA-humpback whales were satellite tagged in the northern Barents Sea during a research cruise. These tags gave long-term information on both the horizontal and vertical (diving) movement patterns. During the same period, another research cruise was conducted to map the abundance of capelin in the whole Barents Sea using acoustic and biological surveying techniques. Combining data from these cruises, gave us the opportunity to investigate the predator-prey-relationships between these two species. The main objective of this study was to investigate the movements and diving behavior of humpback whales in relation to the capelin distribution in the Barents Sea. Specifically, we examined (1) if humpback whale movements were influenced by diurnal variations in light levels, (2) individual variation in the whales' behavioral responses to capelin density, and (3) whether their diving patterns change when the whales leave the Barents Sea.

3 Methods

3.1 Study area

The Barents Sea is a large shelf sea, located north of Norway and west of the Russian island Novaya Zemlya (Sakshaug, 1997). The northern boundary is between Frans Josef Land and the archipelagos of Spitsbergen, whereas the western boundary is usually considered as the continental edge at 10° – 15°E (Gjøsæter et al., 2009). The inflow of cold water from the Artic Ocean in the north, and warmer water from the Norwegian Sea in the west, brings very different physical characteristics and meet in a dynamic water mass we call the Polar Front (Wassmann et al., 2006). More than 20% of the Barents Sea is shallower than 100 meters, and the deepest troughs are deeper than 400 meters (Gjøsæter et al., 2009). With a complex bathymetry, the Barents Sea has several large shallow banks and deep troughs, and an average depth of 230 meters (Wassmann et al., 2006).

The tagging was conducted between 4th and 9th of September 2018 in the northern Barents Sea (figure A1). The research cruse was a collaboration between the Arctic University of Norway and Institute of Marine Research (IMR). The capelin data was collected during a yearly joint Norwegian/Russian ecosystem cruise between August and October 2018 in the Barents Sea and adjacent waters. The collaboration has been conducted yearly since 1986, and the Institute of Marine Research (IMR) is collecting data in Norwegian waters and the Knipovich Polar Reseach Institute of Marine Fisheries and Oceanography (PINRO) in Russian waters. This collaborative work aims to monitor abiotic and biotic factors and potential changes of these in the Barents Sea, capelin is one of the species that have been monitored.

3.2 Tagging

Whales were slowly approached, and tagging was conducted from a 20 ft RIB boat (rigid inflatable boat). Wildlife computers SPLASH-302 and SPOT-303 tags (www.wildlifecomputers.com //Wildlife Computers, Redmond, WA) were deployed using an Aerial Rocket Tagging System (ARTS launcher, www.restech.com). We aimed for tag placement below the dorsal fin, as described by Andrews et al. (2019) (figure 1). This is also the area where the blubber contains the most connective tissue and an area that is also

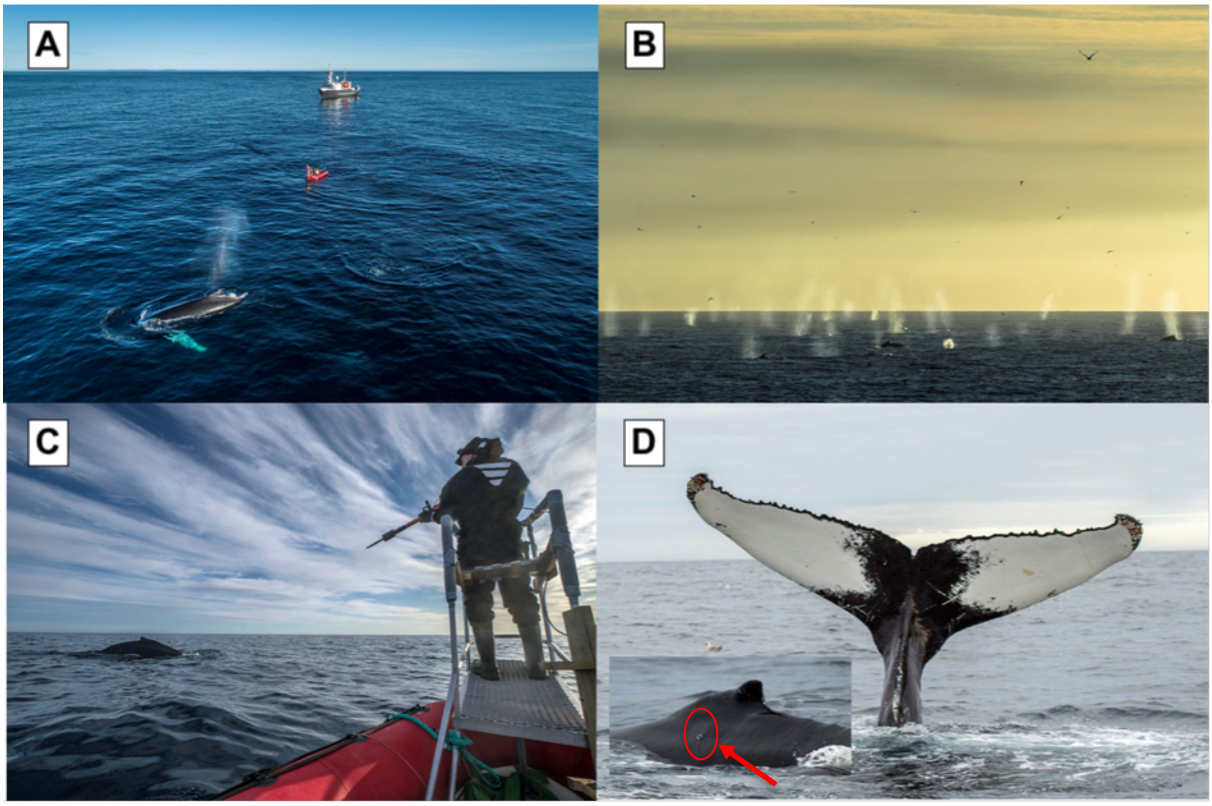

Figure 2: (A) picture of the RIB in relation to the whale. (B) photo of the specific area, where you can see a lot of humpback whale blows and some dorsal fins. (C) Tagging was conducted from the front of the RIB, pictured here. (D) photo ID of one humpback whale tail and tag placement, as indicated by red circle and arrow. Photos: Audun Rikardsen (top) & Lisa Kettemer (bottom).

exposed to air when surfacing (A. Rikardsen, personal communication, November 10, 2021). The tags were about 20 cm in length and equipped with anchors/petals that kept the tag in place in the blubber. To decrease risk of infection 70% ethanol was used to sterilize the darts before deployment. At each deployment event, the date, location, whale's reaction to deployment was recorded. Nine adult size animals and one calf were tagged. If possible, photographs of the flukes were taken, enabling identification of the individual whales. This prevented animals from being tagged twice. The tagging was approved by the Norwegian Food Safety Authority (Mattilsynet) under permit FOTS ID 14135 2017/279575.

The five SPOT-tags we used gave the horizontal position. They were programmed to send about 15 transmission/hour for the first four months, then 12 transmissions/hour for the following three months and then 80 transmission per day until the battery ran out or the tag fell out. The five SPLASH-tags are more advanced, and in addition to horizontal position also give some information on the diving behavior of the tagged animal. It can for example give the start and end of a dive, its maximum depth and the "behavioral shape" of a dive; V-, U, and square shape. The shape of the dive was defined onboard the tag and sent as messages to satellites. Algorithms within the tag define the dive shapes based on how much of the dive time was spent at 'bottom' depth. The bottom depth is considered all depth reading >= 80% of the maximum depth observed for the dive. Square shaped dives are when more than half of the dive time is spent at the bottom. U-shaped dives are if between 20% and 50% of the total dive time is spent at the bottom. V-shaped dives are if less than 20% of the total dive time is spent at the bottom. As the SPLASH tags collected different and more data, this type of tag had different settings. It was set to send about 400 transmission per day from midnight.

3.3 Tagging data collection and processing

Each tag was assigned a unique five- or six-digits, hereby described as the 'id' number of the tag and whale. When the dry sensor of the tag is in air, it sends a data message (SPLASH) or position transmission (SPOT and SPLASH) to ARGOS-satellites with a delay of about 45 second to the next message to be sent. The satellites need a minimum of three received transmissions within a time frame to calculate a position. These messages are received by one or multiple satellites and the CLS-ARGOS service conduct post-processing, calculation, and pre-filtering (Kalman filter), to estimate tag location points. Based on the number of messages received by each satellite, each raw location point is classified into one of seven location classes, based on quality. Data points with unknown uncertainty (quality=Z) was assigned class B, as this is the class of most uncertainty. R Statistical Software (v4.1.1; R Core Team 2021), was used for all subsequent data processing and analysis. A state-space model (Correlated Random Walk, CRW) was used to reconstruct the most likely path an animal took based on the pre-filtered ARGOS position estimates. The CRW converts the non-uniform time series to a regularized path (Johnson et al., 2008), accounting for location uncertainty and irregular transmissions (Jonsen et al., 2005). The CRW was created using the ‘fit_ssm’ function from the ‘FoieGras’ package (v0.7.6; Jonsen et al 2020; Jonsen et al 2019; Jonsen & Patterson 2020). Specifically, the model used was set to estimate whale locations at three-hour intervals. The number of signals sent from the whale and received by the satellite are based on many variables (specific tag height location on animal, surfacing interval of animal, orbiting satellites available, and more (this is a noncomplete list)), that can cause gaps in the data. Gaps that were over 24 hours were split into two tracks, as they created unlikely loops for the splash tags in our CRW as the model had to estimate multiple consecutive points with no updated change in whale turning angle or speed. Due to different programming, the spot tracks were split when gaps larger than 10 hours occurred. A new track was considered when it had at least 20 consecutive raw data points and there was at least one position each day.

3.3.1 Move persistence

To characterize an animal’s behavior mode a behavioral index, move persistence (g_t) can be used (Breed et al., 2012). Using the positional displacement of the modeled consecutive tracking points, move persistence values are estimated. The autocorrelation of consecutive displacements accounts for an animal’s changes in both direction and speed. Move persistence values range from 0 to 1, where 0 represents area restricted movement behavior with more changes in direction, whereas 1 would be less change of direction and more consistent speed (Jonsen et al 2020; Jonsen et al 2019; Jonsen & Patterson 2020). Here, we used low move persistence values to indicate possible foraging activity, and high values for transiting behavior. From the ‘foieGras’ package, the ‘fit_mpm’ function was used to calculate move persistence (v 0.7.6; Jonsen et al 2020; Jonsen et al 2019; Jonsen & Patterson 2020).

3.4 Diving data

Investigating the humpback whales’ dives or vertical characteristics will give more specific information that can indicate feeding (Pedersen, 2020). The amount of time the humpback whale uses at the maximum depth of a dive can possibly indicate prey choice, as prey aggregate at different depths. We will use the dive shape, depth, and duration, and compare diving behavior from the feeding area to the migration.

With the move persistence values we were able to determine the start of migration for each individual quite accurately. The cut-off point is considered when the individual starts swimming with high directionality towards the south or west (figure A5; figure A7). One individual (ID: 167842) had a large gap in transmissions (figure A3), between spending time in the south-eastern part of the Barents Sea and migrating out of the Barents Sea. This whale lost its tag shortly after, so it was not included in the migration dive estimates. Hereafter 'feeding dives' is also referred to as dives conducted 'within the Barents Sea', and 'migration dives' to 'outside the Barents Sea'.

The start and end of the dive was when the whale passed 2 or 1 meter, respectively, but the tag was set to only store dives deeper than 15m depth that lasted for more than 2 min. When the whale came 'back' from a dive the surface interval timer started going when the whale passed 1 meter, and until the next dive was started recording. The tag then only sends a random subsample of the dives per day.

3.5 Environmental variables

3.5.1 Observed capelin biomass – INLA-field

The Norwegian Institute of Marine Research (IMR) has been monitoring the capelin distribution in the Barents Sea since 1972. In 1975, the monitoring became a part of a joint-research program between IMR and Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO) in Russia (Gjøsæter et al., 1998). The main purpose was to monitor the commercial fish stocks, collect information for stock assessment and advice for fisheries management (Eriksen et al., 2018). In 2004 multiple surveys in the autumn were merged into the first "Barents Sea Ecosystem Survey" by IMR and PINRO, allowing for wider sampling scope. The survey runs annually in August-September, with the objective both to monitor commercial fish stock for stock assessment and to record biotic and abiotic factors and changes in these to understand the trophic relations in the Barents Sea better (Eriksen et al., 2018). Using four to five ships, the survey is designed to visit an equally spaced station grid with 35 nautical miles between each station, where the ships collect trawl data, and other abiotic data. The vessels continuously sample acoustic data at different frequencies along the transects while surveying. The acoustic data are scrutinized and allocated to target species on board using information from the trawl data, and knowledge about acoustic features of the target species. The scrutinized acoustic data were stored in units of Nautical area Scattering coefficients (NASC; m^2/nmi^2)(Maclennan et al., 2002) at 10 m vertical and 1 nautical mile horizontal resolution. The acoustic data allocated to capelin were used for investigation of diurnal vertical migration for capelin and potential spatial and temporal overlap with the dives of humpback whales. To find the density of capelin, my supervisor Emma Vogel combined the NASC values and trawl samples, by using StoX software (Johnsen et al., 2019) and the R-package 'RstoX' (Holmin et al., 2020). This is used to create an Integrated Nested Laplace Approximation (INLA) field of capelin biomass. A detailed description of the estimation and creation of the INLA field can be found in Vogel et al. (2021).

3.5.2 Light intensity

In this study we will use sun angle as a measure of light intensity, which in turn is a proxy for diurnal vertical migration of capelin (Gjøsæter, 1998; Mowbray, 2002). During analysis we used the 'solarpos' function in the 'maptools' package to estimate the sun angle for each humpback whale location point (v1.1.2; Bivand & Lewin-Koh 2021).

3.6 Modelling approach

To investigate how humpback whale movement characteristics (represented by the move persistence index, g_t) is influenced by (1) horizontal capelin biomass, (2) light intensity as a proxy for vertical capelin biomass, we used a mixed effect modeling approach developed especially for animal movement data. In this study we used the 'mpmm' package in R (v0.2.1; Auger-Méthé et al., 2017; Jonsen et al., 2019); it assesses individual and population level responses to the chosen covariates, based on the move persistence index values (Jonsen et al., 2020). Based on the location and time for each whale track coordinate, a corresponding capelin biomass value was extracted from the INLA generated distribution. The sun angle value was extracted using the same method, from the 'maptools' package as described earlier. Thereafter, 9 candidate models were evaluated: (1) ~ biomass + sun angle + (biomass + sun angle | id), (2) ~ biomass + sun angle + (sun angle | id), (3) ~ biomass + sun angle + (biomass | id), (4) biomass + sun angle + (1 | id), (5) ~ sun angle + (sun angle | id), (6) ~sun angle + (1 | id), (7) biomass + (biomass | id), (8) ~ biomass + (1 | id), and (9) ~ 1 + (1 | id). As the capelin biomass distribution covered a limited geographic and timely range, only whale track location points within the interpolated field and during the capelin survey time (15.08.2018 – 30.09.2018) were considered in each model. One individual (ID: 167842) had <10 raw coordinates that fell into previously described requisites and was therefore left out of this model. Each of the nine models were ranked based on the Akaike Information Criterion (ΔAIC) and likelihood ratio (lr) tests.

4 Results

The SPOT tags transmitted in average 91 days (range = 24 –184 days), whereas the SPLASH tags transmitted on average 154 days (range = 60 – 223 days) (Table 1). We were able to follow two SPOT- and two SPLASH-tagged whales when they initiated their southward migration (SPOT id: 47597, 47599; SPLASH id: 167844, 47570) and they on average continued to send data for another 79 days (range= 46 – 132). The whale that initiated their southward migration first did so November 16th (ID 47597), while the latest started swimming south on January 17th (ID 47599) (table 1).

Across the five whales equipped with SPLASH tags the total number of dives recorded was 14 155, ranging between 120 and 5852 recorded dives per individual whale (table 2). The maximum recorded dive depth for an individual whale was 352 meters (range 320m-352m, for the five individuals), while their average dive depth across all individuals was 109 meters. The dives lasted in average for 4 minutes and 20 seconds with a range from 2min (programmed in the tag as the shortest recorded dive) to 24 minutes and 30 seconds.

*Table 2: Tag and tagging information. Each ID number is given by Argos CLS (FRANCE). Last day of transmission is when the tag sent it lasts transmission. * Date leaving = the date when the whale passed the Barents Sea border = NA, if the tag stopped transmitting or fell off before swimming past the Bear Island border.*

							WITHIN THE BARENTS SEA					OUTSIDE THE BARENTS SEA			
ID	Tag type	Tagging date	Last day of trans	Tag length (days)	#raw pos	Date leaving*	Tag dur (days)	#raw pos	# filtered pos	# dives recorded	Max depth (m)	Tag dur (days)	#raw pos	#dives recorded	Max depth (m)
167842	Splash	8.9.18	9.3.19	161	375	NA	161	375	437	120	320	NA	NA	NA	NA
167843	Splash	5.9.18	22.12.18	108	1569	NA	108	1572	847	3900	328	NA	NA	NA	NA
167844	Splash	4.9.18	9.4.19	217	2344	12.1.19	130	2247	1032	5704	352	87	126	148	34
167845	Splash	4.9.18	3.11.18	60	1302	NA	60	1302	457	2839	336	NA	NA	NA	NA
47570	Splash	9.9.18	20.4.19	223	1280	9.12.18	91	948	709	970	344	132	345	474	296
47596	Spot	4.9.18	17.11.18	74	1637	NA	74	1637	551	NA	NA	NA	NA	NA	NA
47597	Spot	4.9.18	6.1.19	124	2827	16.11.18	73	2332	583	NA	NA	51	552	NA	NA
47599	Spot	4.9.18	4.3.19	181	3465	17.1.19	135	3168	1048	NA	NA	46	507	NA	NA
84494	Spot	5.9.18	29.9.18	24	848	NA	24	848	191	NA	NA	NA	NA	NA	NA
171987	Spot	5.9.18	28.10.18	53	859	NA	53	859	390	NA	NA	NA	NA	NA	NA

Table 2: Diving information gathered from SPLASH satellite tags. The table is divided by area where the dives were conducted: within or outside the Barents Sea. Dive shape referring to the time at 'depth', read more in section 3.2. ID numbers are given by the tag manufacturer. 'NA' is reported if the tag did not record dives during this time, i.e. had fallen off or the battery had run out.

	WITHIN THE BARENTS SEA												OUTSIDE THE BARENTS SEA					
	V-SHAPED DIVES			U-SHAPED DIVES			SQUARE-SHAPED DIVES			ACROSS ALL DIVE SHAPES			SHAPES			ACROSS ALL DIVE SHAPES		
ID	% V shape	Avg depth (m)	Avg dur (min)	% U shape	Avg depth (m)	Avg dur (min)	% square shape	Avg depth (m)	Avg dur (min)	Avg depth (m)	Avg dur (min)	% dives > 80 m	% V shape	% U shape	% square shape	Avg depth (m)	Avg dur (min)	% dives > 80 m
167842	10,8	101,3	11,1	31,7	115,7	6,0	57,5	113,8	8,3	113,0	7,9	60,0 %	NA	NA	NA	NA	NA	NA
167843	1,3	108,9	7,0	23,9	112,5	5,0	74,8	115,6	5,6	114,7	5,5	57,0 %	NA	NA	NA	NA	NA	NA
167844	4,0	111,1	9,3	30,2	110,9	6,5	65,7	109,4	7,1	109,9	7,0	57,7 %	11,49	71,62	16,89	21,3	3,4	2,0 %
167845	3,5	81,8	5,1	33,2	111,2	4,6	63,3	12,3	5,5	110,9	5,2	54,7 %	NA	NA	NA	NA	NA	NA
47570	3,9	74,8	4,1	56,9	94,6	3,7	39,2	98,0	5,0	95,1	4,2	38,2 %	4,01	68,35	27,64	74,0	4,0	30,4 %
Average	4,5	93,7	7,1	38,3	105,3	5,1	57,2	93,0	6,2	105,6	5,8	53,5 %	7,75	69,99	22,26	47,7	3,7	16 %

4.1 Horizontal movement of humpback whales in association to the capelin distribution

In general, there was a good overlap between the horizontal humpback whale movement and the estimated capelin distribution. Within the Barents Sea, the humpback whales spent the majority of time in the north-central waters of the area (figure 2). Within September, the humpback whale tracks were restricted to one particular area close to the tagging location in the northern Barents Sea (figure 3). Feeding movement mode, as indicated by low move persistence values, suggests multiple foraging hotspots in the area (figure 3). Between these clusters, there seems to be tracks with high move persistence values, indicating transiting behavior between viable patches.

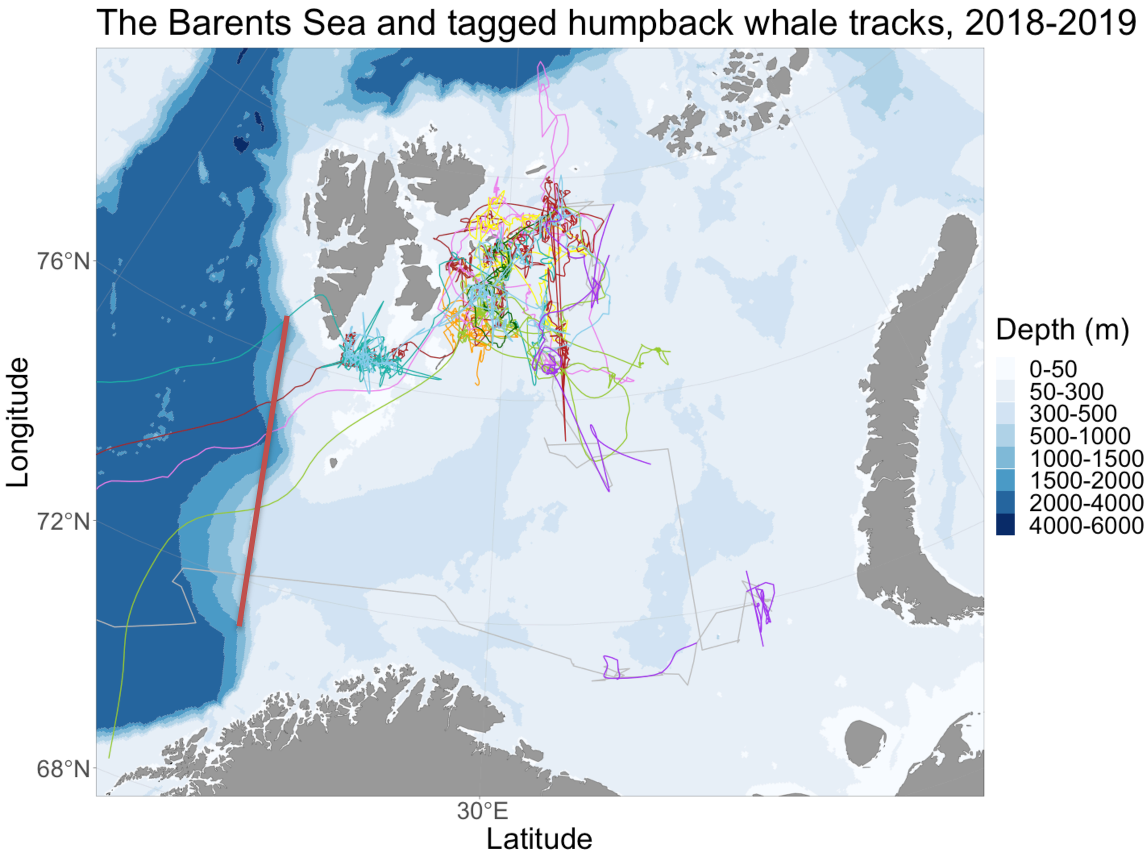

Figure 2: Humpback whale CRW tracks from the whales tagged in the northern Barents Sea in the beginning of September 2018. The map shows the study area, and the bathymetry in the Barents Sea. The thick red almost vertical line is an approximate west border of the Barents Sea. One individual (ID: 167842) had to be split into several tracks (purple color) as there were big gaps in the data. For this individual we also mapped the raw data, with grey color, to visualize the beginning of migration for this whale.

The capelin horizontal distribution during September shows the highest relative density aggregations in the northern Barents Sea (figure A2). Overlapping the humpback whale tracks and the capelin relative density map, showed a clear overlap for the area use (figure 4). Even though most of the humpback whale tracks are in high-relative density areas, some individuals occasionally also traveled outside this area.

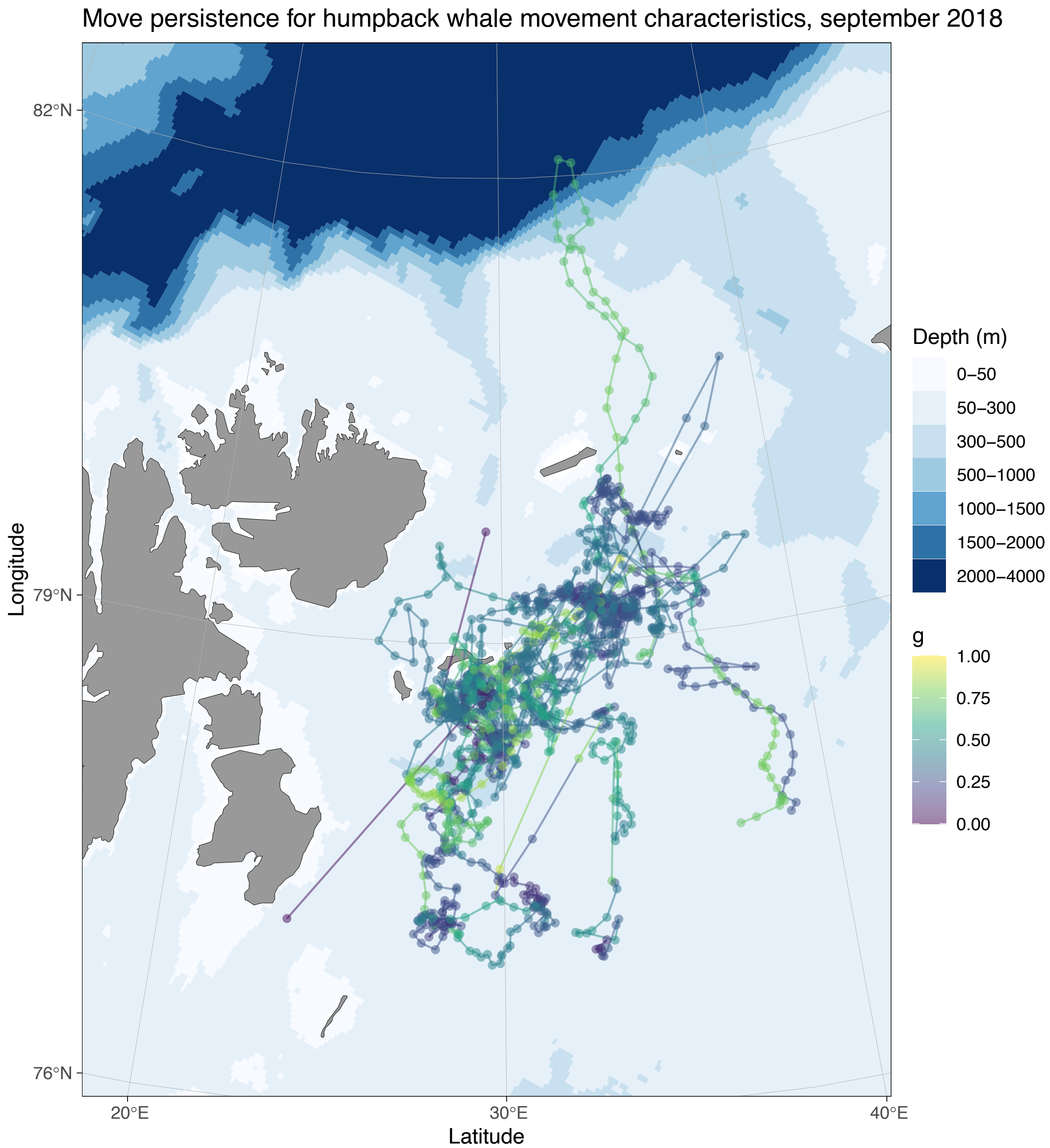

Figure 3: Humpback whale tracks with move persistence values in the northern Barents Sea. High values of g indicate transiting behavior and low values indicate feeding behavior. This is data from all the whales in September 2018.

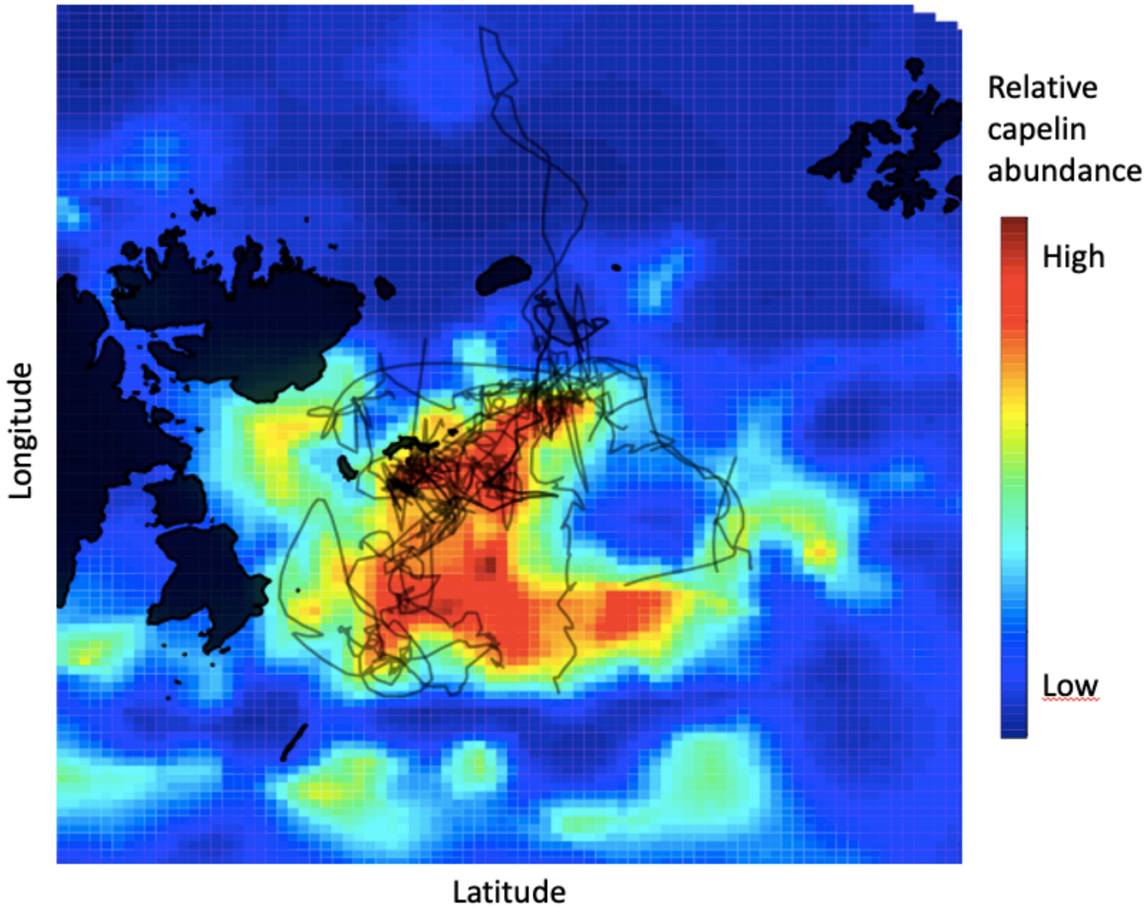

Figure 4: Map of the northern Barents Sea with the relative capelin density distribution, based on spatial analysis of observed capelin biomass using INLA. The black lines show the humpback whale tracks for September 2018.

4.2 Humpback whale diurnal diving behavior in relation to capelin distribution in the water column

The humpback whales generally dove deeper during the daytime and shallower at night, mirroring the capelin vertical migration (estimated for September) (figure 5F). This was especially seen in September and October (figure 5A and 5B)

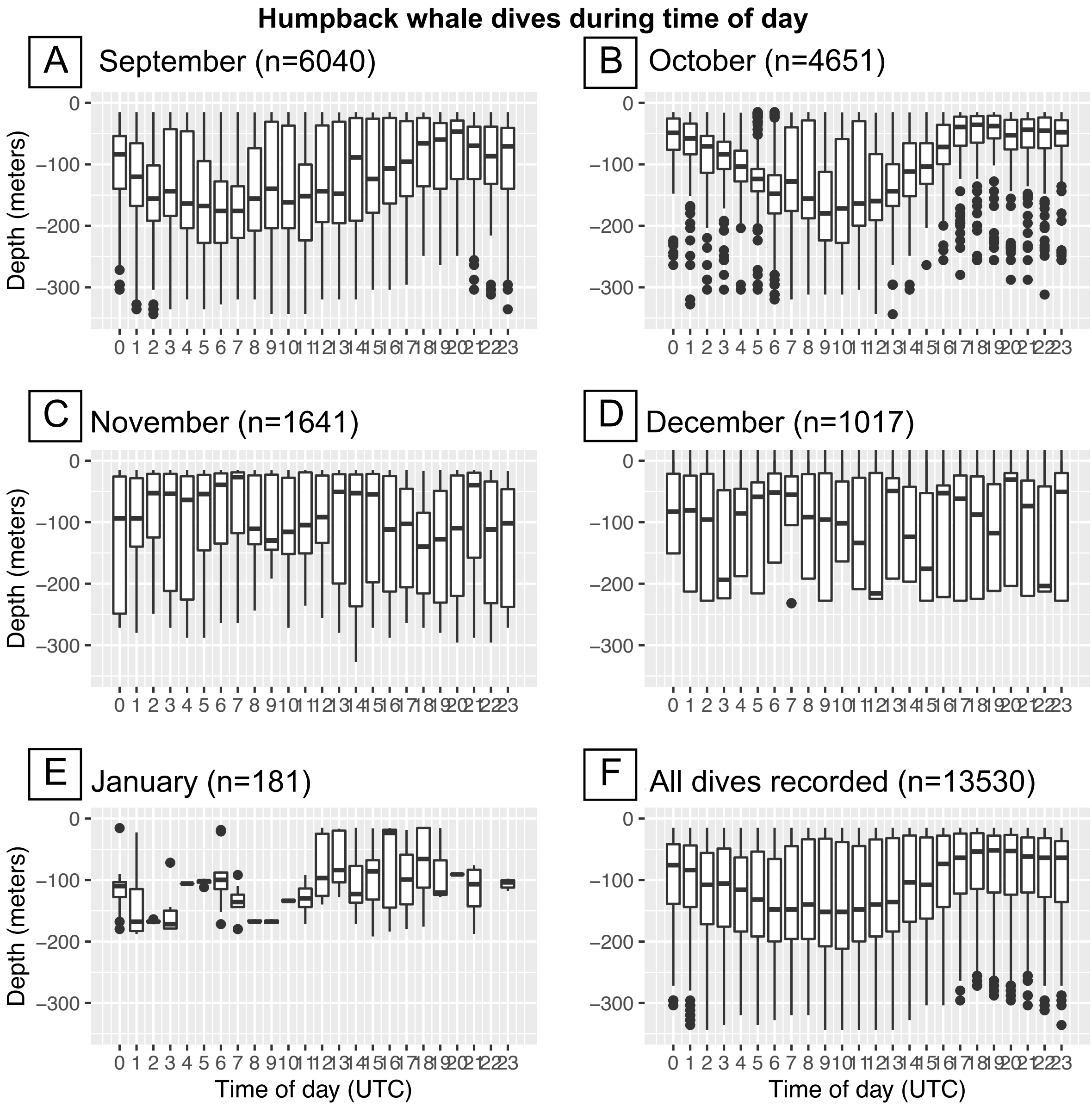

Figure 5: Boxplot of humpback whale diving depth, throughout the day. The thick black horizontal line denotes the median, 50% of the data lies within the white box, the vertical lines represent high/low values (highest/lowest value within 1.5(interquartile range) and dots are per definition considered outliers. The number of dives is denoted with, n. Showing dives conducted in (A) September, (B) October, (C) November, (D) December and (E) in January. (F) Shows all the dives recorded throughout the whole period.*

When the days became shorter and with less daylight in November - January the diurnal diving pattern of humpback whales became generally less clear with a more uniform diving depth during the day and night (figure 5C-E).

Feeding behavior of humpback whales, as indicated by low move persistence values, were found to be extensively during daylight hours for all individuals, except for one individual that seemingly fed mostly during the night (figure 7).

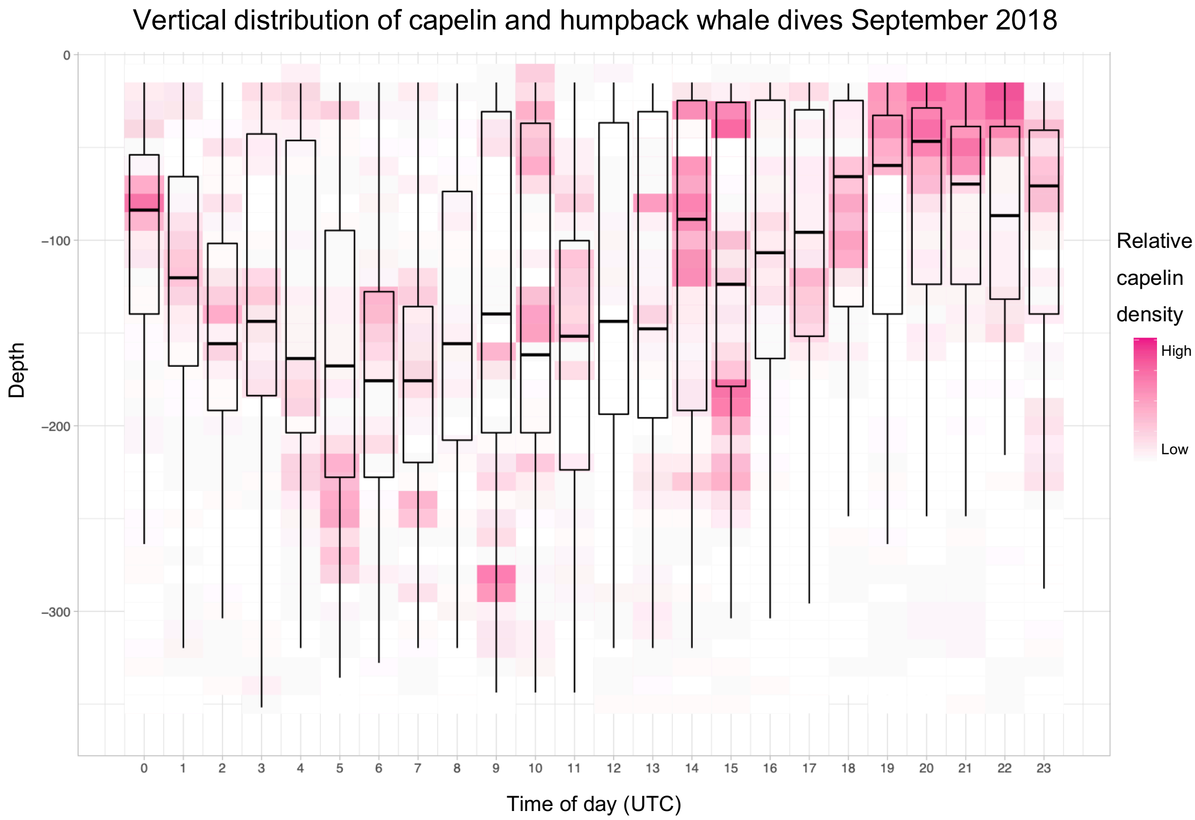

Figure 6: The white and pink background shows the relative capelin density throughout the water column. The black boxplot shows the humpback whale diving depth per hour of day in September. The thick black horizontal line denotes the median, 50% of the data lies within the white box and the vertical lines represent high/low values (highest/lowest value within 1.5(interquartile range).*

4.3 Individual variation in whale's behavioral response to capelin density

In our mixed effect model, g_t we found that humpback whale movement was driven by the capelin horizontal distribution and sun angle, as a proxy for capelin vertical distribution (table 3). In addition, the humpback whales had individual responses and reacted with different intensities to horizontal and vertical capelin density distribution (figure 7). These were the results of the move persistence mixed effect model. All nine mixed effect models converged. The model that best explained humpback whale movement mode, had move persistence as a function of horizontal and vertical capelin density, knowing that individual humpback whales have different move persistence baselines, and the relationship may vary among individuals ((1) ~ biomass + sun angle + (biomass + sun angle | id)).

Table 3: Model rankings by the change in Akaike Information Criterion (ΔAIC) and likelihood ratios (lr) for the move persistence mixed effect models fit to the 10 foraging humpback whales. Note: the absolute ΔAIC and lr for the best ranked model are in the first, and other models and consecutive values are relative to these values. Random slopes and effects are in parenthesis. All models converged.

Model formula	df	ΔAIC	lr
~biomass + sun angle + (biomass + sun angle|id)	**13**	**-2247,54**	**-2273,54**
~biomass + (biomass|id)	9	12,05	20,05
~biomass + sun angle + (biomass|id)	10	13,60	19,60
~biomass + sun angle + (sun angle|id)	10	16,86	22,86
~biomass + (1|id)	7	18,58	30,58
~sun angle + (sun angle|id)	9	19,28	27,28
~bimoss + sun angle (1|id)	8	20,66	30,66
~1 + (1|id)	6	23,79	37,79
~sun angle + (1|id)	7	24,71	36,71

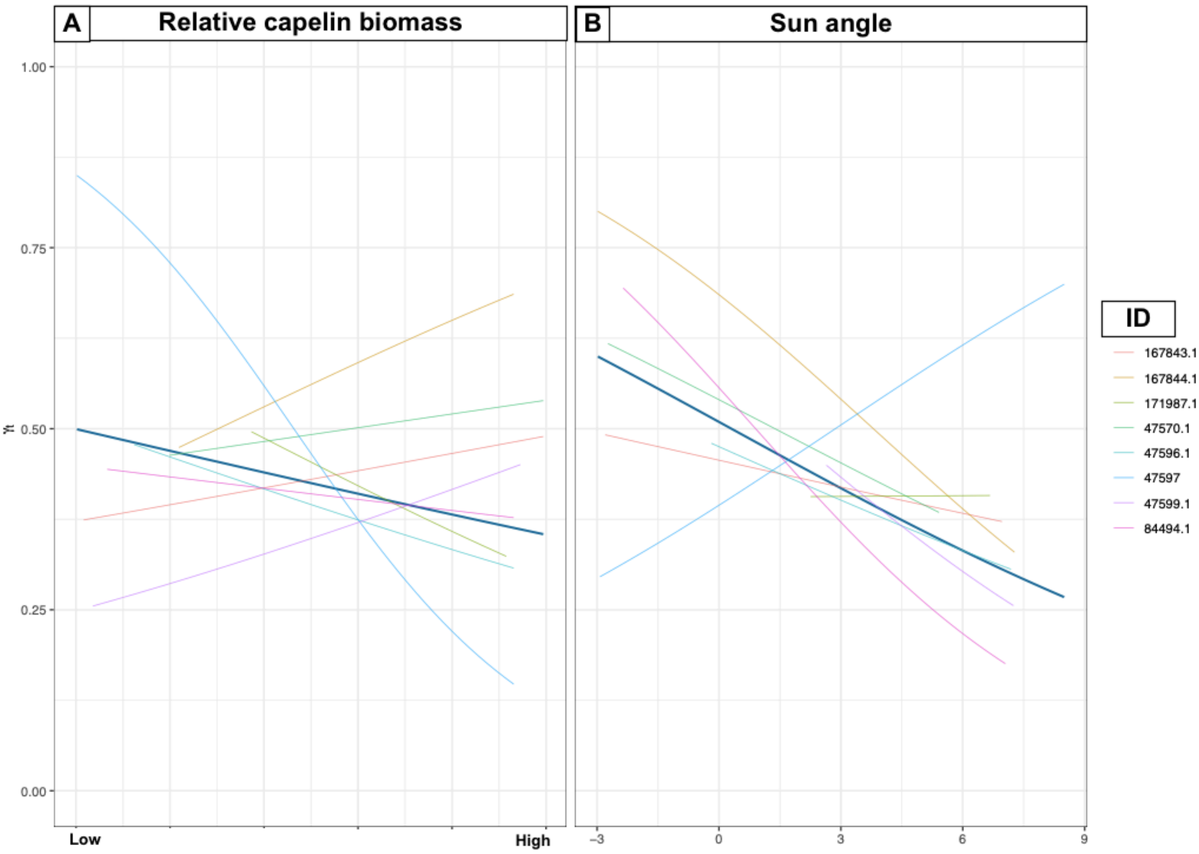

Figure 7: Most parsimonious model from mixed effect analysis. Grouped fixed (dark blue) and individual random (each one color) effects relationship between move persistence γ_t and A) the relative capelin biomass, and B) sun angle. Each panel show the random intercept and slopes of the most parsimonious model from table 3, which was (g_t ~ biomass + sun angle + (biomass + sun angle | id)). Low relative move persistence values indicate feeding, while high indicate transiting. It is important to note that all whales have different move persistence baselines.

4.4 Comparing diving behavior of humpback whales inside and outside the Barents Sea

We found large differences in diving behavior within the Barents Sea and outside the Barents Sea. Data from two of our tagged humpback whales that retained their SPLASH-tags after leaving the Barents Sea indicated that they had deeper and longer dives while feeding in the northern Barents Sea and shallower and shorter dives when they had left the Barents Sea (figure 8). We also found a clear difference in dive shapes within and outside the Barents Sea, meaning they used a higher percentage of the total dive time at deeper depths within the foraging area. While seemingly feeding in the northern Barents Sea there was a trend that humpback whales had their deepest and longest dives around noon (figure 8 A and 8 C). However, when the same whales started their southward migration, this trend was not found (figure 8 B and 8 D).

Square shaped dives (= spending >50% of the dive time below the 'depth threshold') was on average the most conducted dive for the tagged adult whales within the Barents Sea (average = 1783 dives) (figure 10). The second most popular dive behavior was U-shaped dives (average = 838 dives). The humpback whales conducted the absolute least number of V-shaped dives (average = 86 dives). The calf (ID: 47570) conducted most U-shaped dives (n=558) and second most square shaped dives (n=380), within the Barents Sea (figure 10).

Within the Barents Sea average diving depth and duration was 106 m and 5 minutes and 48 seconds. 54% of the dives inside the Barents Sea were below 80 m/deep dives (table 3). However, during migration these averages are 48 m and 3 minutes and 42 seconds, and 16% of the dives were below 80 meters (table 3). On average, the surface intervals within the Barents Sea were 4 minutes and 30 seconds (figure 9). However, outside the Barents Sea the average surface interval was 25 minutes and 20 seconds (figure 9). In addition, humpback whales have a clear majority of square shaped dives (57%) in their feeding grounds, whereas U shaped dives were the majority (69%) outside the Barents Sea (table 3). Important to note that the calf was one of the two whales with dive recorder that had their tag on when starting to migrate.

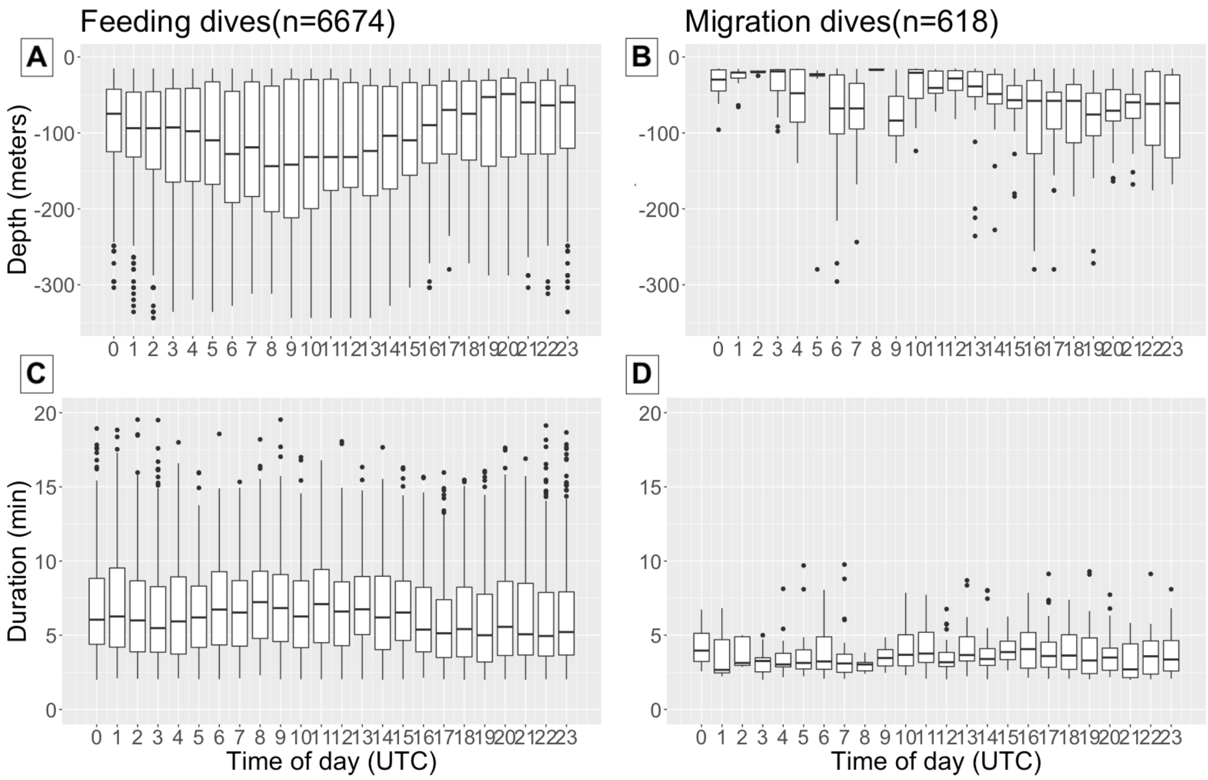

Figure 8: Boxplots comparing humpback whale feeding dives and migration dives. This figure is comparing the two whales that had their tag on while migrating southward to when these two whales were in the Barents Sea, feeding. (A) Showing dive depth while feeding within the Barents Sea. (B) Display dive depth of the whales after migration had started. (C) Showing dive duration within the Barents Sea. (D) Displaying dive duration after migration had started. The thick black horizontal line denotes the median, 50% of the data lies within the white box, the vertical lines represent high/low values (highest/lowest value within 1.5(interquartile range) and dots are per definition considered outliers. n denotes the number of dives in each category.*

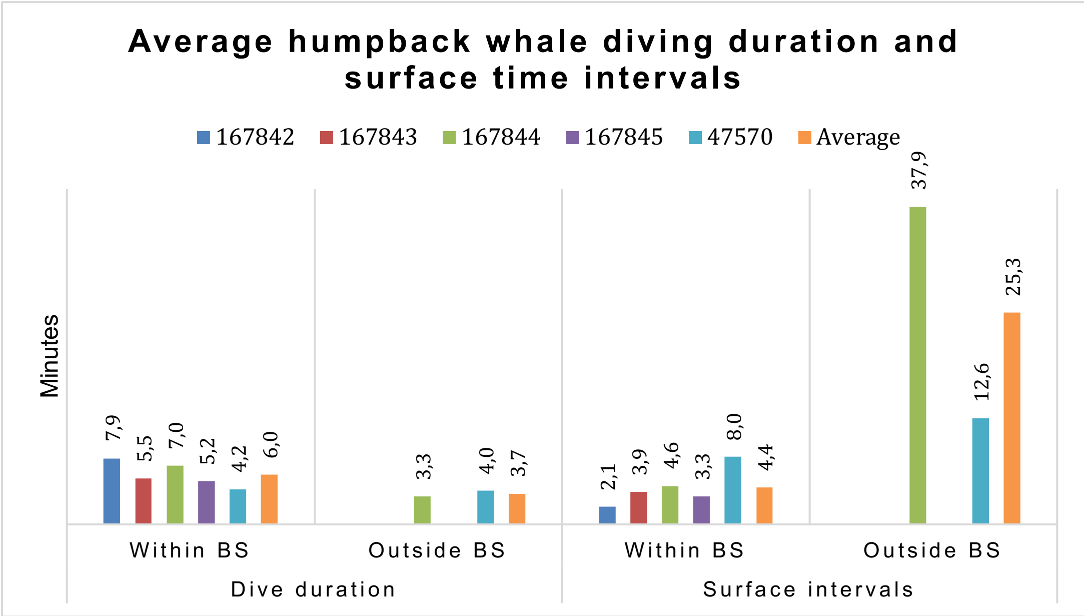

Figure 9: Histogram showing average dive duration for each whale (different colors) on the left, within and outside the Barents Sea. On the right, is a display of average surface interval for each whale, within and outside the Barents Sea. Only two whales had their tag on when leaving the Barents Sea. The average (orange color) is the average of each available whale's average, not the average of the whole dataset.

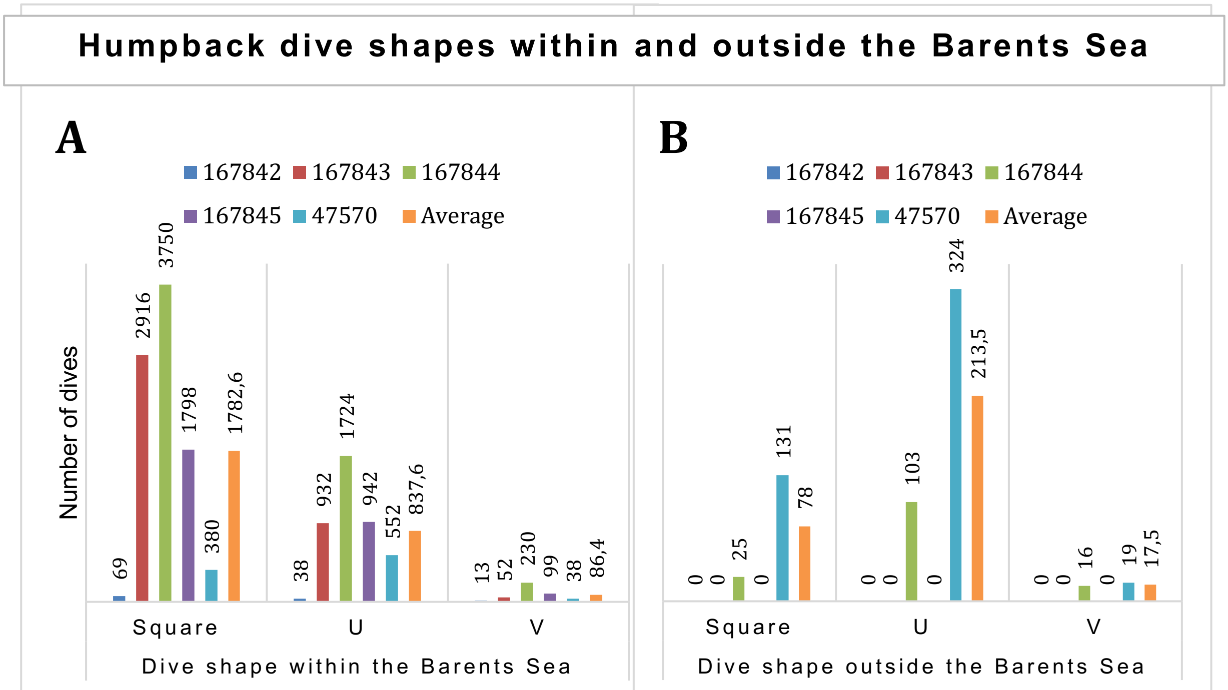

Figure 10: Histogram showing the total number of dives recorded per dive shape for each whale, (A) within and (B) outside the Barents Sea. Dive shapes as recorded from the tag, according to Wildlife computers system, is a percentage system of how much time is spent below 80% of the maximum depth of the dive. Square shaped dives are when more than half of the time is spent at the 'bottom' (80% of the max depth). If between 20% and 50% of the dive is spent at the 'bottom', it is recognized as a U-shaped dive. When less than 20% of the dive is spent at the 'bottom', the dive classifies as a V-shaped dive. Orange bare denotes the average of the available data. Note that the scaling between (A) and (B) are different and not directly comparable.

5 Discussion

To our knowledge, this is the first study on humpback whales that investigates their long-term movements and diving patterns in relation to density estimates of their assumed main prey over a large area. Our findings confirmed spatial and temporal overlap in the humpback whale and capelin distributions for September in the northern Barents Sea, both horizontally and vertically in the water. In addition, our behavioral index results indicate humpback whale feeding behavior is driven by capelin abundance. Previous studies that suggest prey choices of humpback whales have used acoustic fish surveys or historical versions of those, paired with spatiotemporal overlap from visual observations of humpback whales at the surface (Ryan et al., 2016; Víkingsson et al., 2015). Others have used archival tags to confirm the same horizontal area use (Dietz et al., 2002; Friedlaender et al., 2016). However, the spatiotemporal method of relating predator-prey assumes that the predators always feed when in proximity of prey. In contrast, with our method we were able to evaluate the co-occurrence of both the predator and prey in the water column as well. Therefore, some spatiotemporal studies have a higher level of uncertainty than our study. In addition, spatiotemporal overlap studies do not take foraging threshold into account. This is a weakness as it has been found that humpback whales only forage if density of prey is of a specific magnitude (Akiyama et al., 2019; Piatt & Methven, 1992). Our study does not take threshold of prey into account. Instead, we use move persistence analysis coupled with the relative density of prey, which leads us to conclude that humpback whales were feeding in the areas with highest capelin density. More precise methods that have been conducted over smaller scales are suction-cup multi-sensor tags (like, depth, angle, acceleration), some also including video-logging (i.e. CATS). However, these types of tags are more often used to study feeding ecology, feeding techniques and fine-scale movements over short periods and small areas because suction cups tags are only attached to the whales for a short time and need to be recovered (Akiyama et al., 2019; Friedlaender et al., 2009; Mastick et al., 2022; Ware et al., 2014). Our study has less high-resolution dive data, but on the contrary, gives general movement patterns over a much larger area and time scale. Studies that combine both these two methods will be very useful in future studies.

Move persistence mixed effect models similar to the one used in this study, have previously been used to study factors that affect foraging choices in other marine mammals. Killer whales (*Orcinus Orca*) movement on the Norwegian shelf was found to be influenced by the density and distribution of its prey, Norwegian Spring-Spawning herring (Vogel et al., 2021). Whereas Jonsen et al. (2019) found two foraging strategies for southern elephant seals (*Mirounga leonina*) in relation to upwelling areas and start of ice cover areas, as a proxy to potential favorable feeding areas. They found that the open ocean foraging seals, showed increased restricted behavior in areas where the up flow of circumpolar deep-water occurred. Secondly, the sea-ice foraging seals showed increased restricted behavior with increasing sea-ice cover. However, neither of these studies used satellite tags that recorded diving depth and could therefore not include diving data in their analysis. In our study the diving data gave an extra dimension that also showed how the predators behave in relation to their prey on a vertical axis, which is important to understand their more direct and detailed interactions.

Even though all whale behavior was found to be driven by capelin density, our results suggested that half of our 10 whales showed strongest signs of feeding behavior when relative capelin biomass was high, and the other half when relative capelin biomass was lower. There may be several possible explanations to this. Firstly, since the prey data was collected from south to north during a period stretching longer than a month, the capelin could move to slightly different areas during this period, and it could lead the distribution estimation to be less accurate. Our estimated relative capelin abundance map is a static snapshot of the capelin distribution that is thought to be representative of the capelin densities in that period. Even so, capelin is a pelagic schooling fish species, with a highly dynamic abundance that may rapidly change as they migrate or move within in area. However, the overall densities were generally high within the main area, and this area overlapped nicely with the majority of the whale tracks during most of the area and time, indicating that all whales were feeding within this main area. Another possible reason could be that the whales were feeding in locally high-density areas, but with a surrounding low-density. Which in turn, the modeling would determine the overall area to be of low or medium relative density. Categorizing prey densities as high and low doesn’t fully take into account the ecological context, and in some situations (size of whale, availability of other prey), optimality may be driven by something other than absolute size.

There were few other potential fish prey species (herring, blue whiting, sand eel, polar cod) for the humpback whales in this northern part of the Barents Sea in 2018 (van der Meeren & Prozorkevich, 2019). The only other possible prey for the whales is krill, a usual prey also for adult capelin. Krill has been found to be the predominant prey for humpback whales in the Southern Ocean (Bettridge et al., 2015). However, the Antarctic region is known for its large densities of krill and many krill fisheries. Since krill are smaller than capelin, a large whale would likely need higher densities of krill to feed successfully. We know there is usually krill in this area in northern Barents Sea, with typical distributions close to the bottom during daytime and higher up in the water column during the night (Eriksen & Dalpadado, 2011; Gjøsæter et al., 1998). However, the krill distributions were in much lower concentrations than the capelin in this particular area during September 2018 (van der Meeren & Prozorkevich, 2019). It could be that the humpback whales feed on both krill and capelin, however this cannot be quantified with this study. Nevertheless, since we know that humpback whales often feed on capelin in the North Atlantic (F. Larsen & Hammond, 2004; Løviknes et al., 2021; Piatt & Methven, 1992; Smith & Pike, 2009; Víkingsson et al., 2015) and that it has been observed surface feeding on capelin in the northern Barents Sea (N. Øien, personal communication, April 5, 2022). Adding on capelins' high energy content (Hop & Gjøsæter, 2013) and the nice correlation we had between humpback whales and the capelin abundance in this study, we believe that it was the main prey for our tagged whales.

On the horizontal plane, the caplin distribution changes throughout the season and depending on life stages (Gjøsæter, 1998). The data used in this study was collected between August 15th and September 29th. Ideally, we would prefer to know the relative density distribution of capelin throughout the year. However, this data is not collected and not easily available. Capelin migrate north and northeastward to feed during the summer and early autumn, and the mature part of the stock start the spawning migration before the onset of polar night (Gjøsæter, 1998). Therefore, it is reasonable to hypothesize that most of the capelin distribution is quite stable within the same general area in the northern Barents Sea, until some year classes (the mature capelin) start their spawning migration in October-November (Gjøsæter, 1998). Since our study shows that the humpback whales seem to reflect much of the capelin distribution, this may also be confirmed by most of the whales staying in more or less the same area until early winter. Although few tagged whales, our results indicate that most of the humpback whales migrate southward to breed during winter. However, it the last years, quite a few humpback and other whales have been seen feeding on spawning capelin on the continental shelf of Finnmark and Troms County (A. Rikardsen, personal communication, February 21, 2022). Suggesting it might be possible that some of the humpback whales do not migrate south to breed, but rather "follow" the mature capelin distribution southward to their spawning grounds.

The calf was one of the individuals that still had its tag on when starting migration. While foraging in the Barents Sea, the calf showed a preference of spending less time at the maximum depth. This correlates with previous knowledge about mother-calf pairs, as calves have been found to 'follow' their mothers to a degree (Tyson et al., 2012). Since we had a low sample size of data outside the Barents Sea, the calf was included in the comparisons regarding dive shape. It is important to note that this individual had a different dive behavior, than the majority within the Barents Sea.

The density values from the capelin surveys found capelin to be deeper and more spread out in the water column during day light hours. During the evening and night, especially during dusk (from 19 to 23), the capelin was found in shallower waters and had the densest aggregations. Our results also found that there were capelin aggregations high up in the water column during the day. This could be due to specific depth preferences of different capelin age classes, as a result of different prey species (Gjøsæter, 1998). Adult capelin have been found to prefer deeper waters during the day, whereas younger capelin tend to stay higher up in the water column during both day and night (Gjøsæter, 1998). This bimodal vertical distribution verifies that at least part of the capelin distribution conducts diurnal vertical migration, that we found our tagged whales to be following. Additionally, at least 25% of the recorded humpback whale dives were shallow dives (<50 meters) during most the daytime. Which could indicate feeding on the younger age classes of capelin.

In our analysis, light intensity was used as a proxy in the move persistence mixed model, to see if the humpback whales followed these dial depth changes in their dives. Our hypothesis for capelin feeding was supported, as our modeling approach found humpback whale behavioral mode to be best described by both capelin distribution and sun angle. Furthermore, this was supported by our mapping of humpback whale dial dive depth. This diving behavior is supported by a previous study conducted in the Gulf of Maine, where the humpback whales have been found to feed on sand lance (Payne et al., 1986). There, sand lance aggregations are found in the open water during the day, then during the night and in periods of low densities they dig themselves into the sandy substrate (Meyer et al., 1979; Winslade, 1974). Humpback whales have been found to bubble net feed on sand lance during the day and change to bottom feeding on the same prey species during the night (Friedlander et al 2009).

Our model found that the humpback whales all respond differently with different intensities to both capelin horizontal distribution and sun angle. This is different to what we hypothesized, as we thought they would all react similarly to a potential prey species. Ochoa-

Zubiri et al. (2017) found individual NEA- humpback whales to have large behavioral differences when studying dive behavior in the Norwegian fjords. It is not uncommon within a species to have individual variation. In a community modeling study, individual variation for predators in relation to prey were found to be more stable in a dynamic community, compared to a model based on partial preference (Okuyama, 2011).

Our results found that 9 of our whales showed a preference for daytime feeding, however one individual mostly fed during the night. A reason for this could be the humpback whales were in different local areas, and maybe the highest capelin densities for the night-feeder was significantly higher during the night. However, is difficult to generalize behavior in such a complex, intelligent species.

An unexpected finding in the study was a trip taken into the Arctic Ocean at 82°N north of Svalbard by one of the whales (ID: 47597). In the beginning of September the humpback whale stayed in high-density capelin areas, with low move persistence values, proposing feeding behavior. Later in September it moved north, with high move persistence (transiting behavior) and came back to the initial starting point in the north-central Barents Sea. This individual was the same one that showed signs of night-time feeding on capelin. This behavior could be a 'partial searching trip', as first described by Van Ruiten (2022) for killer whales.

Diving behavior as the humpback whales undergo migration has been described for the first-time using satellite tracking data. In addition, this study compares diving behavior within and outside a feeding area. Even though this dataset is small, it can contribute valuable information to the larger conversation about behavior and feeding patterns that is difficult to obtain and can be used as a baseline for future studies.

We found a significant difference in dive duration, dive depth and shape of dives when comparing dives inside and outside the Barents Sea, which supports our hypothesis that they would be different. Previous studies have suggested that feeding dives are more energetically demanding (Goldbogen et al., 2008; Iwata et al., 2021; Owen et al., 2017), however to our knowledge no other studies have investigated how they are different. In this study we used move persistence and directionality to find the start point for migration and compared the behavior "within" and "outside" the feeding ground.

In sum we conclude that the energy rich and abundant capelin is seemingly a very important food source that shapes the feeding behavior of the NEA-humpback whales on their main feeding ground. Capelin is an important energy source that likely makes their long breeding migration possible and shapes their population dynamics. Any future large changes in the abundance and distribution of capelin in the Barents Sea, would therefore likely also have an indirect effect on the NEA-humpback whale population.

6 Reference list

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Appendix A

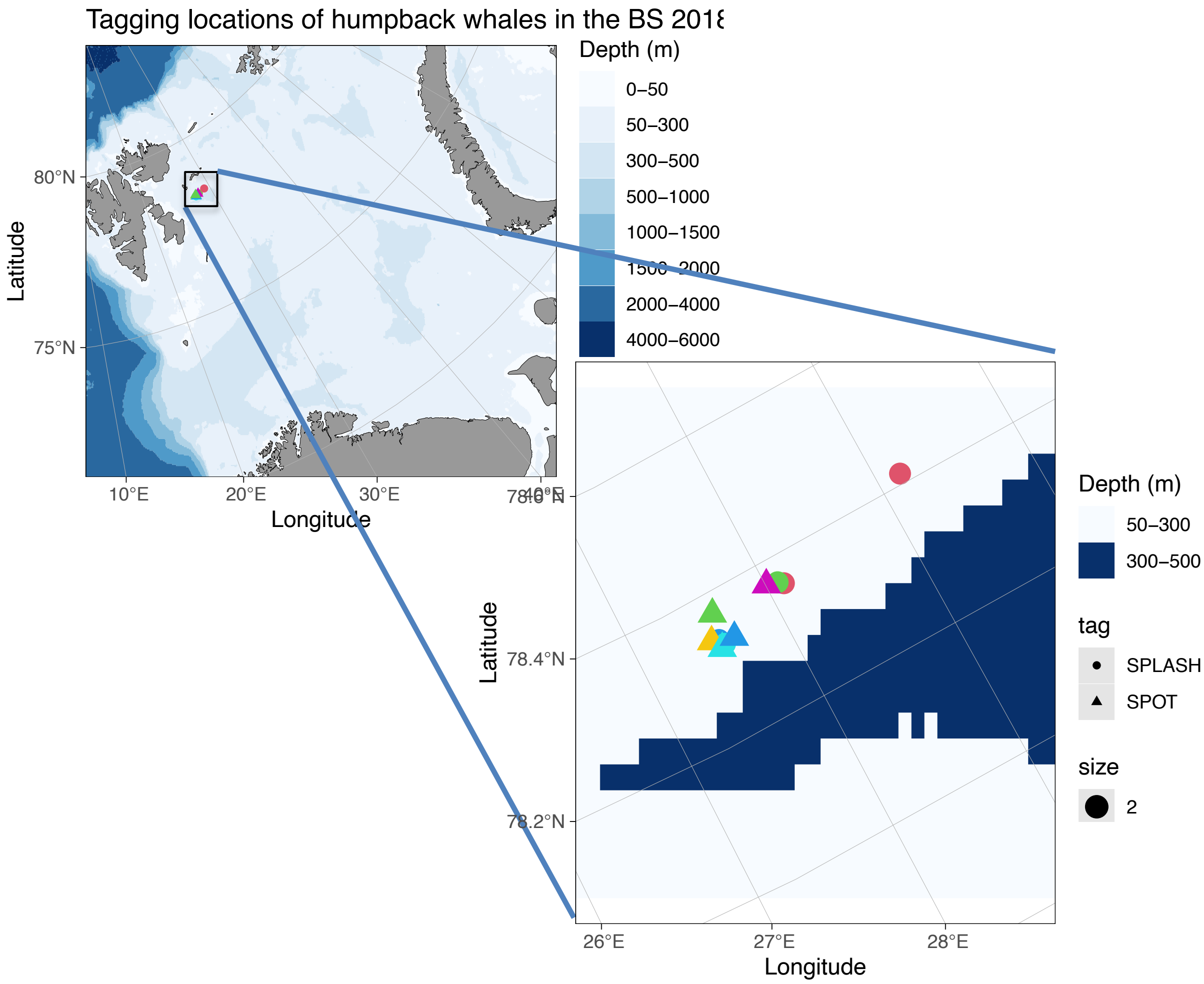

Figure A1: Tagging locations of humpback whales in the Barents Sea in September 2018. Circle dots denote SPLASH tagging location and triangle marks denote SPOT tagging locations. Be aware that the coloration in the maps are somewhat different.

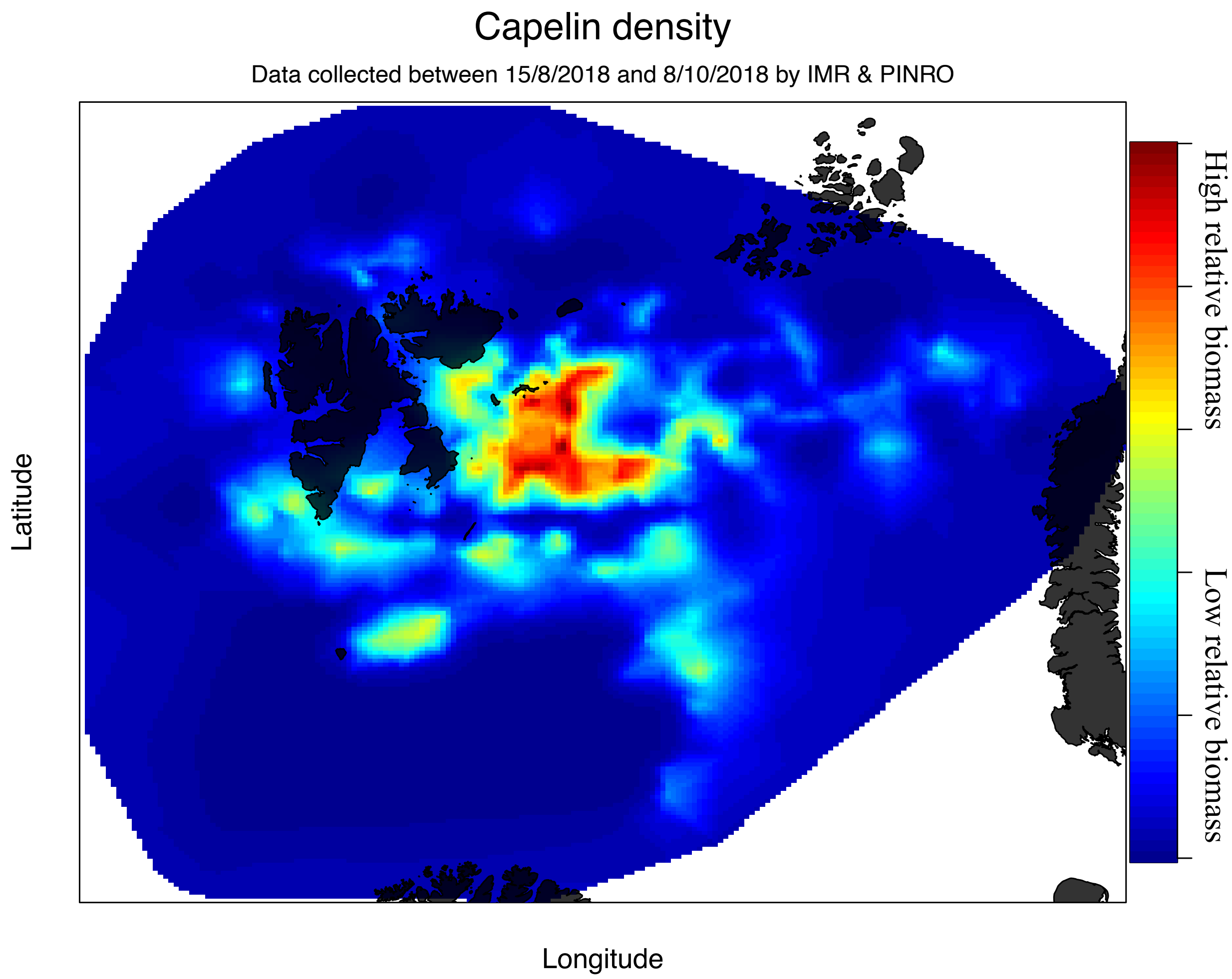

Figure A2: Relative capelin density distribution map based on spatial analysis of observed capelin biomass using INLA. Red areas display high relative density areas of capelin, and dark blue indicates low relative density areas.

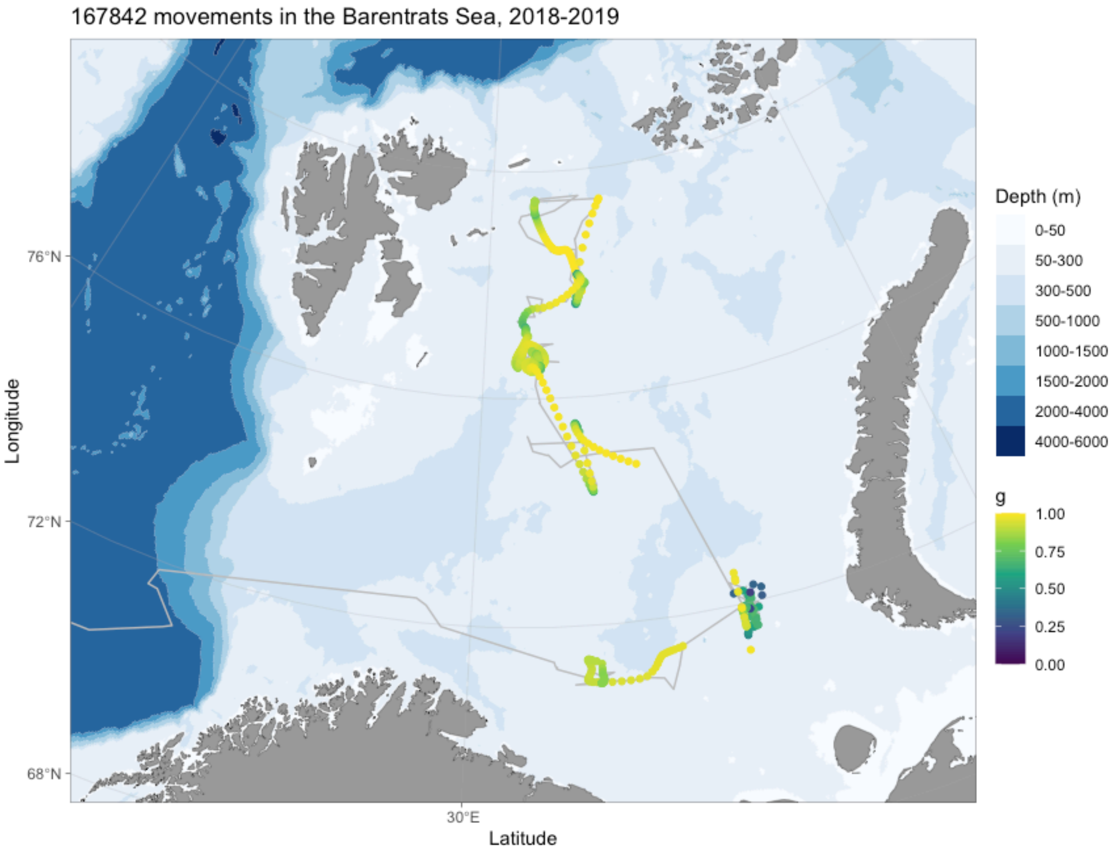

Figure A3: Humpback whale 167842 tagged with a splash tag 8.9.2018. Last date of transmission was 9.3.2019. The tag fell off or stopped transmitting during the migration, before the whale reached the breeding area. Grey lines behind colored dots indicate raw data track. The colored dots indicate humpback whale track and behavioral mode. High move persistence (g) values (lighter colors) indicate transiting behavior, and low values (darker colors) indicate foraging behavior. Individual whales have different move persistence baselines.

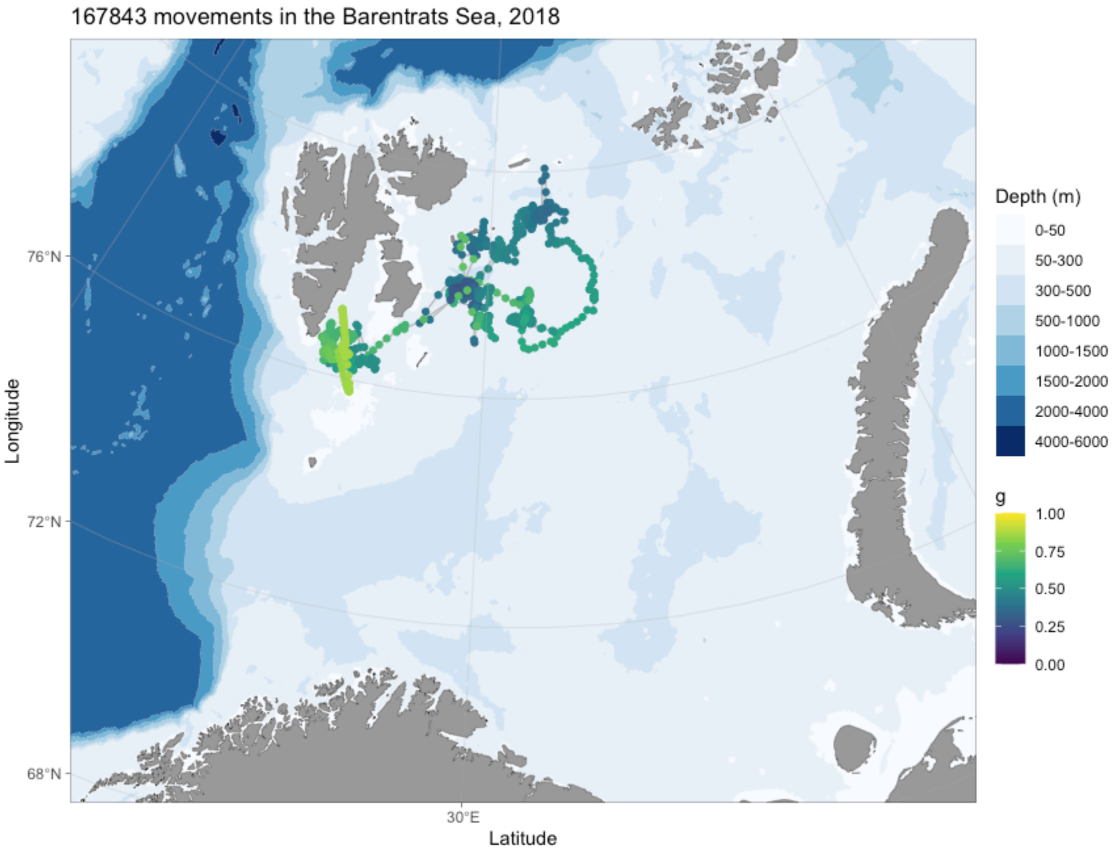

Figure A4: Humpback whale 167843 tagged with a splash tag 5.9.2018. Last date of transmission was 22.12.2018. The tag fell off or stopped transmitting while the whale was in the Barents Sea. Grey lines behind colored dots indicate Correlated Random Walk track. The colored dots indicate humpback whale track and behavioral mode. High move persistence (g) values (lighter colors) indicate transiting behavior, and low values (darker colors) indicate foraging behavior. Individual whales have different move persistence baselines.

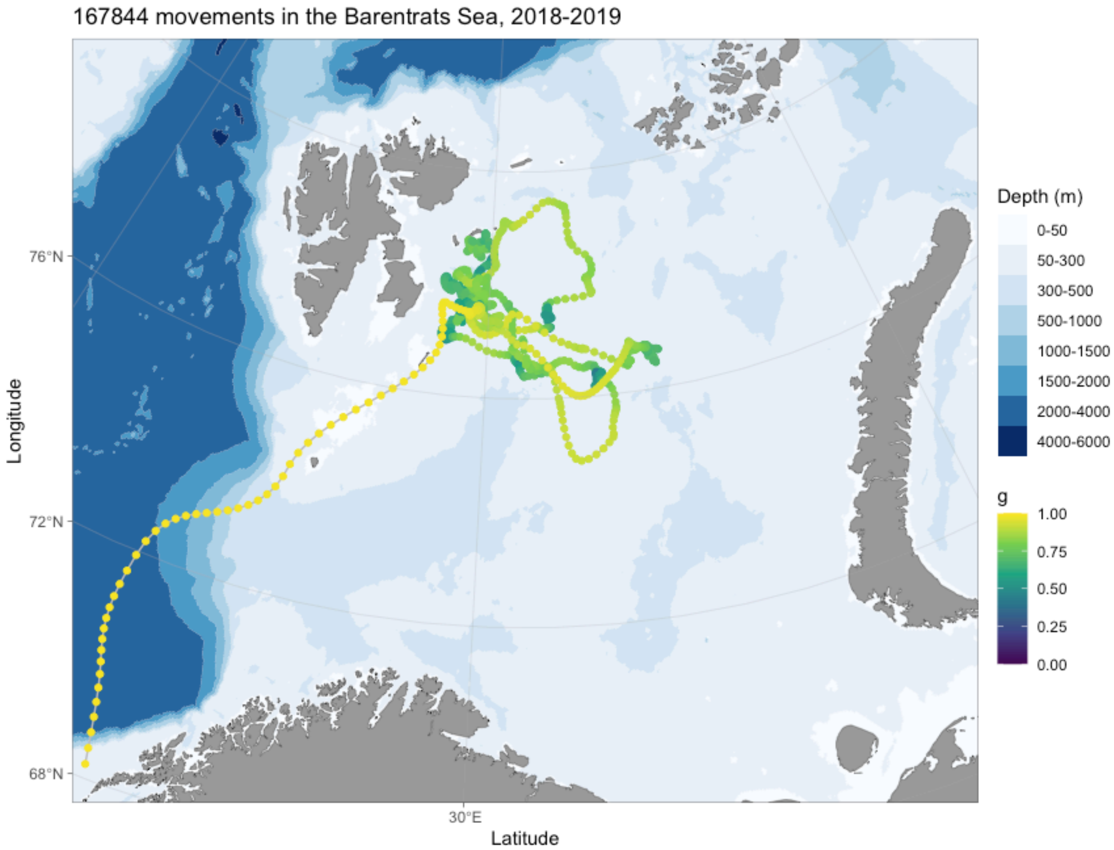

Figure A5: Humpback whale 167844 tagged with a splash tag 4.9.2018. Last date of transmission was 9.4.2019. The tag fell off or stopped transmitting as the whale was in the deep waters east of the Island of Guadeloupe. Grey lines behind colored dots indicate Correlated Random Walk track. The colored dots indicate humpback whale track and behavioral mode. High move persistence (g) values (lighter colors) indicate transiting behavior, and low values (darker colors) indicate foraging behavior. Individual whales have different move persistence baselines.

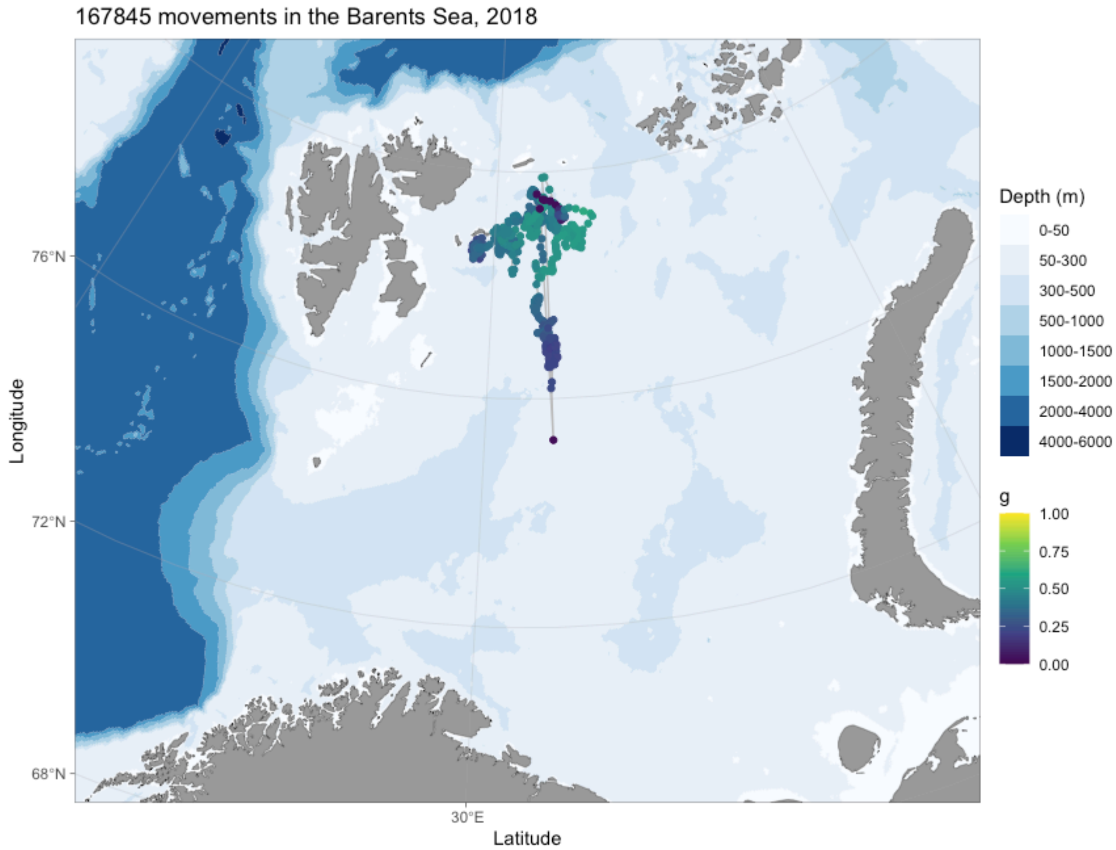

Figure A6: Humpback whale 167845 tagged with a splash tag 4.9.2018. Last date of transmission was 3.11.2018. The tag fell off or stopped transmitting while the whale was in the Barents Sea. Grey lines behind colored dots indicate Correlated Random Walk track. The colored dots indicate humpback whale track and behavioral mode. High move persistence (g) values (lighter colors) indicate transiting behavior, and low values (darker colors) indicate foraging behavior. Individual whales have different move persistence baselines.

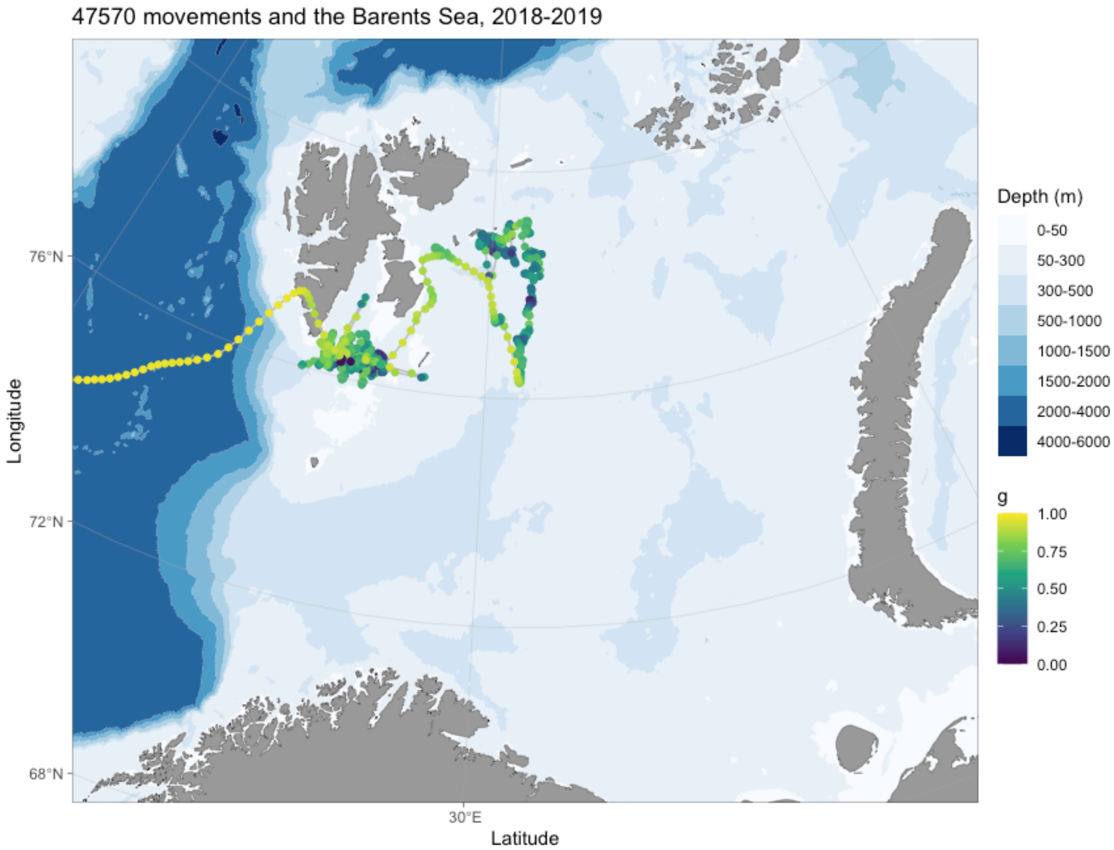

Figure A7: Humpback whale 47570 tagged with a splash tag 9.9.2018. Last date of transmission was 20.4.2019. The whale swam north of Iceland, down to the West Indies and started it migration north again before the tag stopped transmitting. Grey lines behind colored dots indicate Correlated Random Walk track. The colored dots indicate humpback whale track and behavioral mode. High move persistence (g) values (lighter colors) indicate transiting behavior, and low values (darker colors) indicate foraging behavior. Individual whales have different move persistence baselines.

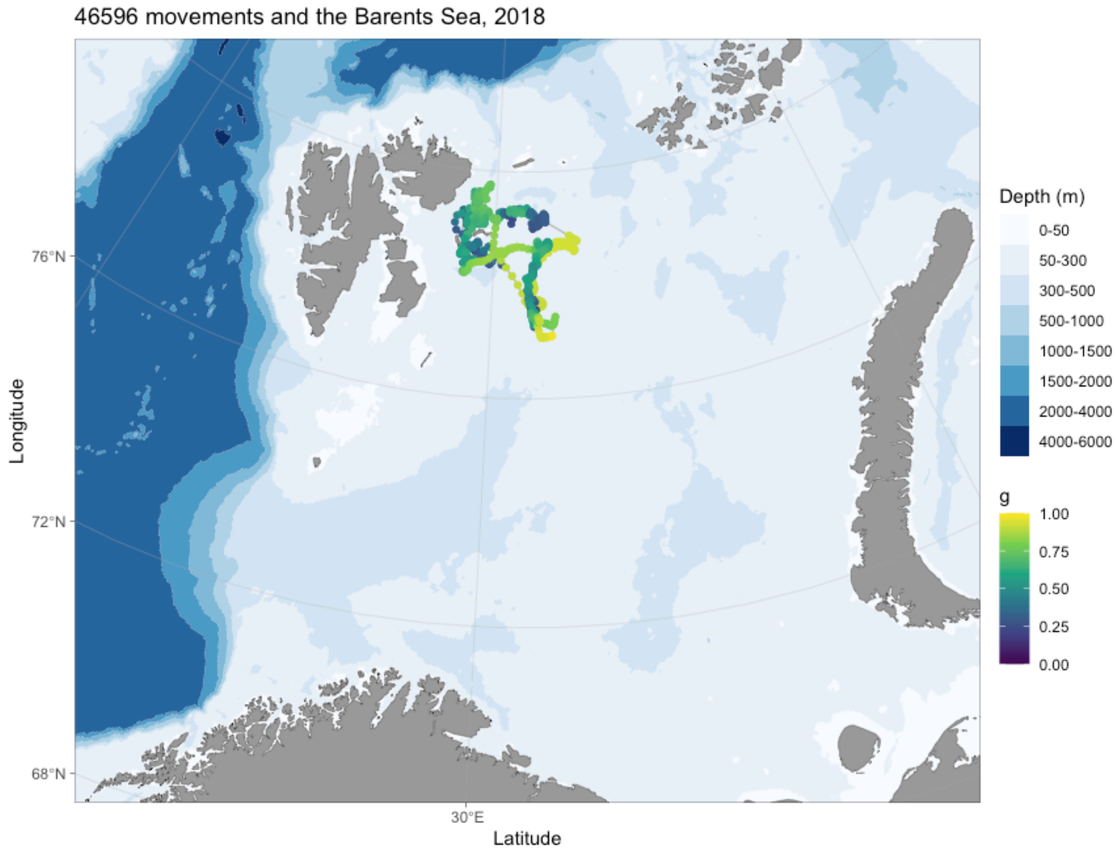

Figure A8: Humpback whale 46956 tagged with a spot tag 4.9.2018. Last date of transmission was 17.11.2018. The tag fell off or stopped transmitting while the whale was in the Barents Sea. Grey lines behind colored dots indicate Correlated Random Walk track. The colored dots indicate humpback whale track and behavioral mode. High move persistence (g) values (lighter colors) indicate transiting behavior, and low values (darker colors) indicate foraging behavior. Individual whales have different move persistence baselines.

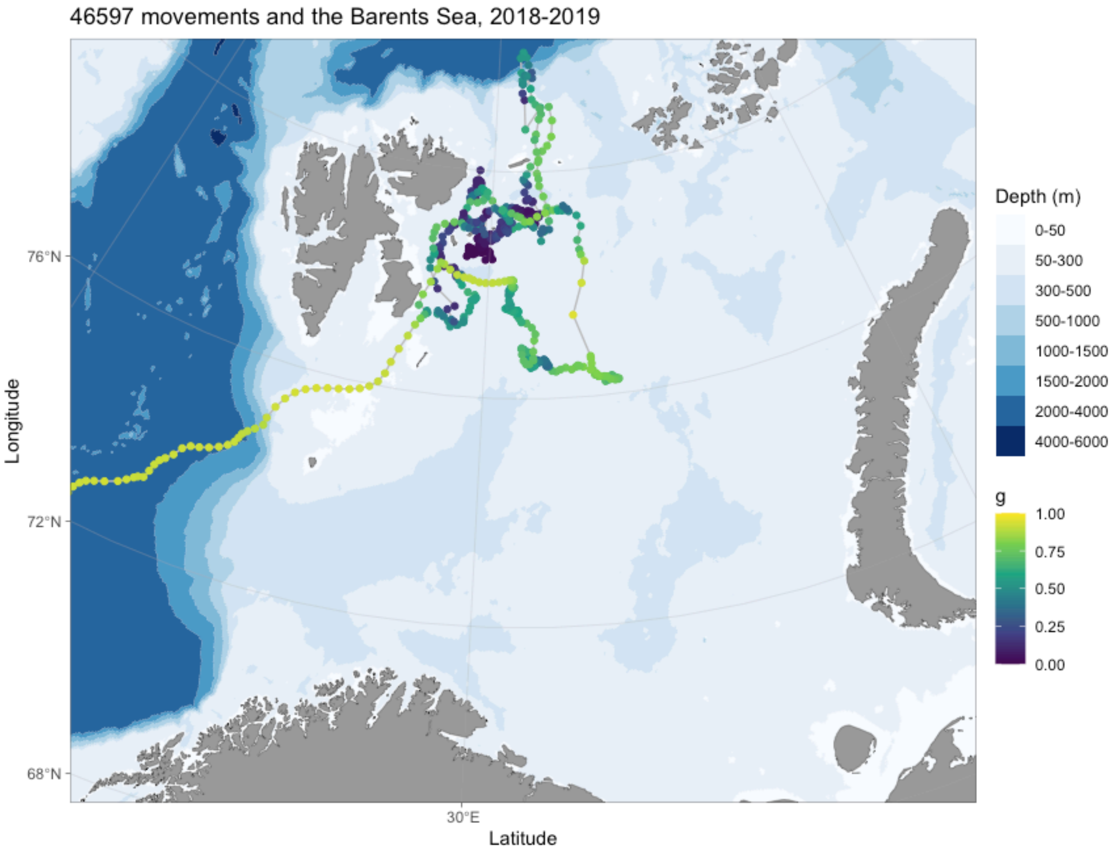

Figure A9: Humpback whale 46597 tagged with a spot tag 4.9.2018. Last date of transmission was 6.1.2019. The tag fell off or stopped transmitting while the whale was migrating southward. Grey lines behind colored dots indicate Correlated Random Walk track. The colored dots indicate humpback whale track and behavioral mode. High move persistence (g) values (lighter colors) indicate transiting behavior, and low values (darker colors) indicate foraging behavior. Individual whales have different move persistence baselines.

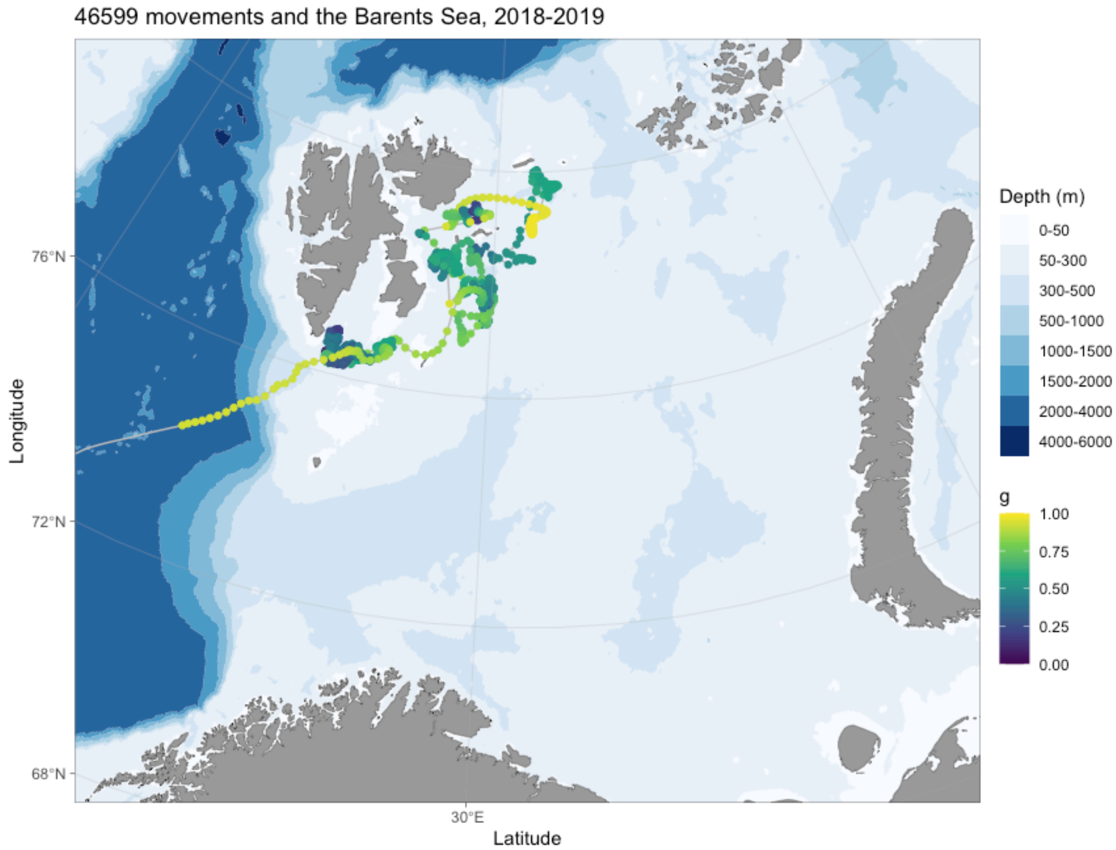

Figure A10: Humpback whale 46599 tagged with a spot tag 4.9.2018. Last date of transmission was 4.3.2019. The tag fell off or stopped transmitting while the whale was migrating southward. Grey lines behind colored dots indicate Correlated Random Walk track. The colored dots indicate humpback whale track and behavioral mode. High move persistence (g) values (lighter colors) indicate transiting behavior, and low values (darker colors) indicate foraging behavior. Individual whales have different move persistence baselines.

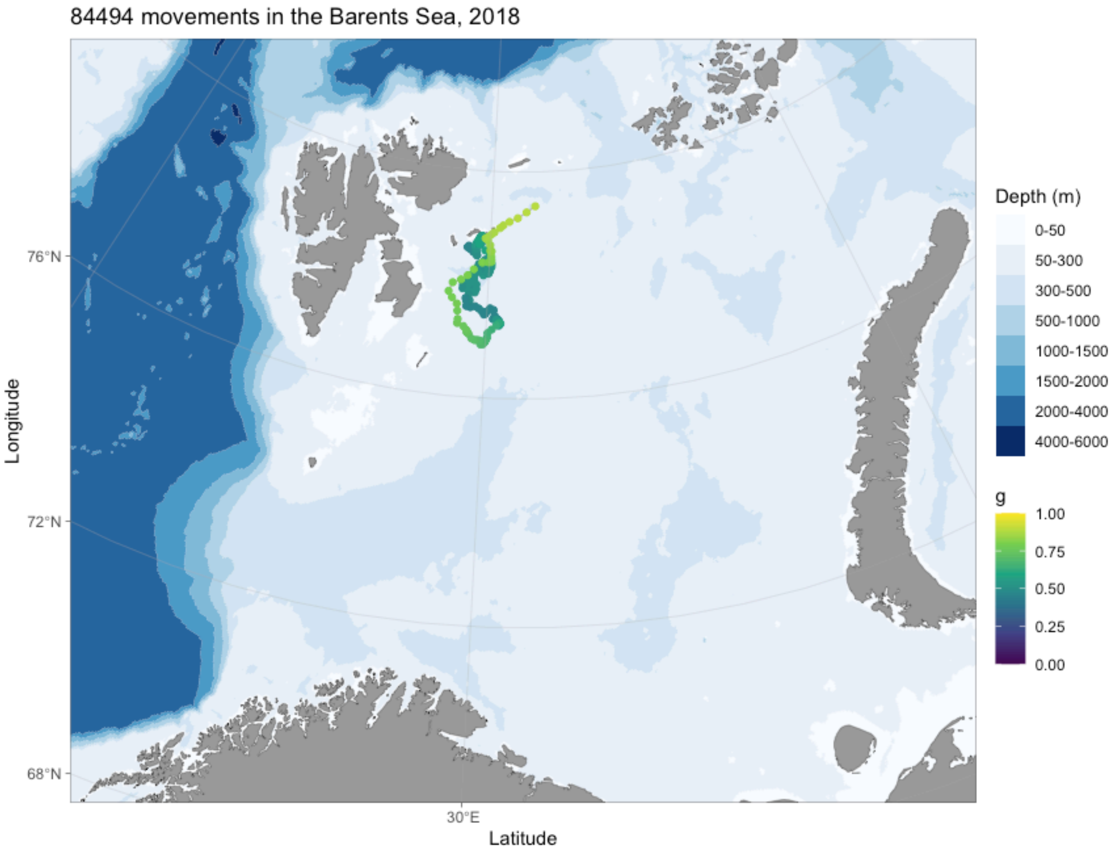

Figure A11: Humpback whale 84494 tagged with a spot tag 5.9.2018. Last date of transmission was 29.9.2018. The tag fell off or stopped transmitting while the whale was within the Barents Sea. Grey lines behind colored dots indicate Correlated Random Walk track. The colored dots indicate humpback whale track and behavioral mode. High move persistence (g) values (lighter colors) indicate transiting behavior, and low values (darker colors) indicate foraging behavior. Individual whales have different move persistence baselines.

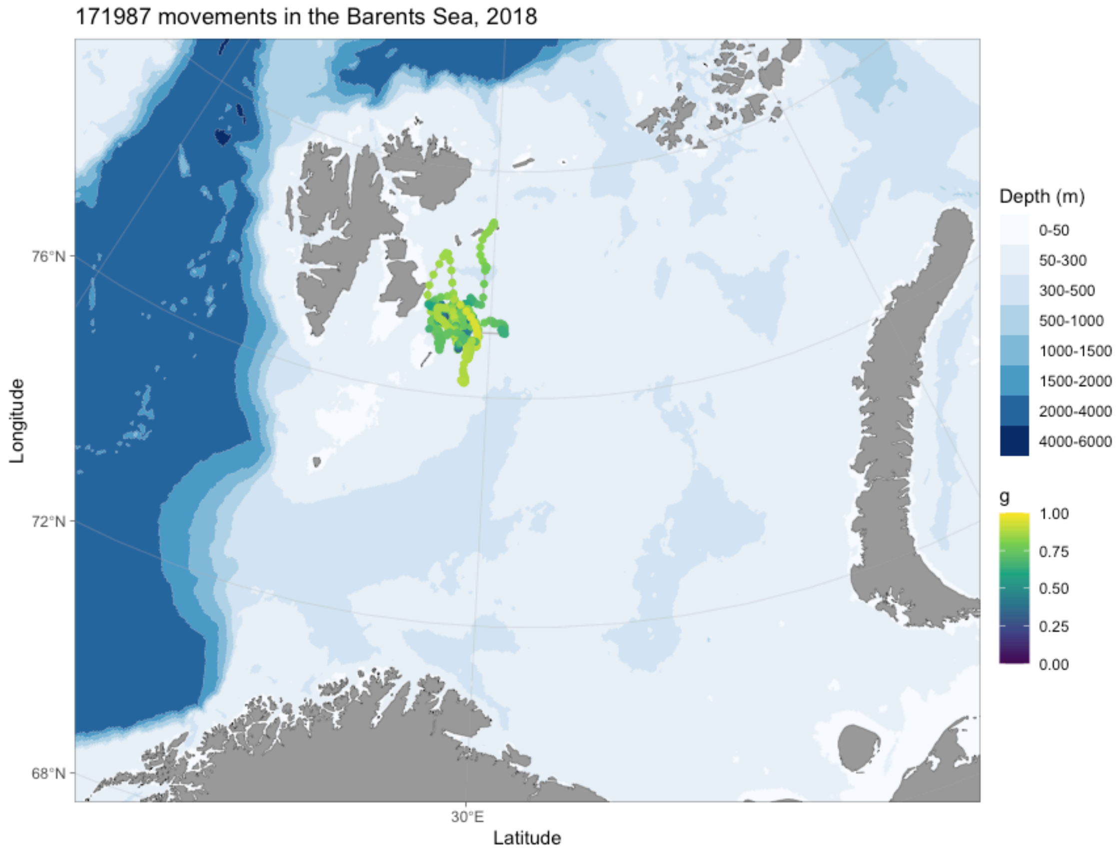

Figure A12: Humpback whale 171987 tagged with a spot tag 5.9.2018. Last date of transmission was 28.10.2018. The tag fell off or stopped transmitting while the whale was within the Barents Sea. Grey lines behind colored dots indicate Correlated Random Walk track. The colored dots indicate humpback whale track and behavioral mode. High move persistence (g) values (lighter colors) indicate transiting behavior, and low values (darker colors) indicate foraging behavior. Individual whales have different move persistence baselines.

Appendix B

```
# Master thesis script
# Created may 2022
# By Stine Skalmerud

####################################################################################################
#Figure 2:
####################################################################################################
#find the data
whale1raw <- read.csv("Barents2018/167842/167842-Locations.csv")
#fit crw with 3 h timestep
fit1 <- fit_ssm(whale1raw, model="crw", time.step=3, control=ssm_control(verbose=1))
crw1 <- grab(fit1, what="predicted", as_sf=FALSE)

#do the above steps for all whale tracks, then bind them together:
allwhales_CRW <- rbind(crw1,crw2,crw3,crw4,crw5,crw6,crw7,crw8,crw9,crw10)

basemap(limits=c(10.638710,55.299474,68.975778,81.750592), rotate=TRUE,bathymetry = TRUE) +
  geom_spatial_path(data=allwhales_CRW, aes(lat,lon), colour=id)+
  labs(title="The Barents Sea and tagged humpback whale tracks, 2018-2019",x="Latitude", y="Longitude")

####################################################################################################
#Figure 3:
####################################################################################################
#Move persistence analysis. Use the fit1 from before:
fmp1<- fit1 %>%
  grab(., "p", as_sf = FALSE) %>%
  select(id, date, lon, lat) %>%
  fit_mpm(., model = "mpm")

#join the mp and crw
whale1 <- join(fit1, fmp1, as_sf = FALSE)
#do the above steps for all tracks, then bind them together:
allwhales_MP <- rbind(whale1,whale2,whale3,whale4,whale5,whale6,whale7,whale8,whale9,whale10)

basemap(limits=c(18.638710,40.299474,76.1,82.750592), rotate=TRUE, bathymetry = TRUE) +
  geom_spatial_path(data=allwhales_CRW, aes(lat,lon), colour=g)+
  geom_spatial_point(data=allwhales_CRW, aes(lat, lon, colour = g)) +
  scale_colour_viridis_c(alpha=0.5,limits = c(0,1)) +
  labs(title="Move persistence for humpback whale movement characteristics, september 2018", x="Latitude", y="Longitude")

####################################################################################################
#Figure 4
####################################################################################################

load("Capelin_2.0/pred.mat.RData")
coast <- readOGR('Capelin_2.0/country.shp')
coast <- spTransform(coast, CRS("+proj=utm +zone=35 +ellps=intl +units=m +no_defs"))
image.plot(pred.mat$x, pred.mat$y, pred.mat$pred, xaxt="n",xlab="",yaxt="n",ylab="")
plot(coast, add=T, col=rgb(0,0,0,.8))
#adding title, axis names, etc
mtext(text="Longitude", side =1, line=1.5, cex=1.2)
mtext(text="Latitude", side=2, line=1.5, cex=1.2)
mtext(text="10 Humpback whale tracks in the Barents Sea", side=3, line=2, cex=1.6)
mtext(text="Humpback whale movement September 2018", side=3, line=0.5, cex=1)

#this shows how to add on one whale track, this has to be done for each tracks:
spot1a <- read.csv("8mars/CRW_spot/spot1/CRW_3h_whale1a_spot.csv")
spot1a <- spot1a[,1:4]
names(spot1a)[3] <- "lat"
names(spot1a)[4] <- "lon"
coordinates(spot1a) <- c('lon', 'lat')
proj4string(spot1a) <- CRS("+proj=longlat +ellps=WGS84 +datum=WGS84")
bb <- bbox(spot1a)
spot1a <- spTransform(spot1a, CRS("+proj=utm +zone=35 +ellps=intl +units=m +no_defs"))
spot1a <- spot1a[which(!duplicated(coordinates(spot1a))),]
lines(spot1a$lon,spot1a$lat, col=rgb(0, 0, 0, 0.5))

####################################################################################################
```

```
#Figure 5
##########################################################################################################
dive.df <- read.csv("total_dive_df_BS.csv")
str(dive.df)
dive.df$Midtime = as.POSIXlt(dive.df$Midtime, format = "%Y-%m-%d %H:%M:%S", tz='UTC')
dive.df$Start = as.POSIXct(dive.df$Start, format = "%Y-%m-%d %H:%M:%S", tz='UTC')
dive.df$End = as.POSIXct(dive.df$End, format = "%Y-%m-%d %H:%M:%S", tz='UTC')
dive.df$Midtime <- as.POSIXct((as.numeric(dive.df$End) + as.numeric(dive.df$Start)) / 2, origin = '1970-01-01',, tz='UTC')
dive.df$DeployID<-as.character(dive.df$DeployID)
dive.df$hour <- dive.df$Midtime$hour #create new column with hour
dive.df$month <- dive.df$Midtime$mon #create new column with hour

sept_dives =subset(dive.df, month=="8")
oct_dives =subset(dive.df, month=="9")
nov_dives =subset(dive.df, month=="10")
dec_dives =subset(dive.df, month=="11")
jan_dives =subset(dive.df, month=="0")

library(gridExtra)

q1 <- ggplot() +
  geom_boxplot(sept_dives, mapping=aes(x=hour, y=-Depth, group=hour)) +
  labs(x="Time of day (UTC)",y="Depth (meters)", title="September dives(n=6040)") +
  scale_x_continuous(breaks=c(0:23), labels=c(0:23),limits=c(-0.5,23.5))+
  scale_y_continuous(limits=c(-350,0))
q2 <- ggplot(oct_dives, aes(x=hour, y=-Depth, group=hour)) +
  geom_boxplot() +
  labs(x="Time of day (UTC)",y="Depth (meters)", title="October dives(n=4651)") +
  scale_x_continuous(breaks=c(0:23), labels=c(0:23),limits=c(-0.5,23.5))+
  scale_y_continuous(limits=c(-350,0))
q3<- ggplot(nov_dives, aes(x=hour, y=-Depth, group=hour)) +
  geom_boxplot() +
  labs(x="Time of day (UTC)",y="Depth (meters)", title="November dives(n=1641)") +
  scale_x_continuous(breaks=c(0:23), labels=c(0:23),limits=c(-0.5,23.5)) +
  scale_y_continuous(limits=c(-350,0))
q4<- ggplot(dec_dives,aes(x=hour, y=-Depth, group=hour)) +
  geom_boxplot(ymin=0,ymax=400) +
  labs(x="Time of day (UTC",y="Depth (meters)", title="December dives(n=1017)") +
  scale_x_continuous(breaks=c(0:23), labels=c(0:23),limits=c(-0.5,23.5))+
  scale_y_continuous(limits=c(-350,0))
q5<- ggplot(jan_dives,aes(x=hour, y=-Depth, group=hour)) +
  geom_boxplot() +
  labs(x="Time of day (UTC)",y="Depth (meters)", title="January dives(n=181)") +
  scale_x_continuous(breaks=c(0:23), labels=c(0:23),limits=c(-0.5,23.5))+
  scale_y_continuous(limits=c(-350,0))
q6<- ggplot(total.dive.dataframe,aes(x=hour, y=-Depth, group=hour)) +
  geom_boxplot() +
  labs(x="Time of day (UTC)",y="Depth (meters)", title="All dives recorded(n=13530)") +
  scale_x_continuous(breaks=c(0:23), labels=c(0:23))+
  scale_y_continuous(limits=c(-350,0))

grid.arrange(top="Humpback whale dives during time of day",q1,q2,q3,q4,q5,q6, ncol=2)

##########################################################################################################
#Figure 6
##########################################################################################################
acu <- read.csv("Acoustic_data.csv")
acu2 = subset(acu, month==9) #take only data from september
dives_BS_3 = subset(dive.df, month==9) #take only data from september

hour1 = subset(dives_BS_3, hour==1)
hour2 = subset(dives_BS_3, hour==2)
hour3 = subset(dives_BS_3, hour==3)
hour4 = subset(dives_BS_3, hour==4)
hour5 = subset(dives_BS_3, hour==5)
hour6 = subset(dives_BS_3, hour==6)
hour7 = subset(dives_BS_3, hour==7)
hour8 = subset(dives_BS_3, hour==8)
hour9 = subset(dives_BS_3, hour==9)
hour10 = subset(dives_BS_3, hour==10)
hour11 = subset(dives_BS_3, hour==11)
```

```
hour12 = subset(dives_BS_3, hour==12)
hour13 = subset(dives_BS_3, hour==13)
hour14 = subset(dives_BS_3, hour==14)
hour15 = subset(dives_BS_3, hour==15)
hour16 = subset(dives_BS_3, hour==16)
hour17 = subset(dives_BS_3, hour==17)
hour18 = subset(dives_BS_3, hour==18)
hour19 = subset(dives_BS_3, hour==19)
hour20 = subset(dives_BS_3, hour==20)
hour21 = subset(dives_BS_3, hour==21)
hour22 = subset(dives_BS_3, hour==22)
hour23 = subset(dives_BS_3, hour==23)
hour0 = subset(dives_BS_3, hour==0)

ggplot()+
  geom_tile(acu2, mapping=aes(y=-(ch*10), x=hour,fill=log(sa+1)))+
  scale_fill_gradient(low = "white", high = "deeppink2") +
  theme_light()+
  scale_y_continuous(limits=c(-360,0))+
  scale_x_continuous(breaks = c(0:23), labels=c(0:23))+
  geom_boxplot(hour0, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour1, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour2, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour3, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour4, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour5, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour6, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour7, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour8, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour9, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour10, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour11, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour12, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour13, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour14, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour15, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour16, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour17, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour18, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour19, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour20, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour21, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour22, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  geom_boxplot(hour23, mapping=aes(y=-Depth, x=hour),color="black", alpha=0) +
  labs(title="Capelin density and humpback whale diving depth, during one day throughout the watercolumn",
       x="Time of day (UTC)", y="Depth")

#########################################################################################################
#Figure 7
#########################################################################################################
#using the crw fits, i had one as the spot tags and the other as splash, but could be done with all in one
splash.crw <- rbind(crw1,crw2,crw3,crw4,crw5)
spot.crw <- rbind(crw6,crw7,crw8,crw9,crw10)

library(sf)
library(sp)
library(maptools)
library(fields)
library(foieGras)
library(data.table)
library(tidyverse)

spot_loc <- grab(spot.crw, what = "p", as_sf = FALSE) %>%
  sf::st_as_sf(., coords = c("lon","lat"), crs = 4326)
splash_loc <- grab(splash.crw, what = "p", as_sf = FALSE) %>%
  sf::st_as_sf(., coords = c("lon","lat"), crs = 4326)

###################################################################################
# sun angle
# check as.posixct / utc zone Oslo..!
coord_cut <-  data.table(
```

```
  x= c(spot_loc$x),
  y= c(spot_loc$y))
Hels <- SpatialPoints((coord_cut), proj4string=CRS("+proj=longlat +datum=WGS84"))
sun.ang <- solarpos(Hels,spot_loc$date)
# SS - do this again with TZ - BE SURE THAT TIME ZONE IS CORRECT.
spot_loc$sun.elevation <- sun.ang[,2]

#splash
coord_cut1 <-  data.table(
  x= c(splash_loc$x),
  y= c(splash_loc$y))
Hels1 <- SpatialPoints((coord_cut1), proj4string=CRS("+proj=longlat +datum=WGS84"))
sun.ang1 <- solarpos(Hels1,splash_loc$date)
splash_loc$sun.elevation <- sun.ang1[,2]
###########################################################################################
# transforming from latlong to utm 35
#Convert to sf object and project to get xy
spot_loc_sf <- spot_loc %>% st_as_sf(coords = c("lon", "lat")) %>% st_set_crs(4326)
prj = "+proj=utm +zone=35 +datum=WGS84 +units=km +no_defs"
spot_loc_sf <- spot_loc_sf %>% st_transform(crs = prj)

library(dplyr)
# Append coordinates to dat
spot_loc.cord <- spot_loc_sf %>% mutate(x = st_coordinates(spot_loc_sf)[,1],
                              y = st_coordinates(spot_loc_sf)[,2])

# Convert the projected locations from metres to kilometres
spot_loc.cord <- spot_loc.cord %>% mutate(x = x*1000,y = y*1000)
prj = "+proj=utm +zone=35 +datum=WGS84 +units=m +no_defs"

#splash
splash_loc_sf <- splash_loc %>% st_as_sf(coords = c("lon", "lat")) %>% st_set_crs(4326)
prj = "+proj=utm +zone=35 +datum=WGS84 +units=km +no_defs"
splash_loc_sf <- splash_loc_sf %>% st_transform(crs = prj)
splash_loc.cord <- splash_loc_sf %>% mutate(x = st_coordinates(splash_loc_sf)[,1],
                                y = st_coordinates(splash_loc_sf)[,2])
splash_loc.cord <- splash_loc.cord %>% mutate(x = x*1000,y = y*1000)
prj = "+proj=utm +zone=35 +datum=WGS84 +units=m +no_defs"

##################################################
# add biomass column/value

load("Capelin_2.0/pred.mat.RData")

#add biomass etc
spot_loc.cord$biomass <- rep(NA, nrow(spot_loc.cord))
splash_loc.cord$biomass <- rep(NA, nrow(splash_loc.cord))

for(i in 1:nrow(spot_loc.cord)) {
  idx <- c(which.min(abs(spot_loc.cord$x[i]-pred.mat$x)),
         which.min(abs(spot_loc.cord$y[i]-pred.mat$y)))
  spot_loc.cord$biomass[i] <- pred.mat$pred[idx[1],idx[2]]
}

for(i in 1:nrow(splash_loc.cord)) {
  idx <- c(which.min(abs(splash_loc.cord$x[i]-pred.mat$x)),
         which.min(abs(splash_loc.cord$y[i]-pred.mat$y)))
  splash_loc.cord$biomass[i] <- pred.mat$pred[idx[1],idx[2]]
}

###########################################################################################
# jmpm
all.ssm <- do.call("rbind", list(spot_loc.cord,splash_loc.cord))

jmpm.spot <- spot.crw %>%
  grab(., "p", as_sf=FALSE) %>%
  dplyr::select(id, date, lon, lat) %>%
  fit_mpm(., model = "jmpm")

jmpm.spot.all <- join(spot.crw, jmpm.spot, as_sf = FALSE)
```

```
jmpm.splash <- splash2.crw %>%
  grab(., "p", as_sf=FALSE) %>%
  dplyr::select(id, date, lon, lat) %>%
  fit_mpm(., model = "jmpm")

jmpm.splash.all <- join(splash2.crw, jmpm.splash, as_sf = FALSE)
#################################################
# add environmental variables
jmpm.spot.all$biomass <- as.numeric(spot_loc.cord$biomass)
jmpm.splash.all$biomass <- as.numeric(splash_loc.cord$biomass)#
#########################################################################################
###  mpmm
#########################################################################################
install.packages("mpmm")
remotes::install_github("ianjonsen/mpmm")
library(mpmm)

grouped_df()
table(jmpm.spot.all$id)
jmpm.spot.all <- jmpm.spot.all[order(jmpm.spot.all$date),]
jmpm.spot.all <- jmpm.spot.all[order(jmpm.spot.all$id),]

jmpm.splash.all <- jmpm.splash.all[order(jmpm.splash.all$date),]
jmpm.splash.all <- jmpm.splash.all[order(jmpm.splash.all$id),]

pos.env.hw1 <- rbind(jmpm.spot.all,jmpm.splash.all)
pos.env.hw1 <- pos.env.hw1[order(pos.env.hw1$date),]
pos.env.hw1 <- pos.env.hw1[order(pos.env.hw1$id),]
#########################################################
#removing NAs
pos.env.hw = subset(pos.env.hw1, biomass!="NA")
###########################################################
mpmm1 <- mpmm::mpmm(formula = ~ biomass + sun.elevation  + (biomass + sun.elevation|id), data=grouped_df(pos.env.hw, 'id'))
mpmm2 <- mpmm::mpmm(formula = ~ biomass + sun.elevation  + (sun.elevation|id), data=grouped_df(pos.env.hw, 'id'))
mpmm3 <- mpmm::mpmm(formula = ~ biomass + sun.elevation  + (biomass|id), data=grouped_df(pos.env.hw, 'id'))
mpmm4 <- mpmm::mpmm(formula = ~ biomass + sun.elevation  + (1|id), data=grouped_df(pos.env.hw, 'id'))
mpmm5 <- mpmm::mpmm(formula = ~ sun.elevation + (sun.elevation|id), data=grouped_df(pos.env.hw,'id'))
mpmm6 <- mpmm::mpmm(formula = ~ sun.elevation + (1|id), data=grouped_df(pos.env.hw,'id'))
mpmm7 <- mpmm::mpmm(formula = ~ biomass + (biomass|id), data=grouped_df(pos.env.hw,'id'))
mpmm8<- mpmm::mpmm(formula = ~ biomass + (1|id), data=grouped_df(pos.env.hw,'id'))
mpmm.int <- mpmm::mpmm(formula = ~ 1 + (1|id), data=grouped_df(pos.env.hw,'id'))

foo <-
  AIC(mpmm1,
      mpmm2,
      mpmm3,
      mpmm4,
      mpmm5,
      mpmm6,
      mpmm7,
      mpmm8,
      mpmm.int)
bar <-
  c(mpmm1$opt.time[1],
    mpmm2$opt.time[1],
    mpmm3$opt.time[1],
    mpmm4$opt.time[1],
    mpmm5$opt.time[1],
    mpmm6$opt.time[1],
    mpmm7$opt.time[1],
    mpmm8$opt.time[1],
    mpmm.int$opt.time[1])

head(INLA.cape.1)
str(bar)
###
foo <- foo %>% mutate(model = rownames(foo)) %>%
  mutate(time = bar) %>%
  .[order(.$AIC), ] %>%
  mutate(dAIC = -1 * round(.$AIC[1] - .$AIC, 2)) %>%
  dplyr::select(3, 1:2, 4) # specify dplyr:: in case raster pkg is loaded
```

```
lrt <-
  function(x, y)
    (x$opt$objective * 2 - y$opt$objective * 2) * -1
m1 <- eval(parse(text = foo$model[1]))
lr <-
  sapply(2:nrow(foo), function(i)
    lrt(m1, eval(parse(text = foo$model[i])))) %>%
  round(., 2)
mc <-
  sapply(1:nrow(foo), function(i)
    as.character(eval(parse(text = foo$model[i]))$call)[2])
foo$dAIC[1] <- AIC(m1) %>% round(., 2)
restab <- foo %>%
  mutate(lr = c(m1$opt$objective * 2, lr)) %>% mutate(model = mc) %>%
  dplyr::select(1:2, 4, 5)

knitr::kable(
  restab,
  align = c("rrrrr"),
  col.names = c("Model formula", "df", "dAIC", "LR"), format = 'latex',
  digits = 2
) %>%
  kableExtra::kable_styling(full_width = F, position = "left")

kable_styling(kable(
  restab,
  align = c("rrrrr"),
  col.names = c("Model formula", "df", "dAIC", "LR"), format = 'latex',
  digits = 2
) )
######################
#Table 3:
######################
kable_styling(kable(restab))
######################
#Figure 7
######################
plot(mpmm1, label=TRUE)
##############################################################################################################
#Figure 8
##############################################################################################################
#feeding dives = feed
#migration dives = mig
m1 <- ggplot() +
  geom_boxplot(feed, mapping=aes(x=hour, y=-Depth, group=hour)) +
  labs(y="Depth (meters)", title="Feeding dives(n=6674)", size=15) +
  theme(text=element_text(size=25))+
  scale_x_continuous(breaks=c(0:23), labels=c(0:23),limits=c(-0.5,23.5))+
  scale_y_continuous(limits=c(-350,0))
m2<- ggplot() +
  geom_boxplot(mig, mapping=aes(x=hour, y=-Depth, group=hour)) +
  labs(title="Migration dives(n=618)", size=15) +
  theme(text=element_text(size=25))+
  scale_x_continuous(breaks=c(0:23), labels=c(0:23),limits=c(-0.5,23.5))+
  scale_y_continuous(limits=c(-350,0))
m3 <- ggplot() +
  geom_boxplot(feed, mapping=aes(x=hour, y=Duration, group=hour)) +
  labs(x="Time of day (UTC)",y="Duration (min)",size=15) +
  theme(text=element_text(size=25))+
  scale_x_continuous(breaks=c(0:23), labels=c(0:23),limits=c(-0.5,23.5))+
  scale_y_continuous(limits=c(0,20))

m4<- ggplot() +
  geom_boxplot(mig, mapping=aes(x=hour, y=Duration, group=hour)) +
  labs(x="Time of day (UTC)", size=25) +2
theme(text=element_text(size=25))+
  scale_x_continuous(breaks=c(0:23), labels=c(0:23),limits=c(-0.5,23.5))+
  scale_y_continuous(limits=c(0,20))

grid.arrange(m1, m2, m3,m4, nrow=2)
```