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Characterizing movement and searching behavior of humpback whales at the North-Norwegian coast

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Cover photo: Surfacing humpback whale (*Megaptera novaeangliae*) during feeding on overwintering herring outside of Skjervøy.

November 2020. Photo: Juni Bjørneset

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Abbreviations

BCPA – Behavioral change point analysis

CC – Concordance criterion

CRW – Correlated random walk

NSD – Net squared displacement

NSS – Norwegian spring-spawning

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As one of my supervisors (Audun) said; when people get tired of reading your thesis, they skip right to the acknowledgements. Whale, hello there!

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1 Abstract

Studying movement patterns of individual animals over time can give insight into how they interact with the environment and optimize their foraging strategies. Humpback whales (*Megaptera novaeangliae*) undertake long seasonal migrations between feeding areas in polar regions during summer/early winter and breeding areas in more tropical areas during late winter/spring. The Norwegian Sea is a part of the humpback whale migration route between the Barents Sea and their southern breeding grounds, and during the last decade several individuals have had up to a three month stop-over period around some specific fjord areas in Northern Norway. Here they feed on Norwegian spring-spawning (NSS-) herring (*Culpea harengus L.)* to seemingly re-fuel before continuing their southwards breeding migration. Their smaller scale movement and individual variation in behavioral patterns during this stop-over period are not well understood, including why some whales have been observed to leave the fjords and then later return within the same season.

Therefore, this study used data from 12 satellite tagged humpback whales and for the first time segmented their tracks into five distinct movement modes; ranging, encamped, nomadic, roundtrip and semi-roundtrip. This was done by using a behavioral change point analysis (BCPA) to pick out homogeneous segments based on persistence velocity at relatively small scales, and then modeled the net squared displacement (NSD) over time to differentiate movement modes. This study also visually identified longer roundtrips away from the fjords that lasted several days and examined movement modes within these.

The most common movement mode was ranging behavior (54%), particularly seen during the start of their southwards migration and in areas outside the fjord systems in late winter, indicating when the whales moved over larger distances in the offshore habitat. Inside the fjord systems, encamped, nomadic, round and semi-roundtrip modes were more prevalent in December-January, suggesting the whales are mainly foraging on overwintering NSS-herring in this area. Half of the whales left the fjords and came back again during the same winter seasons, and these trips lasted from 4-22 days and were conducted in late December or January. During these trips, 60% of their behavior consisted of ranging behavior, sometimes split by shorter periods of encamped, roundtrips or nomadic behavior. We hypothesize that these trips may serve as "searching trips" where the whales search for better feeding opportunities outside the fjord systems, and if better foraging conditions are not found, they return to the fjords to continue their feeding. This study serves as a baseline for future studies investigating both this theory and humpback whale behavior in general, and confirms that the method is useful to analyze smaller scale movement patterns of satellite tagged whales.

2 Introduction

Knowledge on animal movement is essential to understand the interaction between organisms and their environment. Studying how and why animals move provide insight into population dynamics and species interactions, as well as understanding future impacts from habitat loss and climate change (Hays et al., 2016; Nowacek et al., 2016; Schick et al., 2008). How individuals adjust to changes in resource availability over space and time is known as resource tracking (Abrahms et al., 2020). In the marine environment, predators such as whales are shown to be strongly influenced by the distribution and behavior of prey (Bestley et al., 2015; Joy et al., 2015; Vogel et al., 2021). However, individual movements are a complex process affected by both biological factors (genotype), external factors (environment), and internal factors (status, history) (Hays et al., 2016; Schick et al., 2008; Shaw, 2020). Together these factors influence and shape the structure and distribution of populations at various spatial and temporal scales (Gurarie et al., 2016; Schick et al., 2008). Spatial and temporal variations of animal movement include everything from daily foraging and random nomadic movements to longer seasonal migrations (Dietz et al., 2020; Mueller, 2008; Singh et al., 2012; Van Ruiten, 2021).

Humpback whales are possibly the mammal that conduct the longest known seasonal migrations, moving between feeding areas in polar regions during summer/early winter to breeding areas in more tropical regions during late winter/spring (Bengtson Nash et al., 2018; Kettemer et al., in press; Straley et al., 2018). Based on genetic studies suggesting limited inter-oceanic gene flow, we consider the species divided into three main populations: The North Atlantic, North Pacific, and Southern Hemisphere population (Baker et al., 1993; Jackson et al., 2014; Ramm, 2020). Among these, individuals in the northeast Atlantic humpback population are assumed to undertake the longest known migration of about 9000km one way from feeding areas in the northern Barents Sea east of Svalbard to the tropical breeding areas in the Caribbean or Cap Verde (Kettemer et al., in press). Humpback whales can use a variety of feeding techniques to capture a variety of prey, but studies on the North Atlantic population have shown lunge feeding is the primary technique for prey capture (Ochoa Zubiri, 2017; Pedersen, 2020). Lunge feeding is performed by opening the mouth to engulf large quantities of prey and water that is later filtered out through the baleen plates, a feeding strategy demanding dense prey aggregations (Goldbogen et al., 2013; Simon et al., 2012). Humpback diet is variable across different populations and feeding grounds, varying

from zooplankton such as krill (*Euphausiacea*), to small schooling fish like capelin (*Mallotus villotus)* and herring (*Culpea harengus)* (Bouchard et al., 2019; Løviknes et al., 2021)

In the last decade, large masses of Norwegian spring-spawning (NSS-) herring (*Culpea harengus L.)* have moved into some specific fjords around Tromsø (2012-2017) and Skjervøy (2016-2022) in Northern Norway, followed by hundreds of humpbacks and killer whales (*Orcinus orca*) (Jourdain & Vongraven, 2017; Kettemer et al., in press; Ramm, 2020; Rikardsen, 2019; Vogel et al., 2021). These areas are located close to one of the assumed northeast Atlantic humpback whale migration routes, and the whales therefore seem to conduct a stop-over to re-fuel before they later migrate south to the southern breeding grounds in the Caribbean (Ramm, 2020). This appearance of the whales near the coast and populated areas enabled us the unique opportunity to study their detailed behavior (Dietz et al., 2020; Mul et al., 2020; Van Ruiten, 2021; Vogel et al., 2021).

The theory of optimal foraging states that animals will adapt their foraging to utilize resources as efficiently as possible (Stephens & Krebs, 1886; Tyson et al., 2016; Werner & Hall, 1974). This includes strategies to maximize net energy intake and decrease costs simultaneously. What to eat, where to find food patches, and how to allocate themselves relative to the patches are all fundamental to optimal foraging theory, and are building blocks of movement patterns (Pyke et al., 1977). The theory predicts that when prey density in an area decline, a predator will either leave the area or switch to a different prey species (Charnov, 1976), as discussed for killer whales by (Vogel et al., 2021). The marine environment is dynamic and prey is often found distributed in patches, implying that predators must choose which prey patch to exploit and when to leave it (Bouchard et al., 2019). How long a predator chooses to remain within a particular prey-patch depends upon the value (energy density) of the present patch, the value of alternate patches, as well as the time it will take transiting between the patches (Akiyama et al., 2019; Charnov, 1976; Van Ruiten, 2021). Theory predicts that a predator will spend more time in valuable patches further away from other patches, and less time in less valuable patches close to other patches. This is known as the marginal value theorem (Charnov, 1976). Based on satellite tracking data, Van Ruiten (2021) discussed this theorem in relation to killer whale behavior. Her data indicated that some individuals left the fjord areas only to return multiple days or weeks later, but the model she used to analyze her data was not fit to identify and describe in detail these excursions (see below). Rikardsen (2019) also claimed that a similar excursion behavior may be seen for humpback whales in the same area, but this is not scientifically documented. This behavior is intriguing because the whales

leave a fjord where there is seemingly still a lot of herring based on fishery statistics (Fiskeridirektoratet, 2022), which is contrary to what optimal foraging theory and marginal value theory would predict (Charnov, 1976; Pyke et al., 1977). To better understand the extent of this excursion behavior, a method is needed to identify and describe the whales behavior during such events (Van Ruiten, 2021).

Recent advances in electronic tagging techniques that collect biotelemetry data now offer opportunities to investigate animal movements in response to variation in space and time across a range of ecological scales (Abrahms et al., 2020; Block et al., 2011). For humpback whales, large scale movement patterns have been extensively documented over the past decades for some populations (Andrews-Goff et al., 2018; Garrigue et al., 2015; Meynecke et al., 2021; Modest et al., 2021; Øien, 2010). However, movement behavior on smaller scales at the level of individuals and characterization of multiple movement modes that extends travelling versus feeding are not properly studied (Meynecke et al., 2021; Shaw, 2020; Valani et al., 2020). Being able to identify distinct movement modes may represent a first step towards a closer investigation of relations between an animal and their physical or biological environment (Fancy et al., 1988).

New methodical techniques have been developed to segment continuous time series data and identify small-scale behavioral modes of animals (Morelle et al., 2017), allowing us to investigate the complexity of foraging strategies and behavioral patterns on both individual and population level. Recently, several studies have used satellite tracking data to describe the killer whale behavior in the fjords of Northern Norway and along the Norwegian coast. These studies used mainly two (Dietz et al., 2020; Vogel et al., 2021) or three (Mul et al., 2020) discrete behavioral modes to describe the behavior; transiting, area restricted search and fishery attraction, or a continuous behavioral index ranging between two behavioral extremes (Vogel et al., 2021). Van Ruiten (2021) took this a step further and classified killer whale movement into five different discrete behavioral modes, including a behavioral mode termed "round trip". This mode is defined by movements away from initial starting location followed by a complete return to the same location. However, her method was not able to identify such "round trips" if they lasted for several days or more, due to how the parameters she used in her model were toned to detect smaller scale behaviors. Thus, we needed a supplemental approach to identify such longer excursions in this study (visual methods, see section 3.7).

Based on the lack of knowledge mentioned above, the main objective of this study was to try to fit the method used of Van Ruiten (2021) on killer whales to characterize humpback whale movement patterns along the Norwegian coastline, and additionally identify potential longer temporary excursions away from the fjords ("Long roundtrips") that was previously not possible with her method. The sub-goals were to;

i. Segment humpback whale tracks into five different movement modes to investigate their behavioral patterns and individual variability.

ii. Examine the order of movement modes, possible relationships between them, and how this change by season and area.

iii. Identify potential longer excursions (several days) away from and back to the fjord systems and investigate movement modes within these.

Humpback behavior based on movement modes will be discussed in the context of theoretical framework of optimal foraging theory and marginal value theorem.

3   Methodology

3.1   Study area

This study is based on tracking data collected from satellite tagged humpback whales from two fjord areas of Northern Norway (around 69-70 °N): Tromsø and Skjervøy area (Fig 1). The Tromsø fjord area consist of four major fjords or sounds surrounding Kvaløya: Ersfjorden, Sessøyfjorden, Vengsøyfjorden and Kaldfjorden. These fjords are relatively narrow and total length of these areas range from 12-16km and consist of both shallow and deep areas (maximum depth ~270 m) (Norgeskart, 2022; Ramm, 2020; Thorsnæs & Askheim, 2020). Skjervøy fjord area is defined as the outer Kvænangen fjord area which splits into two major inner fjord branches; Reisafjorden (southern area) and the inner parts of Kvænangen (southeast) (Fig.1 and 3). Kvænangen fjord is generally wider and more open (15 km at its widest) than the Tromsø fjords and has a maximum length of 74km from the fjord mouth to the bottom of the Kvænangen branch (Sørstraumen). It generally has steeper sides and less shallow areas than the Tromsø area, and has a maximum depth of 400-450m (Knutsen et al., 2018).

During the last decade, a substantial portion of the NSS-herring population has overwintered in these fjord areas before they migrate to their spawning areas on the continental shelf along the Norwegian coast from Troms to Møre (Vogel et al., 2021). The rest of the population overwinter in the Norwegian Sea, including on the continental shelf of the coast of Northern Norway (Salthaug & Stenevik, 2020). In the fjord areas, the herring overwintering outside Tromsø took place from 2012-2017 and in the Skjervøy area since 2016 until today. These large aggregations of overwintering herring inside the fjords attracts humpback whales, killer whales, and large fishing fleets competing for this common resource. The presence of the whales close to shore in these areas provides a unique opportunity to do research on these species (Mul et al., 2020; Ramm, 2020; Rikardsen, 2019).
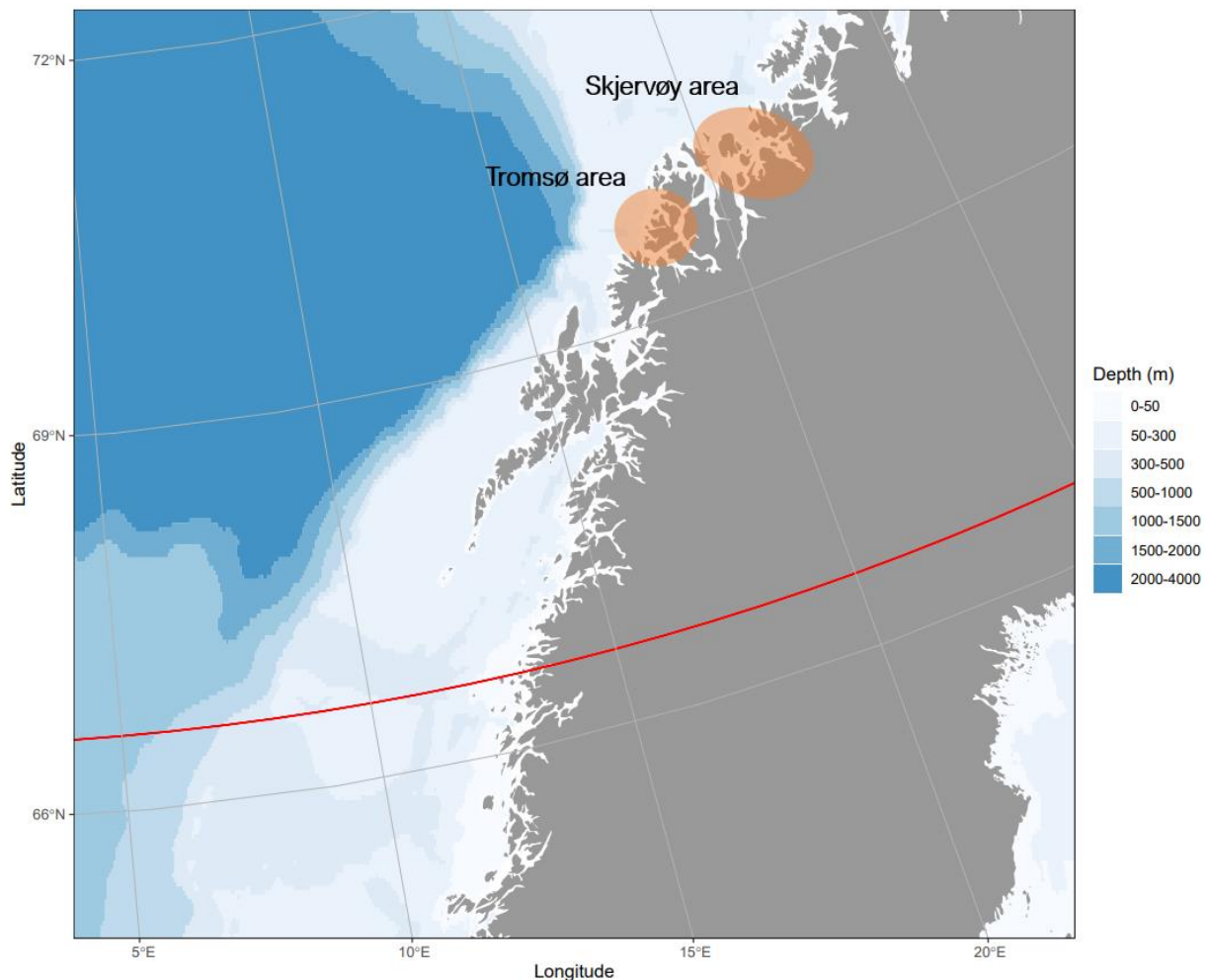
Figure 1: Map of the Northern Norway study area. Fjord-areas where tagging was conducted over a temporal extent of 4 years (2016-2019) are indicated with red circles. Since all whales that passed the Arctic Circle (66°33'N, red line) seemed to had started their breeding migration, the analysis for this study focused on the area north of this latitude.

3.2 Tagging

The tagging was done over a four-year time-period (2016-2019) from December to January in both fjord areas (see Appendix A). Argos Satellite tags (SPOT 320/303, Wildlife Computers, Redmond WA, USA) were deployed using the best practice guidelines for cetacean tagging (Andrews et al., 2019). The tagging was approved by the Norwegian Food Safety Authority (Mattilsynet), under permit FOTS ID 14135, report nr. 2017/279575. We used a 26-ft open RIB (rigid inflatable boat) or a 22ft aluminum boat equipped with a tagging platform in the front and an air-powered rifle (ARTS, www.restech.no) to attach the tags transdermally into the skin and blubber layer where stainless steel anchors kept the tag in place until the tag was shed from the whale (Fig.2). Tag placement will affect the quality and amount of data received by the ARGOS satellites (Mul et al., 2019), as the tag only transmit when exposed to air. Therefore, for tag attachment we aimed for the area just below the dorsal fin which

contain most connective tissue in the blubber and is exposed to air when surfacing (Andrews et al., 2019; A. Rikardsen, personal communication, November 10, 2021). To reduce the risk of infection, darts were disinfected with 70% ethanol both prior and just before deployment.

Tags were programmed to transmit about 16 times per hour for the first three months, then the number of transmissions was reduced to 14-12 transmissions per hour for the following four months, and after that to about 80 transmissions per day until the tag either fell off the whale or the battery died. Photographs were taken for photo-ID purposes to identify the whales. Additionally, biopsies (skin and blubber samples) were opportunistically taken for use in other projects.

Figure 2: Satellite tagging of one of the humpback whales in Kaldfjord (Tromsø area) in 2016. The SPOT 320/303 Argos Satellite tag is attached transdermal (inserted tag shown as a small circle below the dorsal fin) while the tag carrier fell off at the impact (seen on right side of the tag). Photo: Ronald Johansen

3.3 Data collection and Processing

Characterizing smaller scale movement patterns of humpback whales requires consistent series of location data without large gaps. Several tracks in the raw data had multiple extended gaps of between 4-10 hours that made the tracking incomplete, therefore these tracks were removed to avoid any spurious data points when further applying the analysis (see section 3.4). This resulted in 12 out of 20 tracks being used in this study. Also, since our

objectives were to study movement patterns and searching behaviors in two fjord-areas of Northern Norway and along the Norwegian coast, whale tracks south of the Arctic Circle approximately 66°N were cut prior to further analysis. South of the Arctic Circle, whales were considered to have started on their breeding migration, and these data were thus not relevant for this study.

Location estimates from tags were provided by the CLS-ARGOS service and prefiltered using a Kalman filter in a state-space framework. All data processing and statistical analyses were performed using 'R' software (R Core Team, 2021). A Correlated Random Walk (CRW) state-space model was applied to convert irregular time series of Argos position estimates to provide a most likely time regularized path along with their uncertainty estimates. The model assumes that the movement characteristics at a given time is correlated with the movement characteristics of the previous location (Johnson et al., 2008). The CRW was applied using the 'fit_ssm' function in the package 'foieGras'(Jonsen et al., 2020), and in this study the time-step was set to three-hour intervals following practices by Vogel et al., 2020 and Van Ruiten 2021 .

3.4 Behavioral change point analysis

Tracks were divided into distinct segments based on movement characteristics by applying a Behavioral Change Point Analysis (BCPA). The BCPA identifies shifts in movement parameter values by sweeping an analysis window over the time series and identifying the most probable change point within each window (Gurarie et al., 2009; Gurarie et al., 2016). Bayesian Information Criterion (BIC) is used to define the significance of changepoints. Longitude-latitude data were converted to Universal Transverse Mercator (UTM) coordinates before the BCPA analysis was applied using the package 'bcpa' (Gurarie, 2014).

In this study the analysis was customized to set a window size of 40, sensitivity parameter (K) of 3, cluster width of 4, and persistence velocity was chosen as our response variable. Persistence velocity was chosen as it is a continuous variable within [0,1], that combines speed and turning angle into one single index of move persistence. The window size represents the minimum temporal scope where you would expect changepoints. A greater window size will include more data points, and therefore increasing the goodness of fit. A smaller window size will identify finer scale structure in the data, at a cost of increased risk of spurious change points (Gurarie et al., 2009; Van Ruiten, 2021). The sensitivity parameter K is adjusted to compensate for possible spurious change points. As a smaller window size is

more sensitive, the K could be adjusted to a smaller value that decreases the sensitivity of the model, while sensitivity may be increased by increasing K when a larger window size is used. The cluster width refers to the temporal range where successive changepoints are assumed to be within the same cluster (Gurarie, 2014; Morelle et al., 2017). Minor changepoints within a small temporal range can be filtered out by increasing the cluster with (Nicholson et al., 2019; Van Ruiten, 2021). In this study the specific parameter values were customized by trial and error, to optimize the detection of smaller scale homogenous behavioral states, while keeping it robust and avoiding spurious change points.

3.5 Candidate Movement Modes

The five movement modes defined in this study are roundtrip, semi-roundtrip, ranging, nomadic and encamped. Since this is the first time this method is applied to humpback whale telemetry data, the modes chosen are similar to the ones applied in previous studies presented by Bunnefeld et al.(2011) for moose (*Alces alces*), Morelle et al. (2017) for wild boar (*Sus scrofa*), and Van Ruiten (2021) for killer whales (*Orcinus orca*). **Roundtrip** means the whale performs a looping behavior where it leaves a starting location and returns to that location at a later stage. **Semi-roundtrip** means the whale leaves a location and returns to a location close to the initial location. **Ranging** is a rapid directional movement defined by an increase in distance from the starting location preceded by slower movements, describing transiting behavior. **Nomadic** is a wandering movement at slower speeds than ranging, defined by a simple linear model or an increase in distance from the starting location. **Encamped** is a sedentary behavior defined by non-directional movements, suggesting behaviors like resting, foraging or high affinity to a certain area.
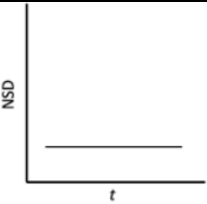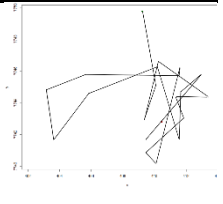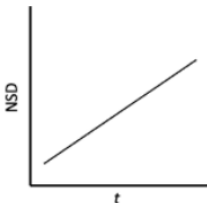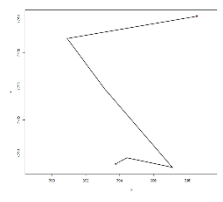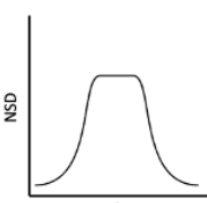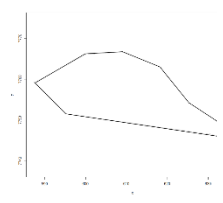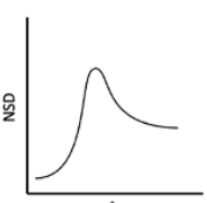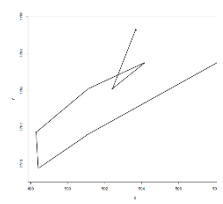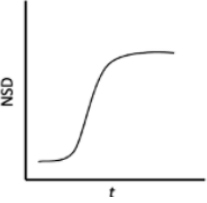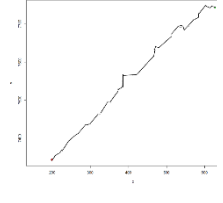
3.6 Classifying Segments

The spatial relationship between net squared displacement (NSD) and time (t) was defined for each movement mode. NSD calculates the squared distances between every GPS location and the initial location of the movement path (Papworth et al., 2012). Distances are squared to cancel directional information, an efficient method to convert movement data from 3D (x,y,z) to 2D (NSD from origin t) allowing further application of simpler statistical models (Morelle et al., 2017) . NSD was calculated for each segment generated by the BCPA, by applying the function 'as.ltraj' from the package 'adehabitatiLT' (Calenge, 2011). As previously described in Bunnefeld et al.(2011), Morelle et al. (2017), and Van Ruiten (2021), mathematical curve equations that best represent each movement mode was selected (Tab 1) . The R package

'FlexParamCurve' (Oswald et al., 2012) and a script supplied by Morelle et al.(2017) and Van Ruiten (2021) (see Appendix C) was used to fit the subsequent mathematical curve equations independently to the NSD data from each segment.

Concordance criterion (CC) was used to evaluate the model fit per segment, for candidate movement modes represented by non-linear equations (Morelle et al., 2017; Singh et al., 2016; Van Ruiten, 2021). The CC measures the degree of accuracy and precision between observed and predicted estimates, and values of CC range from -1 to 1. Values close to 0 represent a lack of fit, larger absolute values represent improved fit, and ± 1 indicates perfect concordance. Each segment is classified as the movement mode with the highest absolute CC value. For the linear equation for constant NSD (NSD=c, tab.1), CC is not applicable, so Akaike Information Criterion (AIC) was used instead. If segments got a CC value above or below a threshold of 0.7, it is considered a poor fit. Poor fitted segments were classified as encamped if the model had the lowest observed AIC. Roundtrips and semi-roundtrips were distinguished by comparing the NSD value at the point of the curve where the y-value changes its sign, to the net change in NSD from start to end of the segment.

Table 1: The five defined movement modes, their corresponding theoretical net squared displacement (NSD) curve, linear or nonlinear mathematical equations and an example of segment path from humpback whale analysis in this study. Parameter descriptions; c constant, t time since departure, a slope, A first curve plateau, A´difference between second and first curve plateaus, k rate of change between initial y value and first plateau, k´ rate of change between first and second plateaus, i inflection point of first curve, i´inflection point of second curve, m shape parameter (changes the inflection point and rate of change) of first curve. See Oswald et al.(2012) for more deetails on equation parameters. See text section 3.5 for description of the different movement modes. Table is adapted with permission from Van Ruiten (2021).

Movement Mode	NSD Curve	Equation	Path example
Encamped		$$NSD = c$$	
Nomadic		$$NSD = a * t$$	
Roundtrip		$$NSD = \frac{A}{1 + m * \exp(-k(t - i))^{\frac{1}{m}}} + \frac{A}{1 + \exp(-k´(t - i´))}$$	
Semi-roundtrip		$$NSD = \frac{A}{1 + m * \exp(-k(t - i))} + \frac{A´}{1 + \exp(-k´(t - i´))}$$	
Ranging		$$NSD = \frac{A}{1 + \exp(-k(t - i))}$$	

3.7 Mapping and visual studies of whale tracks; identifying long roundtrips

The methods described in chapter 3.5 and 3.6 above were not well suited for identifying roundtrips on a larger scale lasting multiple days with various lengths (days-weeks). As the temporal span of the long roundtrips might vary tremendously, first obstacle was finding suitable values for the adjustable parameters in the BCPA by trial for each individual whale. Secondly, the BCPA identifies significant changepoints in movement parameters (speed, turning angle), meaning if the whale changed its behavior remarkably within the in-and-out of fjord excursion, the long roundtrip behavior we aimed for in this study would not be identified. Hence, a more efficient way to investigate long roundtrips were to plot CRW whale tracks of three-hour timesteps on maps to visually observe movement patterns using the R package 'ggOceanMaps' (Vihtakari 2020) and 'leaflet' (Cheng, 2022). The term "complete long roundtrip" in this study is defined as a looping behavior, where a whale leaves a specific fjord area, and later crosses the borderline of the initial fjord area multiple days later. If a whale leaves a specific fjord area, performs a looping behavior offshore lasting multiple days before it returns to another fjord area, this was defined as a "partial long roundtrip». Fjord borders were found in Fjordkatalogen (Miljødirektoratet, 2022) and used to define the fjord areas (Fig.3).

The identification of long roundtrips was combined with the segmentation and classification of movement modes (Chapter 3.4-3.6) to examine which movement modes were performed during the potential offshore excursions.
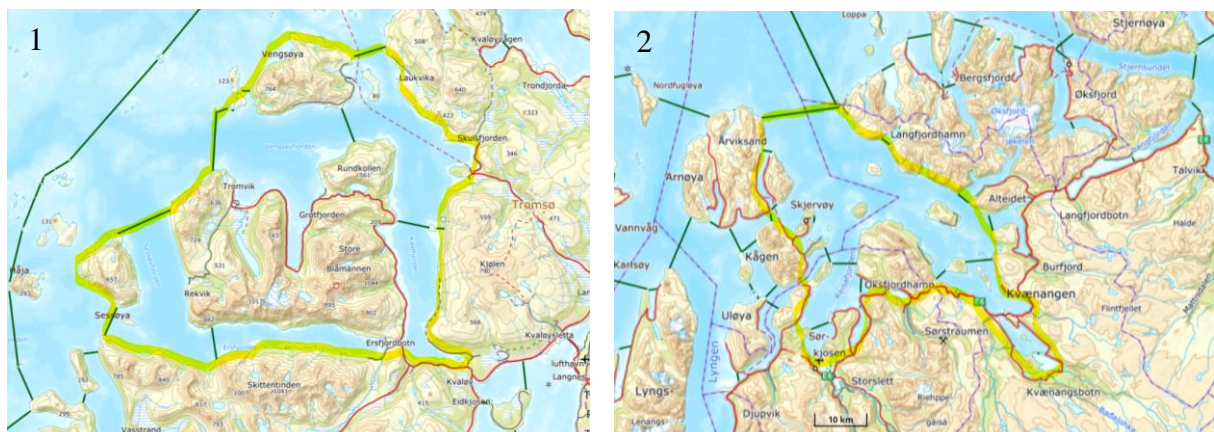
Figure 3: Map of Tromsø area (1) and Skjervøy area (2) with fjord borders taken from Fjordkatalogen highlighted in yellow (Miljødirektoratet, 2022).

4 Results

4.1 Tracking

The main migration pattern of the selected 12 humpback whales showed aggregations in the fjords where they were tagged (Tromsø and Skjervøy area), followed by an extensive use of the Norwegian continental shelf before they migrated southward and passed the Arctic Circle (Fig.4). Out of the 12 tagged individuals included in this study, the average time spent in the area of interest (North-Norwegian coast above the Arctic Circle) from time of tagging until they passed south of this limit was 36 days (8-69). Total extracted positions per individual whale range from 140 to 2357, with an average of 1160 (Tab. 2). Total number of positions per individual after applying the correlated random walk model was on average 275 (63-538) (Tab. 2). Most whales left the fjord areas in January. They travelled south of the Arctic Circle in January or February, with the latest whale crossing this latitude March 19th (Tab.2).

Table 2: Tracking and tagging data of the 12 humpback whales used in this study from time of tagging until they passed the Arctic Circle (AC). Tag deployment dates span from December 13th 2016 to January 8th 2019. Two whales never passed the AC because the tag stopped transmitting, these are marked with (*).

Tagging location	Whale ID	Deployment date	Days before passing AC	Total extracted positions	Number of CRW positions	Leaving fjord areas	Leaving AC
Tromsø	166150	15.01.2017	23	1036	179	16.01.2017	06.02.2017
Tromsø	166149	10.01.2017	69	2357	538	07.2.2017	19.03.2017
Tromsø	166148	22.12.2016	44	1566	270	25.01.2017	03.02.2017
Tromsø	166146	13.12.2016	15	584	119	27.12.2016	*
Tromsø	166145	24.01.2017	12	140	90	31.01.2017	*
Tromsø	166143	05.01.2017	8	212	63	05.01.2017	12.01.2017
Tromsø	166142	04.01.2017	34	1373	266	11.01.2017	06.02.2017
Skjervøy	83287	04.12.2018	57	1797	450	15.01.2019	29.01.2019
Skjervøy	83278	08.01.2019	39	1232	304	29.01.2019	15.02.2019
Skjervøy	83274	03.12.2018	31	936	239	29.12.2019	02.01.2019
Skjervøy	83271	03.12.2018	58	1517	456	09.01.2019	29.01.2019
Skjervøy	47598	19.01.2018	42	1176	331	20.01.2018	01.03.2018
Average:			36	1160	275		
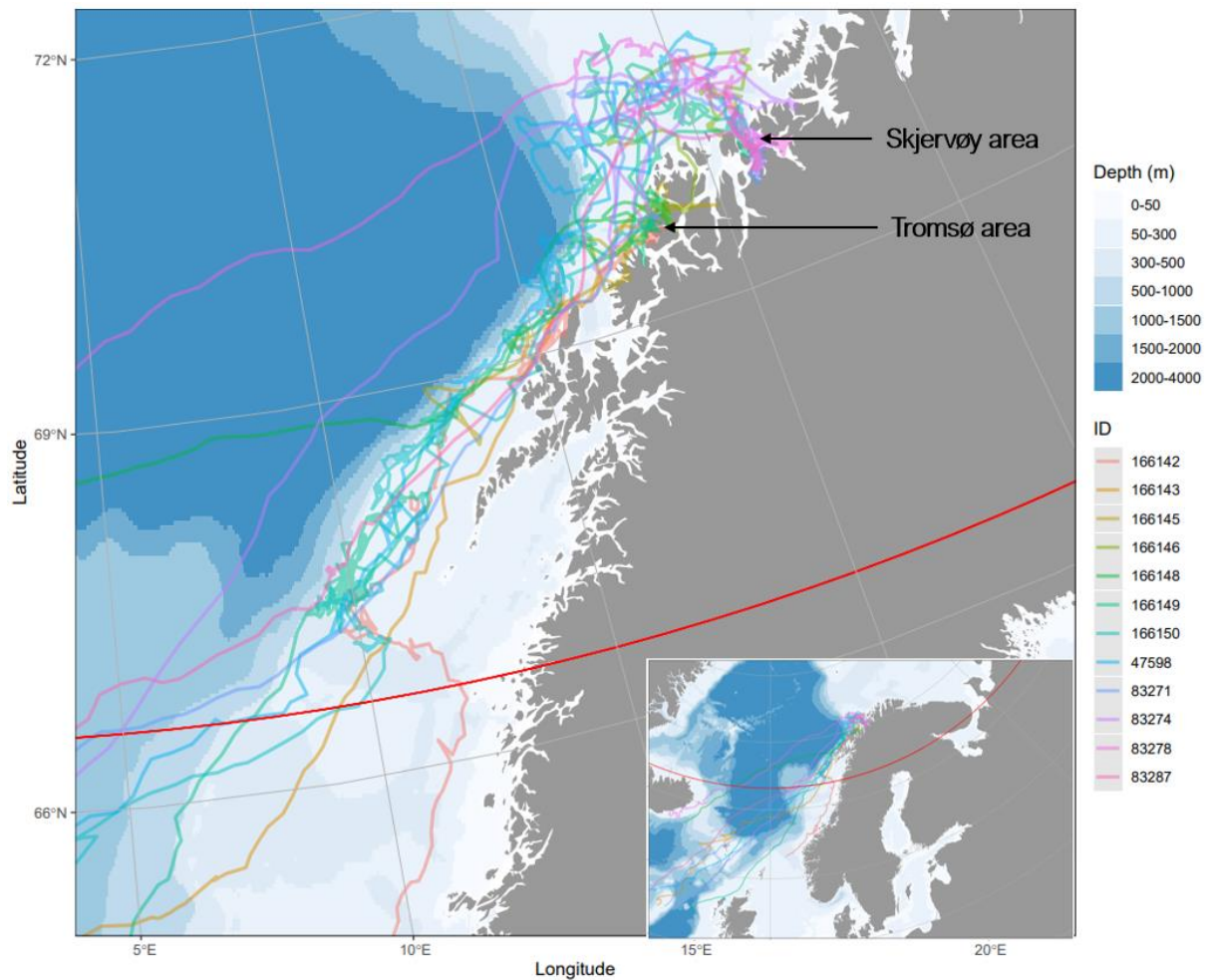
Figure 4: Tracks of the selected 12 satellite tagged humpback whales (2016-2019) along the coast of Northern Norway. The Arctic Circle (66°33'N) represented on this map as a red line, was set as the southern border for the study since the whales then seemingly had started on their southward breeding migration. The small map shows the tracks including the Norwegian Sea. Individual whale tracks are color coded by unique tag ID numbers.

4.2 Segmentation and classification

Out of the identified behavioral movement modes, ranging behavior was the overall most common (Tab.3), making up 54% of all whale tracks. Further, the following most common identified movement modes were nomadic (10%), encamped (9%) and roundtrip (8%) respectively. The least common movement mode was semi-roundtrip (2%). In total, the whale tracks were divided into 290 segments generated through the BCPA analysis. Classification of candidate movement modes succeeded for 243 segments (83,79%), while 47 segments (16,2%) of all whale tracks remained unclassified. Unclassified segments are shorter in both duration and total distance traveled compared to the other modes, meaning undefined segments make up less than 16% of the total length of all whale tracks.

Table 3: Descriptive statistics for each classified movement mode. N is number of segments classified per mode. Duration, total distance traveled, and speed in mean±SD.

Movement mode	N	Duration (h)	Total distance traveled (km)	Speed (km/h)
Roundtrip	22	42,0±18,3	84,7±49,5	3,0±1,5
Semi-roundtrip	6	30,5±10,1	58,2±23,4	2,8±0,8
Ranging	158	30,3±14,5	102,6±93,8	4,7±2,8
Nomadic	31	30,3±12,4	81,2±56,3	4,1±2,6
Encamped	26	46,7±14,8	64,1±28,5	2,1±1,1
Undefined	47	20,87±12,6	46,3±29,7	4,1±3,3
Total	290	33,7±14,0	73,3±47,0	3,6±1,9

4.3 Sequential patterns and seasonal trends

When examining the order of movement modes, ranging behavior was the most common second mode to follow any first mode (Fig.5, Tab.4). Ranging behavior often appeared repeatedly, where a segment classified as ranging was followed by a second segment also classified as ranging, as well as it occurred in between other modes. All whale tracks contain a dominant proportion of ranging behavior distributed throughout the whole track (see Appendix B), with the relative amount in relation to other modes increasing from mid-January towards the spring months after leaving the fjord areas (Fig.5). The opposite trend applies for encamped, nomadic, roundtrip and semi-roundtrips. These behaviors are most prevalent in the beginning of the whale track in December and January when the whales are located within the fjord systems, while the frequency decreases throughout the track. Through February-March after leaving the fjord systems the transition to these movement modes is rare.
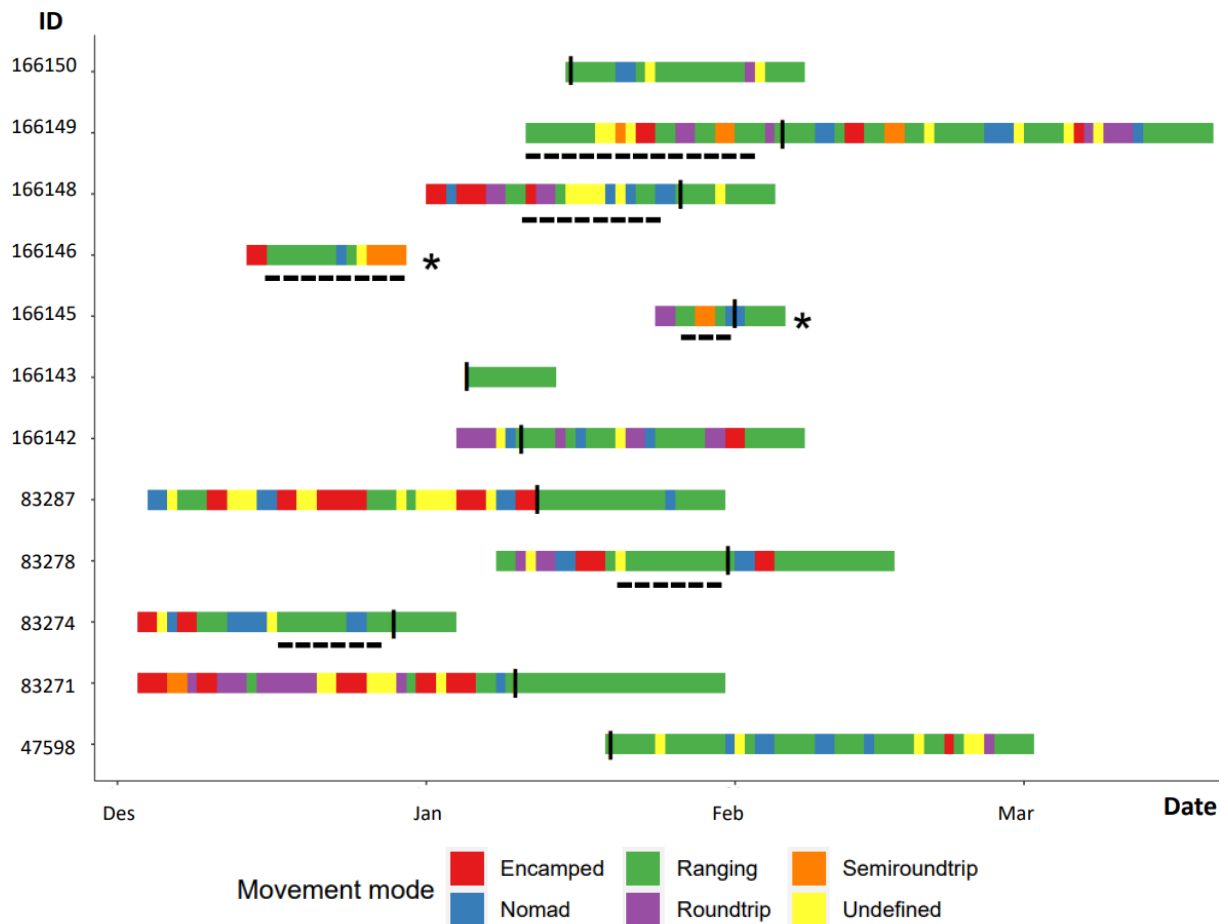
Figure 5: Sequences of movement modes for each individual whale (ID, y-axis) over time (x-axis) during winter and spring across a temporal span of four years (2016-2019) for 12 satellite tagged humpback whales at the Tromsø and Skjervøy fjord areas. Counting from the origin, the bottom five whales (47598-83287) were tagged in Skjervøy area, while the top seven whales (166142-166150) are tagged in Tromsø Area. Whale tracks end where the whales crossed south of the Arctic Circle. Two whales never passed the Arctic Circle, these are marked with (*). Each color represents a movement mode. Black dotted lines represent the long roundtrips out from and back to the fjord areas. Vertical lines indicate when the whale left the fjord areas for the last time before starting on their southward breeding migration.

Table 4: Contingency table with summarized counts of movement mode transitions from 12 satellite tagged humpback whales. The conditional probability of "Second Mode" occurring given the "First Mode" already occurred are represented in percentage in the parentheses.

		Second mode					
		Encamped	Round	Semi-round	Nomad	Ranging	Undefined
First mode	Encamped	3 (11,5)	4 (15,3)	1(3,8)	1 (3,8)	11(42,3)	6(23,0)
	Round	2 (9,1)	2 (9,1)	0	2 (9,1)	9 (40,1)	7 (31,8)
	Semi-round	0	1(12,5)	1(12,5)	0	4(50,0)	2(25,0)
	Nomad	6(17,6)	0	0	4(11,1)	16(47,1)	8(23,5)
	Ranging	6(4,0)	6(4,0)	4(2,7)	17(11,5)	97(65,1)	17(11,5)
	Undefined	7(13,2)	7(13,2)	3(5,5)	7(13,2)	19(35,8)	10(18,8)

4.4 Visually identified long roundtrips

Half of the whales performed some sort of complete or partial long roundtrip away from the fjord systems where they were tagged, lasting for 4-22 days (average ~11 days) (Fig.6). All long roundtrips are conducted in late December or late January. Whale 83278 performed a complete long roundtrip (9 days), leaving Kvænangen fjord Skjervøy area January 20th, going for a trip on the shelf before returning to the initial fjord January 28th. Whale 166148 did a complete long roundtrip (10 days) from Vengsøyfjorden Tromsø area, leaving January 11th and returning January 20th. Whale 166149 was tagged in Sessøyfjorden Tromsø area January 11th, moved north and entered Kvænangen fjord Skjervøy area January 18th, before returning in Tromsø area outside of Vengsøya February 2nd (22 days). Whale 166145 did a complete trip lasting for 4 days differing from the rest of the trips by being conducted outside fjords of Senja instead of Tromsø or Skjervøy area.

Two whales performed partial trips entering both Tromsø and Skjervøy area. Whale 166146 was tagged in Tromsø area, performed a looping behavior offshore before returning a bit further north closer to Skjervøy area 9 days later. Whale 83274 was tagged in Kvænangen Skjervøy area December 18th, entered Tromsø area December 22nd, before returning a bit north of Kvænangen December 27th (10 days).
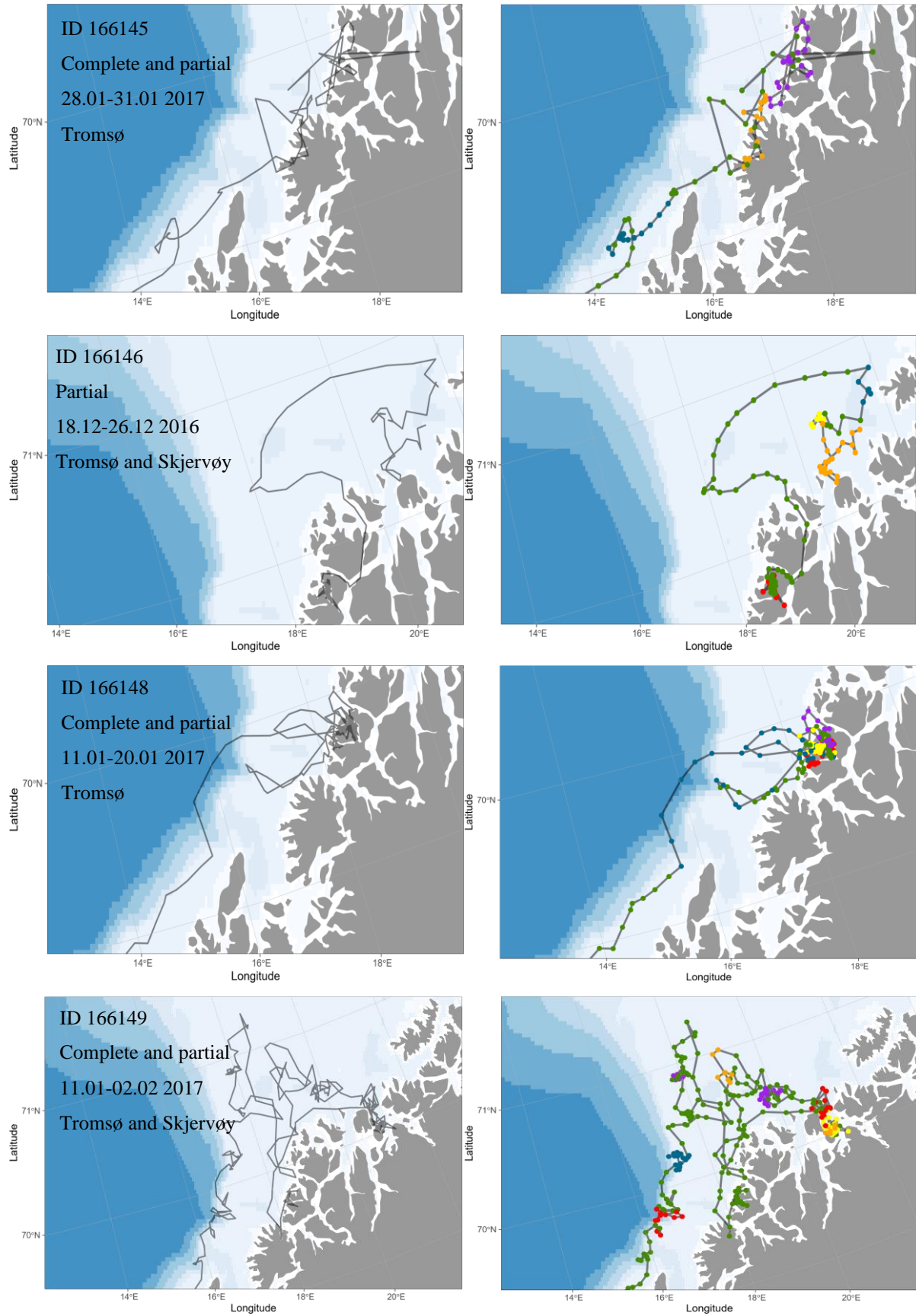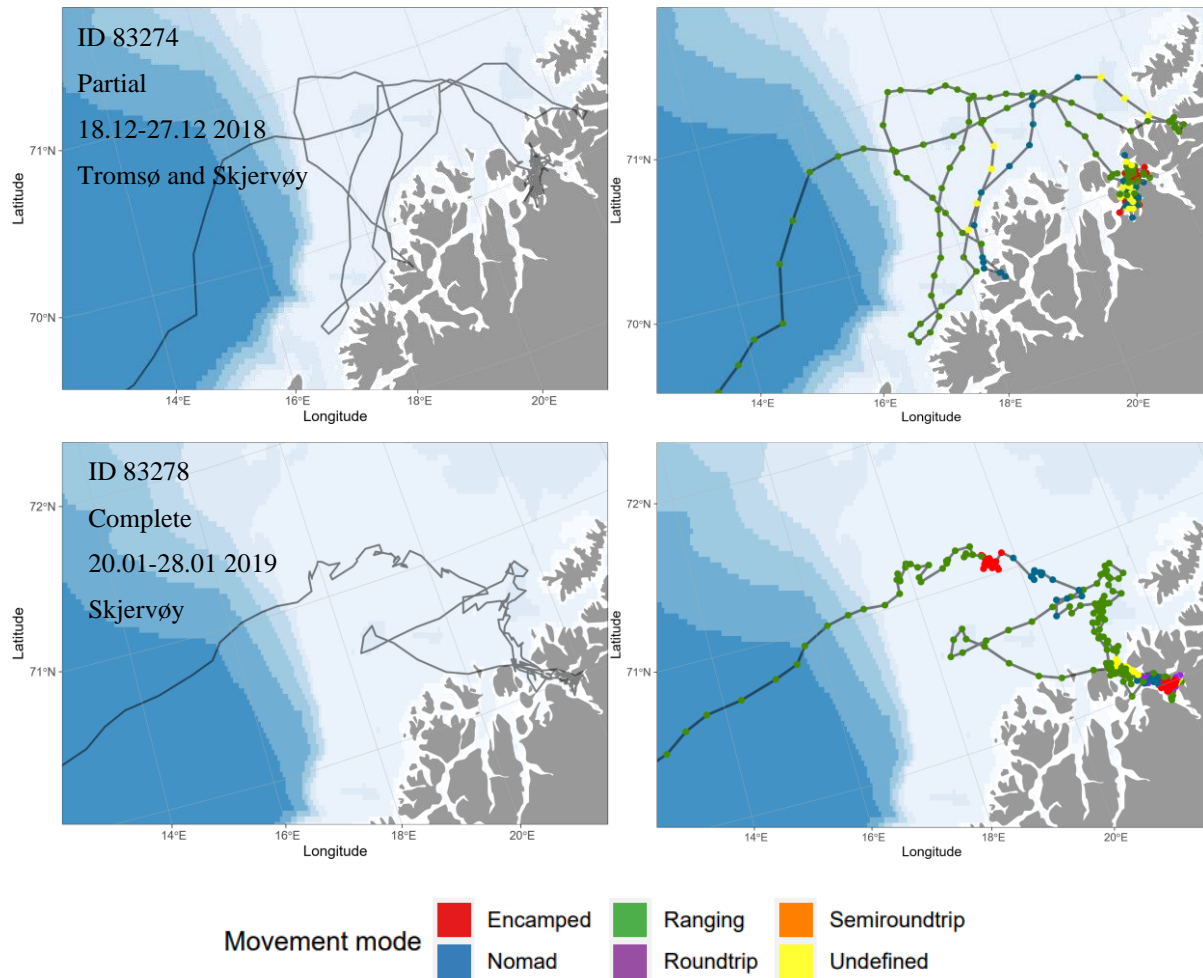
Figure 6: Overview of partial- and complete long roundtrips found in six of the 12 analyzed whales. Individual whales are presented per row. On each row, the maps to the left and right are showing the same whale track, but to the right, tracks are segmented and colored by the corresponding movement mode classified. What type of trip (partial VS complete), dates of the trip, and at what area the trip was conducted (Skjervøy and/or Tromsø area) are presented in the left corner of each map.

4.5 Movement modes within long roundtrips

Within the six documented long roundtrips, 60% of the whale tracks were classified as ranging behavior. Roundtrip, semi-roundtrip and encamped constituted 5%, nomadic 10%, while 15% of the segments within long roundtrips were not classified. Ranging was dominating offshore within the loops. The remaining modes were more frequent inside the fjord systems and sometimes found in shorter sections offshore (166149 and 83278) (Fig.6).

5 Discussion

This is the first study that have classified humpback whale tracking data into five distinct movement modes, and we were able to do this successfully for ~84% of all segments generated through the BCPA. Thus, this may imply that the methods are viable for exploring and describing how individual humpback whales are behaving in a more detailed manner than has previously been described. Previous studies have used mainly two (Dietz et al., 2020; Vogel et al., 2021) or three (Mul et al., 2020) behavioral modes to describe animal behaviors of transiting, area restricted search (localized) and fishery attraction, or a continuous behavioral index ranging between two behavioral extremes (Vogel et al., 2021). Our study identified the additional behaviors of roundtrip, semi-roundtrip, and nomadic behavior, inspired by Van Ruiten (2021) and Morelle et al. (2017). The remaining ~16% of generated segments were not able to classify into one of the chosen movement modes in this study, but unclassified segments are shorter in both duration and total distance traveled compared to those successfully classified. That means undefined behavior make up a good deal less than 16% of the total length of all whale tracks, indicating that the five movement modes applied in this study are fit to describe most of the humpback whales' behavior.

Out of all movement modes, ranging was the most frequently occurring behavior, constituting for more than ½ of all generated segments. Ranging is characterized by straight and faster movement, suggesting a behavior where the animal is simply passing through an area. This is similar to the commonly assessed transiting behavior in former studies (Cerchio et al., 2016; Riekkola et al., 2019). Encamped mode, characterized by slower speed and increased turning rates, represented about 1/10 of all segments. Such movement, also termed area-restricted search, would equate to a forager staying in a prey patch, suggesting behaviors of intensified foraging (Fauchald & Tveraa, 2003; Hays et al., 2016). Most encamped behaviors occurred inside the fjord areas, thus aligning with the principle of resource tracking (Abrahms et al., 2020) as we know these areas had high herring abundance during the same period (Ramm, 2020; Vogel, 2020; Vogel et al., 2021). The relationship between ranging and encamped mode is comparable to the commonly assessed travelling versus feeding behavior in previous studies (Bartoń & Hovestadt, 2013; Cerchio et al., 2016; Riekkola et al., 2019). Empirical studies have implied a gradual transition between ranging and encamped/foraging behaviors, indicating the switchover is not necessarily immediate, and the models with only two modes like travelling vs feeding are too simple (Bartoń & Hovestadt, 2013; Benhamou, 1992). This

study shows that searching behavior among humpback whales can be characterized in a more complex way than travelling versus feeding or ranging versus encamped.

In addition to the two common modes used to describe humpback and other whale species behaviors, we characterized three novel movement modes for humpback whales, including two types of trips (round and semi-roundtrip), and nomadic behavior that constituted totally 1/5 of all generated segments. When it comes to individual variability, nomadic and roundtrip behavior was performed by all whales except one, that left the fjords straight away for migration. As most of the individual whales are spending quite some time in these modes, these behaviors appear to be favored by selection and are expected to be beneficial somehow (Tyson et al., 2016). According to marginal value theory we assume that if prey density in a patch has fallen, the whales should start looking for another prey patch or switch to a substitute prey (Charnov, 1976). Under these conditions, nomadic behavior could likely be associated to actions of search during foraging conducted when prey density in the current patch has declined. The same applies for roundtrip, when during a roundtrip the whales failed to discover a more valuable prey patch and instead return to the initial one. Semi-roundtrip behavior could be the result of a whale relocating and ending up within a new prey patch further away from the initial one, substantiated by predictions of marginal value theory that a predator will spend more time in valuable patches further away from other patches, and less time in less valuable patches close to other patches (Charnov, 1976). Optimal foraging is only one factor influencing the way animals move, they can move for a wide variety of reasons. Competition, predation, and anthropogenic disturbances are just a few other possible reasons an animal might change its behavior and/or relocate. (Hays et al., 2016; Schick et al., 2008). Anyhow, we know marine animals are shown to be strongly influenced by the distribution of prey (Bestley et al., 2015; Vogel et al., 2021), and according to the concept of resource tracking (Abrahams et al., 2020), we can assume that regardless of what caused the relocation, where they stopped for their next location was most likely related to the discovery of a valuable food patch.

The overall order and patterns of movement modes change by season. Collectively, all whale tracks show an increased relative amount of ranging behavior towards spring (February-March). This is when the density of NSS herring inside the fjords decrease and the whales begin to leave the fjord areas (Vogel et al., 2021). It is also the time when humpback whales usually initiate their breeding migration (Kettemer et al., in press; Modest et al., 2021;

Rikardsen, 2019), so the increased dominance of ranging behavior towards this period could be explained by these two factors. Within the fjord areas earlier in the season, the modes encamped, nomadic, round, and semi-roundtrips were more prevalent, suggesting that these modes are likely to be associated with foraging on overwintering NSS-herring. We also found a main pattern in how the modes were sequenced, showing that all modes are most likely to be followed by ranging behavior. This was consistent with ranging being the most common overall movement mode. Other than this, there was no clear pattern in the order of movement modes, indicating there is no relationship between them to possibly predict which modes are most likely to follow each other.

The modes considered in this study were similar to those used by Van Ruiten (2021) on satellite data from killer whales in the same area, making it possible to compare the movement across the two separate species. For the killer whales they found a high degree of individual variation and no clear patterns in the sequence analysis of movement modes. Killer whales and humpback whales have different foraging tactics and different life strategies (Jourdain & Vongraven, 2017; Mastick et al., 2022; Vogel et al., 2021). Contrasting the more unpredictable switches in movement modes found in the killer whales, humpback whales, being highly migratory animals, may have been expected to have more predictable changes in their movement patterns as a function of seasonality. That was confirmed in our study. Despite the differences on overall patterns, looking at movement modes by area, both species show similar trends with roundtrips, semi-roundtrips and encamped/resident behavior dominating in the fjord areas, while ranging/transiting and nomadic is more associated with the offshore habitats. These trends are consistent with predictions based on both marginal value and optimal foraging theory (Charnov, 1976; Stephens & Krebs, 1886). As mentioned before, encamped behavior is similar to area restricted search, illustrated by reduced speeds and increased turning rates, suggesting intensified foraging. Switching between prey patches could possibly be described by round and semi-roundtrips. The fact that both killer whales and humpback whales show these behaviors in areas of assumingly high prey density strengthens the suggestion that these movement modes represent strategies of optimal foraging.

We did not find any clear difference in movement patterns of the humpback whales between the two fjord areas (Tromsø and Skjervøy) of interest, implying that any difference in these fjord characteristics were not a major factor influencing movement mode selection of

humpback whales. Instead, seasonality, and presumably prey distribution as discussed above had a stronger influence on movement modes.

This study is also the first to describe long excursions away from and back to a feeding area with assumed high prey density. Based on optimal foraging theory, we would expect the whales to stay in the fjord areas with high herring density, feeding continuously until the continuation of their migration. However, results in this study found that half of the whales left the fjords to go on multiday offshore excursions lasting from a few days up to three weeks and then later returned within the same season. According to theory, the humpback whales should spend most of their time in areas with high prey density and decrease the time spent transiting between foraging areas (Bella-Fernández et al., 2021; Charnov, 1976). One possible explanation for why they still leave may be that surplus energy gained from the fjord areas makes it possible to conduct these excursions to search for even richer prey patches (Bonte et al., 2012), as we know some of the herring aggregate and overwinters on the continental shelves off the coast -instead of in the fjords (Vogel et al., 2021).

The excursion phenomenon is similar to the roundtrip and semi-roundtrips defined as movement modes, except this is on a larger scale, both spatially and temporally, therefore termed "long roundtrip" in this study. As discussed previously in the context of marginal value theory for round- and semi-roundtrip (movement modes), we hypothesize "long roundtrip" behavior could be associated to actions of search when prey density in the fjords decline. Interestingly, even if the whales are tagged during separate years, these excursions all take place at seemingly similar times, in late December or late January. Usually some of the herring starts to slowly move out of the fjords from mid-December and throughout January (A. Rikardsen, personal communication, March 25, 2022). After feeding in an area for a while, the whales may have noticed that parts of the herring started to slowly pull out of the fjords at that time, and therefore decided to "check" the area outside of the fjords for better opportunities. Additionally, the fact that the time of departure for the humpback whale breeding migration is approaching could possibly make the whales become more restless in this period (Kettemer et al., in press; Modest et al.,2021). According to the classical optimal foraging theory (Charnov 1976), animals should ideally have full information about their environment to take optimal decisions about where and when to search for resources. However, foragers cannot always possess ultimate information about their environment; they must be in a certain distance to their prey to detect it (Bartoń & Hovestadt, 2013). So, if the whales did not find better opportunities in the offshore habitat, they simply returned based on

memory because they know the original foraging ground was better, resulting in the long roundtrip behavior, possibly then better defined as a searching trip.

Examining what modes make up these longer excursions further support the theory that this is a searching trip. In fact, 60% of the long roundtrips were classified as ranging behavior, suggesting that the whales spent most of their time on the shelf searching through a larger area deprived of finding valuable food patches that was worth stopping for. It appears whales move mainly by ranging until possibly encountering something to change their behavior, that leads them to switch movement mode. Encamped, nomadic, round, and semi-round trips are mostly found inside the fjord areas, but in some cases also documented offshore on the shelfs in shorter sections. Performing ranging behavior for a while before suddenly switching to encamped mode could suggest the whale ran into a prey patch. That is perhaps what was happening during a partial long roundtrip; probably they eventually found an area with more herring, and thus did not return to the same starting point. In a future study it would be interesting to combine data on prey abundance (if available) with the humpback whales to confirm or reject this hypothesis, something similar to what Vogel et al. (2021) did using two movement modes of killer whale behavior in relation to herring density. Adding more movement modes could then possibly describe more of the behavior and the relationship with prey abundance over a large area. Anyhow, the switch to other modes than ranging on the shelfs could also partly be related to other events than foraging, e.g. resting or socializing, as humpback whales are known to perform social behavior and surface activities in the form peduncle throws and tail slapping, and then be more stationary during this period (Meynecke & Liebsch, 2021). However, based on the fact that herring is also known to overwinter on the continental shelf (Salthaug & Stenevik, 2020), and that the whales should be more likely to socialize within the fjord areas where there are possibly higher densities of whales, we believe that this long roundtrip behavior is related to searching for food before they initiate their southward breeding migration.

Some humpback whales might also be attracted to fishing vessels, like Mul et al., (2020) described for killer whales. In general, humpback whales seem to be less attracted to fishing boats than killer whales, although some individuals appear to specialize in events of fishing boats and killer whales engaged (A. Rikardsen, personal communication, January 12, 2022). We know fisheries and marine mammals target the same resources, but in general, the extent to which anthropogenic activities determine animal behavior is largely unknown (Hays et al.,

2016). Late December when some of these long roundtrips occurred, overlaps with when fisheries operating in the fjords of Tromsø and Skjervøy stop fishing due to Christmas holidays (Fiskeridirektoratet, 2022; Norges Sildesalgslag, 2022). That may indicate the whales exploit the aggregations of fishing vessels and killer whales when foraging on NSS herring inside the fjords, but when the aggregations dissolve due to the holidays, they permit themselves to search on larger areas for prey hotspots. There is not enough data to reject or conclude this hypothesis. An approach for further investigation could be visual studies observing whale behavior closely around fishing vessels in addition to more tagged individuals. More tagged individuals would always strengthen a scientific argument, but considering ethical aspects, one should note there is a rational question how many individuals to tag to get enough data and at the same time avoiding unnecessary disturbance (Andrews et al., 2019; Mul et al., 2019). We do not have enormous amounts of whales in this study (12), but presumably enough to be representative of the population. The fact that we are reusing data already collected over a four-year time-period to explore it even more is also a huge positive. Nevertheless, the fact that some of these long roundtrips occurred during the time of fishery holidays seems notable and might be worth further exploration in future studies.

This study aimed to characterize smaller scale movement patterns and searching behavior of humpback whales at the North-Norwegian coast, however it should be considered that the methods used are restricted to some degree by a few factors limiting what scale of movement we were able to identify. The BCPA comes with three adjustable parameters; the window size, sensitivity parameter K and the cluster width, which all affects the results and sensitivity of analysis. There is no automatic way to know the optimal value of these for our data specifically, so this was decided by testing values that balanced the minimum temporal scope within expected change points against desired power (Gurarie et al., 2009; Van Ruiten, 2021) to aim for the scales of interest. The analysis was applied to data with 3-hour timesteps, excluding all behavioral change points within a temporal span smaller than 3 hours. Whales dive, and satellite tags only receive signals during the small fraction of time when the animals are close to surface, resulting in unpredictable time intervals per signal and restricted quality compared to tracking data from terrestrial animals (Bunnefeld et al., 2011; Morelle et al., 2017). This could prospectively explain some of the undefined segments in our results, or maybe humpback whale behavior simply does not always fit perfectly into the exact modes chosen in this study. If aimed to detect even more fine-scale humpback whale behavior targeting specific feeding events at hourly time scales or less, this would demand a different

tag, like for instance the CATS Cam, a multi-sensor wildlife recorder with higher temporal resolution, HD video, and hydrophone (Ratsimbazafindranahaka et al., 2022). The downside of these tags is they have a lower recording time (often just a couple of hours), so they would for instance not be able to identify the long roundtrips or movement modes in relation to seasons. Nonetheless, our results were able to describe multiple movement modes at small-intermediate scales and individual variation in behavioral patterns during the stop-over period in the North-Norwegian fjords and thus fill in some knowledge gaps about humpback whale behavior.

Despite some limitations, we conclude that characterizing distinct multiple movement modes like we did in this study is a promising approach for future studies to achieve a more detailed examination of movement behavior of satellite tagged whales. Similar to what Van Ruiten (2021) confirmed for killer whales, we here confirm that this method is also applicable for humpback whales, and thus possibly other whale species. Our tagged humpback whales showed complex strategies on varied spatiotemporal forms during their re-fueling stop-over in Northern Norway, before they continued their migration to southern breeding grounds. One of these strategies was longer excursions away from and back to the fjord areas, where the whales seemingly search for better feeding opportunities outside the fjord systems, and if that is not found, they return to the fjords to continue their feeding. These excursions were defined visually as the current model (BCPA+NSD) was not suitable to identify them, but using the model to characterize movement modes within these trips was successful and supported the assumption that these excursions were most likely related to searching for prey. To better verify the results found and discussed in this study, one could include vertical movement of the whales and prey distributions. Finally, mapping multiple movement modes may give a better understanding of how the whales are spending their time, with potential for also identifying prey hotspots or critical areas for the whales. Such information serves an important role notifying policy makers about areas of protection as well as areas where whale and anthropogenic activity might influence each other. This study may serve as a baseline for future studies investigating the unique long roundtrip behavior further, as well as humpback behavior in general within various environments.

Reference List

Abrahms, B., Aikens, E. O., Armstrong, J. B., Deacy, W. W., Kauffman, M. J., & Merkle, J. A. (2020). Emerging perspectives on resource tracking and animal movement ecology. *Trends in Ecology & Evolution*, *36*(4), 308-320.

Akiyama, Y., Akamatsu, T., Rasmussen, M. H., Iversen, M. R., Iwata, T., Goto, Y., Aoki, K., & Sato, K. (2019). Leave or stay? Video-logger revealed foraging efficiency of humpback whales under temporal change in prey density. *PloS one, 14*(2), e0211138.

Andrews-Goff, V., Bestley, S., Gales, N., Laverick, S., Paton, D., Polanowski, A., Schmitt, N., & Double, M. (2018). Humpback whale migrations to Antarctic summer foraging grounds through the southwest Pacific Ocean. *Scientific Reports, 8*(1), 1-14.

Andrews, R. D., Baird, R. W., Calambokidis, J., Goertz, C. E. C., Gulland, F. M. D., Heide-Jorgensen, M. P., Hooker, S. K., Johnson, M., Mate, B., Mitani, Y., Nowacek, D. P., Owen, K., Quakenbush, L. T., Raverty, S., Robbins, J., Schorr, G. S., Shpak, O. V., Townsend Jr, F. I., Uhart, M., Wells, R. S., & Zerbini, A. N. (2019). Best practice guidelines for cetacean tagging. *The journal of cetacean research and management, 20*(1), 27-66. https://doi.org/10.47536/jcrm.v20i1.237

Baker, C., Perry, A., Bannister, J., Weinrich, M., Abernethy, R. B., Calambokidis, J., Lien, J., Lambertsen, R., Ramirez, J. U., & Vasquez, O. (1993). Abundant mitochondrial DNA variation and world-wide population structure in humpback whales. *Proceedings of the National Academy of Sciences, 90*(17), 8239-8243.

Bartoń, K. A., & Hovestadt, T. (2013). Prey density, value, and spatial distribution affect the efficiency of area-concentrated search. *Journal of theoretical biology, 316*, 61-69.

Bella-Fernández, M., Suero Suñé, M., & Gil-Gómez de Liaño, B. (2021). Foraging behavior in visual search: A review of theoretical and mathematical models in humans and animals. *Psychological research*, 86, 331-349.

Bengtson Nash, S. M., Castrillon, J., Eisenmann, P., Fry, B., Shuker, J. D., Cropp, R. A., Dawson, A., Bignert, A., Bohlin-Nizzetto, P., & Waugh, C. A. (2018). Signals from the south; humpback whales carry messages of Antarctic sea-ice ecosystem variability. *Global Change Biology, 24*(4), 1500-1510.

Benhamou, S. (1992). Efficiency of area-concentrated searching behaviour in a continuous patchy environment. *Journal of theoretical biology, 159*(1), 67-81.

Bestley, S., Jonsen, I. D., Hindell, M. A., Harcourt, R. G., & Gales, N. J. (2015). Taking animal tracking to new depths: synthesizing horizontal–vertical movement relationships for four marine predators. *Ecology, 96*(2), 417-427.

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., Hazen, E. L., Foley, D. G., Breed, G., & Harrison, A.-L. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature, 475*(7354), 86-90.

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., & Saastamoinen, M. (2012). Costs of dispersal. *Biological reviews, 87*(2), 290-312.

Bouchard, B., Barnagaud, J.-Y., Poupard, M., Glotin, H., Gauffier, P., Torres Ortiz, S., Lisney, T. J., Campagna, S., Rasmussen, M., & Célérier, A. (2019). Behavioural responses of humpback whales to food-related chemical stimuli. *PloS one, 14*(2), e0212515.

Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C. M., Dettki, H., Solberg, E. J., & Ericsson, G. (2011). A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology, 80*(2), 466-476.

Calenge, C. (2011). Analysis of animal movements in R: the adehabitatLT package. *R Foundation for Statistical Computing*, *Vienna.*

Cerchio, S., Trudelle, L., Zerbini, A. N., Charrassin, J.-B., Geyer, Y., Mayer, F. X., Andrianarivelo, N., Jung, J.-L., Adam, O., & Rosenbaum, H. C. (2016). Satellite telemetry of humpback whales off Madagascar reveals insights on breeding behavior and long-range movements within the southwest Indian Ocean. *Marine Ecology Progress Series, 562*, 193-209.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical population biology, 9*(2), 129-136.

Cheng, J., Karambelkar, B., & Xie, Y. (2022). leaflet: Create Interactive Web Maps with the JavaScript 'Leaflet' Library. R package version 2.1.1. https://CRAN.R-project.org/package=leaflet

Dietz, R., Rikardsen, A. H., Biuw, M., Kleivane, L., Noer, C. L., Stalder, D., van Beest, F. M., Rigét, F. F., Sonne, C., & Hansen, M. (2020). Migratory and diurnal activity of North Atlantic killer whales (*Orcinus orca*) off northern Norway. *Journal of Experimental Marine Biology and Ecology, 533*, 151456.

Fancy, S. G., Pank, L. F., Douglas, D. C., Curby, C. H., & Garner, G. W. (1988). Satellite telemetry: a new tool for wildlife research and management. Fish and Wildlife Service Washington DC.

Fauchald, P., & Tveraa, T. (2003). Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology, 84*(2), 282-288.

Fiskeridirektoratet. (2022). *Fangst fordelt på måned.* https://www.fiskeridir.no/Yrkesfiske/Tall-og-analyse/Fangst-og-kvoter/Fangst/Fangst-fordelt-paa-maaned

Garrigue, C., Clapham, P. J., Geyer, Y., Kennedy, A. S., & Zerbini, A. N. (2015). Satellite tracking reveals novel migratory patterns and the importance of seamounts for endangered South Pacific humpback whales. *Royal Society open science, 2*(11), 150489.

Goldbogen, J. A., Friedlaender, A. S., Calambokidis, J., McKenna, M. F., Simon, M., & Nowacek, D. P. (2013). Integrative approaches to the study of baleen whale diving behavior, feeding performance, and foraging ecology. *BioScience, 63*(2), 90-100.

Gurarie, E., Andrews, R. D., & Laidre, K. L. (2009). A novel method for identifying behavioural changes in animal movement data. *Ecology letters, 12*(5), 395-408.

Gurarie, E., Bracis, C., Delgado, M., Meckley, T. D., Kojola, I., & Wagner, C. M. (2016). What is the animal doing? Tools for exploring behavioural structure in animal movements. *Journal of Animal Ecology, 85*(1), 69-84.

Hays, G. C., Ferreira, L. C., Sequeira, A. M., Meekan, M. G., Duarte, C. M., Bailey, H., Bailleul, F., Bowen, W. D., Caley, M. J., Costa, D. P., Eguíluz, V.M, Fossette, S., Friedlaender, A.S., Gales, N., Gleiss, A. C., Gunn, J., Page 30 of 39 Harcourt, R., Hazen, E.L., Heithaus, M. R., Heupel, M.,…Thums, M. (2016). Key questions in marine megafauna movement ecology. *Trends in Ecology & Evolution, 31*(6), 463-475.

Jackson, J. A., Steel, D. J., Beerli, P., Congdon, B. C., Olavarría, C., Leslie, M. S., Pomilla, C., Rosenbaum, H., & Baker, C. S. (2014). Global diversity and oceanic divergence of humpback whales (*Megaptera novaeangliae*). *Proceedings of the Royal Society B: Biological Sciences, 281*(1786), 20133222.

Johnson, D. S., London, J. M., Lea, M.-A., & Durban, J. W. (2008). Continuous-time correlated random walk model for animal telemetry data. *Ecology, 89*(5), 1208-1215.

Jonsen, I. D., Patterson, T. A., Costa, D. P., Doherty, P. D., Godley, B. J., Grecian, W. J., Guinet, C., Hoenner, X., Kienle, S. S., & Robinson, P. W. (2020). A continuous-time state-space model for rapid quality control of argos locations from animal-borne tags. *Movement ecology, 8*(1), 1-13.

Jourdain, E., & Vongraven, D. (2017). Humpback whale (*Megaptera novaeangliae*) and killer whale (*Orcinus orca*) feeding aggregations for foraging on herring (*Clupea harengus*) in Northern Norway. *Mammalian Biology, 86*(1), 27-32.

Joy, R., Dowd, M. G., Battaile, B. C., Lestenkof, P. M., Sterling, J. T., Trites, A. W., & Routledge, R. D. (2015). Linking northern fur seal dive behavior to environmental variables in the eastern Bering Sea. *Ecosphere, 6*(5), 1-22.

Kettemer, L.E., Rikardsen, A.H., Biuw, M., Broms, F., Mul, E., & Blanchet, M.-A. (in press). Round-trip migration and energy budget of a breeding female humpback whale in the Northeast Atlantic. *PloSOne.*

Knutsen, T., Hosia, A., Falkenhaug, T., Skern-Mauritzen, R., Wiebe, P. H., Larsen, R. B., Aglen, A., & Berg, E. (2018). Coincident mass occurrence of gelatinous zooplankton in northern Norway. *Frontiers in Marine Science, 5*, 158.

Løviknes, S., Jensen, K. H., Krafft, B. A., Anthonypillai, V., & Nøttestad, L. (2021). Feeding Hotspots and Distribution of Fin and Humpback Whales in the Norwegian Sea From 2013 to 2018. *Frontiers in Marine Science, 8*, 6.

Mastick, N. C., Wiley, D., Cade, D. E., Ware, C., Parks, S. E., & Friedlaender, A. S. (2022). The effect of group size on individual behavior of bubble-net feeding humpback whales in the southern Gulf of Maine. *Marine Mammal Science*.

Meynecke, J.-O., De Bie, J., Menzel Barraqueta, J.-L., Seyboth, E., Prakash Dey, S., Lee, S., Samanta, S., Vichi, M., Findlay, K., Roychoudhury, A., & Mackey,B. (2021). The role of environmental drivers in humpback whale distribution, movement and behaviour: a review. *Frontiers in Marine Science*, 1685.

Meynecke, J.-O., & Liebsch, N. (2021). Asset Tracking Whales—First Deployment of a Custom-Made GPS/GSM Suction Cup Tag on Migrating Humpback Whales. *Journal of Marine Science and Engineering, 9*(6), 597.

Miljødirektoratet. (2022). *Fjordkatalogen.* https://kartkatalog.miljodirektoratet.no/MapService/Details/fjordkatalogen

Modest, M., Irvine, L., Andrews-Goff, V., Gough, W., Johnston, D., Nowacek, D., Pallin, L., Read, A., Moore, R. T., & Friedlaender, A. (2021). First description of migratory behavior of humpback whales from an Antarctic feeding ground to a tropical calving ground. *Animal Biotelemetry, 9*(1), 1-16.

Morelle, K., Bunnefeld, N., Lejeune, P., & Oswald, S. A. (2017). From animal tracks to fine-scale movement modes: a straightforward approach for identifying multiple spatial movement patterns. *Methods in Ecology and Evolution, 8*(11), 1488-1498.

Mueller, T. (2008). *Animal distributions and movement behaviors in relation to resource dynamics*. [Doctoral dissertation, University of Maryland, College Park].

Mul, E., Blanchet, M.-A., Biuw, M., & Rikardsen, A. (2019). Implications of tag positioning and performance on the analysis of cetacean movement. *Animal Biotelemetry, 7*(1), 11

Mul, E., Blanchet, M.-A., McClintock, B. T., Grecian, W. J., Biuw, M., & Rikardsen, A. (2020). Killer whales are attracted to herring fishing vessels. *Marine Ecology Progress Series, 652*, 1-13.

Nicholson, K. L., Warren, M. J., Rostan, C., Månsson, J., Paragi, T. F., & Sand, H. (2019). Using fine-scale movement patterns to infer ungulate parturition. *Ecological indicators, 101*, 22-30.

Norgeskart. (2022). *Vengsøyfjorden.* https://www.norgeskart.no/#!?project=seeiendom&layers=1008,1015&zoom=11&lat=7748620.14&lon=634334.00&markerLat=7748620.1355836755&markerLon=634333.9978310559&panel=searchOptionsPanel&sok=Vengs%C3%B8yfjorden&p=searchOptionsPanel

Norges Sildesalgslag (2022). *Innmeldingsjournal.*
https://www.sildelaget.no/no/kvoter-og-fangst/fangst/innmeldingsjournal/

Nowacek, D. P., Christiansen, F., Bejder, L., Goldbogen, J. A., & Friedlaender, A. S. (2016). Studying cetacean behaviour: new technological approaches and conservation applications. *Animal Behaviour, 120*, 235-244.

Ochoa Zubiri, K. (2017). *Diving behaviour of humpback whales feeding on overwintering herring in North-Norwegian fjords* [Master's thesis, UiT Norges arktiske universitet]. Munin.

Oswald, S. A., Nisbet, I. C., Chiaradia, A., & Arnold, J. M. (2012). FlexParamCurve: R package for flexible fitting of nonlinear parametric curves. *Methods in Ecology and Evolution, 3*(6), 1073-1077.

Papworth, S. K., Bunnefeld, N., Slocombe, K., & Milner-Gulland, E. (2012). Movement ecology of human resource users: using net squared displacement, biased random bridges and resource utilization functions to quantify hunter and gatherer behaviour. *Methods in Ecology and Evolution, 3*(3), 584-594.

Pedersen, M. A. (2020). *Foraging behaviour of humpback whales (Megaptera novaeangliae): Automatic detection of feeding lunges from two-dimensional data* [Master's thesis, UiT Norges arktiske universitet]. Munin.

Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal foraging: a selective review of theory and tests. *The quarterly review of biology, 52*(2), 137-154.

Tyson, R. B., Friedlaender, A. S., & Nowacek, D. P. (2016). Does optimal foraging theory predict the foraging performance of a large air-breathing marine predator?. *Animal Behaviour*, *116*, 223-235.

Ramm, T. (2020). *Hungry during migration? Humpback whale movement from the Barents Sea to a feeding stopover in northern Norway revealed by photo-ID analysis* [Master's thesis, UiT Norges arktiske universitet]. Munin.

Ratsimbazafindranahaka, M. N., Huetz, C., Andrianarimisa, A., Reidenberg, J. S., Saloma, A., Adam, O., & Charrier, I. (2022). Characterizing the suckling behavior by video and 3D-accelerometry in humpback whale calves on a breeding ground. *PeerJ, 10*, e12945.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Riekkola, L., Andrews-Goff, V., Friedlaender, A., Constantine, R., & Zerbini, A. N. (2019). Environmental drivers of humpback whale foraging behavior in the remote Southern Ocean. *Journal of experimental marine biology and ecology, 517*, 1-12.

Rikardsen, A. (2019). *Vinterkval*. To-Foto AS.

Salthaug, A., & Stenevik, K. (2020, November 6). *Kommer silda inn i fjordene i Nord-Norge i vinter?*. Havforskningsinstituttet. https://www.hi.no/hi/nyheter/2020/november/kommer-silda-inn-i-fjordene-i-nord-norge-i-vinter

Schick, R. S., Loarie, S. R., Colchero, F., Best, B. D., Boustany, A., Conde, D. A., Halpin, P. N., Joppa, L. N., McClellan, C. M., & Clark, J. S. (2008). Understanding movement data and movement processes: current and emerging directions. *Ecology letters, 11*(12), 1338-1350.

Shaw, A. K. (2020). Causes and consequences of individual variation in animal movement. *Movement ecology, 8*(1), 1-12.

Simon, M., Johnson, M., & Madsen, P. T. (2012). Keeping momentum with a mouthful of water: behavior and kinematics of humpback whale lunge feeding. *Journal of Experimental Biology, 215*(21), 3786-3798.

Singh, N. J., Allen, A. M., & Ericsson, G. (2016). Quantifying migration behaviour using net squared displacement approach: clarifications and caveats. *PloS one, 11*(3), e0149594.

Singh, N. J., Börger, L., Dettki, H., Bunnefeld, N., & Ericsson, G. (2012). From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological Applications, 22*(7), 2007-2020.

Stephens, D.W., & Krebs, J.R. (1886). *Foraging Theory* (Vol.1). Princeton University Press.

Straley, J. M., Moran, J. R., Boswell, K. M., Vollenweider, J. J., Heintz, R. A., Quinn II, T. J., Witteveen, B. H., & Rice, S. D. (2018). Seasonal presence and potential influence of humpback whales on wintering Pacific herring populations in the Gulf of Alaska. *Deep Sea Research Part II: Topical Studies in Oceanography, 147*, 173-186.

Thorsnæs, G., & Askheim, S. (2020, July 6). *Ersfjorden*. Store norske leksikon. https://snl.no/Ersfjorden

Valani, R., Meynecke, J.-O., & Olsen, M. T. (2020). Presence and movement of humpback whale (*Megaptera novaeangliae*) mother-calf pairs in the Gold Coast, Australia. *Marine and Freshwater Behaviour and Physiology, 53*(5-6), 251-263. https://doi.org/10.1080/10236244.2020.1850177

Van Ruiten, M. (2021). *A new look at whale behavior: identifying multiple spatial movement patterns of Norwegian killer whales* [Master's thesis, UiT Norges arktiske universitet]. Munin.

Vihtakari, M. (2020). ggOceanMaps: Plot Data on Oceanographic Maps using 'ggplot2'. R package version 0.4.3. https://mikkovihtakari.github.io/ggOceanMaps

Vogel, E. F. (2020). *The influence of herring (Clupea harengus) biomass and distribution on killer whale (Orcinus orca) movements on the Norwegian shelf* [Master's thesis, UiT Norges arktiske universitet]. Munin.

Vogel, E. F., Biuw, M., Blanchet, M.-A., Jonsen, I. D., Mul, E., Johnsen, E., Hjøllo, S. S., Olsen, M. T., Dietz, R., & Rikardsen, A. (2021). Killer whale movements on the Norwegian shelf are associated with herring density. *Marine Ecology Progress Series, 665*, 217-231.

Werner, E. E., & Hall, D. J. (1974). Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology, 55*(5), 1042-1052.

Øien, N. (2010). Knølhvalen-en langpendler mellom Karibia og Barentshavet. *Ottar, 2010*(280), 57-62.

Appendix A

Table S1: Tagging info from raw data of all 20 satellite tagged humpback whales over four field seasons, tagged between 24.11.2015 and 8.01.2019 in Tromsø and Skjervøy area in Northern Norway. Data is collected from tag deployment date until the tag quit transmitting. The 12 whales used in this study are placed above the red line. Remaining 8 whales below the red line were not used in analysis due to few total extracted positions or multiple gaps throughout the track on 4-10 hours that made the tracking incomplete. They were removed to avoid spurious change points when further applying the analysis.

| Tagging Location	Whale ID	Tag deployment date	Days before passing AC	Total extracted positions	Leaving fjord areas	Leaving AC	Last date with data
Tromsø	166150	15.01.2017	317	3763	16.01.2017	06.02.2017	27.11.2017
Tromsø	166149	10.01.2017	117	3060	07.2.2017	19.03.2017	06.05.2017
Tromsø	166148	22.12.2016	46	1621	25.01.2017	03.02.2017	06.02.2017
Tromsø	166146	13.12.2016	15	584	27.12.2016	27.12.2016	27.12.2016
Tromsø	166145	24.01.2017	12	142	31.01.2017	04.02.2017	04.02.2017
Tromsø	166143	05.01.2017	45	547	05.01.2017	12.01.2017	18.02.2017
Tromsø	166142	04.01.2017	121	3147	11.01.2017	06.02.2017	04.05.2017
Skjervøy	83287	04.12.2018	136	3243	15.01.2019	29.01.2019	17.04.2019
Skjervøy	83278	08.01.2019	337	4358	29.01.2019	15.02.2019	06.12.2019
Skjervøy	83274	03.12.2018	78	1520	29.12.2019	02.01.2019	17.02.2019
Skjervøy	83271	03.12.2018	105	2072	09.01.2019	29.01.2019	16.03.2019
Skjervøy	47598	19.01.2018	134	2244	20.01.2018	01.03.2018	01.06.2018
Tromsø	152129	02.12.2015	20	114	-	22.02.2015	22.02.2015
Skjervøy	83280	04.01.2019	4	4	-	08.01.2019	08.01.2019
Tromsø	152134	24.11.2015	27	367	-	20.12.2015	20.12.2015
Tromsø	152139	20.11.2016	10	272	-	30.11.2016	30.11.2016
Tromsø	166140	20.11.2016	12	242	-	01.12.2016	01.12.2016
Tromsø	166141	13.12.2016	1	11	-	13.12.2016	13.12.2016
Tromsø	166147	13.12.2016	2	56	-	15.12.2016	15.12.2016
Skjervøy	174062	01.08.2018	1	8	-	01.08.2018	01.08.2018

Appendix B
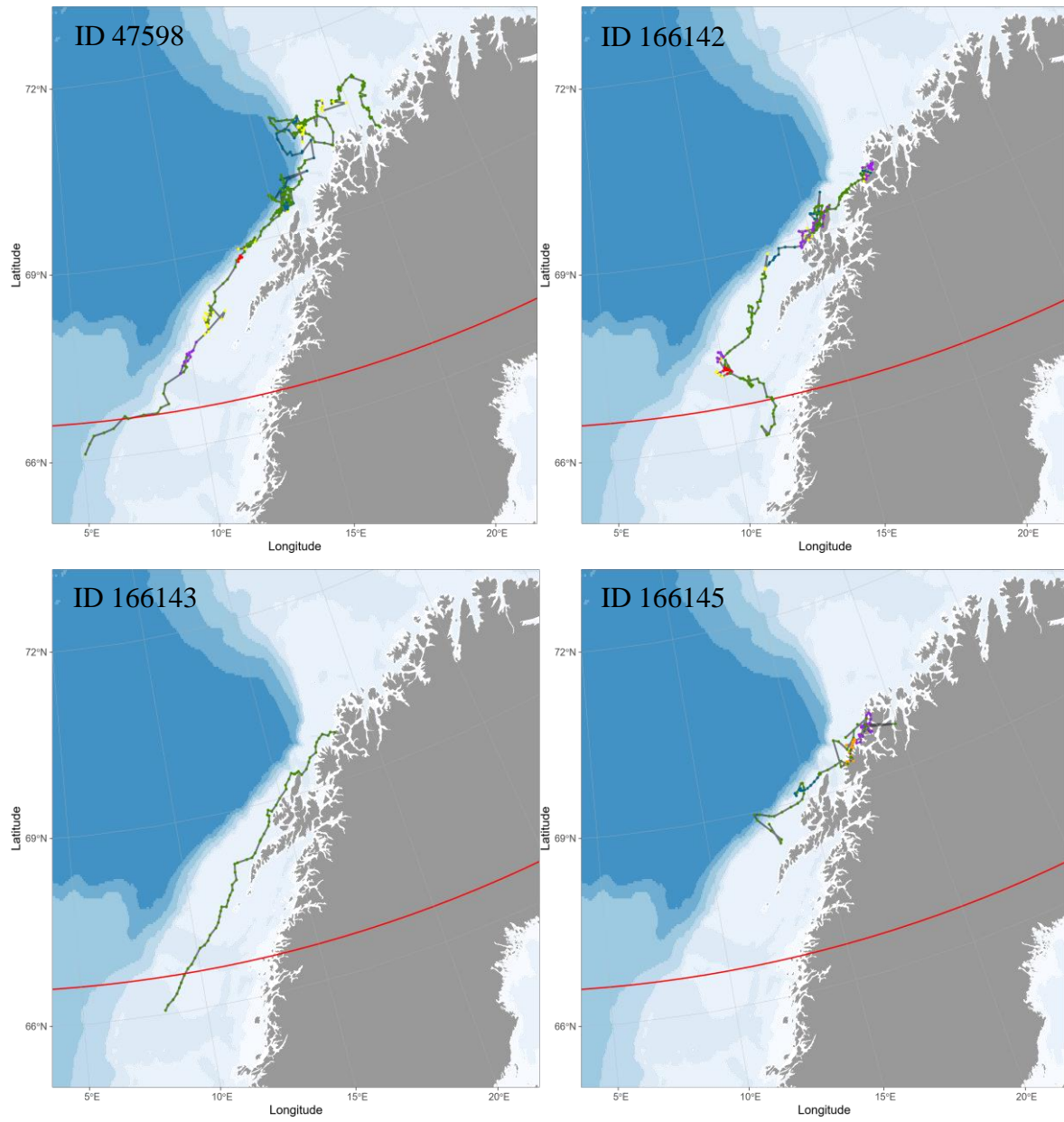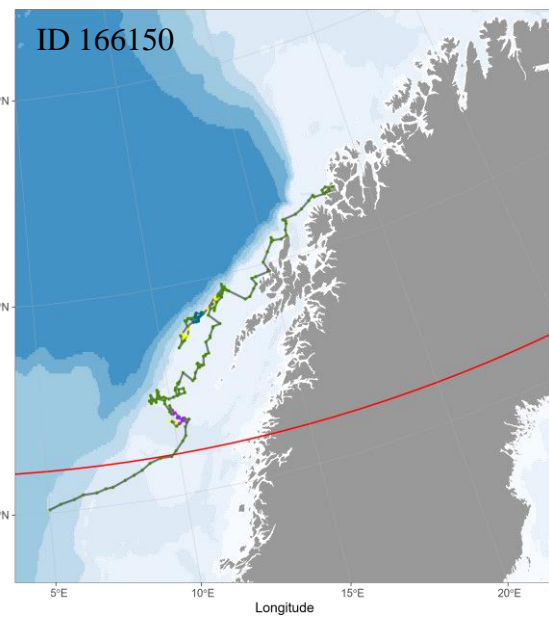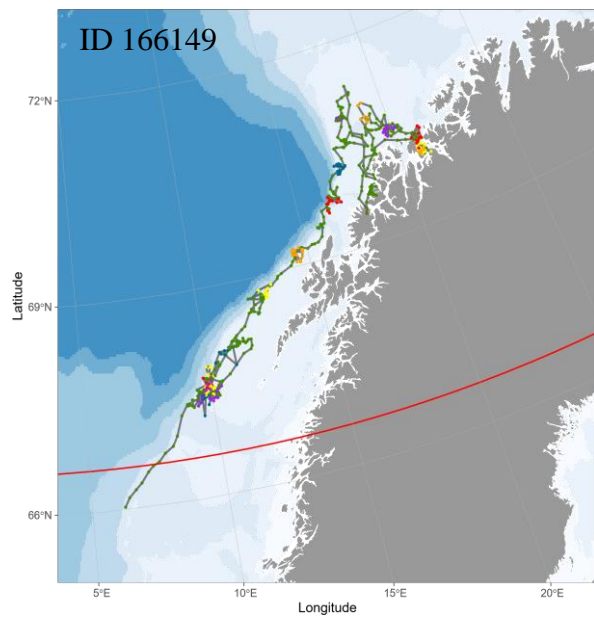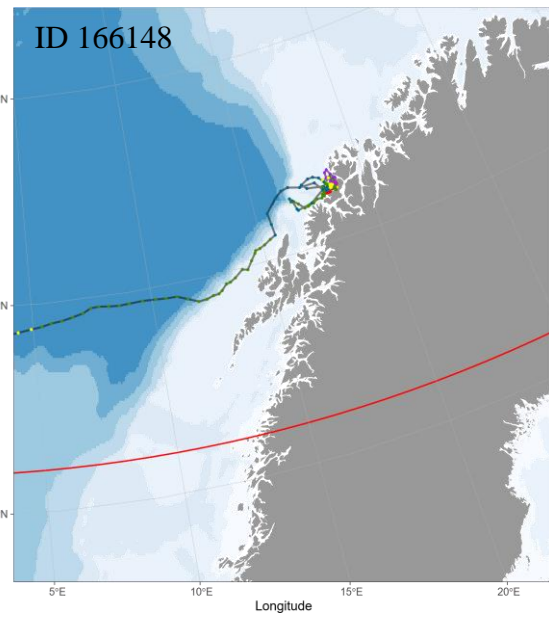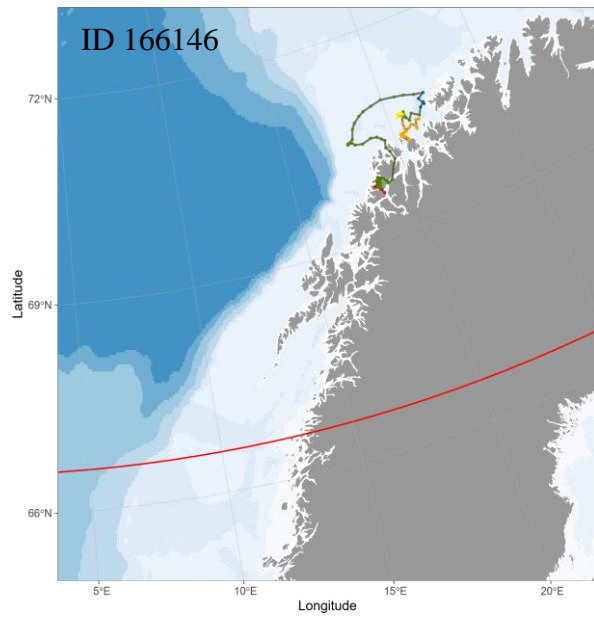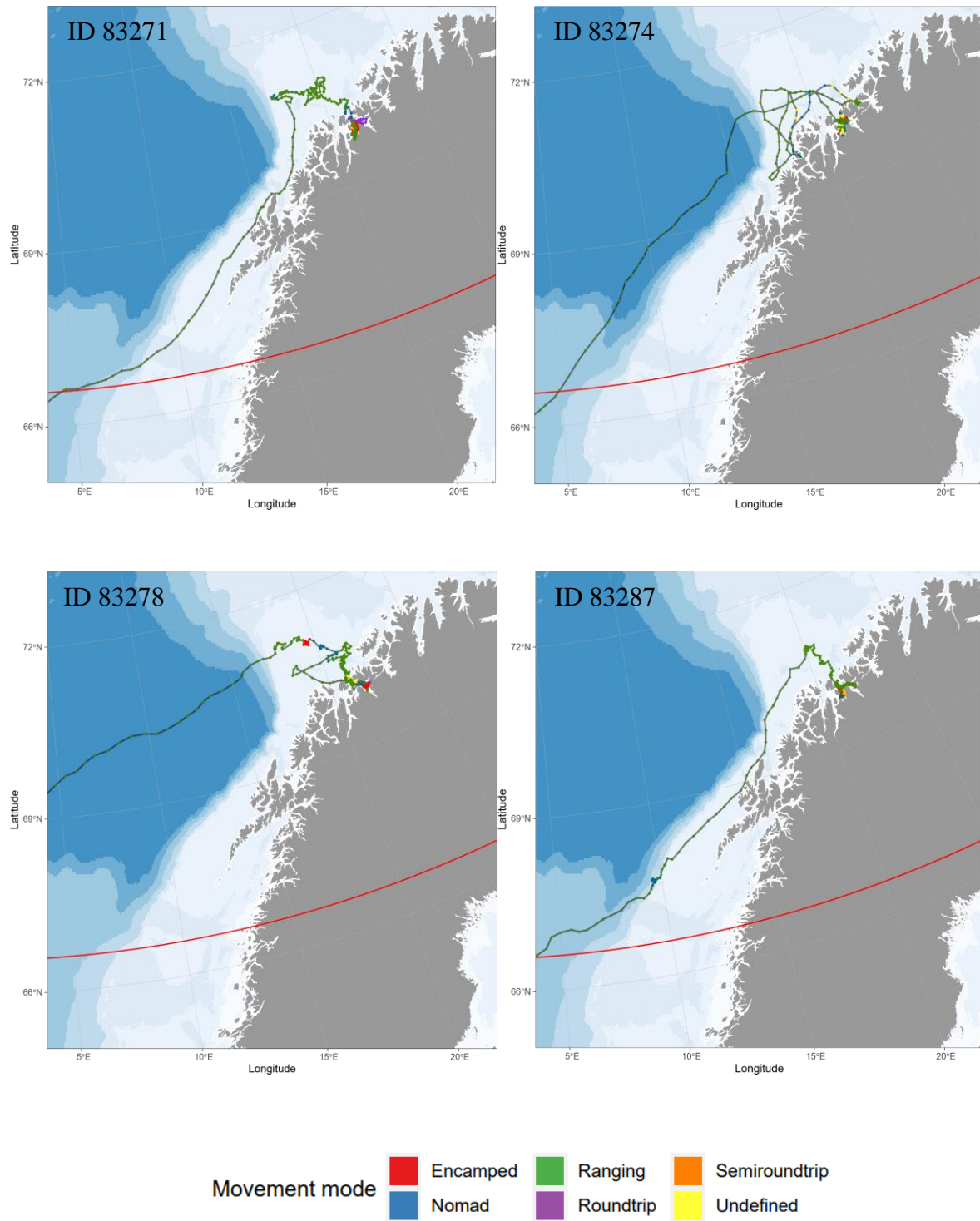
Figure S1: Maps of 12 satellite tagged humpback whales (2016-2019) along the Norwegian coast north of the Arctic Circle (66°33'N). Tracks are segmented and color coded by the corresponding movement mode classified.

Appendix C

```
########################################################################
###SEGMENTING WHALE TRACKS AND CLASSIFYING MOVEMENT MODES

# load necessary packages
library(move)
library(adehabitatLT)
library(bcpa)
library(FlexParamCurve)
library(circular)
library(reshape)
library(nls2)
library(mapproj)
library(ggmap)
library(ggplot2)
library(writexl)
library(dplyr)

###### FUNCTIONS #############
#----- Concordance Criteria function ----------
CC<- function(nsd_data, fitted_val){
  cc<-1 - (sum((nsd_data - fitted_val)^2) /
        (sum((nsd_data - mean(nsd_data))^2) +
          sum((fitted_val - mean(fitted_val))^2) +
          length(nsd_data)*((mean(nsd_data)-
                    mean(fitted_val))^2) ))}

###################################
# 1. GET THE DATA

whales.crw <- read.csv("166146pc.csv", dec = ".", header = T)
whales.crw$id<-as.factor(whales.crw$id)
whales.crw$date<- as.POSIXct(whales.crw$date,format="%Y-%m-%d
%H:%M:%S",tz="UTC")

###################################
# 2. BCPA analysis (Gurarie et al. 2009)

#Subset humpback whale by ID
hw<- subset(whales.utm, id == "166146")
hw<- hw[order(hw$date),]

Simp<- hw[,c("date","x.1","y.1")]
mytrack <- MakeTrack(Simp$x.1,Simp$y.1,Simp$date)
names(Simp) <- c("Time","X","Y")
class(Simp)<- c("track", "data.frame")
Simp.VT<- GetVT(Simp)

#WINDOW SWEEP
```

```
Simp.ws <- WindowSweep(Simp.VT,"V*cos(Theta)", #log(V), V*cos(Theta)
             windowsize = 40,
             K = 3)


cps<-ChangePointSummary(Simp.ws,clusterwidth=4)
cps<- cps[[1]]


###################################
# 3. ADD SEGMENTS NUMBERS TO INDIVIDUAL TRACK DATA

cps$timestamp<- as.POSIXct(strptime(cps$middle.POSIX,"%Y-%m-%d %H:%M:%S"))
dataseg<- NULL

for (i in 1:(nrow(cps)+1)) {
  if (i==1) {segment.i<- subset(hw, date<cps$timestamp[i])}
  if (i==(nrow(cps)+1)) {segment.i<- subset(hw, date>cps$timestamp[i-1])}
  if (i>1 & i<(nrow(cps)+1)) {segment.i<- subset(hw, date>cps$timestamp[i-1]
&date<cps$timestamp[i]) }
  if (length(segment.i[,1]) > 0) {segment.i$segment<- i}
  dataseg<- rbind(dataseg, segment.i)
}

#reorder and rename
d1 <- dataseg
d1$date <- as.POSIXct(strptime(d1$date,"%Y-%m-%d %H:%M:%S"))
d1 <- d1[which(!duplicated(d1$date)), ]
d1<- d1[order(d1$date),]
d1 <- na.omit(d1)

datetime<- d1$date
coord<-data.frame((d1$x.1),(d1$y.1))

# make ltraj: a trajectory of all there locations
d2<-as.ltraj(coord,datetime,
        as.character(d1$id),
        burst=d1$segment,
        typeII=TRUE)


###################################
# 4. EXTRACT NSD FOR EACH SEGMENT

datansd<-NULL

for(n in 1:length(summary(d2)[,1])) {
  nsdall<-d2[[n]][,8]
  nsdtimeall<-d2[[n]][,3]
  nsdtimestartzero<-d2[[n]][,3]-d2[[n]][1,3]
  nsdid<-rep(as.vector(summary(d2)[n,1]),
        length.out=summary(d2)[n,3])
  nsdtrip<-rep(as.vector(summary(d2)[n,2]),length.out=summary(d2)[n,3])
```

```
    datansd1<-data.frame(nsdall,nsdtimeall,nsdtimestartzero,nsdid,nsdtrip)
    datansd<-rbind(datansd,datansd1)
}
head(datansd)

datansd$zero1<-as.numeric(unclass(datansd$nsdtimestartzero))
# making seconds since trip start numeric
datansd$zerostart<-datansd$zero1/60
#changing the time since trip start from seconds to minutes
datansd$zerostart<-datansd$zerostart/60
#changing the time since trip start from min to hrs

datansd1<-na.omit(datansd)

##################################
# 5. TESTING THE CANDIDATE MODELS

d3 <- datansd1
names(d3)
d3$NSD <- (d3$nsdall)
d3$nsdtrip<-factor(d3$nsdtrip,levels=unique(d3$nsdtrip))
d1g <- groupedData(zerostart~NSD|nsdtrip,data=d3)

data1<-NULL

pdf("hw.166146.pdf",height = 5, width = 5)

for (i in unique(d1g$nsdtrip)) {

 #rm(myoptions)
 rm(list=ls(pattern = "richardsR"), envir = FlexParamCurve:::FPCEnv)
 rm(list=ls(pattern = "richardsR"), envir = .GlobalEnv)

 data_id<- subset(d1g, nsdtrip==i)
 trip<- unique(data_id$nsdtrip)

 plot(data_id$zerostart, data_id$NSD, pch=16, xlab="time(hrs)", ylab="Net squared
displacement")

 modpar.mono<- try(modpar(data_id$zerostart, data_id$NSD,pn.options=
"myoptions.monotonic",verbose = T, force4par = TRUE))# for monotonic curve (e.g.
dispersal)
 modpar.nonm<- try(modpar(data_id$zerostart, data_id$NSD,pn.options=
"myoptions",verbose = T))# for non-monotonic curve


 if(class(modpar.mono) == "try-error") {next}
 if(class(modpar.nonm) == "try-error") {next}
 Ri<-myoptions$Ri
 RM<-myoptions$RM
```

RANGING : MOD 32

```
mod32 <-try(nls(NSD~SSposnegRichards(zerostart, Asym = Asym,K = K, Infl= Infl,
                    modno = 32,pn.options =
"myoptions.monotonic"),data=data_id,control=list(tol=10)))

#derive starting parameters for fixed effects
if(class(mod32) == "try-error") {
  CC_mod32 <- 0
}
if(class(mod32) != "try-error") {
  CC_mod32 <- CC(data_id$NSD,fitted(mod32))
  aic_mod32 <- AIC(mod32)
  lines(data_id$zerostart, predict(mod32), col="blue")
}
```

ROUNDTRIP : MOD 2

```
mod2 <-try(nls(NSD~SSposnegRichards(zerostart, Asym = Asym,K = K, Infl=
Infl,M=M,RM=RM, RAsym = RAsym, Rk = Rk, Ri=Ri,
                    modno = 2,pn.options = "myoptions"),
        data=data_id,
        control=list(tol=10)))

#derive starting parameters for fixed effects
if(class(mod2) == "try-error") {
  CC_mod2 <- 0
}
if(class(mod2) != "try-error") {
  CC_mod2 <- CC(data_id$NSD,fitted(mod2))
  aic_mod2 <- AIC(mod2)
  lines(data_id$zerostart, predict(mod2), col="green")
  df2 <- data.frame(data_id$zerostart,predict(mod2))
  names(df2) <- c("x", "y")
}
```

ROUNDTRIP-PARTIAL: MOD 22

```
mod22 <-try(nls(NSD~SSposnegRichards(zerostart, Asym = Asym,K = K, Infl=
Infl,RAsym = RAsym,Ri=Ri, Rk = Rk, RM=RM,
                    modno = 22,pn.options = "myoptions"),
        data=data_id,
        control=list(tol=10))) #algorithm = "plinear"

#derive starting parameters for fixed effects
if(class(mod22) == "try-error") {
  CC_mod22 <- 0
}
```

```
if(class(mod22) != "try-error") {
  CC_mod22 <- CC(data_id$NSD,fitted(mod22))
  aic_mod22 <- AIC(mod22)
  lines(data_id$zerostart, predict(mod22), col="red")
  df22 <- data.frame(data_id$zerostart,predict(mod22))
  names(df22) <- c("x", "y")
}

#### ENCAMPED

hr<- try(lm(NSD~1, data=data_id))

#derive starting parameters for fixed effects
if(class(hr) == "try-error") {
  CC_hr<- 0
}
if(class(hr) != "try-error") {
  CC_hr<- CC(data_id$NSD,fitted(hr))
  aic_hr<- AIC(hr)
  lines(data_id$zerostart, predict(hr), col="gray")
}

#### NOMADIC

nom1 <- try(lm(NSD  ~ zerostart,data=data_id),silent=TRUE)
#derive starting parameters for fixed effects
if(class(nom1) == "try-error") {
  CC_nom1 <- 0
}
if(class(nom1) != "try-error") {
  CC_nom1 <- CC(data_id$NSD,fitted(nom1))
  aic_nom1 <- AIC(nom1)
  lines(data_id$zerostart, predict(nom1), col="black", lty=2)
}

legend("topleft",c(paste("mod32=",round(CC_mod32,2)),
            paste("mod2=",round(CC_mod2,2)),
            paste("mod22=",round(CC_mod22,2)),
            paste("nomad=",round(CC_nom1,2)),
            paste("hr (aic)=",round(aic_hr,2))),
     text.col=c("blue","green","red","black","gray"),cex=.7)

data1$trip <- levels(trip)
data1$CC_mod32 <- CC_mod32
data1$CC_mod2 <- CC_mod2
data1$CC_mod22 <- CC_mod22
data1$CC_nom1 <- CC_nom1
data1$CC_hr <- CC_hr
data1$aic_mod32 <- aic_mod32
data1$aic_mod2 <- aic_mod2
```

```r
data1$aic_mod22 <- aic_mod22
data1$aic_nom1 <- aic_nom1
data1$aic_hr <- aic_hr

# Select model with the highest CC
model<- list(mod32, mod2, mod22, nom1, hr)
cc <- data.frame(CC_mod32,CC_mod2,CC_mod22,CC_nom1,CC_hr)
best.cc <- cc[which(cc==max(cc[1,],na.rm=T))]
aic<- data.frame(aic_mod32,aic_mod2,aic_mod22,aic_nom1,aic_hr)
best.aic<- aic[which(aic==min(aic[1,],na.rm=T))]

if (names(best.aic)=="aic_hr" | (best.cc <.7 & CC_nom1 <.4)) { # | aic$aic_hr/min(aic) <
1.01 ...
  best.model<- hr
  strategy<- "encamped"
}
if (names(best.cc)=="CC_nom1" | (best.cc <.7 & CC_nom1 > .4))  {
  best.model<- nom1
  strategy<- "nomad"
}
if (names(best.cc)=="CC_mod32" & best.cc >.7)  {
  best.model<- mod32
  strategy<- "ranging"
}
if (names(best.cc)=="CC_mod22" & best.cc >.7)  {
  strategy<- ifelse (1.5*(predict(mod22)[length(predict(mod22))]) >= max(predict(mod22)) ,
            "ranging",
            ifelse (predict(mod22)[length(predict(mod22))] <= max(df22[df22$x
<abs(coef(mod22)[3]),]$y) ,
                  "round-trip","semi-round-trip"))
  best.model<- mod22
}
if (names(best.cc)=="CC_mod2" & best.cc >.7)  {
  strategy<- ifelse (1.5*(predict(mod2)[length(predict(mod2))]) >= max(predict(mod2)) ,
            "ranging",
            ifelse (predict(mod2)[length(predict(mod2))] <= max(df2[df2$x
<abs(coef(mod2)[3]),]$y) ,
                  "round-trip","semi-round-trip"))
  best.model<- mod2
}

predW<- predict(best.model)
# add result on the plot
title(paste("hw.166146pc trip nÂ°", trip,"-",strategy, sep=""))

}

dev.off()

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

###CREATE MAP (INDIVIDUAL WHALE BY MOVEMENT MODE)

```
###################################
#.1 DOWNLOAD NECESSARY PACKAGES

library(ggplot2)
library(ggOceanMaps)
library(tidyverse)

###################################
#2. GET THE DATA

whale<-X166146mode
whale$id=as.character(whale$id)
whale<-subset(whale, select=c(1,3,4,5,6,7,8,9,10,11,12))
colnames(whale)<-c("ID","date","lon","lat","x","y","x.1","y.1","segment", "Mode", "Mode.")

###################################
#3. CREATE THE MAP

dt <- data.frame(lon = c(seq(-180:180), seq(30:30)), lat = 66.6)
dt
c<-basemap(limits = c(5,23 ,65, 72), bathymetry = TRUE, land.border.col = NA)+
  geom_spatial_path(data = whale, shape = 20, alpha = 0.5, aes(x = lon, y = lat), size =
0.7)+labs(x="Longitude", y="Latitude")+
  geom_spatial_path(data = dt, aes(x=lon, y=lat),color="red")+
  geom_spatial_point(data = whale,shape = 20, alpha = 1, aes(x = lon, y = lat, color=Mode),
size = 1)
c
c + scale_colour_manual(values = c("red", "deepskyblue4", "chartreuse4", "purple", "orange",
"yellow"))

###############################################################################

###LEAFLET INTERACTIVE MAP

###################################
#1. DOWNLOAD NECESSARY PACKAGES

library(leaflet)
library(sp)

###################################
#2. GET THE DATA

raw<-read.csv("rawcopy.csv", header = TRUE)
View(raw)
raw$DeployID=as.character(raw$DeployID)
raw$DeployID=as.factor(raw$DeployID)
```

```
subset.whales=subset(raw,DeployID=="166148")
subset.whales
```

```
###################################
#3. CREATE MAP
```

```
m <-leaflet() %>%   #creating a pipe cntr+shift+m
  addTiles() %>%
  addMarkers(data = subset.whales, lng =~lon, lat = ~lat, popup = ~date)
m
```

###

SEQUENCE FIGURE

```
###################################
#1. DOWNLOAD NECESSARY PACKAGES
library(RColorBrewer)
library(ggplot2)
library(lubridate)
```

```
###################################
#2. GET THE DATA
```

```
combined <- read.csv("combined3.csv", dec = ".", header = T)
combined1<-subset(combined, select = c(1,3,4,5,6,7,8,9,10,11))
colnames(combined1)<-c("id", "date", "lon", "lat", "x", "y", "x.1", "y.1","segment","Mode")
combined1$date<-as.POSIXct(combined1$date, format = "%Y-%m-%d %H:%M:%S", tz=
"UTC")
```

```
###################################
#3. CONVERT TO JULIAN DAY
```

```
combined1$Julianday<-as.numeric(format(combined1$date, "%j"))
j2d<-function(n){
  n<-ifelse(n<180, n+365,n)#wrap a mid year
  d<-as.Date("2015-01-01")+n
  return(d)
}
combined1$Jdate<-j2d(combined1$Julianday)
```

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

#4. CREATE THE FIGURE

```
ggplot()+
  geom_point(data=combined1, shape=15, aes(x=Jdate, y=as.factor(id), color=
factor(Mode),group=id),size=6,alpha=1)+
theme(panel.background = element_rect(fill = "white", colour = "white"),
    panel.grid.major = element_blank(),
    panel.grid.minor = element_blank(),
    axis.line = element_line(size = 0.3, linetype = "solid", colour = "black"),
    legend.position="bottom",
    legend.text = element_text(size=9),
    legend.key.size = unit(0.5,"line"),
    axis.text = element_text(size=9)) +
  scale_color_brewer(palette ="Set1", na.value="grey") +
  labs(x = "Date", y = "ID", color = "Movement mode")
```


###