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

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Research Article

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Abstract

Background: Studying movement patterns of individual animals over time can give insight into how they interact with the environment and optimize foraging strategies. Humpback whales (*Megaptera novaeangliae*) undertake long seasonal migrations between feeding areas in polar regions and breeding grounds in tropical areas. During the last decade, several individuals have had up to a three month stop-over period around specific fjord-areas in Northern Norway to feed on Norwegian spring-spawning (NSS -) herring (*Culpea harengus L.)*. Their behavioral patterns during this period are not well understood, including why some whales seemingly leave the fjords and then later return within the same season.

Methods: Here we for the first-time classified humpback whale tracks into five distinct movement modes; ranging, encamped, nomadic, roundtrip and semi-roundtrip. A behavioral change point analysis (BCPA) was used to select homogeneous segments based on persistence velocity. Then, net squared displacement (NSD) over time was modeled 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.

Results: Inside the fjord systems, encamped mode was most prevalent in December-January, suggesting the whales were mainly foraging on overwintering NSS-herring in this area. During the same winter seasons, half of the whales left the fjords and then returned. We hypothesize that these trips serve as 'searching trips' during which the whales seek better feeding opportunities outside the fjords. If better foraging conditions are not found, they return to the fjords to continue their feeding. The overall most common mode was ranging (54%), particularly seen during the start of their southwards migration and in areas outside the fjord systems, indicating that the whales mainly moved over larger distances in the offshore habitat.

Conclusion: This study serves as a baseline for future studies investigating both the searching trip theory and humpback whale behavior in general, and confirms that this method is useful to analyze smaller scale movement patterns of satellite tagged whales.

Keywords: Humpback whale, *Megaptera novaeangliae,* Satellite telemetry, movement ecology, foraging behavior

Background

Knowledge on animal movement is essential to understand the interaction between organisms and their environment. In the marine environment, predators such as whales are shown to be strongly influenced by the distribution and behavior of prey (1-4). However, individual movements are a complex process affected by both biological factors (genotype), external factors (environment), and internal factors (status, history) (5-7). Together, these factors influence and shape the structure and distribution of populations at various spatial and temporal scales (6, 8).

Humpback whales conduct some of the longest known seasonal migrations of all mammals, moving between feeding areas in polar regions during summer/early winter to breeding areas in more tropical regions during late winter/spring (9-11). Based on genetic studies suggesting limited gene flow between ocean basins, we consider the species divided into three main populations: The North Atlantic, North Pacific, and Southern Hemisphere population (12-14). Among these, the Northeast Atlantic humpback population is assumed to undertake the longest migration, about 9000km one way from feeding areas in the northern Barents Sea to tropical breeding areas in the Caribbean or Cap Verde (10).

Humpback whale 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 (*Clupea harengus)* (15, 16). In the last decade, large masses of Norwegian spring-spawning (NSS-) herring (*Clupea harengus L.)* have aggregated in specific fjord systems in Troms, Northern Norway in winter, followed by hundreds of humpback and killer whales (*Orcinus orca*) (3, 10, 17, 18). These areas are located close to one of the assumed migration routes of humpbacks to and from the Barents Sea summer feeding grounds, and the wintertime feeding may therefore represent a stop-over to re-fuel before they later migrate to the southern breeding grounds in the (14, 19).This occurrence of whales near the coast and populated areas enabled us the unique opportunity to study their detailed behavior (3, 20-22).

According to *optimal foraging theory,* animals will adapt their foraging to utilize resources as efficiently as possible (23-25). 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 contributing to shaping movement patterns (26). 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 (27), as discussed for killer whales and humpback whales by Vogel et.al 2023 (3, 4) . 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 (15). 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 (22, 27, 28). Marginal value theory predicts that a predator will leave the current patch when energy consumption rate within the patch reduces to the average energy consumption rate in the environment (27). Marginal value theorem has been examined in Norwegian killer whales (22), and found that some whales left the herring rich fjord areas only to return multiple days or weeks later, however the model used to analyze the data was unable to adequately identify and describe in detail these excursions (see below). Similar excursion behavior has been described for humpback whales in the same area by Rikardsen 2019 (18). This behavior is intriguing because the whales leave a fjord where there is seemingly higher herring density than outside based on fishery statistics (29). Such behavior could appear contrary to what optimal foraging theory and marginal value theory would predict (26, 27). However, net energy intake is determined by energy intake minus energy expenditure, and there are several factors affecting whether this behavior is contrary with theory. If the competition becomes very high for the resource patches inside the fjords, then it might be more profitable to leave in search for other patches. To better understand the extent of this excursion behavior, a method is needed to identify and describe the whales behavior during such events (22).

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 (30, 31). For humpback whales, large-scale movement patterns have been extensively documented over the past decades for some populations (32-36). However, movement behavior at smaller scales, and characterization of multiple movement modes that extends travelling versus feeding are not properly studied (7, 37, 38). 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 (39).

New methodical techniques have been developed to segment continuous time series data and identify small-scale behavioral modes of animals (40), 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 killer whale behavior along the Norwegian coast using a range of behavioral indexes, from area restricted search and fishery attraction, to a continuous behavioral index ranging between two behavioral extremes. While these studies typically utilized two (3, 20) or three (21) discrete behavioral modes to describe behavior, some used continuous behavioral indexes (3). A killer whale study from 2021 (22) 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 the initial starting location followed by a complete return to the same location. However, “round trips” spanning multiple days were not identified, due to how the parameters in the applied model were tuned to detect smaller scale behaviors. Therefore, this warrants a concurrent supplemental approach to identify such longer excursions in this study (visual methods, see section 3.7).

The main objective of this study was to characterize humpback whale movement patterns along the Norwegian coastline, and additionally identify potential longer temporary excursions away from the fjords (“Long roundtrips”). Our first sub-goal was to segment humpback whale tracks into five different movement modes to investigate their behavioral patterns and individual variability. Secondly, we wanted to examine the order of movement modes, possible relationships between them, and how this change by season and area. Finally, we tried to identify potential longer excursions (several days) away from and back to the fjord systems, and investigated movement modes within these excursions. Humpback behavior based on movement modes will be discussed in the context of theoretical framework of optimal foraging theory and marginal value theorem.

Methods

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 (Figure 1). The Tromsø fjord area consists 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 12-16 km and consist of both shallow and deep areas (maximum depth ~270 m) (14, 41, 42). 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). Kvænangen fjord is generally wider and more open (15 km at its widest) than the Tromsø fjords and has a maximum length of 74 km 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 400-450 m (43).

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 (3). The rest of the population overwinter in the Norwegian Sea, including on the continental shelf of the coast of Northern Norway (44). 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 attract 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 (14, 18, 21).

Tagging/Instrumentation

The tagging was done over a four-year time-period (2016-2019) from December to January in both fjord areas (see Additional file 1). Argos Satellite tags (SPOT 302/303, Wildlife Computers, Redmond WA, USA) were deployed using the best practice guidelines for cetacean tagging (45).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. Tag placement will affect the quality and amount of data received by the ARGOS satellites (46), as the tag only transmit when exposed to air. Therefore, for tag attachment we aimed for the area just below the dorsal fin which is exposed to air when surfacing (45). This region also contains the thickest layer of blubber and has a significant amount of connective tissue within it, which aids to keep the tag in place. 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.

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 (47). The CRW was applied using the 'fit_ssm' function in the package 'foieGras' (48) and in this study the time-step was set to three-hour intervals following practices by Vogel et al., 2020 (49) and Van Ruiten 2021 (22).

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 (8, 50). 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' (50).

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 (22, 50). 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 (22, 40). Minor changepoints within a small temporal range can be filtered out by increasing the cluster width (22, 51). 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.

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) (52) for moose (*Alces alces*), Morelle et al. (2017) (40) for wild boar (*Sus scrofa*), and Van Ruiten (2021) (22) 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.

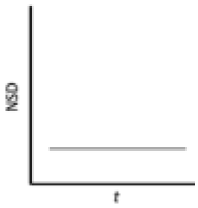
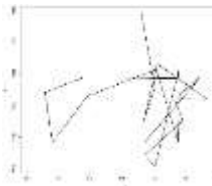
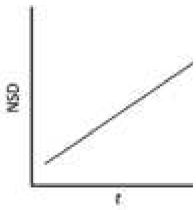
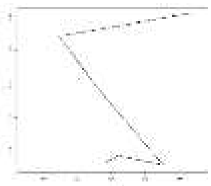
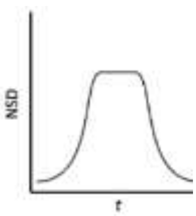
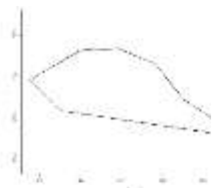
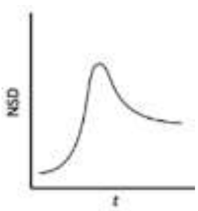
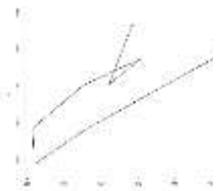
Classifying segments

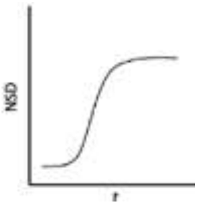
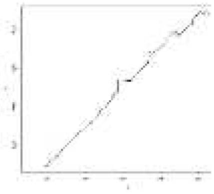
The spatial relationship between net squared displacement (NSD) and time (t) was defined for each movement mode. NSD calculates the squared distances between every GPS location and the initial location of the movement path (53). Distances are squared to cancel directional information, an efficient method to convert movement data from 3D (x,y,z) to 2D (NSD from origin t) allowing further application of simpler statistical models (40). NSD was calculated for each segment generated by the BCPA, by applying the function ‘as.ltraj’ from the package ‘adehabitatiLT’ (54). As previously described in Bunnefeld et al. (2011) (52), Morelle et al. (2017) (40), and Van Ruiten (2021) (22), mathematical curve equations that best represent each movement mode was selected (Table 1) . The R package

‘FlexParamCurve’ (55) and a script supplied by Morelle et al. (2017) (40) and Van Ruiten (2021) (22) (see Additional file 3) 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 (22, 40, 56). 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, Table 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) (55) 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) (22).

Movement Mode	NSD Curve	Equation	Path example
Encamped		$NSD = c$	
Nomadic		$NSD = a * t$	
Roundtrip		$NSD = \frac{A}{1 + m * \exp\left(-k(t-i)\right)^{\frac{1}{m}}} + \frac{A}{1 + \exp\left(-k'(t-i')\right)}$	
Semi-roundtrip		$NSD = \frac{A}{1 + m * \exp\left(-k(t-i)\right)} + \frac{A'}{1 + \exp\left(-k'(t-i')\right)}$	

Ranging		$NSD = \frac{A}{1 + \exp\left(-k(t-i)\right)}$	

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' (57) and 'leaflet' (58). 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 (59) and used to define the fjord areas.

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.

Results

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 (Figure 1). 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 (ranging between 8-69 days). Total extracted positions per individual whale range from 140 to 2357, with an average of 1160 (Table 2). Total number of positions per individual after applying the correlated random walk model was on average 275 (ranging between 63-538) (Table 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 19^{th} (Table 2).

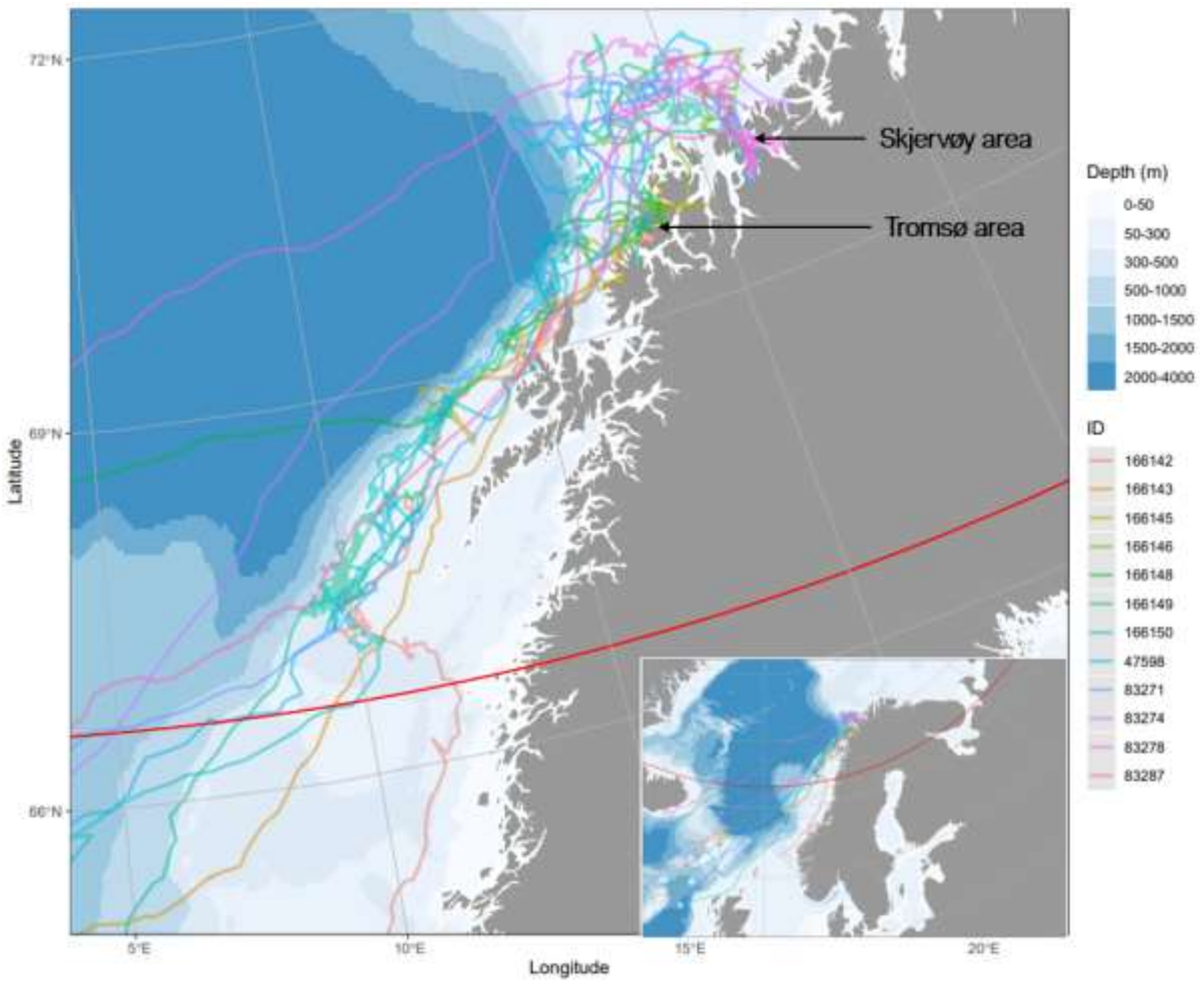


Figure 1: Tracks of the selected 12 satellite tagged humpback whales (2016-2019) along the coast of Northern Norway. The Arctic Circle (66°33'N) represented on this map as a red line, was set as the southern border for the study since the whales then seemingly had started on their southward breeding migration. The small map shows the tracks including the Norwegian Sea. Individual whale tracks are color coded by unique tag ID numbers.

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		

Segmentation and classification

Out of the identified behavioral movement modes, ranging behavior was the overall most common (Table 3), making up 54% of all whale tracks. Further, the following most 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 in 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 the 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

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 (Figure 2, Table 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 Additional file 2), with the relative amount in relation to other modes increasing from mid-January towards the spring months after leaving the fjord areas (Figure 2). 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.

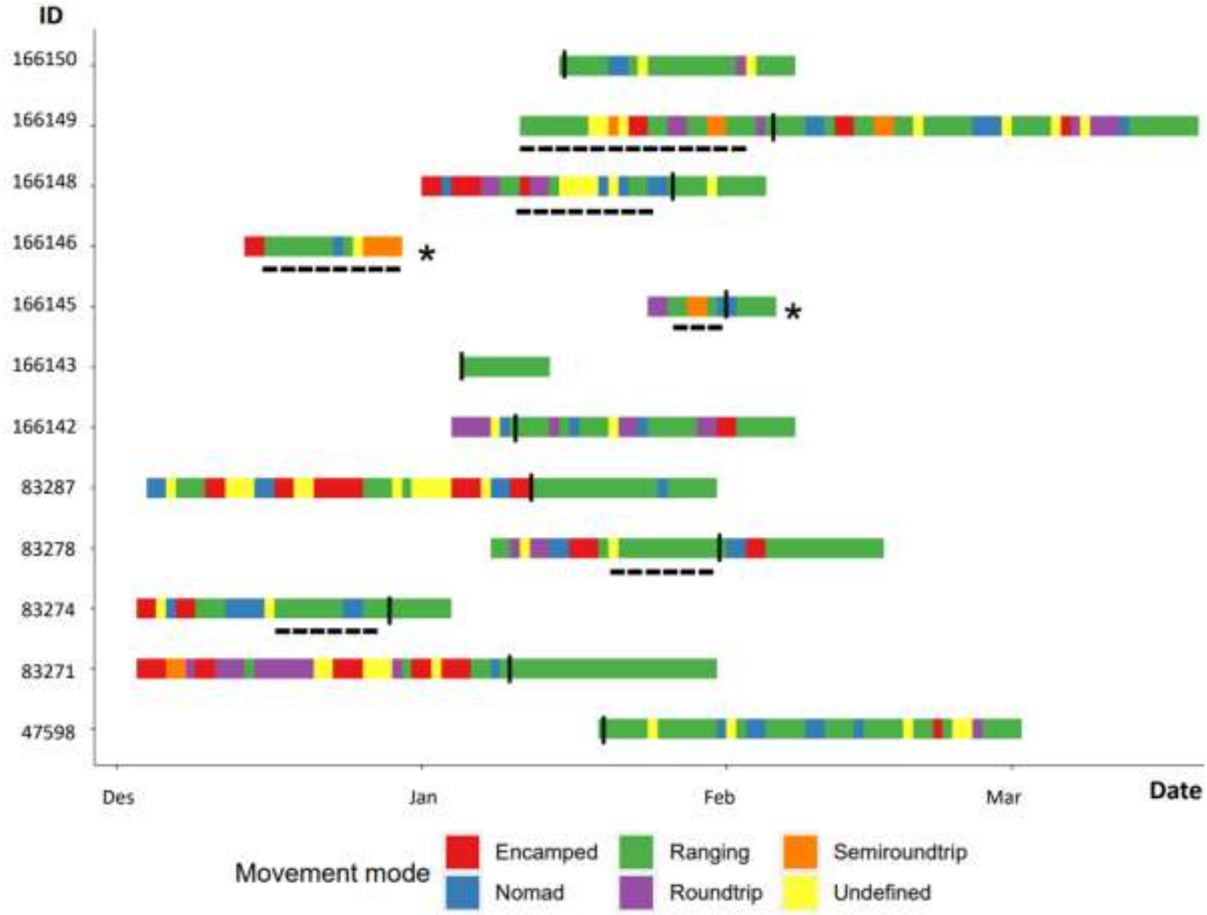


Figure 2*:* Sequences of movement modes for each individual whale (ID, y-axis) over time (x-axis) during winter and spring across a temporal span of four years (2016-2019) for 12 satellite tagged humpback whales at the Tromsø and Skjervøy fjord areas. Counting from the origin, the bottom five whales (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.

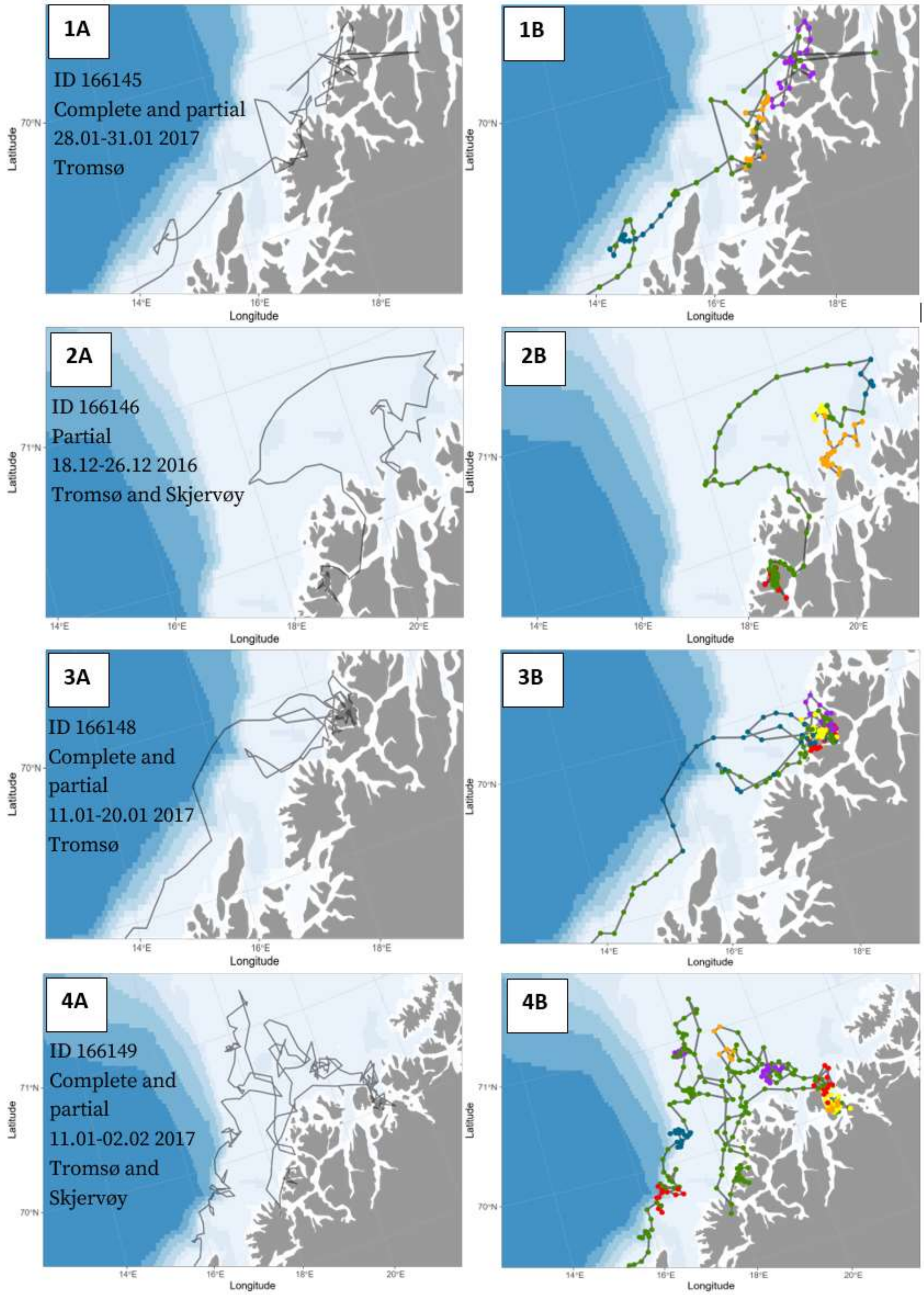
		Second mode					
		Encamped	Round	Semi-round	Nomad	Ranging	Undefined
First mode	Encamped	3 (11,5)	4 (15,3)	1 (3,8)	1 (3,8)	11 (42,3)	6 (23,0)
	Round	2 (9,1)	2 (9,1)	0	2 (9,1)	9 (40,1)	7 (31,8)
	Semi-round	0	1 (12,5)	1 (12,5)	0	4 (50,0)	2 (25,0)
	Nomad	6 (17,6)	0	0	4 (11,1)	16 (47,1)	8 (23,5)
	Ranging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

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) (Figure 3). All long roundtrips were 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 continental 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).


1A
ID 166145
Complete and partial
28.01-31.01 2017
Tromsø
1B
2A
ID 166146
Partial
18.12-26.12 2016
Tromsø and Skjervøy
2B
3A
ID 166148
Complete and
partial
11.01-20.01 2017
Tromsø
3B
4A
ID 166149
Complete and
partial
11.01-02.02 2017
Tromsø and
Skjervøy
4B
Latitude
Longitude
70°N
71°N
14°E
16°E
18°E
20°E

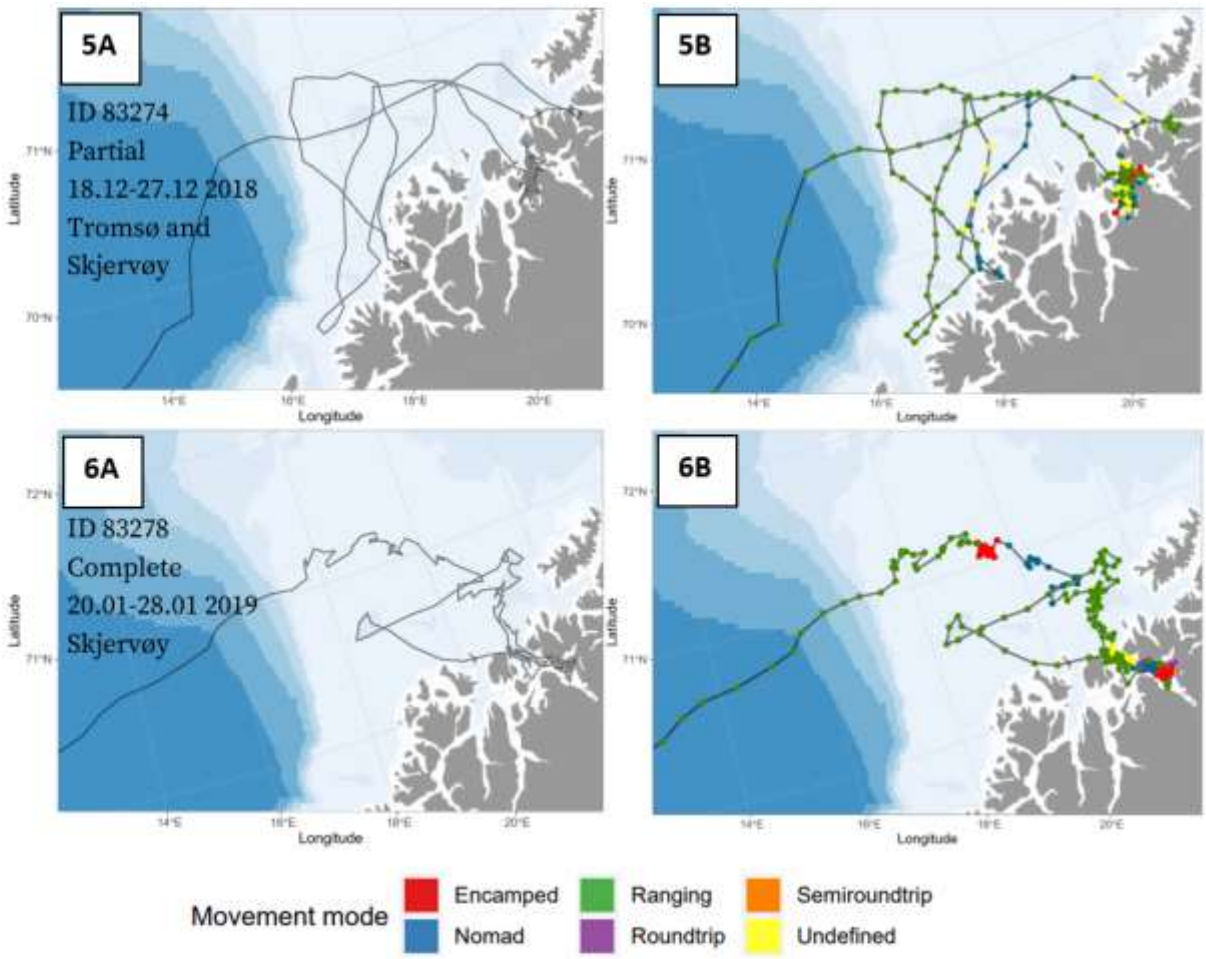


Figure 3: Overview of partial- and complete long roundtrips found in six of the 12 analyzed whales. Individual whales are presented per row. On each row, the maps to the left and right show the same whale track, but to the right, tracks are segmented and colored by the corresponding movement mode classified. 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.

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 (roundtrip, semi-roundtrip, encamped and nomadic) were more frequent inside the fjord systems and sometimes found in shorter sections offshore (166149 and 83278) (Figure 3).

Discussion

This is the first study that has classified humpback whale tracking data into five distinct movement modes, successfully for ~84% of all segments generated through the BCPA. The remaining ~16% of generated segments could not be classified into one of the chosen movement modes due to their shorter durations and total distances traveled compared to those successfully classified. Still, undefined segments make up a small part of the total length of all whale tracks, suggesting that the five movement modes are suitable for describing most humpback whale behavior. This may provide a more detailed understanding of individual humpback whale behavior.

Ranging was the overall most frequent behavior, constituting for more than ½ of all generated segments. Ranging is characterized by straight and faster movement, resembling transiting behavior in former studies (60, 61). Encamped mode, characterized by slower speed and increased turning rates, indicated intensified foraging, and were often seen in fjord areas with high herring abundance (3, 5, 14, 49, 62). This behavior represented about 1/10 of all segments, but dominated within the fjord systems. The relationship between ranging and encamped mode was not immediate, suggesting a more complex behavioral shift than previous studies assessing transiting versus feeding have described (3, 20, 21, 60, 61, 63, 64).

This study introduced three additional movement modes for humpback whales compared to traditional modelling of whale tracks. This included two types of trips (round and semi-roundtrip), and nomadic behavior, totaling 1/5 of all segments. Nomadic and roundtrip behavior was performed by all whales except one, that left the fjords straight away for migration. The behaviors appear to be favored by natural selection, possibly driven by changes in prey density and distribution (24, 30). Nomadic behavior could likely be associated to actions of search during foraging conducted when prey density in the current prey-patch has declined. The same applies for roundtrip, if the whales failed to discover a more valuable prey patch during the trip, they instead returned 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 (27). Competition, predation, and anthropogenic disturbances are just a few other possible reasons an animal might change its behavior and/or relocate (5, 6). Given that marine animals are shown to be strongly influenced by the distribution of prey (1, 3), we can assume that regardless of what caused the relocation, their subsequent location was most likely related to the discovery of a valuable food patch.

The occurrence of movement modes changed by season and habitat. In December-January, encamped, nomadic, round, and semi-roundtrip were the most common behaviors dominating inside the fjord systems, suggesting that these modes are linked to foraging activities on overwintering NSS-herring. All whale tracks showed an increased relative amount of ranging behavior towards spring (February-March) and in the offshore habitat. This is coinciding with the time humpback whales usually initiate their breeding migration (10, 18, 35) and the NSS herring density inside the fjords start to decrease (3). There was no clear pattern in the order of movement modes.

This study is also the first to identify and describe humpback whale long excursions away from feeding areas, contradicting optimal foraging theory. 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 (27, 65). However, results 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. One possible explanation for why they 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 (66), as we know some of the herring aggregate and overwinters on the continental shelves off the coast - instead of in the fjords (3).

The "long roundtrip" phenomenon in this study is similar to the way roundtrips and semi-roundtrips work, except it occurs over a larger area and a longer period of time. As discussed 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. Although the whales are tagged during separate years, the excursions consistently occurred around the same times, in late December or late January. This timing coincides with the gradual movement of herring out of the fjords, which begins in mid-December and continues throughout January (18). It is plausible that, after feeding in a particular area for some time, the whales observed the herring's gradual departure from the fjords and decided to explore the offshore habitat for potentially better foraging opportunities.

Furthermore, the approaching time for the humpback whale breeding migration might contribute to increased restlessness among the whales during this period (10, 35). However, foragers do not always possess comprehensive information about their environment; they must maintain at a certain distance to their prey to detect it efficiently (63). So, if the whales did not find better opportunities in the offshore habitat, they likely relied on their memory and returned to their original foraging grounds, resulting in the long roundtrip behavior, possibly better defined as a searching trip.

Examining what modes make up these longer excursions further supports the theory that these trips primarily serve a searching purpose. The long roundtrips consisted of mainly ranging behavior (60%), suggesting that the whales spent most of their time on the shelf searching through a larger area, where valuable food patches worth stopping for appeared to be scarce. Encamped, nomadic, round, and semi-round trips are mostly found inside the fjord areas, but in some cases also documented offshore on the shelves in shorter sections. The transition from ranging behavior to encamped mode during a long roundtrip could suggest a potential encounter with a prey patch. During a partial long roundtrip is it plausible that the whales located a region with a more abundant prey patch, and thus did not return to the original starting point.

In a future study it would be worthwhile to incorporate data on prey abundance (if available) in conjunction with the humpback whale data to confirm or reject this hypothesis (3). Anyhow, the shift away from ranging behavior on the shelfs could be influenced by other events than foraging, e.g. resting or socializing. Humpback whales are known to engage in social behaviors and surface activities, including peduncle throws and tail slapping, during which they tend to be more stationary (37). However, considering the presence of overwintering herring on the continental shelf (44), and the likelihood of higher whale densities within the fjord areas for socializing, we contend that the "long roundtrip" behavior primarily revolves around food-seeking activities as a precursor to their southward breeding migration.

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 affect the results and sensitivity of the analysis. Determining the optimal values for these parameters specific to our dataset required a careful balance between minimizing the temporal scope around expected change points and achieving the desired analytical power (22, 50). The analysis was applied to data with 3-hour timesteps, excluding all behavioral change points within smaller temporal spans. Whales dive, and satellite tags only receive signals when the whales surface, resulting in unpredictable time intervals per signal and restricted quality compared to tracking data from terrestrial animals (40, 52). This could prospectively explain some of the undefined segments in our results or suggest humpback whale behavior does not always align precisely with the predefined modes used 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/or hydrophone (67). The downside of these tags is they have limited recording durations, often just a few hours, so they would not be able to identify the long roundtrips or movement modes in relation to seasons. Nonetheless, our results successfully described multiple movement modes at small to intermediate scales, revealing individual variations in behavioral patterns during the stop-over period in North-Norwegian fjords and thus fill inn some knowledge gaps about humpback whale behavior.

Conclusions

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. The satellite-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 in 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.

Abbreviations

AIC: Akaike information criteria; BCPA: Behavioral change point analysis; CRW: Correlated random walk; BIC: Bayesian information criterion; CC: Concordance criterion; NSD: Net squared displacement; NSS: Norwegian spring-spawning.

Declarations

Ethics approval and consent to participate

Tagging procedures were approved by the Norwegian Food Safety Authorities (Mattilsynet), under the permit: FOTS-ID 14135, and evaluated by an accredited veterinarian (Mattilsynet Report nr. 2017/279575).

Consent for publication

Not applicable.

Availability of data and materials

Data can be available upon request.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

All authors have agreed to be listed and approve the submitted version of the manuscript. IYU, EFV and AHR conceived of and designed the study; AHR provided funding; EFV, MB and AHR performed the field work; IYU, MVR and EFV performed the analysis; IYU, EFV, MB and AHR contributed data or analysis tools; IYU, EFV and AHR drafted the manuscript; IYU, EFV, MB, MVR and AHR approved of the final version of the manuscript.

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