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Characterizing humpback whale behavior along the North-Norwegian coast

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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 3-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 To investigate whale behavior during this seasonal stopover, we 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 manually 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.

Conclusions 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 could be useful to analyze local scale movement patterns of satellite tagged whales.

Keywords Humpback whale, *Megaptera novaeangliae*, Satellite telemetry, Movement ecology, Foraging behavior

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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 internal factors (e.g. genotype, status, history), and external factors (e.g. environment, competition) [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, where they stay during summer to early winter, to breeding areas in more tropical regions, where they stay during late winter to spring [9–11]. Based on genetic studies suggesting limited gene flow between ocean basins, the species is considered to be divided into three main populations: The North Atlantic, North Pacific, and Southern Hemisphere population [12–14]. Among these, one individual of the North Atlantic population undertook the longest recorded humpback whale migration, covering about 9000 km one-way from feeding areas in the northern Barents Sea to tropical breeding areas in the Caribbean or Cape Verde [10]. This confirms previous observations of these long-ranging migrations based on photo-ID [10, 15].

Humpback whale diet is variable across different populations and feeding grounds based on prey availability and predictability, varying from zooplankton such as krill (*Euphausiacea*), to small schooling fish like capelin (*Mallotus villotus*) and herring (*Clupea harengus*) [16, 17]. In the Northeast Atlantic, humpback whales exhibit a preference for krill and small schooling fish species, including herring, capelin, blue whiting (*Micromesistius poutassou*) and mackerel (*Scomber scombrus*) [17–19]. Over 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, 20, 21]. 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 increase energy reserves before they later migrate to the southern breeding grounds in the Caribbean [14, 20]. The establishment of these foraging sites in northern Norway coincided with the occurrence of dense herring concentrations in these fjord systems from 2010 onwards, with potential future shifts as herring migration patterns change [15, 21]. Before 2010, herring in northern Norway overwintered mainly in offshore waters northwest of Andøya island [22]. However, since 2010, there has been a shift, where the dense herring concentrations appearing along the coast and in fjords have influenced the distribution of humpback and killer whales, leading to a northward shift within fjord systems [3, 4, 10]. The altered migration and overwintering patterns are attributed to strong age classes dominating school behavior [15, 17–19, 21, 22]. The foraging site in northern Norway has become a significant part of the annual routine for some northeast Atlantic humpback whales. This occurrence of whales near the coast and populated areas provided a unique opportunity to study their detailed behavior [3, 23–25].

According to *optimal foraging theory,* animals will adapt their foraging behavior to allocate resources as efficiently as possible [26–28]. 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 [29]. The theory predicts that when prey density in an area declines, the net foraging efficiency declines and a predator may choose to switch to a different prey species, or move to a different prey patch of equal or better quality [30]. Evidence of this behavior have been shown for killer whales and humpback whales in Norwegian waters by Vogel et al. [3, 4]. Given the dynamic nature of the marine environment, where prey distribution is often patchy and changing over time, predators have to strategically manage their resource utilization to maximize their net energy intake. As prey density declines within an exploited patch, predators may benefit from transitioning to a different patch with higher prey density [15]. How long a predator chooses to remain within a particular prey-patch depends upon the value (energy density) of the present patch, the expected value of alternate patches, as well as the time it will take transiting between the patches [27, 30, 31]. 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 [30]. Marginal value theory has been examined in Norwegian killer whales [25], and it was determined 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. Similar excursion behavior has been described for humpback whales in the same area by Rikardsen [20]. This behavior is intriguing because the whales leave a fjord where there is seemingly higher herring density than outside based on fishery statistics [32]. Such behavior could appear contrary to what optimal foraging theory and marginal value theory would predict [33, 34]. However, net energy intake is determined by energy intake minus energy expenditure, and there are several factors affecting whether this behavior is contrary to 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 [25].

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 [33, 34]. For humpback whales, both large-scale and smaller-scale movement patterns have been extensively documented over the past decades for some populations [35–40]. Recent research on humpback whales along the Norwegian coastline has focused on examining more long-range migration routes, and has documented specific fjords in Northern Norway as foraging grounds before the whales proceed with their migration [10, 15, 41]. However, no studies to date have undertaken an analysis of their behavior within these fjords, characterizing multiple movement modes that extends beyond the common distinction between directed movements (taken to represent 'travelling') versus meandering movements within a region (often assumed to represent 'searching' or 'feeding') [7, 42, 43]. Being able to identify distinct movement modes is important to understand relations between an animal and their physical or biological environment [25, 44].

New methodical techniques have been developed to segment continuous time series data and identify small-scale behavioral modes of animals [45], 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 [3, 23, 24]. While these studies typically utilized two [3, 23] or three [24] discrete behavioral modes to describe behavior, some used continuous behavioral indices [3]. A killer whale study in our region from 2021 [25] took this a step further and classified killer whale movement into five different discrete behavioral modes. Applying a similar method on humpback whales in the same area could be useful to fill knowledge gaps about behavior in the fjord areas, and also provides the opportunity for comparison with killer whales in the same area.

The main objective of this study was to characterize humpback whale movement patterns during their seasonal stopover along the North-Norwegian coast. Additionally, we aimed to identify and describe extended temporary excursions beyond the fjords frequently observed in our satellite telemetry data and supported from repeated photo-ID sightings in different fjord systems. Our initial sub-goal involved segmenting humpback whale tracks into five distinct movement modes to examine their behavioral patterns and individual variability. Subsequently, we investigated the sequential order of movement modes, potential interrelationships between them, and how these dynamics varied by season and geographic area. Lastly, our exploration extended to the identification and analysis of longer excursions, lasting more than 3 days, away from and back to the fjord systems, encompassing an investigation into movement modes within these extended excursions.

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 (Figs. 1 and 2). 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 to 16 km and consist of both shallow and deep areas (maximum depth ~ 270 m) [15, 46, 47]. 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 is generally deeper than the Tromsø area with a maximum depth of 400–450 m [47].

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 [48]. In the fjord areas, the herring overwintering outside Tromsø and Skjervøy took place from 2010 onwards [3, 22, 48]. These large aggregations of overwintering herring inside the fjords attract humpback whales, killer whales, and large fishing fleets competing for this common resource [3, 10, 14, 15]. The exact number of humpback whales out of the total population entering the fjords on their migration down is not known. However, estimates based on photo-identification analysis in Norwegian waters suggest that perhaps 400–500 individuals are present at one point or another during a given season on these overwintering grounds inside the fjords [14]. With the estimated humpback whale abundance in the Norwegian Sea and Barents Sea at about 10,708 [49], it suggests that approximately 3–4% of the population visits the fjords. The presence of

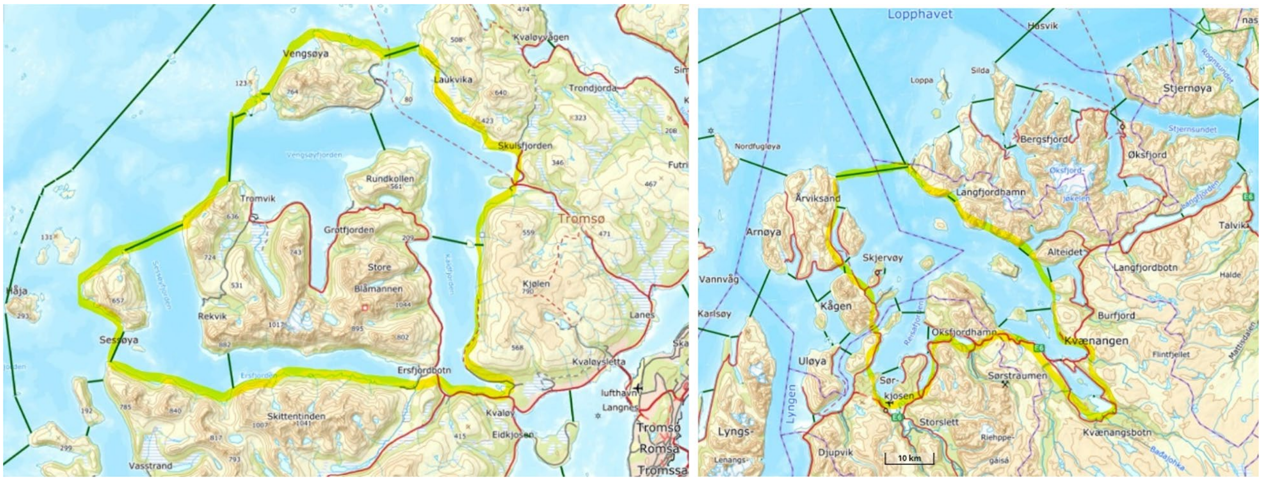


Fig. 1 Map of Tromsø area to the left, and Skjervøy area to the right, with fjord borders sourced from Fjordkatalogen. kartkatalog.miljodirektoratet.no/MapService/Details/fjordkatalogen

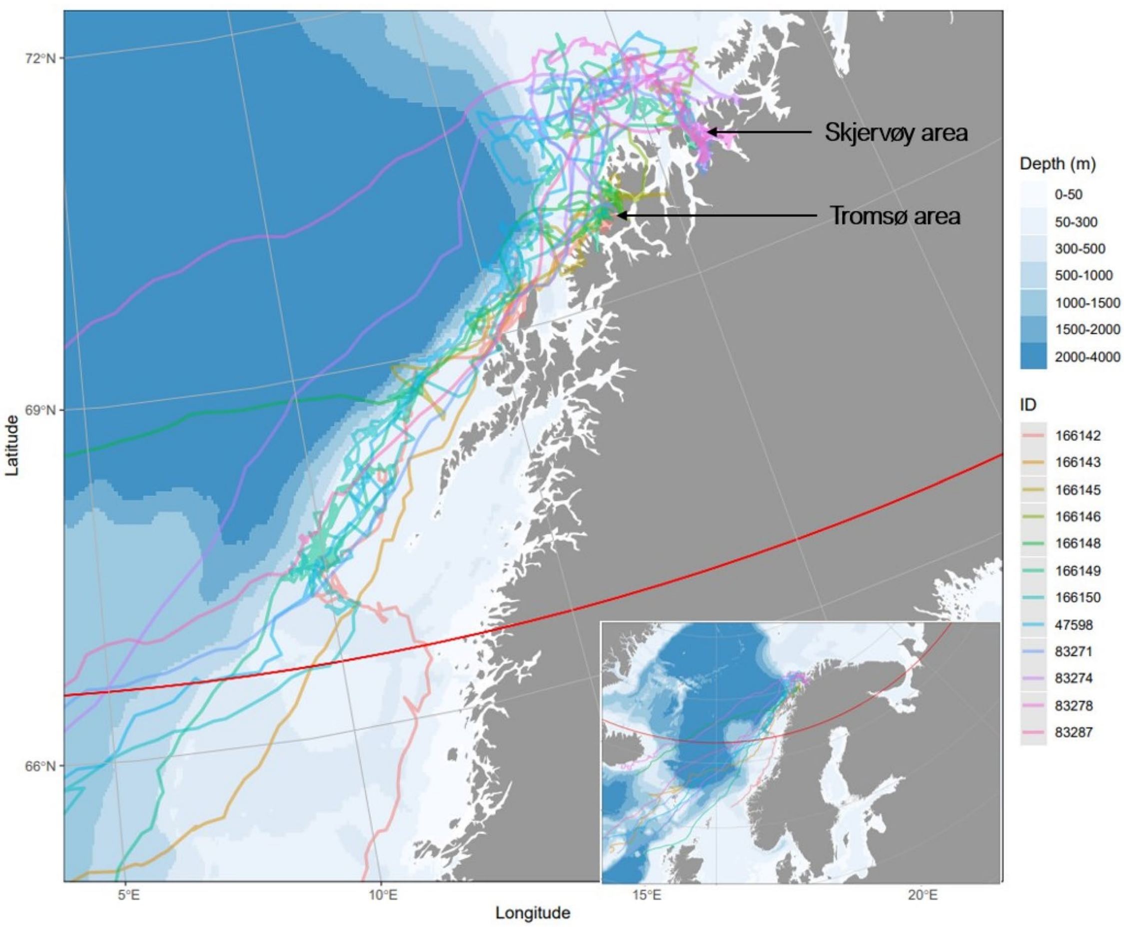


Fig. 2 Tracks of the selected 12 satellite tagged humpback whales (2016–2019) along the coast of Northern Norway. The Arctic Circle (66° 33′ N) represented on this map as a red line, was set as the southern border for the study since beyond this point the whales had seemingly started on their southward breeding migration. The small map shows the tracks including the Norwegian Sea. Individual whale tracks are color coded by unique tag ID numbers

the whales close to shore in these areas provides a unique opportunity to do research on this species [15, 22, 24].

Tagging/instrumentation

The tagging was done over a 4-year timeperiod (2016–2019) from December to January in both fjord areas (see Supplemental Table S1). Argos Satellite tags (SPOT 302/303, Wildlife Computers, Redmond WA, USA) were deployed on 20 individual humpback whales, using the best practice guidelines for cetacean tagging [50]. 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 22 ft 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 [51], as the tags 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 [50]. 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 to fieldwork and just before deployment.

Tags were programmed to transmit about 16 times per hour for the first 3 months, then the number of transmissions was reduced to 14–12 transmissions per hour for the following 4 months, and after that to about 3–4 transmissions per hour until the tag either fell off the whale or the battery died. Photographs were taken for individual whale photo-identification.

Data collection and processing

Characterizing movement patterns of humpback whales on a local scale (within a fjord or between fjord areas) requires a consistent series of location data without large gaps. Several tracks in the raw data had multiple extended gaps of between 4 and 10 h that made the tracking incomplete, therefore these tracks were removed to avoid any spurious data points when further applying the analysis. 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 on a local scale 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, the analysed whales did not return to any fjord systems and were consequently considered to have initiated their breeding migration. Therefore, they were deemed not relevant for the scope of this study.

Location estimates from tags were provided by the CLS–ARGOS service and prefiltered using a Kalman filter in a state-space framework, following the approach described in Lopez et al. [52]. 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 [53]. The CRW was applied using the 'fit_ssm' function in the package 'foieGras' [54] and the time step was set to 3-h intervals following practices by Vogel et al. [55] and Van Ruiten [25].

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 points within each window [8, 56]. 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' [56].

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 (V_p) was chosen as it is a continuous variable within (0,1), that combines speed and turning angle into one single index of movement persistence. V_p was calculated by mapping the UTM coordinates from our dataset and extracting velocity and angle information from the trajectory data. The window size specifies the number of consecutive data points that are considered together to assess the behavior of the animal. A greater window size will include more data points, and thus increase the goodness of fit. A smaller window size will identify finer-scale structures in the data, but at the increased risk of spurious change points that might not be significant or representative of the animal's behavior [25, 56]. The sensitivity parameter K is adjusted to compensate for possible spurious change points. As a smaller window size is more sensitive, a lower K decreases sensitivity, requiring stronger evidence for identifying change points [25, 45]. The cluster width refers to the temporal range where successive changepoints are considered to be within the same cluster [25, 57]. A decreased cluster width enhances sensitivity to short-term changes but comes with the trade-off of an increased risk of false positives. 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. In the BCPA analysis, the chosen window size of 40 implies that 40 datapoints are considered in each window sweep to identify change points in the dataset. Given the 3-h timestep between data points, this means changepoints were defined within a time frame of 120 h. A detailed description of the BCPA methodology can be found in Gurarie et al. [56].

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. [58] for moose (*Alces alces*), Morelle et al. [45] for wild boar (*Sus scrofa*), and Van Ruiten [25] 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. Roundtrip and semi-roundtrip were differentiated by comparing NSD value at the initial inflection point (NSD_{inf}) to the overall change in NSD from the beginning to the end of the segment (NSD_{net}). Segments were classified as a roundtrip if $NSD_{inf} > NSD_{net}$, and as semi-roundtrip if $NSD_{inf} < NSD_{net}$. 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. Speeds were determined based on the distance travelled away from the starting position over a certain number of hours.

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 location and the initial location of the movement path [59]. 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 [45]. NSD was calculated for each segment generated by the BCPA, by applying the function 'as.ltraj' from the package 'adehabitatiLT' [60]. As previously described in Bunnefeld et al. [58], Morelle et al. [45], and Van Ruiten [25], mathematical curve equations that best represent each movement mode were selected (Table 1). The R package 'FlexParamCurve' [61] and a script supplied by Morelle et al. [45] and Van Ruiten [25] (see Supplemental script 1) was used to fit the subsequent mathematical curve equations independently to the NSD data from each segment.

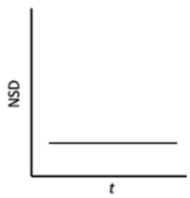
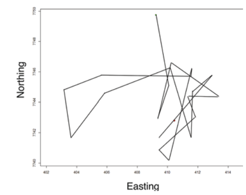
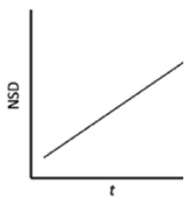
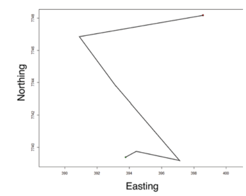
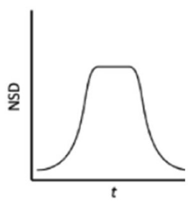
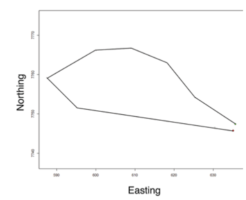
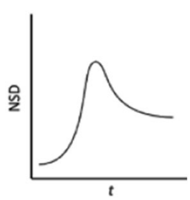
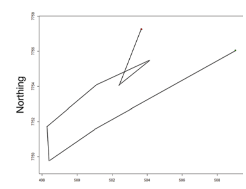
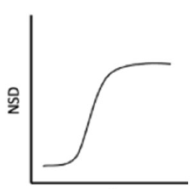
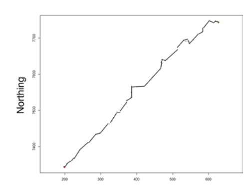
Concordance criterion (CC) was used to evaluate the model fit per segment, for candidate movement modes represented by non-linear equations [25, 45, 62]. CC quantifies the accuracy and precision between observed and predicted estimates, with values ranging from -1 to 1. Values close to 0 indicate a lack of fit, while larger absolute values suggest an improved fit, and ± 1 indicates perfect concordance. Each segment is categorized based on the movement mode with the highest absolute CC value.

For the linear equation involving constant NSD ($NSD = c$, Table 1), CC is not applicable. In such cases, we used the Akaike Information Criterion (AIC) instead. Segments with CC values above or below a threshold of 0.7 are considered poorly fitted. If a segment is poorly fitted, we classify it as encamped, given that the model has the lowest observed AIC.

Mapping and visual examination of whale tracks; identifying and characterizing long roundtrips

The methods outlined in the preceding sections did not allow for identification of longer roundtrips, lasting multiple days with varying durations (from 3 days to weeks). The primary challenge arose in determining appropriate values for the adjustable parameters in the BCPA model for each individual whale, given the substantial variability in the temporal extent of these prolonged roundtrip behaviors. The BCPA identifies significant changepoints in movement parameters, such as speed and turning angle. Consequently, if a whale undergoes a marked behavioral change during a long roundtrip excursion, the targeted long roundtrip behavior in this study may be split into shorter segments, and therefore not be accurately identified. Hence, a more efficient way to identify long roundtrips was to plot CRW whale tracks of 3-h timesteps on maps to visually observe movement patterns using the R package 'ggOceanMaps' [63] and 'leaflet' [64]. As the longest segment identified with the BCPA model in our study was 70 h (2.9 days), the definition of "long roundtrip" was set to 3 days or more. The term "complete long

Table 1 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. Table is adapted with permission from Van Ruiten [25]

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

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. [61] for more details on equation parameters. See text for description of the different movement modes

roundtrip" in this study is defined as a looping behavior, where a whale leaves a specific fjord area, and later re-enters the initial fjord area more than 3 days later. If a whale leaves a specific fjord area, performs a looping behavior offshore lasting more than 3 days before it returns to another fjord area, this was defined as a "partial long roundtrip". Fjord borders utilized to define fjord areas were sourced from Fjordkatalogen (Fig. 1) [65].

Smaller-scale behavioral movement modes performed within the long roundtrips were explored, aiming to understand how whales were spending their time during these 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 (Fig. 2). 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) was 36 days, with individual durations ranging from 8 to 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 and 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 19th (Table 2).

Segmentation and classification

Based on hours spent in each behavioral movement mode, ranging behavior was the overall most common (Table 3), making up 53.04% of all whale tracks. The following most common movement modes were encamped (13.45%), undefined (10.87%), nomadic (10.40%) and roundtrip (10.23%), respectively. The least common movement mode was semi-roundtrip (2.03%). In total, the whale tracks were divided into 290 segments generated through the BCPA analysis. Classification of candidate movement modes succeeded in 243 segments (83.8%), 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. While not all whales displayed all five movement modes, ranging behavior was observed in all individuals. Additionally, among the other movement modes, encamped, nomadic, roundtrip and undefined modes were evenly represented within each deployment. Semi-roundtrips were only exhibited by four individuals. The use of five movement modes was justified by statisticaly comparing the average value of each modes move persistnace (Supplemental text 1 and Figure S1).

Table 3 Descriptive statistics for each classified movement mode

Movement mode	*N*	Duration (h)	Total distance traveled (km)	Speed (km/h)
Roundtrip	22	42.0 ± 18	84.7 ± 49	3.0 ± 1
Semi-roundtrip	6	30.5 ± 10	58.2 ± 23	2.8 ± 1
Rging	158	30.3 ± 14	102.6 ± 93	4.7 ± 2
Nomadic	31	30.3 ± 12	81.2 ± 56	4.1 ± 2
Encamped	26	46.7 ± 14	64.1 ± 28	2.1 ± 1
Undefined	47	20.8 ± 12	46.3 ± 29	4.1 ± 3
Total	290	200.6 ± 34	437.1 ± 127	20.8 ± 5
Mean	48.3	33.4 ± 9.3	73.3 ± 47	3.6 ± 2

N is the number of segments classified per mode. Duration, total distance traveled, and speed, are all shown in mean ± SD

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. 3, Table 4). Ranging behavior often appeared repeatedly, where a segment classified as ranging was followed by a second segment also classified as ranging. Ranging also sometimes occurred in-between

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)

Tagging location	Whale ID	Deployment date	Tracking duration (days)	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		

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 (*)

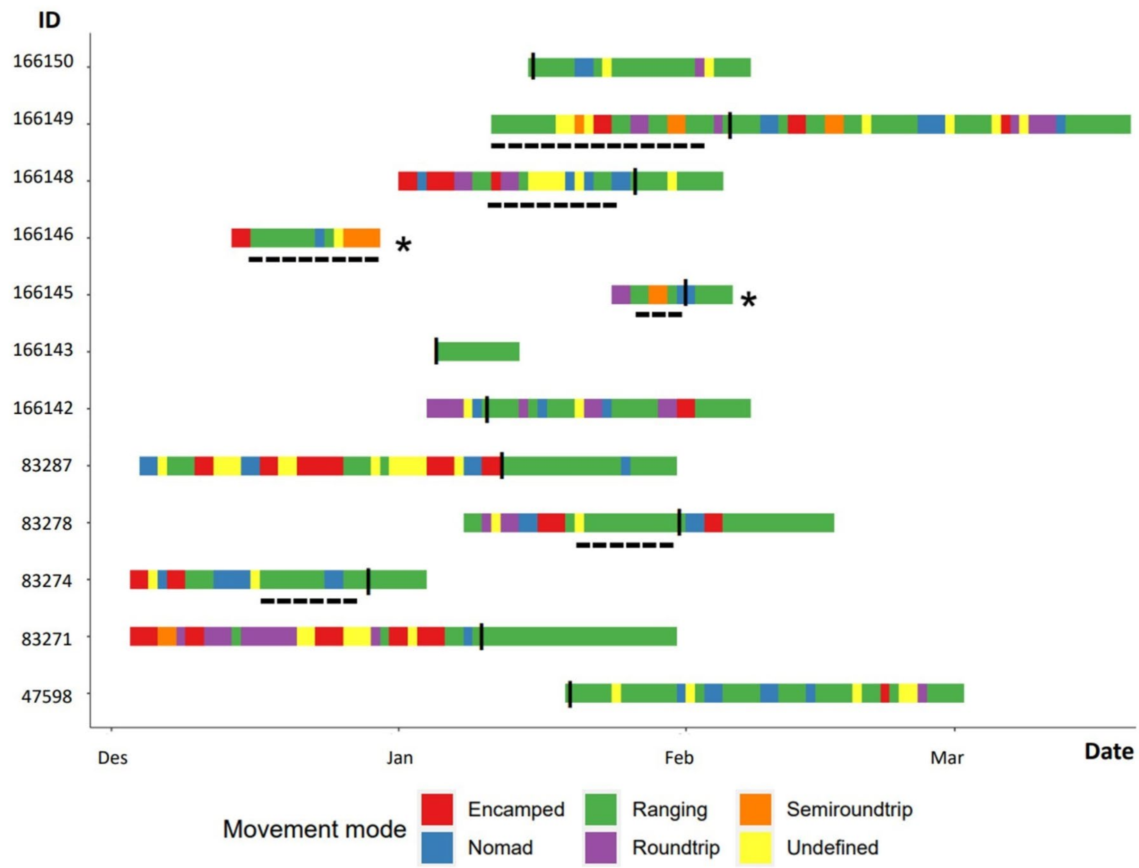


Fig. 3 Sequences of movement modes for each individual whale (ID, *y*-axis) over time (month, *x*-axis) during winter and spring across a temporal span of 4 years (2016–2019) for 12 satellite tagged humpback whales at the Tromsø and Skjervøy fjord areas. Counting from the origin, the bottom five whales (47598–83287) were tagged in Skjervøy area, while the top seven whales (166142–166150) were 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

	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)
Nomadic	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)

The conditional probability of "Second Mode" occurring given the "First Mode" already occurred are represented in percentage in the parentheses

other modes. All whale tracks contain a dominant proportion of ranging behavior distributed throughout the whole track (see Supplemental Figure S2), with the relative amount in relation to other modes increasing from mid-January towards the spring months (February–March) after leaving the fjord areas (Fig. 3). 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 was rare.

Visually identified long roundtrips

Half of the whales performed at least one complete and/or partial long roundtrip away from the fjord systems where they were tagged, lasting for 4–22 days (average ~ 11 days) (Fig. 4). 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. Three whales (166145, 166148 and 166149), left the initial tagging area (Tromsø) and transited to a different fjord area, defined as a partial long roundtrip. Thereafter, they returned to the initial fjord area (Tromsø). Therefore, these whales conducted both a partial and a complete long roundtrip. Whale 166148 completed a full long roundtrip (10 days) from the Vengsøyfjorden Tromsø area, departing on January 11th and returning on January 20th. This whale subsequently undertook a partial roundtrip on the shelf before beginning its southward migration. Whale 166149 was tagged in Sessøyfjorden in the Tromsø area January 11th, moved north and entered Kvænangen fjord Skjervøy area January 18th, before returning to the Tromsø area February 2nd (22 days). Whale 166145 completed a long roundtrip from the Tromsø area lasting for 4 days, including a transit to and movements within the fjords of Senja island before returning to Tromsø (Fig. 4).

Two whales performed partial roundtrips 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).

Movement modes within long roundtrips

Within the six documented long roundtrips, 60% of the segments were classified as ranging behavior. Some individuals completed a roundtrip and/or a semiroundtrip as part of the long roundtrip. Roundtrip and semiroundtrip both constituted 5% of the classified segments within the long roundtrips. Encamped accounted for 5%, nomadic for 10%, while 15% of the segments within the long roundtrips were not classified. Ranging was dominating in the areas outside the fjord systems. The remaining modes (roundtrip, semi-roundtrip, encamped and nomadic) were more frequent inside the fjord systems, but also occasionally found in shorter sections offshore (166149 and 83278) (Fig. 4).

Discussion

This is the first study to characterize humpback whale movement patterns during their seasonal stopover at the North-Norwegian coast. Classification of movement modes was successful 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 half of all generated segments. Ranging is characterized by straight and fast movement (4.7 km/h), resembling transiting behavior in former studies [66, 67]. Encamped mode, characterized by slower speeds (2.1 km/h) and increased turning rates, could indicate intensified foraging, and was often seen in fjord areas with high herring abundance [3, 5, 14, 55, 68]. This behavior represented about one-tenth of all segments, but dominated within the fjord systems. The distinction between ranging and encamped modes is similar to the commonly assessed transiting versus area-restricted search behaviors in previous studies [3, 23, 24, 66, 67, 69, 70]. Models with only two modes, such as transiting versus area-restricted search, are commonly understood to be an oversimplification [69, 70]. This study suggests that movement behavior of humpback whales is more complex than these binary classifications. While our analysis identifies five distinct modes, it is important to note that the number of behavioral modes that can be effectively classified likely depends on the scale and resolution of the data collected. Although the classification process with five movement modes can be completed and covers a significant percentage of all segments (84%), further research is needed to validate the ecological significance of these additional modes.

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 one-fifth of all segments. Nomadic and roundtrip behavior was performed by all whales except one, which left the fjords for migration immediately after tagging. The behaviors are possibly driven by changes in prey density and distribution [27, 33]. Nomadic behavior may

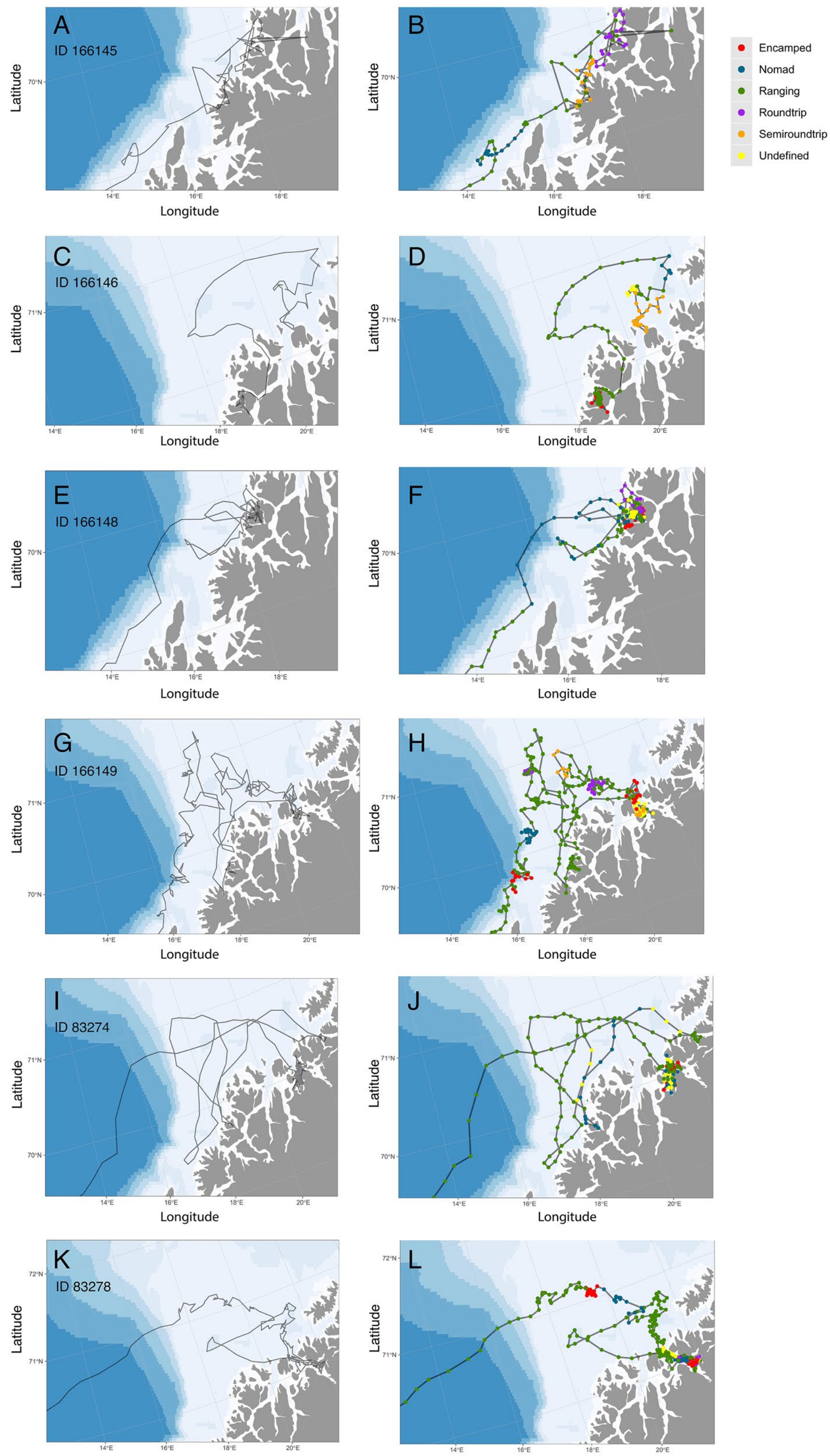


Fig. 4 Overview of partial- and complete long roundtrips conducted by six of the 12 analyzed whales. Individual whales are presented per row and marked with whale ID. On each row, the maps to the left and right show the same whale track, but to the right, tracks are segmented and colored by the corresponding movement mode classified

be linked to search activities conducted during foraging, for instance if a whale starts searching for an alternative prey patch in response to a decline in foraging success in the current patch. 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 where 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 [30]. 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 that the humpback whales' shift in behavior is affected by prey densities [3].

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, which could suggest 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, 22, 38] and the NSS herring density inside the fjords starts to decrease [3]. There was no clear pattern in the order of movement modes. This agrees with findings from a similar analysis on killer whales [25], suggesting that factors influencing movements include prey and environmental factors such as season and habitat, rather than specific sequences.

This study is also the first to identify and describe humpback whale long excursions away from inland feeding areas. 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 [30, 71]. However, results found that half of the whales left the fjords to go on multiday offshore excursions lasting from a few days up to 3 weeks before later returning to the initial fjord 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 [72], such as to where some of the herring aggregate and overwinter 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 declines. Although the whales were 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 [22]. 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, 38]. However, foragers do not always possess comprehensive information about their environment; they must maintain a certain distance to their prey to detect it efficiently [69]. 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 provides insights into the nature of these trips. Movement mode statistics for whales that engaged in a long roundtrip were not remarkably different from those that were not. The long roundtrips consisted of mainly ranging behavior (60%), suggesting that the whales were moving through a larger area. 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 it is plausible that the whales located a region with a more abundant prey patch, and thus did not return to the original starting point.

In any case, the shift away from ranging behavior on the shelves could be influenced by events other than foraging. Competition, predation, and anthropogenic disturbances are just a few other possible reasons an animal might change its behavior and/or relocate from one area to another [5, 6]. Marine mammals often target the same resources and areas as, for instance, commercial and recreational fishing [6, 24, 73–75]. Prey resources are also often present in areas where other human activities occur, for instance related to offshore energy industry or military naval activities [73–75]. In addition, whale aggregations may also lead to an interest in direct tourist activities, such as whale watching. All the above may influence the behavior of whales, by eliciting either avoidance or attraction movements. Several studies investigate the effects of noise from boat traffic and offshore energy installations, particularly concerning various whale species that rely on sound for communication over long distances, as well as for echolocation to find food and navigate [73–75]. Operational interactions with fisheries, such as entanglement in fishing nets, as well as increased foraging opportunities that attract whales to fishing vessels, have been documented in Norwegian waters [24]. Shift in movement patterns could also be caused by 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 [42]. Given the absence of specific prey data or environmental information, we cannot draw firm conclusions about the entire set of drivers behind observed humpback whale movements. Future studies incorporating detailed prey and environmental data could provide a more robust foundation for understanding the driving factors behind the observed movement patterns.

This study aimed to characterize local 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 [25, 51]. Other increasingly used methods for capturing complex behavioral patterns from whale telemetry data exist, such as hidden Markov Models (HMMs) [76, 77] and the move persistence model within aniMotum [78]. However, BCPA was chosen due to the specific objectives and context of our study, as it was used in the particular studies that inspired our work, offering clear benefits for comparative analyses and interpretability.

In the visual representation of humpback whale movement modes (Fig. 4), segments that appear similar on the map may actually represent different time scales (e.g., movements occurring over shorter or longer durations). This can cause certain movement patterns, such as seemingly looping behaviors (roundtrips), to appear in different colors than expected (e.g., a behavior expected to be purple may appear green). This apparent misclassification arises because the temporal aspect is not visible on the map, leading to visual inconsistencies that do not necessarily indicate inaccuracies in the underlying classification methodology. Despite these visual inconsistencies, NSD remains a valuable method for characterizing movement patterns over time, as it provides insights into the temporal dynamics of whale behavior that are not captured by spatial data alone. The maps, despite their limitations, are still useful for visualizing general movement trajectories and identifying potential areas of interest or behavioral changes.

Errors and irregular time series associated with Argos data could also potentially influence behavioral classification. There are several potential reasons for intermittent longer gaps in the location data. For instance, poor coverage could result from whales having entered into narrow fjords surrounded by steep mountain sides, limiting the time period during one satellite pass for which transmissions could be received [3, 52, 54]. More than one signal must be received in order for the Argos system to estimate a position. It is also possible that high swell conditions, especially in combination with tags being positioned slightly low on the body of a whale, can limit the transmissions sent from a tag [50]. The analysis was applied to data with 3-h 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 [45, 58]. 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 [79]. 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. Palacios et al. [80] introduced the RDW tag, an advanced Argos tag that could possibly serve as an intermediary between traditional Argos tags and CATS cam. This innovative satellite telemetry device enables prolonged observation of large whale movements and dive behaviors without the need for recovery [80]. The study showcases the tag's effectiveness through validation experiments and simulations, offering transformative insights into whale physiology, behavior, and ecology over extensive geographic ranges and multi-month timescales. In a future study, such a tag may potentially mitigate some of the weaknesses inherent in this current study. 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 in some knowledge gaps about humpback whale behavior.

Conclusions

The satellite-tagged humpback whales showed complex strategies on varied spatiotemporal forms during their stop-over to increase energy reserves in Northern Norway, before they continued their migration to southern breeding grounds. One of these strategies involved longer excursions away from and back to the fjord areas. During these excursions, it seemed that the whales engaged in behavior that might have suggested searching for enhanced feeding opportunities beyond the fjord systems. In the absence of concrete evidence supporting this interpretation, it should be noted that this speculation requires further investigation and data on, for example, prey distributions and vertical movement of the whales. Nevertheless, the observed pattern involved a return to the fjords to resume their feeding activities. This behavior might have been indicative of a search-and-return pattern to foraging grounds, though definitive conclusions await additional empirical support. 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. 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

Supplementary Information

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Supplementary Material 1.

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Author 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, MV and EFV performed the analysis; IYU, EFV, MB, MV and AHR contributed data or analysis tools; IYU, EFV and AHR drafted the manuscript; IYU, EFV, MB, MV and AHR approved of the final version of the manuscript.

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Availability of data and materials

Data can be available upon request.

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.

Competing interests

The authors declare no competing interests.

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