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A new look at whale behavior: identifying multiple spatial movement patterns of Norwegian killer whales

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Cover photo: Male killer whale (Orcinus orca) traveling through Kvænangen fjord, Northern Norway in late November 2020. Photo: Meghan Van Ruiten

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Abbreviations

BCPA – Behavioral change point analysis

CC – Concordance criterion

CRW – Correlated random walk

NSD – Net squared displacement

NSS – Norwegian spring-spawning

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1 Abstract

Studying an animal's movement patterns in both space and time can shed light on the strategies individuals use to optimize foraging and adapt to seasonal and environmental variation. Killer whales (*Orcinus orca*) are dynamic, apex predators inhabiting all the world's oceans, preying and specializing on a wide variety of prey. Over the last decade, large numbers of Norwegian killer whales have been found feeding on high concentrations of over-wintering Norwegian spring-spawning (NSS) herring (*Clupea harengus*) in fjords of northern Norway, before often traveling to southern herring spawning grounds to continue their feeding. Smaller-scale movement patterns across habitats are less understood. This study classified Norwegian killer whale movement into five different movement modes based on satellite tracking data. To do this we used a behavioral change point analysis (BCPA) to select robust, homogeneous velocity-persistence states at intermediate scales and then modeled the net squared displacement (NSD) over time to differentiate movement patterns. The identified modes were residence/restricted area search, transiting/traveling, nomadic/wandering modes, as well as unique round trip and partial trip behavioral movements. Totally 95.4% of segments were classified into candidate movement modes. Collective whale movement showed consistent use of all classified behavioral movement modes across differing key herring associated areas suggesting the novel candidate modes proposed reflect strategies for optimal foraging. Individual variation in movement patterns suggests potential divergent foraging strategies among individuals or groups of Norwegian killer whales, and highlights the gaps in knowledge regarding the variation of smaller-scale search and dispersal movements in this species. Sequence analysis of behavioral modes reveals no clear patterns at intermediate spatiotemporal scales, suggesting environmental or prey field factors having more influence over movement decision making. This study can serve as a baseline for future comparative studies regarding fine-scale behaviors of Norwegian killer whales, as well as analyzing satellite tracking data of other marine animals.

2 Introduction

Understanding how and why animals move is a fundamental question within ecology. Animals are able to adapt different complex behaviors and movement strategies in order to interact with and utilize resources within varying environments (Mueller & Fagan, 2008; Nathan et al., 2008; Schick et al., 2008). Movement can occur at various spatial and temporal scales and in a variety of forms, from daily foraging, seasonal migrations, permanent dispersals to random nomadic movements depending on the requirements of the individual and the availability of resources (Mueller, 2008; Giuggioli & Bartumeus, 2010). While there might be some general approaches for optimizing movement, there are substantial differences between species and even populations. Movement is a complex process that depends on an animal's internal state, physiological limits, and environmental factors (Shaw, 2020). All of these factors affect and result in a movement path containing a combination of different behavioral movements, shaping the distribution and structure of populations (Schick et al., 2008; Gurarie et al., 2016). Thus, knowledge of movement patterns and frequencies of movement is essential in understanding an animal's ecology (Hansson et al., 2014).

In the marine environment, the movement and behavior of marine predators are often influenced by their prey distribution and abundance (Womble et al., 2014). For example, if predators specialize on prey that migrates then the predators are likely to follow their prey during their migration (e.g., Abrahms et al., 2019). In contrast, if predators specialize on non-migratory prey then they are likely to be more resident and instead exhibit different localized searching strategies, such as near-far searches (Motro & Shmida, 1995; Ford et al., 1998; Reluga & Shaw, 2015). Alternatively, predators that are more generalists, or able to feed on multiple prey species, may exhibit varying movement patterns and strategies in order to obtain the particular prey species they are targeting (Suryan et al., 2000). *Optimal foraging theory* suggests that to maximize fitness, an animal will adapt foraging strategies that increase food intake and decrease costs, maximizing net energy gained and ultimately increasing fitness (Pyke et al., 1977). Prey sources are often unpredictable and patchily distributed in marine environments, and thus predators must decide which prey patch it will exploit and when it will leave (Doniol-Valcroze et al., 2011). The *marginal value theory* predicts that within patchy environments, a predator should leave the current patch when the energy intake rate drops to the average capture rate, or in other words, they will spend relatively more time within valuable patches that are farther from other patches, and less time in patches that are less valuable and

nearer to other patches (Charnov, 1976). This means that the time an individual spends within a patch depends upon the value of the current patch, the value of other patches, and the time it would take to travel to the next patch (Werner & Hall, 1974; Cowie, 1977; Pyke, 1984). Thus, studying an animal's movement patterns and variations in both space and time can shed light on the strategies individuals use to search a given area and optimize foraging (Weimerskirch et al., 2005; Doniol-Valcroze et al., 2011; Reluga & Shaw, 2015). While prey distribution and abundance can influence a predator's movements to a large degree, other intra-, interspecific and abiotic interactions must also be considered. For example, high densities of predators can lead to resource competition among individuals or groups and result in increased dispersal rates (Matthysen, 2005). Alternatively, dispersal patterns may arise when individuals are locating mates, e.g., with males being more likely to search for areas with more females and fewer males (van Overveld et al., 2014). Therefore, variation in some movements may be due to local population dynamics. Similarly, variations within environments or habitats can lead to differences in movement, such as unpredictability in surroundings can result in random or nomadic movements of marine predators (Mueller & Fagan, 2008).

Killer whales (*Orcinus orca*) are dynamic, apex predators with a global distribution that are known to display a large variety of behaviors and movements (Ford, 2009; de Bruyn et al., 2013). These large, toothed whales inhabit all the world's oceans preying on a wide variety of prey, including fish, seals, seabirds, and other cetaceans (de Bruyn et al., 2013). While killer whales are considered generalists on the species level, specialized diets, and movement patterns have led to the evolution of killer whale ecotypes that exploit specific prey species and ecological niches (Foote et al., 2009, 2010; Ford, 2009; Morin et al., 2015). For example, in the northeast Pacific and Antarctica multiple ecotypes, which have overlapping geographic ranges, have been defined based on the relationship between specific prey and/or movement patterns (Ford et al., 1998; Andrews et al., 2008). In the northeast Atlantic, including the Norwegian coast, the estimated population of killer whales is about 15,000 individuals (Leonard & Øien, 2019), where many are present year-round along the Norwegian coast (near and offshore) but also regularly found near Iceland, Svalbard and in the Barents Sea (Jourdain et al., 2019; Dietz et al., 2020). North Atlantic killer whales display both local and long-distance movements, and studies have shown a strong association between the Norwegian killer whales' movements and the Norwegian spring-spawning (NSS) herrings' (*Culpea harengus*) distribution and migration patterns (Similä & Ugarte, 1993; Similä et al., 1996; Jourdain et al., 2019; Vogel et al., 2021). However, recent studies also show that these whales, or perhaps specific groups, also prey upon

other fish species, marine mammals, and seabirds during parts of the year (Vester & Hammerschmidt, 2013; Jourdain et al., 2017, 2020a). Consequently, the level of specialization in their diets remains relatively unclear.

In the past decade, a large portion of the NSS herring stock has overwintered (November-January) in specific fjord areas of northern Norway. In late winter/early spring the herring leave these fjords to spawn on the continental banks from Troms county to the southern coast of western Norway (Møre) (Rikardsen, 2019; Toresen et al., 2019). These dense winter aggregations of herring attract large numbers of killer whales, other predators and people, both in the fjords and at the herring spawning grounds. Although the movement of Norwegian killer whales has been studied in detail in some respects (e.g., Dietz et al., 2020; Mul et al., 2020; Vogel et al., 2021), discrete patterns in killer whale movement are rarely identified. Foraging theory predicts that these killer whales should take advantage of this abundance of herring by spending most of their time in areas of high prey density and reducing their time in areas of low prey density, thus movement should reflect strategies that optimize foraging. However, recent studies and observations (e.g., Rikardsen, 2019; Jourdain et al., 2020b; Mul et al., 2020) are identifying various behaviors that expand upon what we know regarding movement patterns among different individuals or populations. For example, even if these killer whales seem to be feeding in areas with high prey density, some appear to perform what has been termed as “scouting” trips or excursions away from areas of dense herring aggregations only to return to the original area after varying amounts of time (Rikardsen, 2019). However, for what reason, to what extent, and how often remains relatively unclear. Another example is that killer whales were found to be attracted to fishing activity in Norway, as it provides an ideal foraging opportunity (Mul et al., 2020). On the other hand, many cetaceans are known to exhibit avoidance behaviors such as long diving times, abrupt turning, and increased swimming speeds in the presence of boat activity (Lusseau, 2003; Davenport & Davenport, 2006). For these killer whales, their movement could be influenced by many factors, and consequently, the movement patterns among individuals or populations could differ among varying environments. Therefore, classifying the Norwegian killer whale’s movement into multiple modes within shorter spatial and temporal scales could potentially help identify both the mentioned and other foraging strategies, determine seasonal distribution, and ultimately yield better quantitative predictions of population dynamics and collective whale behavior.

Identifying finer-scale movements and behaviors such as foraging, resting, dispersing, searching, or wandering has always been a challenge, but the advances in biotelemetry have

revolutionized the way we collect and analyze animal movement (Fancy et al., 1988). Biotelemetry, including satellite tagging and tracking, is a method that is becoming more frequently used to assess movement and behavior of whales in the last decade (e.g., Andrews et al., 2008; Mate et al., 2011; Prieto et al., 2014). With new methodical approaches we can now identify multiple behavioral movements from continuous time series data (e.g., Morelle et al., 2017). Additionally, these new methods allow us to explore the concepts of search and uncertainty in foraging theory, and better integrate individual variability in order to answer questions about the efficiency of foraging strategies. Therefore, the main objective of this study was to segment the tracks of satellite-tagged Norwegian killer whales into five discrete movement modes by combining two valid modeling approaches. More specifically, the first algorithm was used to segment the tracks based on persistence velocity and the second classified these segments into specific movement modes based on net squared displacement over time. This segmentation and classification allowed us to examine, (1) variations between individual whales as compared to the collective in relation to both seasonality and geographical location, and (2) the sequences of movement types to assess possible relationships. Finally, we discussed the relationships between the movement modes and the potential whale behavior in the context of the theoretical framework of the optimal foraging theorem.

3 Materials and Methods

3.1 Study Area

The study area covered the coastal region of the Norwegian Sea. Norwegian spring-spawning (NSS) herring (*Culpea harengus*) has one of its main spawning areas off the coast of Møre from February to March, but herring spawning areas also extend as north as Vesterålen and Troms (Fig. 1, Toresen et al., 2000). During winter, NSS herring seem to be following deep ocean trenches that start at the edge of the Norwegian continental shelf and lead into northern coastal waters, with one of these trenches leading into Kvænangen fjord and its surroundings (Rikardsen, 2019). In recent years, the 2013 year-class herring has been dominating the overwintering herring in Kvænangen fjord in northern Norway before migrating south to spawn during the spring off the coast of western Norway, attracting large numbers of killer whales (*Orcinus orca*) to these areas (Rikardsen, 2019; Toresen et al., 2019). Kvænangen fjord has a total length of 74 km with maximum depths of around 400 to 450 m. The fjord is mostly wide with the mouth being 15 km and the main fjord area contains several islands, side fjords and branches (Fig. 1, Larsen, 1997). The fieldwork for this study was conducted over one winter field season in northern Norway and the west coast of Norway (Fig. 1). The majority of tagging occurred between late October through February in the Kvænangen fjord (2018-2019). From late February to early March 2019, additional tagging occurred in southern Norwegian coastal waters off the coast of Møre in collaboration with the Norwegian Coast Guard (Fig. 1).

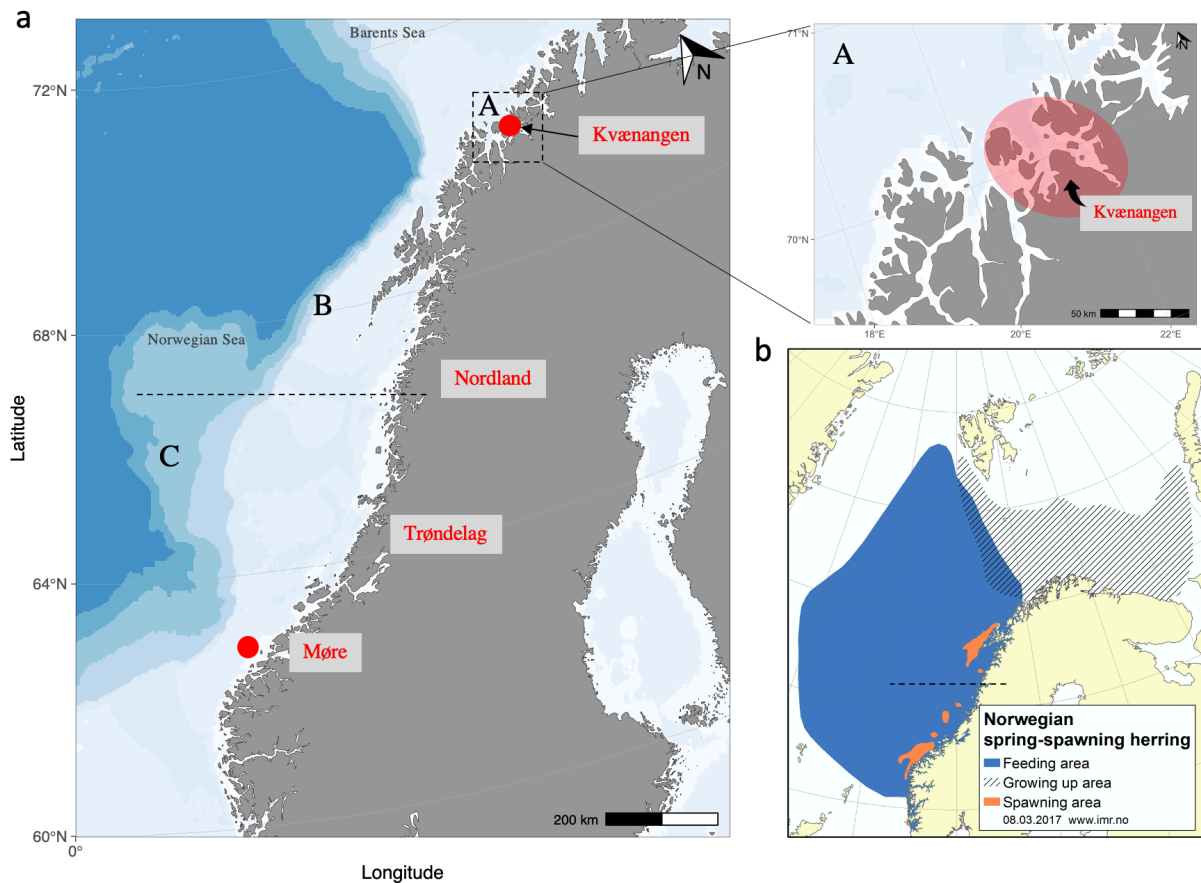


Figure 1 Maps of the Norwegian study area. In panel (a), the tagging sites are indicated with red circles. Core areas of killer whale and Norwegian spring-spawning (NSS) herring overlap are designated by zones A, B, and C. Zone A refers to Kvænangen fjord where the NSS herring overwintered for the 2018/2019 season. Zone B refers to the Norwegian shelf when whales leave the fjord for the last time. Zone C is referring to a main southern spawning ground for the NSS herring, which in this study we define as being below 67°N. The dotted lines represent the general partitioning of defined zones. The inset shows Kvænangen fjord in more detail. Panel (b) is taken from www.imr.no (2017) and illustrates the distribution and general migration pathways of NSS herring.

3.2 Tagging

Whales were approached and tagged from a 26-ft open RIB (Rigid inflatable boat) in the northern fjords and in a 22-ft water jet driven coast guard patrol boat at the coastal banks off Møre in the period from the end of October 2018 to mid-February 2019. Wildlife Computers SPOT5 or SPOT6 Limpet Argos transmitters (www.wildlifecomputers.com) were deployed using an Aerial Rocket Tagging System (www.restech.no). We aimed for tag placement in the center of the dorsal fin as tag placement can have an influence on the quality of data (Andrews et al., 2013; Mul et al., 2019). Tags were surface-mounted using two 68-mm titanium subdermal darts extending from the base of the tags, which penetrate through the skin and anchor in the dense connective tissue layers (collagen) in the dorsal fin (Andrews et al., 2013; Andrews et al., 2019). The darts were sterilized before deployment with 70% ethanol to decrease the risk of infection. For the first 45 days tags were programmed to transmit 14-15 times every hour to obtain high temporal resolution during the initial tagging period. In the following 35-45 days

the transmission rate was reduced to 8-10 transmissions per hour to extend battery life. Finally, the transmission rate was further reduced to 55 transmissions per day until the battery failed or the tag detaches from the whale. Since our objective was to identify multiple movement modes over a relatively stable period of time, we removed whale tracks that contained fewer than 100 raw position estimates from further analysis, resulting in 13 out of 18 individual tracks being used in this study.

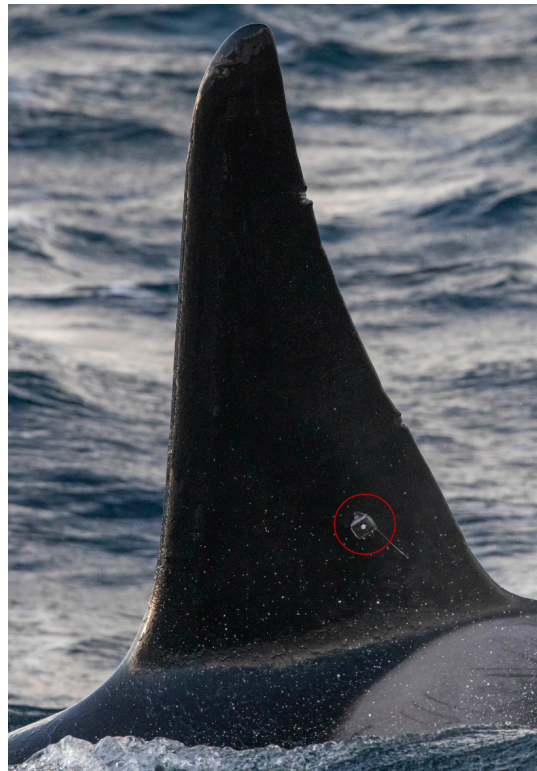


Figure 2 Shows deployed SPOT5 Limpet Argos transmitter on the dorsal fin of adult male killer whale off coast of Møre (2020). Red circle highlights tag placement. Photo by: Audun Rikardsen.

3.3 Data Collection and Processing

Geographic position estimates of tags were calculated by the CLS-ARGOS service and prefiltered using a Kalman filter in a state-space framework. All subsequent data processing and statistical analyses were performed using ‘R’ software (R Development Core Team, 2020). We applied a Correlated Random Walk (CRW) state-space model to reconstruct the most likely path based on the pre-filtered Argos position estimates, using the ‘fit_ssm’ function from the ‘foieGras’ package (Jonsen & Patterson, 2020). This approach converts the irregular and relatively noisy time series of Argos position estimates to a time regularized path. The CRW model assumes that the movement characteristics at one location are correlated with the characteristics at the previous location (Johnson et al., 2008) while taking into account the

location error and irregular transmissions (Jonsen et al., 2005). The model was set to compute location estimates at two-hour intervals. Since one of our objectives was to study behavioral variation at different seasonal locations, all whale location points were designated as being either in zone A, B, or C. Zone A is referring to Kvænangen fjord where the NSS herring overwintered for the 2018/2019 season and the primary whale tagging location. Zone B is referring to the Norwegian continental shelf when whales leave the fjord for the last time. Zone C is referring to a main southern herring spawning area along the western coast of Norway, which for the purpose of this study we define as being below 67°N (Fig.1).

3.4 Behavioral Change Point Analysis

For this study, we applied a Behavioral Change Point Analysis (BCPA) to automatically segment the tracks into distinct segments in terms of movement characteristics. This method was chosen because it allows for the identification of behavioral structures in the tracking data without any prior assumptions regarding movement parameters (Gurarie et al., 2009, 2016). The BCPA is a likelihood-based method that identifies significant changes in movement parameters (mean, variance, or continuous autocorrelation) underlying locational time-series data by sweeping an analysis window over the time-series to identify the most likely changepoint and using Bayesian Information Criterion (BIC) to determine the significance of changepoints (Gurarie et al., 2009). First, the longitude-latitude data was converted to Universal Transverse Mercator (UTM) coordinates then we ran our BCPA analysis using the ‘bcpa’ package (Gurarie, 2014), and customized our analysis to use persistence velocity as our response variable, moving window size of 50, sensitivity (K) of 3 and cluster width of 3.

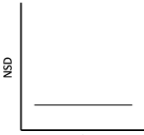
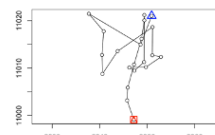
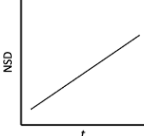
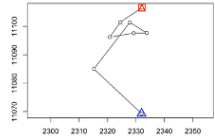
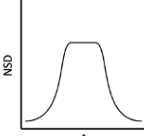
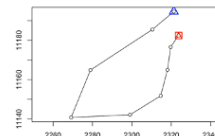
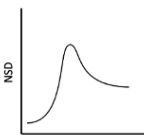
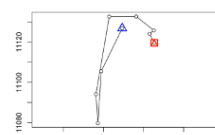
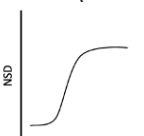
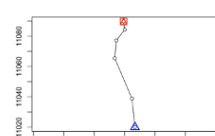
Persistence velocity was chosen as it provides a rather robust time-series variable by including speed and turning angle. The window size refers to the minimum temporal scope within which changepoints are expected. The greater the size of the window, the greater the power of the model selection at a cost of identifying finer-scale behavioral shifts. Smaller window sizes identify the finer-scale behavioral shifts, but at the increased risk of spurious change points (Gurarie et al., 2009). To compensate for possible spurious change points, we adjusted the K or sensitivity parameter. The cluster width was increased to filter away minor change points within a small temporal range. Analysis parameters were selected to optimize the detection of robust, homogeneous velocity-persistence states (along a whale track) while reducing spurious short behavioral states.

We then calculated net squared displacement (NSD) for each separate segment. NSD is the Euclidian squared distance between the first location of a segment and the subsequent relocations. We used the function ‘as.ltraj’ from the package ‘adehabitatLT’ (Calenge, 2011) to obtain NSD of each segment. NSD is regularly used in modeling larger migratory movements of animals (Bunnefeld et al., 2011), however, it can be rationally applied to smaller-scale movements (Singh et al., 2016; Morelle et al., 2017).

3.5 Candidate Movement Modes

For this study, we first defined several candidate movement modes. This approach allows us to take advantage of the existing knowledge or expectations about the whale’s spatial behavior while providing us with the opportunity to test for the presence of alternative movement modes (Morelle et al., 2017). Since this is a first-time application to killer whale telemetry data, the candidate movement modes were adapted from the movement modes presented by Bunnefeld et al. (2011) and Morelle et al. (2017), who tested these candidate modes using Global Positioning System (GPS) data of moose (*Alces alces*) and wild boar (*Sus scrofa*). The five candidate spatial modes used in this study were (1) residence: defined by non-directional movement, behavior suggestive of foraging, resting, or high affinity to a specific area, (2) round trips: longer movements away from initial starting location followed by a complete return to the initial location, (3) partial trips: longer movements away from initial starting location followed by a partial or incomplete return to the initial location, (4) nomadic: defined by a simple linear model or an increase in distance from the initial location, and (5) transiting: defined by an increase in distance from the initial location followed or preceded by slower movements (Tab. 1).

Table 1 The defined candidate movement modes for killer whales, their corresponding theoretical net squared displacement (NSD) curve, linear or nonlinear mathematical equations and an example of segment path (blue triangle indicating starting point and the red square indicating the end point). Parameters description: c constant, a slope, t time since departure, A first curve plateau, A' difference between second and first curve plateaus, k rate of change between initial γ 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 (for more details on equation parameters see Oswald et al., 2012).

Candidate mode	NSD curve	Equation	Path example
Resident		$NSD = c$	
Nomad		$NSD = a \cdot t$	
Round trip		$NSD = \frac{A}{1 + m \cdot \exp(-k(t - i))^{1/m}} + \frac{A'}{1 + \exp(-k'(t - i'))}$	
Partial trip		$NSD = \frac{A}{1 + \exp(-k(t - i))} + \frac{A'}{1 + \exp(-k'(t - i'))}$	
Transit		$NSD = \frac{A}{1 + \exp(-k(t - i))}$	

3.6 Classifying Segments

For each of the candidate movement modes, we defined the spatial relationship of NSD and time for each movement mode (Tab. 1). Then we picked specific mathematical curve equations, suggested by Bunnefeld et al. (2011) and Morelle et al. (2017), that best represent each movement mode (Tab. 1). We then fitted the corresponding nonlinear or linear mathematical curve equations separately to the NSD data from each segment using the ‘FlexParamCurve’ package (Oswald et al., 2012) and an adapted script provided by Morelle et al. (2017).

We used Concordance Criterion (CC) to test the relative goodness-of-fit (Singh et al., 2012; Morelle et al., 2017) for the candidate movement modes for each segment. The values of CC fall between ranges from 0 (no correlation) to ± 1 (perfect concordance) representing the concordance between the observed and predicted values. The Akaike Information Criterion (AIC) is used to assess the goodness-of-fit of residence mode as the CC is not applicable for

the linear model ($NSD = c$, Tab. 1). Each segment is subsequently classified as the movement mode with the highest CC value. For segments with poor fitting CC values (i.e., above/below a threshold of 0.7), they were classified as residence mode if the model has the lowest observed AIC. We differentiated between round and partial trips by comparing the NSD value at the first inflection point, or the point on the curve where the curvature changes its sign, to the net change in NSD from the start to the end of the segment, so $NSD_{inf} > NSD_{net}$ indicated round trip movement, otherwise indicated partial trip. Unclassified segments with 4 or less positional locations and tracks ending in a partial trip (total of 14 segments) were removed from further analysis. We also conducted a chi-square analysis to test the null hypothesis that movement modes are independent of previous modes across all whales.

4 Results

4.1 Tracking

Average satellite tag longevity was 44 days, ranging from 12 to 78 days. Average extracted geographical positions was 864 points, ranging from 109 to 1594 points (Tab. 2). Timing of migration and arrival at the herring (*Culpea harengus*) spawning grounds in zone C (Fig. 1) varied among individuals, with killer whales (*Orcinus orca*) leaving the fjords between early December to early February and arriving at southern herring spawning grounds in February (Tab. 2). Whales tagged outside Møre stayed relatively close to tagging location area in the first two weeks after tagging. Of these whales, ID 83754 and ID 83755 had the shortest tracks, lasting 12 and 14 days respectively. Whale 179032 showed high fidelity to Møre tagging site for approximately two weeks but then traveled further south and then north again into the Norwegian Sea and the last positions indicated it was heading further off the Norwegian shelf (Fig. 3, supplementary Fig. 1).

Table 2 Tagging information from 13 killer whales used in analysis, tracked between October 26th, 2018 and March 26th, 2019 in Norway. Tagging locations are partitioned by the black line. Zone A refers to Kvænangen fjord where the NSS herring overwintered for the 2018/2019 season. Zone C is referring to a main southern spawning ground for the NSS herring, which in this study we define as being below 67°N. Individuals with NA indicate that they never made it to the other zones. Note that the individuals tagged in Møre remain in zone C for entirety of tracking time.

Location	Whale ID	Sex	Tagging position	Deployment date	Leave zone A date	Arrival at zone C date	Last date	Total tag longevity (days)	Total extracted positions
Kvænangen	54013	Male	70.07, 21.09	2018-10-26	NA	NA	2018-12-03	39	681
	53561	Male	70, 21.12	2018-10-28	2018-12-10	NA	2018-12-20	54	1041
	53559	Male	70.24, 21.03	2018-11-06	2019-01-01	NA	2019-01-02	57	1112
	54011	Male	70.25, 21.1	2018-11-06	2019-01-01	NA	2019-01-09	65	1267
	83761	Male	70, 21.07	2018-11-13	2018-12-06	NA	2018-12-09	27	557
	83760	Male	70.24, 21.08	2018-11-16	2018-12-16	NA	2018-12-26	41	866
	53557	Male	69.98, 21.12	2019-01-04	2019-02-06	2019-02-27	2019-03-23	79	1594
	83764	Male	69.93, 21.17	2019-01-06	2019-01-30	NA	2019-02-04	29	498
	83756	Male	69.99, 21.66	2019-01-08	2019-02-09	2019-02-15	2019-03-13	64	1301
	83768	Male	70, 21.17	2019-01-23	2019-01-27	2019-02-09	2019-03-26	63	1271
Møre	83755	Male	63.13, 6.74	2019-02-16	NA	NA	2019-02-28	13	109
	83754	Male	63.12, 6.62	2019-02-17	NA	NA	2019-03-01	12	176
	179032	Male	63.2, 6.75	2019-02-17	NA	NA	2019-03-26	38	754

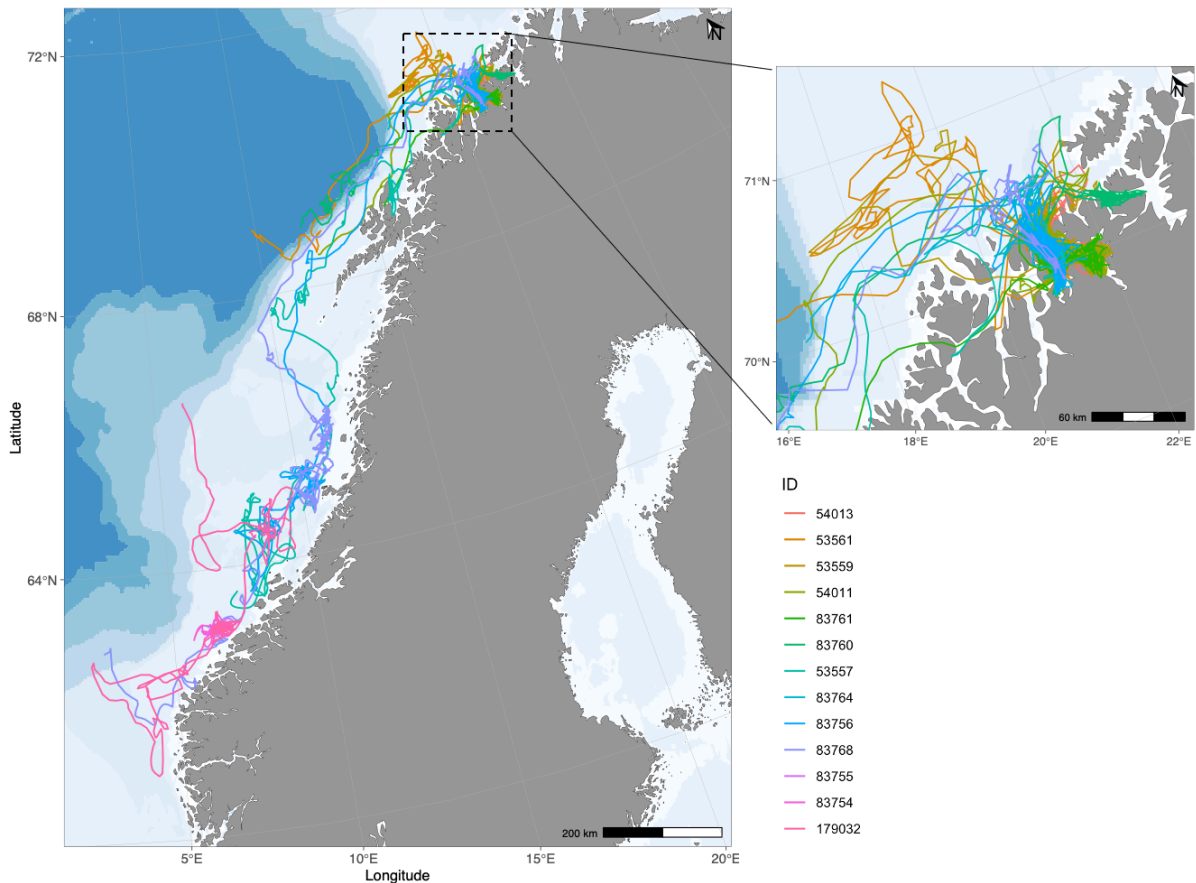


Figure 3 Map of satellite tagged killer whale tracks along the Norwegian coast during the winter and spring of 2018/2019. Tracking data from individual whales collected are depicted and color coded by unique tag ID numbers. The inset shows Kvænangen fjord and surrounding area in more detail.

4.2 Spatial and temporal trends

Examining spatial distributions showed several distinct collections of movement modes at various locations. Collective resident areas were exhibited mainly in Kvænangen fjord, Trøndelag, Møre (Fig. 4). Round and partial trips were highly associated with these common residence areas but also occurred of waters along the Norwegian shelf to a lesser degree (Fig. 4a). Transiting movements showed common traveling corridors among whales, with most notable being along the Norwegian shelf as whales leave Kvænangen fjord. Nomadic movements were typically found around the resident areas identified (Fig. 4) but also found as intermediate states during longer traveling events, specifically as whales migrate south (Figs. 4, 5). A closer look at Kvænangen fjord and the surrounding area (Fig. 4b) highlights overlap of all modes but also revealed some differences in the distribution range between the movement modes. Specifically, majority of movement was within the fjord but there also was activity outside the fjord near the Norwegian shelf (Fig. 4b) which was seen when the whales leave the fjord for the last time and start migrating south (Fig. 5). Some round trip and nomadic positions

were seen just outside the main fjord area, while residence and partial trip locations were mainly focused within the main fjord area (Fig. 4b). Additionally, transiting positions showed the overall extent of the tagged whales' distribution (Fig. 4), suggesting high site fidelity during this period.

Transiting and trips (both round and partial) appeared to be more associated with fluctuations along the latitudinal and longitudinal scales, while residence and nomadic modes were relatively more stable (Fig. 5). Whales tagged in Kvæningen fjord started migrating south at different times but there appeared to be two main time frames, with individuals either leaving in December or leaving in late January to early February (Fig. 5, 6). After whales left the Kvæningen fjord to migrate to the southern herring spawning ground they seemed to show two approaches. Either they exhibited faster movement towards southern latitudes, mainly consisting of transiting behavior, or a more gradual movement towards southern latitudes, consisting of several different behaviors (Fig. 5). The spatial maps and longitudinal scale fluctuations showed that whales migrating south stayed near or on the edge of the Norwegian continental shelf before traveling to the coastal waters of Trøndelag and Møre (Fig. 5, 6).

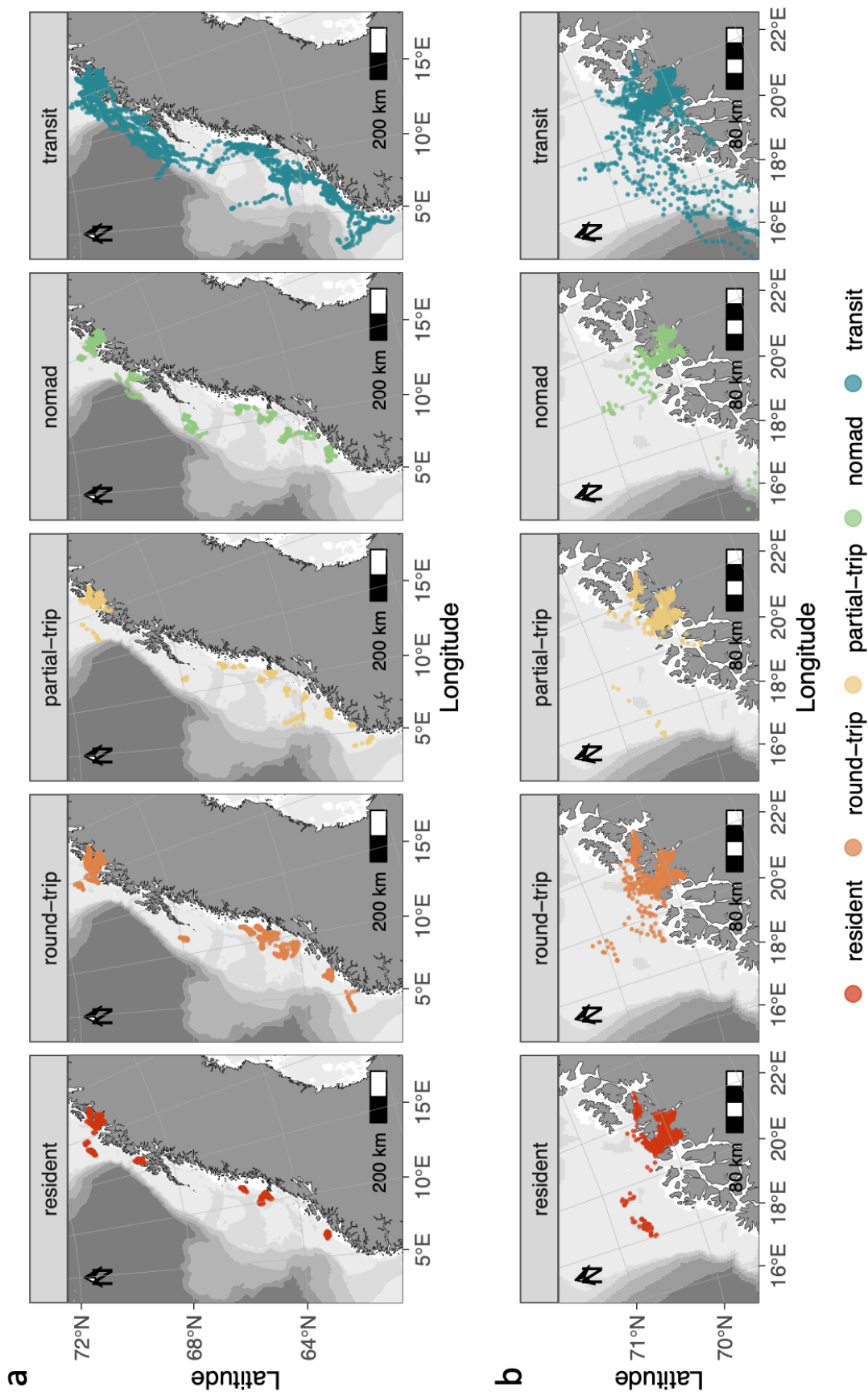
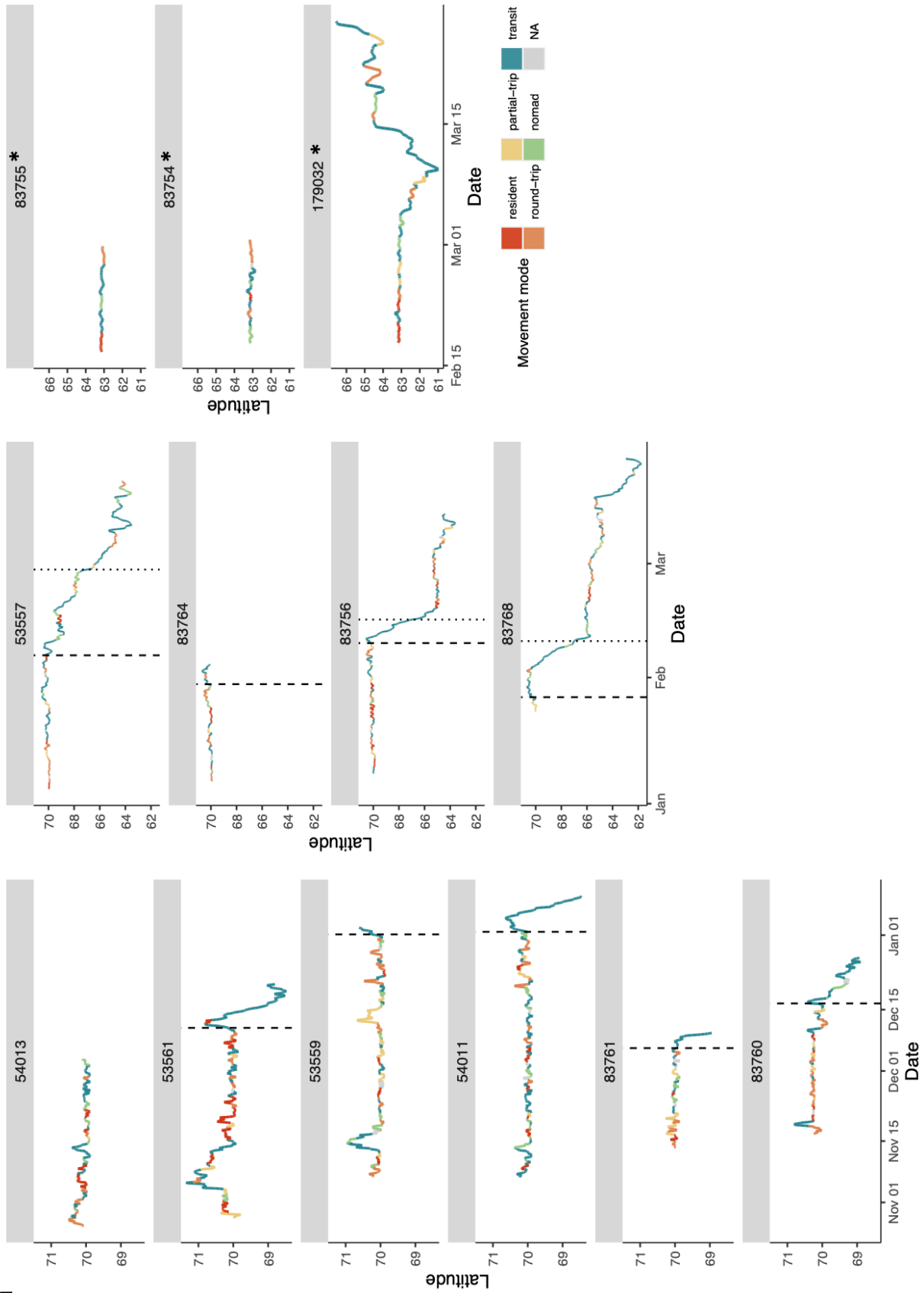


Figure 4 Distribution maps of geographic positions of 13 tagged killer whales in Norway separated by movement mode. Panel (b) shows inset of Kvaenangen fjord and surrounding area in more detail.

a



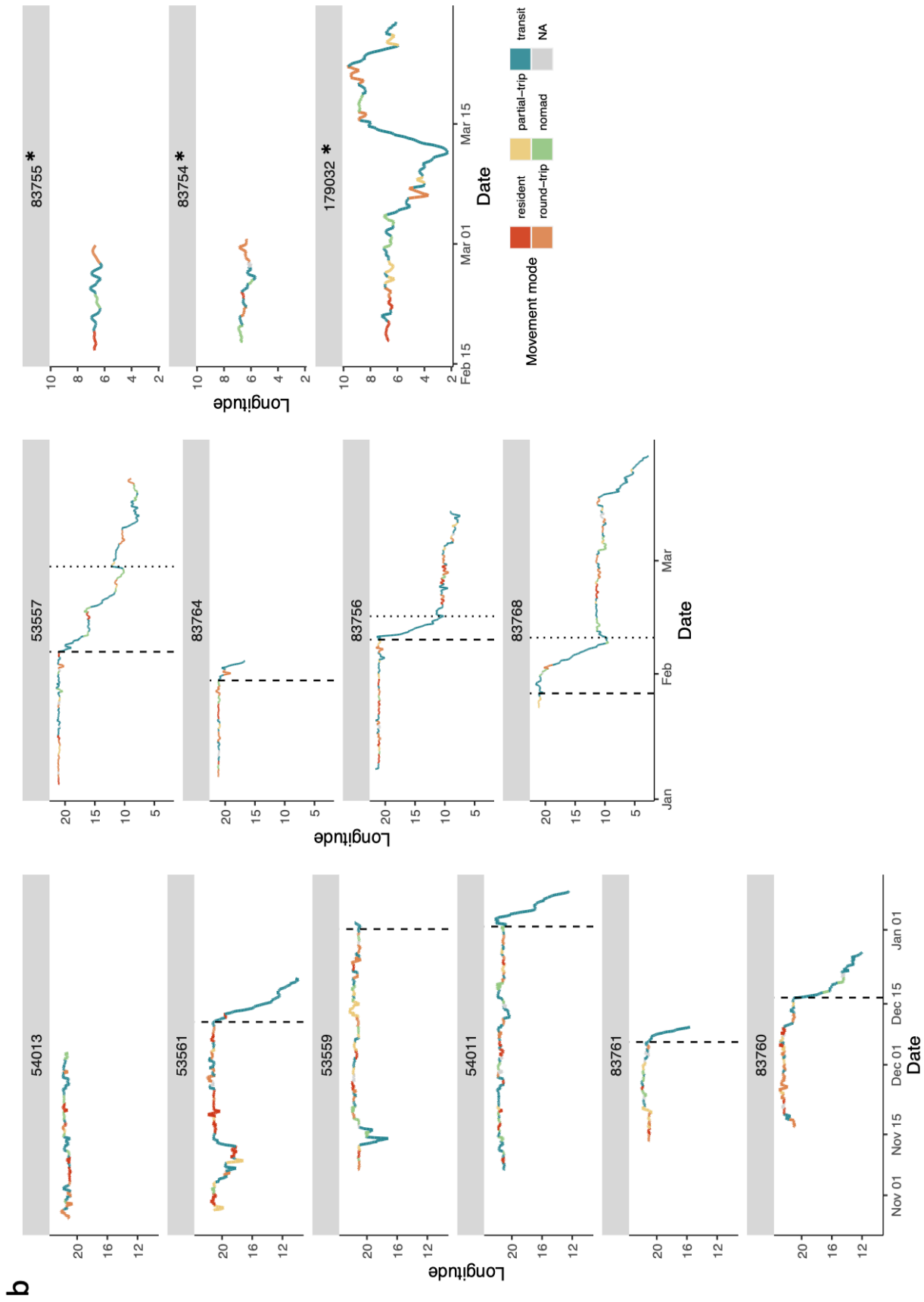


Figure 5 Latitudinal (panel a) and longitudinal (panel b) movements of 13 satellite tagged killer whales in Norway during the winter of 2018/2019, showing the spatiotemporal extent of classified movement modes. Dashed line indicates when those individuals in Kvænangen fjord (zone A) leave the fjord and the dotted line indicates when they reach southern herring spawning grounds (zone C). Individuals tagged off Møre are indicated by (*). Note that figures are organized into columns with similar time scales for easier comparison.

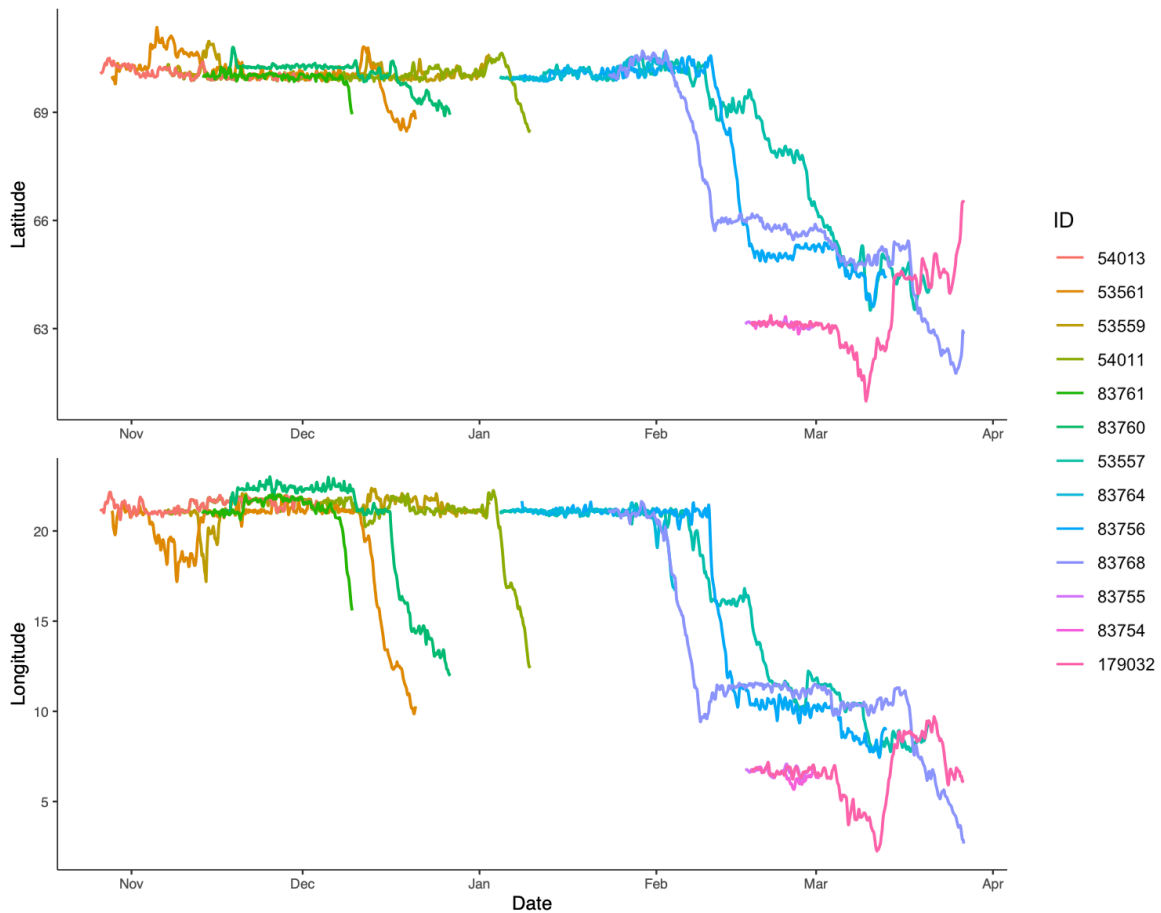


Figure 6 Shows summarized view of latitudinal and longitudinal movements for 13 satellite tagged killer whales in Norway over time (2018/2019).

4.3 Segmentation and classification characteristics

The BCPA analysis produced a combined total of 528 segments. Across all whale tracks, 504 (95.4%) segments were successfully classified into candidate movement modes, leaving only 24 (4.6%) segments unclassified. The majority of whales (10 out of 13) displayed all behavioral modes, the exception being partial-trip mode in the two shortest tracks (ID83755, 83754) (Fig. 7). The average segment duration (range: 6 - 68 hours) was 23.8 (± 11.8) hours, and the average total distance traveled (range: 7.8 - 296.9 km) was 64.2 (± 44.4) km (Tab. 3).

Total time allotment to the different movement modes varied among zones and individuals (Fig. 7). Collectively, transiting mode was the dominating mode accounting for 32%, 71%, and 48% of the total time among zones A, B, and C respectively (Fig. 7). In zones A and C, round trips accounted for 21% and 20% respectively, while in zone B nomadic movements accounted for 12% of collective time allocation (Fig. 7). Zones A and C had resident mode accounting for 18% and 10% of total time, while zone B only had 5% of

residence. Density plots of segment duration values for all movement modes in three zones and across individuals are shown in Figure 6. The duration values for the movement modes across all areas tended to have a broader distribution, with some modes (e.g., resident and nomadic) having more distinct bimodal distribution (Fig. 8a). Movement modes in zones A and C had overall a wider distribution but with peaks at shorter duration times, while zone B had overall slightly longer durations with more distinct peaks. However, these more distinctive peaks in zone B are likely an artifact from lack of tracking time in that zone. The duration values for the movement modes across individuals exhibited unimodal, bimodal, and more variable distributions, illustrating a high degree of within-individual variation in movement characteristics (Fig. 8b).

Table 3 Central tendency and variability (mean \pm SD) of descriptive statistics for each of the classified movement modes.

Movement mode	N	Duration (h)	Total distance traveled (km)	Speed (km/h)	Persistence Velocity	Net Displacement (km)
Resident	54	32.1 \pm 12.7	67.9 \pm 37.1	2.2 \pm 0.9	1.0 \pm 0.7	11.3 \pm 14.4
Round trip	86	27.5 \pm 11.0	67.9 \pm 38.9	2.6 \pm 1.2	1.5 \pm 1.1	14.1 \pm 19.3
Partial trip	47	25.5 \pm 12.0	64.9 \pm 40.4	2.7 \pm 1.5	1.6 \pm 1.3	24.1 \pm 31.1
Nomad	60	25.8 \pm 12.4	61.2 \pm 39.9	2.4 \pm 1.0	1.2 \pm 1.1	28.2 \pm 33.9
Transit	257	20.6 \pm 10.5	64.6 \pm 49.9	3.2 \pm 2.0	2.2 \pm 1.9	57.3 \pm 82.2
Unclassified	24	17.0 \pm 6.8	44.6 \pm 27.9	2.6 \pm 1.3	1.1 \pm 1.1	10.4 \pm 10.2
Total	528	23.8 \pm 11.8	64.2 \pm 44.4	2.8 \pm 1.7	1.7 \pm 1.6	42.3 \pm 70.4

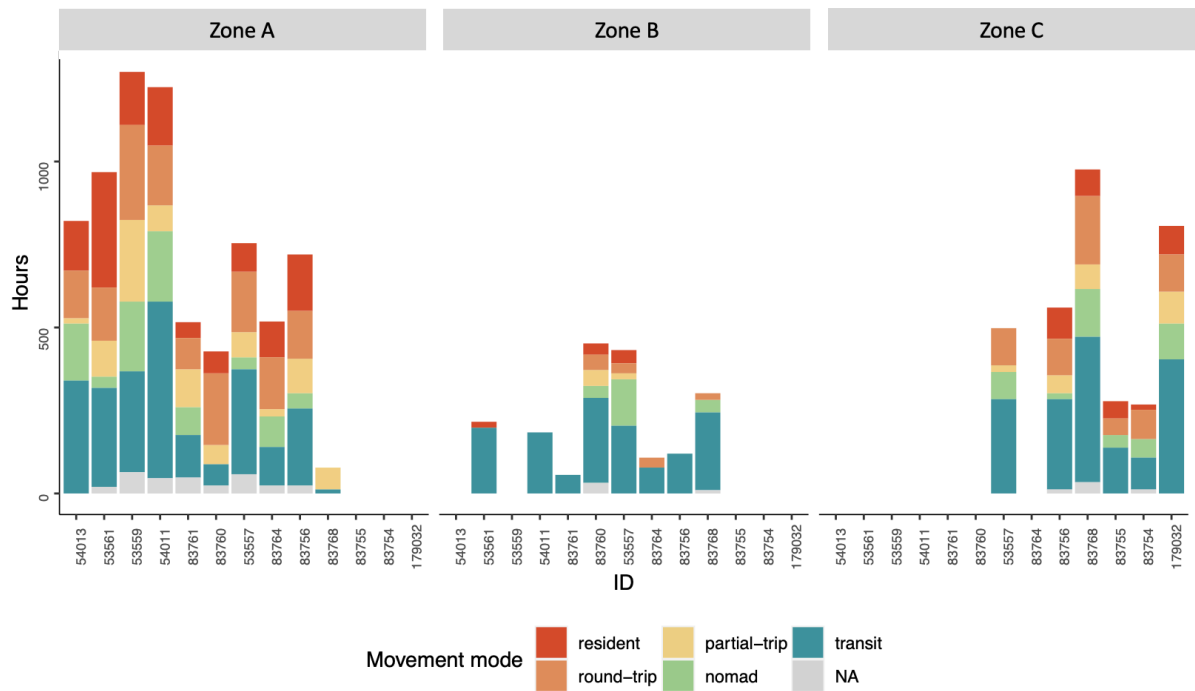


Figure 7 Total time (h) allocation of classified movement modes for all tagged killer whales separated by the defined zones A, B, and C during the winter and spring of 2018/2019. Zone A refers to Kvænangen fjord where the NSS herring overwintered for the 2018/2019 season. Zone B refers to the Norwegian shelf when whales leave the fjord for the last time. Zone C is referring to a main southern spawning ground for the NSS herring, which in this study we define as being below 67°N.

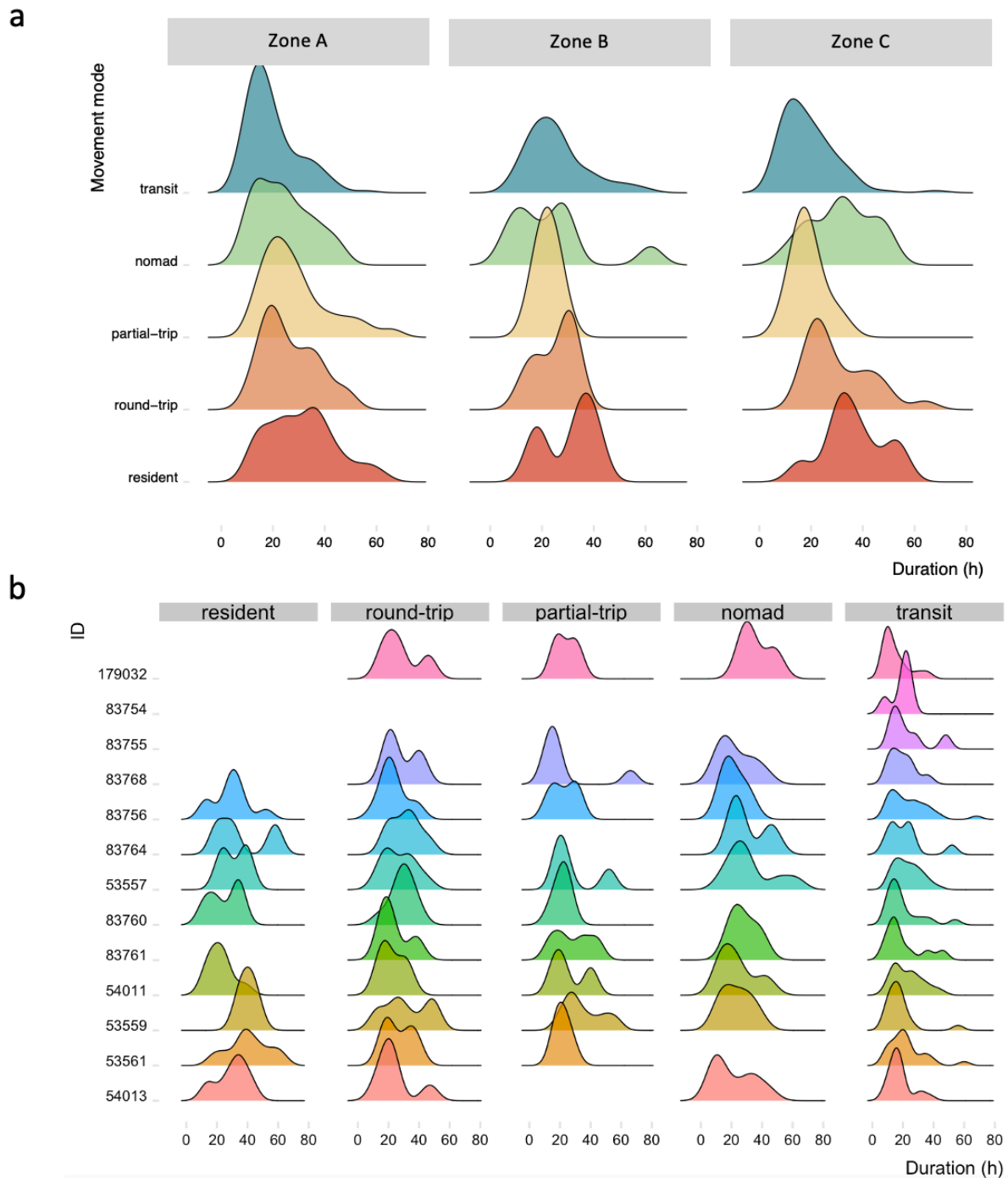


Figure 8 Panel (a) shows density plots of duration values of classified segments for all tagged killer whales in the three defined zones. Zone A refers to Kvænangen fjord where the NSS herring overwintered for the 2018/2019 season. Zone B refers to the Norwegian shelf when whales leave the fjord for the last time. Zone C is referring to a main southern spawning ground for the NSS herring, which in this study we define as being below 67°N. Panel (b) shows density plots of duration values of classified segments per individual. Note that missing curves indicate too few values for accurate representation of that field, for more information of individual movement characteristics refer to supplementary table 1.

4.4 Sequential patterns

We found every kind of transition exhibited across tracks collectively (Fig. 9). However, some individual tracks did not exhibit certain transitions. For example, in the two shortest tracks (ID 83755 and 83754) there was no classified partial trip mode and so no transition was observed. From looking at the collective sequences and transitions of movement modes we found that transiting was the most frequent and probable mode, with round trips being the second, whereas partial trips were the least frequent (Fig. 9, Tab. 4). Transiting modes commonly appeared in doubles or multiples before another mode occurred, or in other words, transiting behavior commonly followed transiting behavior. Results from a Chi-square test of independence, testing if the subsequent behavior is independent of current behavior, show that these two variables are independent, $X^2(16, N = 528) = 13.4, p = 0.6$ (Tab. 4).

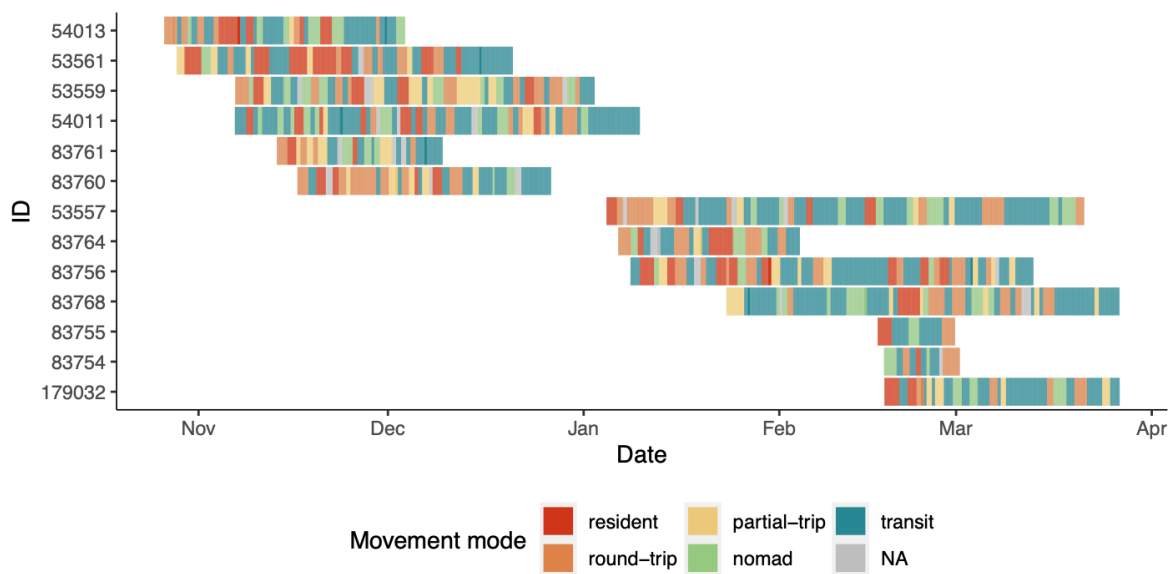


Figure 9 Shows the sequences of movement modes for 13 satellite tagged killer whales over time during the winter and spring of 2018/2019.

Table 4 Contingency table summarizing the counts of all observed movement mode transitions of 13 satellite tagged killer whales. The probability (conditional) of 'second mode' occurring given the 'first mode' are represented by the values in parentheses.

		Second mode				
		Resident	Round-trip	Partial-trip	Nomad	Transit
First mode	Resident	7 (0.13)	10 (0.19)	7 (0.13)	8 (0.15)	20 (0.38)
	Round-trip	8 (0.10)	14 (0.18)	11 (0.14)	7 (0.09)	38 (0.49)
	Partial-trip	5 (0.11)	6 (0.14)	1 (0.02)	5 (0.11)	27 (0.61)
	Nomad	6 (0.11)	10 (0.18)	6 (0.11)	4 (0.07)	30 (0.54)
	Transit	22 (0.09)	36 (0.15)	18 (0.08)	29 (0.12)	133 (0.56)

5 Discussion

This study successfully classified Norwegian killer whale (*Orcinus orca*) movement behavior into five different behavioral movement modes based on satellite tracking data. Earlier studies have commonly classified tracking data of killer whales and other whale species into two or three behavioral states or movement modes (e.g., Prieto et al., 2014; Jimenez Lopez et al., 2019; Dietz et al., 2020; Mul et al., 2020) or instead of discrete behaviors, classifying movements by a continuous scale of movement behavior (e.g., Vogel et al., 2021). What is new with this study is that we have also identified nomadic, round and partial trip modes in addition to the more common resident/restricted area search and transiting modes. To do this we combined two methods as proposed by Morelle et al. (2017). The behavioral change point analysis (BCPA) was able to select robust, homogeneous velocity-persistence states at intermediate scales and modeling the net squared displacement (NSD) objectively differentiated movement patterns and was robust to medium sampling intervals.

Our study identified seasonal distributions of known and novel movement strategies of Norwegian killer whales. At the large-scale population perspective, the killer whales demonstrated a clear shift from home-ranging behavior within a northern fjord area with known high density of overwintering Norwegian spring-spawning (NSS) herring (*Clupea harengus*) in November to January, to migratory behavior in January to February, and back to home-ranging behavior when they reached the southern spawning areas in February to March. At the individual level and intermediate spatiotemporal scales, we found a high degree of individual and behavioral variation within three key areas (herring overwintering and southern spawning areas, and the continental shelf area in-between these two areas). Both collective and individual whale movement patterns illustrated that all classified movement modes were used to varying degrees across multiple areas coinciding high prey abundance, which suggest that the movement strategies presented here are likely associated to optimal foraging strategies. While collective sequence analysis of movement modes revealed no significant patterns at intermediate spatiotemporal scales, this further informs futures studies by suggesting, that at this scale, individual tendencies in movement, environmental or prey field factors likely have more influence over movement and behavioral decisions.

The spatial distributions of the movement modes revealed several distinct collections of all the movement modes overlapping. This was seen to a large degree at locations corresponding with known herring associated areas, i.e., Kvænangen fjord and southern herring spawning

grounds (Fig. 1, 3). In range-resident species, individuals may match settlement choices to their prey type and hence occur in certain environments (Mueller, 2008) and foraging theory predicts that these killer whales should spend most of their time in areas of high prey density and reducing their time in areas of low prey density (Pyke et al., 1977). NSS herring is known to be an important prey species for killer whales in Norway (Similä et al., 1996; Jourdain et al., 2019; Vogel et al., 2021). We presume that the observed seasonal shifts in core use areas, specifically when whales leave Kvænangen fjord and migrate south, are related to the NSS herring movements (Vogel et al., 2021). Our study shows that the 10 whales tagged in Kvænangen stayed in or near the fjord during winter, when large masses of herring overwinter in the area (Rikardsen, 2019). The whales then left the fjord between early December to early February and moved south, that is until tags stopped transmitting, to the NSS herring spawning grounds along Nordland, Trøndelag and Møre. The three whales tagged near Møre were observed feeding on herring and sometimes also in the same area as fishing vessels (A. Rikardsen, personal communication), further suggesting that the whales were still continuing to feed on herring in these waters. However, we cannot verify all the potential prey types these whales may have targeted after leaving Kvænangen fjord, as some Norwegian killer whales could potentially switching to other prey species for a short period while migrating south and isotope analysis indicates heterogeneity between individuals' dietary patterns (Jourdain et al., 2017, 2020). Regardless, the time the killer whales allocated to these main herring foraging areas indicates that these are profitable areas and thus, the defined movement modes in this study are likely reflective of behavioral movements or strategies that optimize foraging.

In this study we aimed to include and explore the concepts of search or dispersal (round and partial trips) and uncertainty (nomadic) in addition to the commonly assessed resident/restricted area search and transiting modes. All behaviors or movements have costs and benefits (Bonte et al., 2012). Collectively, if a movement or strategy is favored by selection then we should expect the benefits of observed movement or strategies to outweigh or reduce the costs (Shaw, 2020). We found that round and partial trips, here referred to as *trips*, as well as nomadic movements were exhibited to a large degree (approximately 37% of all classified behavior) throughout all whale tracks. These trips were concentrated in areas of residence further suggesting that these behaviors are strategies related, in some degree, to optimal foraging. Residence is characterized by non-directional movement with typically decreased travel speeds and increased turning rates. Given the scales in this study, residence behavior observed is likely representative of intensive foraging within the given areas (Charnov, 1976;

Jonsen et al., 2005). If the whales are feeding in an area where prey density has fallen below a specific threshold value, they must decide to either leave the area in search of locations with higher prey densities or switch to alternative prey species (Suryan et al., 2000; Witteveen et al., 2008). Then, according to theory, the most expected cause of these trips is that it is a common tactic used to disperse and search a given area for differing prey patches. It is likely that these whales travel to areas where they had previously been feeding at some time, or perhaps a perform a 'blind' search. Then if they do not find any food or better prey patch, they would return to the initial area and continue feeding there or try another strategy. A second, or additional possibility is that this pattern (depending on the temporal scale) may partly reflect the whale's response to local fishing activity as described in Mul et al. (2020). That study showed that whales were often attracted to and benefitted from fishing activity, particularly in Kvænangen fjord. The start of fishing activity within a given area triggered a change in killer whale movements that had similar spatial signatures to our smaller-scaled round and partial trips. While we found no evidence for trips being more or less frequent at certain times, the distances and durations of trips did tend to increase closer to end of the year before individuals left the fjord to travel south in December (Fig. 5). Perhaps when fisheries were active, the whales were more likely to stay within the areas of the fishing boats (Kvænangen fjord) but when the fishing activity stops for the holidays, the whales started to move over larger areas, and eventually leave the area. Similarly, this behavior could be seen more frequently before fishery activity starts (e.g. in a period in early late October/early November). This question may be answered with additional data from fisheries and more individual whale tracks. Finally, a third possibility is that these trips reflect a simple dispersal strategy related to local population dynamics. Density dependent dispersal is not well studied in killer whales, however some competition/dispersal movement has been studied among other dolphin or whale species and suggests dispersal movements can occur in larger populations (e.g., Sueyro et al., 2018) or related to genders, with usually males competing for females and females competing for food (Silva et al., 2008; Bearzi et al., 2011). Despite what we cannot conclude as the exact reason for this trip behavior, it is reasonable to assume that many of these movements must have an advantageous reason likely related to searching for beneficial prey patches, and/or a combination of these factors.

Interestingly, two whales in our study (ID 53559 and 53561) that were tagged in Kvænangen fjord made extensive multi day excursions to outside of Kvænangen fjord towards the Norwegian shelf in November and then returned (supplementary Fig. 1). The first whale

(ID 53561) left Kvænanen fjord in early November for almost two weeks and exhibited resident, transiting, round and partial trip modes near the Norwegian shelf. The second whale (ID 53559) left Kvænanen fjord mid-November for four days but only exhibited nomadic and transiting modes near the Norwegian shelf. This is interesting because the first whale spent a few days in resident mode, but the second whale did not, even though it traveled to same area. As discussed above, leaving the fjord may be related to searching for a more valuable prey patches or perhaps a response from unknown cues that attract the whales to outside of the fjord. Regardless, the whales differed in behavior suggesting that a prey patch was near the Norwegian shelf, but the second whale that arrived slightly later to the same area may have been too late and the prey patch likely had moved or diminished since the whale did not show residence behavior and had an overall shorter ‘trip’. These noteworthy excursions visually resembled round trip behavior on a larger scale than what was aimed for in this study, due to the parameters set in the BCPA analysis. In other words, the parameters we set for the BCPA in this study were selected to optimize the detection of robust change points within a set temporal range (window size parameter). Future applications of this analysis could be tailored more to automatically identify these larger multi day trips but at the cost of overlooking finer-scale behaviors exhibited along the way. Alternatively, multiple separate BCPA analyses could also be applied to include both very large- and small-scale movements or otherwise combining other methods (e.g., first passage time with BCPA) may prove more beneficial.

In contrast to the complete or partial round trips, the nomadic movements had wide-ranging characteristics and irregular patterns which were likely driven by environmental factors and/or unpredictable prey patches (Teitelbaum & Mueller, 2019). Our study finds that nomadic movements were found across all areas but had less overlap with the other modes while also commonly seen in-between long transiting periods. If these whales are following the NSS herring migration south, then these occasional nomadic movements likely reflect predator-prey encounters or uncertainty in a whale’s trajectory (Vogel et al., 2021). Alternatively, nomadic tendencies have been previously documented, through photo identification and observations, in Norwegian killer whales and were suggested to be more male specific and possibly a mating strategy (Blix et al., 1995). Nevertheless, the reasons behind the observed nomadic behavior in the present study still remains uncertain.

The density distributions of the movement modes across individuals and collective distributions at differing regions yielded insight into the observed variability of Norwegian killer whale movement behaviors, at both the population and individual level. Population

density distributions across different regions were compared to see if durations of behavioral movements in certain areas changed. Movement modes in Kvænangen fjord and in southern spawning areas had similar distribution patterns which had peaks at shorter duration times than along the Norwegian shelf. This is likely due to the herring not being as densely aggregated as it was in the fjords and whales must travel longer distances between prey patches as the herring move south. The durations of most behavioral modes had fairly wide unimodal peaks in differing areas suggesting greater variation of mode durations within and among individuals. Residence duration values along the Norwegian shelf and in southern herring spawning areas had a more bimodal distribution, but this is likely due to limited data in those areas and interpretations should be considered more lightly. Individual density distributions for different behaviors were compared to examine the inter- and intra-individual variation in behavioral movements. Distributions in durations of behaviors were unimodal, bimodal or multimodal. The wide unimodal distributions imply greater within individual variation, while bimodal and multimodal patterns in the distribution of movements suggests either a) the classified movement modes could be representative of multiple different behaviors with similar spatial patterns, example being search versus dispersal, or b) some other environmental or prey field factor could have influenced the amount of time given to certain movements. Overall, the density distributions implied a high degree of movement mode variation across areas and individual whales.

This study also aimed to examine killer whales' movements in a sequential order. However, we did not find any statistical support indicating that previous behaviors/movements influenced subsequent ones. The high variability suggests that transitions to new movements are likely more influenced by individual propensities in movement or environmental factors rather than the previous behavior. One interesting result from looking at the sequences of behaviors was that transiting was the most frequent and probable mode. Transiting behavior occurred frequently together and at smaller scales concentrated in areas we found residence behavior. These groupings of transiting segments are likely representative of different subcategories of transiting, such as short- or medium-distance transiting between prey patches. This is further supported upon visual inspection of classified tracks, which shows that whales tended to travel straight for varying periods of time before abruptly changing trajectories only to continue traveling straight again. Sequence analysis can reveal the groupings in which behaviors occur and so define the relationships which need to be explained. Patterns may not be seen due to the data being pooled across all individuals and areas, but this was done to

compensate for a limited sample. Another reason may be that they are not limited energetically in these areas and therefore can afford more ‘expensive’ or spontaneous behaviors (Bonte et al., 2012). Perhaps offshore sequence patterns in movement may be more apparent and beneficial in a less predictable environment. With a larger dataset and extended tracking data sequence patterns may become more clear or comparable at certain scales among individuals or in different areas.

Overall, a high degree of behavioral movement variation was observed across individuals. The high variability in movement patterns can be explained several ways but we suggest two main explanations. The first and most probable explanation is that movement patterns reflect inter-individual differences in foraging strategies. Strategies or inclinations towards certain movements may be the result of cultural transmission within groups, rather than prey preference. Cultural transmission has been documented amongst killer whale acoustics, foraging strategies, and habitat preferences (de Bruyn et al., 2013; Foote et al., 2016). Perhaps some individuals in our study could be better at sit-and-wait strategy and exploiting the local resources while others are better at search and navigational foraging or some adapting both. For example, those individuals spending more residence time within Kvænangen fjord may be better at timing local foraging events or are more attracted to fishing activity as it provides an easy meal for the whales (Mul et al., 2020). In the eastern north Pacific, two different populations of killer whales have overlapping distribution, but these populations have differing specialized diets. Transient killer whales have a larger spatial distribution, feed mainly on marine mammals and exhibit search and navigational foraging. The resident killer whales have a smaller distribution, feed exclusively on fish and squid and are better at sit-and-wait strategy (Ford et al., 1998). Besides diet, the differences in spatial movements are a large indicator of the differing populations. If Norwegian killer whales are mostly feeding on herring, then the variations in movements could reveal differing local populations or groups with varying foraging strategies even when preying on the same species (Hawkes, 2009).

The second prospective explanation for variability is that there may be gender- or competition-associated differences in movement patterns. It is common among mammals for the social organization to be dominated by female philopatry and male dispersal (Greenwood, 1980). Few studies have explored competition/dispersal and sexual segregation of killer whales within foraging behavior. Beerman et al. (2016) found that adult male and female killer whales movements overlapped spatially while resting, traveling and socializing, but during feeding, females foraged nearshore in shallower waters, while adult males were widely distributed

throughout the study area. In other cases, males often disperse from their maternal pod and become termed "roving" males, spending periods of time alone, and sometimes joining pods that contain potentially reproductive females (Baird & Whitehead, 2000). Considering that the tagged individuals in this study were all males and large numbers of killer whales aggregate within the fjord and in the southern herring spawning grounds, this may account for the overall high degree of transiting and dispersal associated behaviors exhibited in this study. Though, telemetry data of female killer whales is lacking and therefore comparisons cannot be made yet. For example, future studies that follow both males and females within one or several pods and/or areas may help to reveal such potential differences.

This study aimed for robust segmentation of killer whale telemetry tracks in order to look at different behaviors over intermediate time scales. However, it is important to note that the BCPA comes with several so called 'turning-knobs' specifically the window size, K , and cluster width that influences the sensitivity of the analysis and track segmentation results. As of now there is no one, automatic way to know what that sensitivity should be for certain spatiotemporal scales, but this analysis could be more tailored to specific behaviors or scales of interest (Gurarie et al., 2009). Our time steps were specified at two-hour intervals, but state switches within intervals should still be considered a possibility, especially smaller scale foraging events. Inner fjord movement patterns were quite various and biological interpretations should be made cautiously. The main reason for this is that Kvænangen fjord is a complex area geographically. This fjord area contains several islands, side fjords and branches (Fig. 1, Larsen, 1997) and so change points detected and subsequent movement classifications may be an artifact of the restricted area and land formations rather than an individual's decision to change behavior. One example being that nomadic and resident mode are very similar in terms of movement characteristics and can be misclassified just by the whale's temporary direction. In other words, if whales make abrupt changes in trajectory around landmasses then it can segment and misclassify the following spatial mode. We accounted for this by decreasing the sensitivity of the BCPA, but regardless this should still be considered. Similarly, round and partial trips were discriminated by inflection point, but the classified partial trips were very similar to round trips, and in some areas a few partial trips had more resemblance to transiting in terms of spatial relocations, so we suggest further post-curve fitting discriminatory criteria when dealing with similar spatial patterns to reduce those outliers.

Finally, tag placement and performance can also affect the interpretation of finer-scale behavior. Vertical tag placement on killer whales' dorsal fins can affect the quality and quantity

of location estimates, with higher placement leading to better tag performance (Mul et al., 2019). With poor tag placement (e.g., below the dorsal fin and low on the animal), there is a likely increase in poor location estimates which can lead to unreliable inferences of movement, especially at smaller scales. In this study we tried to account for positional errors and misidentification of behaviors by implementing the correlated random walk with a two-hour time step and optimizing the BCPA to intermediate temporal scales. This allowed us to decrease the chances of spurious location estimates altering overall NSD model fitting. For smaller scale behavior like single feeding events in hourly or less time scales, tag placement and performance should be considered as a covariate (Mul et al., 2019).

The Norwegian killer whale's movement can take on a variety of spatiotemporal forms, which depends on an individual's perception of external factors, in combination with its genotype, and internal state (Shaw, 2020). For these killer whales, we found that the candidate movement modes presented here are shared collectively in areas of high herring abundance but the degree to which these modes are favored varies among individuals. While it is possible that most of the whales in our study continue to target herring even after the spawning events, it is not known if these behaviors/movement modes persist beyond the herring spawning period. Determining if these behavioral movements persist across all seasons could help resolve whether these killer whales are mainly feeding on herring year-round, or if there is a change in behavioral movements then this could indicate prey-switching. Furthermore, these discrete behaviors could be compared with the relative biomass distributions of prey species or anthropogenic factors to investigate their influence on whale behaviors (e.g., Mul et al., 2020; Vogel et al., 2021). There are many different methods to analyze telemetry data and each comes with strengths and weaknesses, where some results found in one analysis can be obscured in another. It can often be useful to explore data using different tools or by combining methods, as we have done in this study. It is important to recognize that the whale's horizontal movement is only part of the picture. Killer whales are highly mobile species and live in complex 3-dimensional environments. Vertical/dive movement or physiological data would be instrumental in understanding these behaviors we have classified in this paper. Regardless, this method remains promising for future research on killer whales, as well as other animals. At the individual level, this analysis is flexible enough to incorporate an unlimited number of behavioral states, as long as they have discernable NSD-time relationships. At the population level we have the potential of linking individual behavior to population dynamics and distribution. In sum, this study can serve as a baseline for future comparative studies regarding

finer-scale behaviors to further develop our knowledge of the foraging or movement strategies among individuals and investigate patterns within varying environments.

6 Literature Cited

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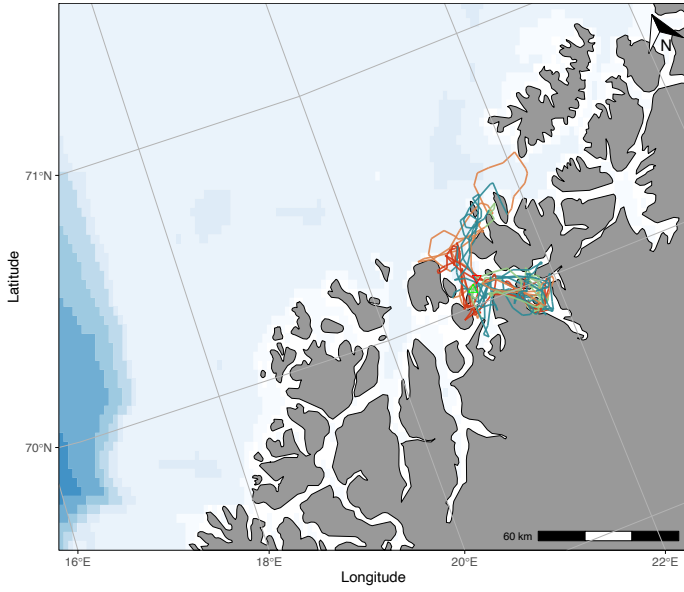
Appendix 1

Table S1 Summarized per individual are the central tendencies and variabilities (mean \pm SD) of descriptive statistics for each of the classified movement modes exhibited.

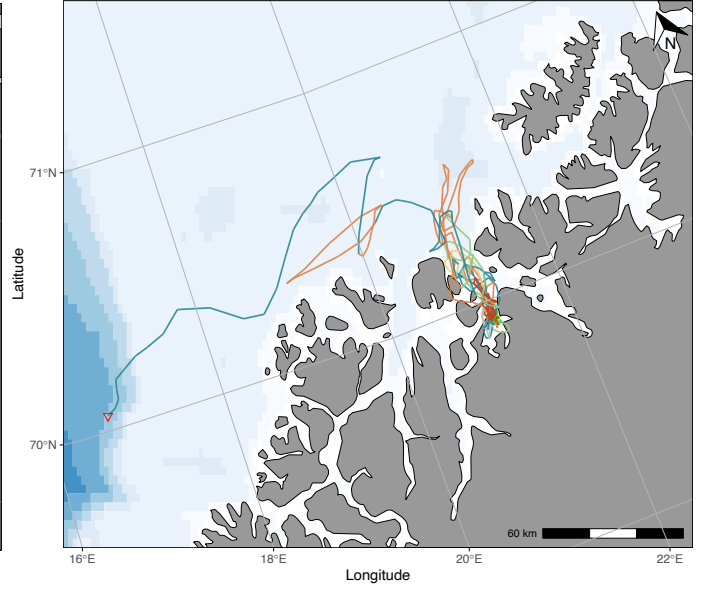
ID	Movement mode	N	Duration (h)	Total distance traveled (km)	Speed (km/h)	Persistence velocity	Net displacement (km)
54013	Resident	5	30.0 \pm 10.6	67.8 \pm 28.8	2.3 \pm 0.7	1.1 \pm 0.6	7.4 \pm 4.5
	Round-trip	6	23.8 \pm 12.1	64.1 \pm 32.3	2.8 \pm 0.9	1.7 \pm 0.7	11.8 \pm 13.5
	Partial-trip	1	16	14.5	0.9	0.5	2.7
	Nomad	8	21.5 \pm 13.7	29.7 \pm 22.9	1.3 \pm 0.4	0.4 \pm 0.4	10.3 \pm 9.4
	Transit	19	17.9 \pm 7.7	36.2 \pm 17.1	2.2 \pm 1.0	1.3 \pm 0.8	19.4 \pm 9.4
	Total	39	21.1 \pm 10.5	42.6 \pm 26.3	2.1 \pm 0.9	1.1 \pm 0.8	14.4 \pm 10.6
53561	Resident	9	40.7 \pm 13.8	112.6 \pm 47.8	2.9 \pm 1.2	1.4 \pm 0.9	10.4 \pm 7.9
	Round-trip	6	26.7 \pm 9.2	69.1 \pm 23.5	2.7 \pm 1.0	1.3 \pm 0.9	9.4 \pm 6.2
	Partial-trip	5	21.6 \pm 4.3	83.5 \pm 59.3	3.9 \pm 2.6	2.9 \pm 2.4	24.3 \pm 21.7
	Nomad	1	34	90.6	2.7	1.1	16.2
	Transit	22	22.5 \pm 12.1	76.2 \pm 57.8	3.2 \pm 1.2	2.2 \pm 1.4	48.2 \pm 37.7
	NA	1	20	30.3	1.5	0.8	12.5
	Total	44	26.9 \pm 13.1	82.8 \pm 52.4	3.1 \pm 1.4	2.0 \pm 1.4	30.9 \pm 32.9
53559	Resident	4	40.0 \pm 5.2	51.4 \pm 13.5	1.3 \pm 0.2	0.4 \pm 0.2	8.7 \pm 2.0
	Round-trip	9	31.8 \pm 14.5	72.2 \pm 41.0	2.4 \pm 1.2	1.5 \pm 1.0	10.0 \pm 10.7
	Partial-trip	7	35.1 \pm 12.9	84.8 \pm 53.5	2.4 \pm 1.3	1.2 \pm 1.3	18.4 \pm 15.3
	Nomad	9	23.3 \pm 9.4	47.3 \pm 20.8	2.1 \pm 0.6	1.0 \pm 0.7	14.6 \pm 8.7
	Transit	17	17.9 \pm 10.9	52.3 \pm 40.0	3.4 \pm 3.4	1.7 \pm 1.7	33.0 \pm 31.3
	NA	3	21.3 \pm 11.0	56.4 \pm 31.6	2.6 \pm 0.5	1.3 \pm 0.8	10.6 \pm 3.4
	Total	49	25.9 \pm 13.3	59.9 \pm 38.4	2.6 \pm 2.2	1.3 \pm 1.3	20.0 \pm 22.1
54011	Resident	8	22.0 \pm 8.1	47.8 \pm 16.4	2.2 \pm 0.4	0.8 \pm 0.6	7.9 \pm 3.5
	Round-trip	8	22.5 \pm 7.6	51.2 \pm 23.5	2.4 \pm 1.2	1.3 \pm 1.3	7.7 \pm 4.6
	Partial-trip	3	26.0 \pm 12.5	50.1 \pm 21.8	1.9 \pm 0.1	1.0 \pm 0.3	15.3 \pm 13.4
	Nomad	9	23.6 \pm 11.6	54.7 \pm 37.9	2.2 \pm 1.0	0.6 \pm 0.9	16.8 \pm 14.2
	Transit	31	23.1 \pm 10.0	52.7 \pm 36.1	2.2 \pm 1.1	1.4 \pm 1.2	31.5 \pm 33.8
	NA	3	15.3 \pm 5.8	45.2 \pm 13.1	3.2 \pm 1.4	2.2 \pm 1.4	9.3 \pm 3.8
	Total	62	22.7 \pm 9.5	51.7 \pm 30.9	2.3 \pm 1.0	1.2 \pm 1.1	21.4 \pm 26.6
83761	Resident	2	24.0 \pm 11.3	48.9 \pm 28.2	2.0 \pm 0.2	0.8 \pm 0.1	2.7 \pm 2.5
	Round-trip	4	23.5 \pm 10.0	44.9 \pm 14.0	2.1 \pm 0.9	1.2 \pm 0.9	2.7 \pm 0.9
	Partial-trip	4	28.5 \pm 13.2	72.2 \pm 36.9	2.7 \pm 1.0	1.4 \pm 0.8	18.0 \pm 9.0
	Nomad	3	28.0 \pm 9.2	57.2 \pm 18.0	2.1 \pm 0.6	0.5 \pm 0.7	10.0 \pm 2.3
	Transit	9	20.4 \pm 12.7	49.3 \pm 72.0	2.0 \pm 1.3	1.1 \pm 1.6	35.1 \pm 69.6
	NA	3	16.0 \pm 2.0	34.1 \pm 24.3	2.0 \pm 1.2	0.2 \pm 0.4	6.3 \pm 3.0
	Total	25	22.9 \pm 10.8	51.3 \pm 46.4	2.2 \pm 1.0	1.0 \pm 1.1	18.1 \pm 42.7
83760	Resident	4	25.0 \pm 10.9	45.3 \pm 29.1	2.0 \pm 1.1	1.1 \pm 1.0	4.2 \pm 1.6
	Round-trip	9	29.1 \pm 7.5	61.6 \pm 30.9	2.0 \pm 0.7	0.8 \pm 0.5	8.4 \pm 5.2
	Partial-trip	5	21.2 \pm 4.6	41.9 \pm 13.0	2.0 \pm 0.6	0.7 \pm 0.5	12.0 \pm 8.9
	Nomad	2	18.0 \pm 17.0	54.4 \pm 41.3	3.5 \pm 1.0	2.6 \pm 0.9	40.6 \pm 24.1
	Transit	16	20.0 \pm 12.1	63.7 \pm 46.0	3.3 \pm 1.8	2.2 \pm 1.9	36.0 \pm 27.1
	NA	3	18.7 \pm 7.6	40.2 \pm 26.0	2.1 \pm 0.9	0.9 \pm 0.7	10.0 \pm 6.6
	Total	39	22.6 \pm 10.4	56.3 \pm 35.9	2.6 \pm 1.4	1.5 \pm 1.4	21.6 \pm 22.9
53557	Resident	4	31.5 \pm 8.9	61.5 \pm 39.0	1.9 \pm 0.9	1.1 \pm 0.8	10.9 \pm 10.9
	Round-trip	12	27.0 \pm 10.5	59.8 \pm 32.4	2.3 \pm 1.2	1.3 \pm 1.0	10.6 \pm 13.2
	Partial-trip	4	28.5 \pm 15.9	52.3 \pm 13.3	2.0 \pm 0.5	1.1 \pm 0.6	20.9 \pm 6.7
	Nomad	8	32.3 \pm 15.9	109.2 \pm 59.0	3.3 \pm 0.9	2.3 \pm 1.0	41.8 \pm 18.7
	Transit	35	23.0 \pm 8.7	74.7 \pm 42.1	3.4 \pm 2.0	2.5 \pm 1.9	47.0 \pm 31.0
	NA	4	14.5 \pm 3.4	28.4 \pm 16.4	1.9 \pm 0.8	0.4 \pm 0.7	6.0 \pm 2.9
	Total	67	25.1 \pm 10.9	71.3 \pm 43.5	2.9 \pm 1.7	2.0 \pm 1.7	33.7 \pm 29.3
83764	Resident	3	36.0 \pm 19.7	41.4 \pm 21.1	1.2 \pm 0.6	0.3 \pm 0.4	3.9 \pm 1.2
	Round-trip	6	31.0 \pm 10.0	79.0 \pm 34.7	2.7 \pm 1.3	1.7 \pm 1.0	10.7 \pm 9.0
	Partial-trip	1	22	41.8	1.9	1.6	15
	Nomad	3	30.7 \pm 13.3	56.2 \pm 25.7	1.9 \pm 0.6	0.9 \pm 0.4	19.3 \pm 15.7
	Transit	9	21.6 \pm 13.0	59.0 \pm 65.6	2.6 \pm 1.3	1.8 \pm 1.2	32.5 \pm 36.9
	NA	2	12.0 \pm 2.8	28.9 \pm 15.3	2.6 \pm 1.9	0.8 \pm 0.3	6.5 \pm 1.7
	Total	24	26.1 \pm 13.3	58.2 \pm 45.8	2.3 \pm 1.2	1.4 \pm 1.0	18.9 \pm 25.4
83756	Resident	9	29.3 \pm 11.9	80.3 \pm 32.4	2.9 \pm 0.9	1.6 \pm 0.7	16.7 \pm 7.9
	Round-trip	11	23.1 \pm 8.4	71.2 \pm 39.7	3.1 \pm 0.9	1.9 \pm 0.9	9.3 \pm 7.9
	Partial-trip	7	22.6 \pm 8.2	57.1 \pm 30.9	2.6 \pm 1.4	1.6 \pm 1.0	19.7 \pm 19.9
	Nomad	3	21.3 \pm 7.6	58.1 \pm 38.2	2.7 \pm 1.7	1.6 \pm 1.9	24.9 \pm 17.7
	Transit	26	24.0 \pm 13.6	89.0 \pm 71.2	3.7 \pm 2.0	2.5 \pm 2.0	54.7 \pm 50.8
	NA	2	18.0 \pm 8.5	62.7 \pm 16.4	4.2 \pm 2.9	2.6 \pm 2.1	15.7 \pm 6.8
	Total	58	24.1 \pm 11.4	77.9 \pm 54.3	3.3 \pm 1.6	2.1 \pm 1.5	33.1 \pm 40.0
83768	Resident	2	40.0 \pm 2.8	79.6 \pm 11.7	2.0 \pm 0.4	0.9 \pm 0.7	6.1 \pm 3.5
	Round-trip	8	28.3 \pm 9.9	65.7 \pm 24.0	2.5 \pm 1.3	1.7 \pm 1.2	11.4 \pm 6.9
	Partial-trip	6	23.3 \pm 21.1	52.3 \pm 38.9	2.4 \pm 0.8	1.4 \pm 0.7	14.1 \pm 9.1
	Nomad	8	22.8 \pm 11.4	67.1 \pm 38.4	3.0 \pm 1.1	1.7 \pm 1.6	33.8 \pm 19.0

	Transit	35	19.5 ± 8.1	70.5 ± 44.0	3.6 ± 2.0	2.5 ± 2.1	49.5 ± 41.4
	NA	2	22.0 ± 17.0	87.4 ± 69.4	3.9 ± 0.1	1.7 ± 1.2	15.0 ± 3.6
	Total	61	22.2 ± 11.2	68.5 ± 39.9	3.2 ± 1.7	2.1 ± 1.8	36.4 ± 36.1
83755	Resident	1	52	37.7	0.7	0.6	1.3
	Round-trip	1	50	49	1	0.9	18.5
	Nomad	1	38	36.7	1	0.7	19
	Transit	6	23.0 ± 13.5	44.2 ± 26.4	1.9 ± 0.5	1.6 ± 0.5	22.6 ± 10.0
	Total	9	30.9 ± 16.4	43.1 ± 21.2	1.6 ± 0.7	1.3 ± 0.6	19.4 ± 10.6
83754	Resident	1	16	32.8	2	0.1	7.9
	Round-trip	2	44.0 ± 28.3	81.6 ± 37.1	2.0 ± 0.4	1.4 ± 0.3	17.3 ± 0.1
	Nomad	2	28.0 ± 25.5	62.3 ± 47.2	2.5 ± 0.6	1.4 ± 0.4	11.6 ± 7.5
	Transit	5	19.2 ± 6.4	46.8 ± 30.7	2.5 ± 1.2	1.6 ± 1.1	20.1 ± 8.1
	NA	1	12	41.2	3.4	0.2	5.6
	Total	11	24.4 ± 16.6	54.2 ± 31.5	2.5 ± 0.9	1.3 ± 0.9	15.6 ± 7.9
179032	Resident	2	43.0 ± 15.6	63.5 ± 21.4	1.5 ± 0.0	0.9 ± 0.1	3.9 ± 1.2
	Round-trip	4	28.0 ± 13.0	132.6 ± 103.2	4.2 ± 2.0	3.2 ± 2.2	21.7 ± 19.2
	Partial-trip	4	24.0 ± 7.1	103.6 ± 42.3	4.5 ± 2.1	3.2 ± 1.5	35.7 ± 21.8
	Nomad	3	36.0 ± 10.6	77.1 ± 16.4	2.3 ± 0.8	1.1 ± 1.1	25.4 ± 8.0
	Transit	27	15.0 ± 8.5	68.0 ± 54.7	4.4 ± 2.8	3.6 ± 2.7	55.0 ± 51.2
	Total	40	20.2 ± 12.2	78.5 ± 58.5	4.1 ± 2.5	3.2 ± 2.5	44.9 ± 45.5
Grand Total		528	23.8 ± 11.8	64.2 ± 44.4	2.8 ± 1.7	1.7 ± 1.6	27.5 ± 32.2

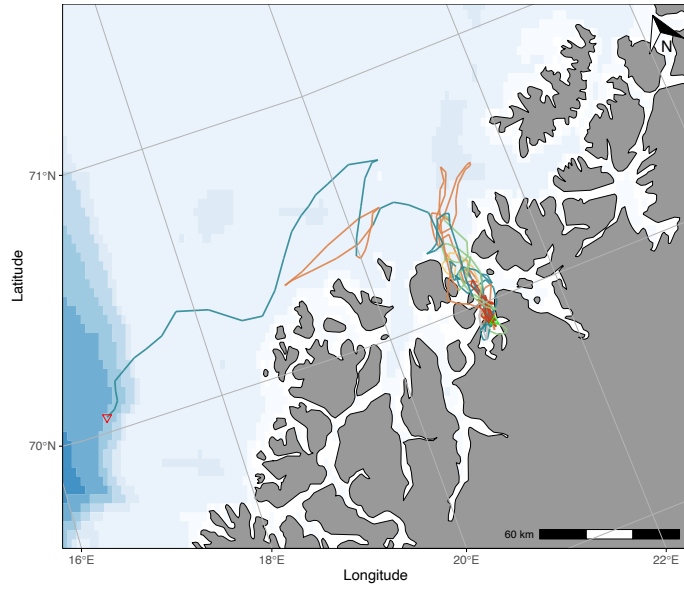
ID 54013



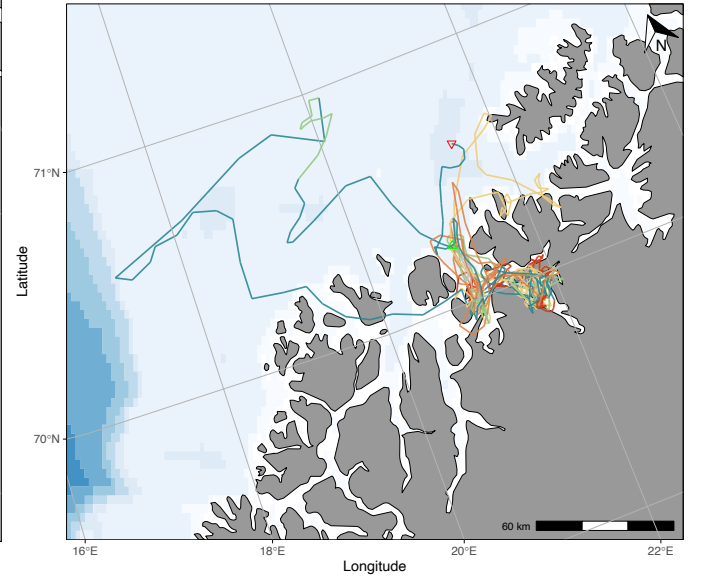
ID 83764



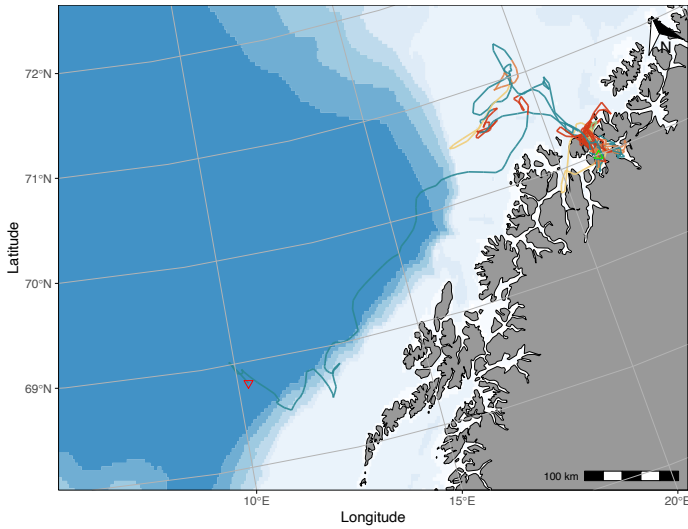
ID 83764



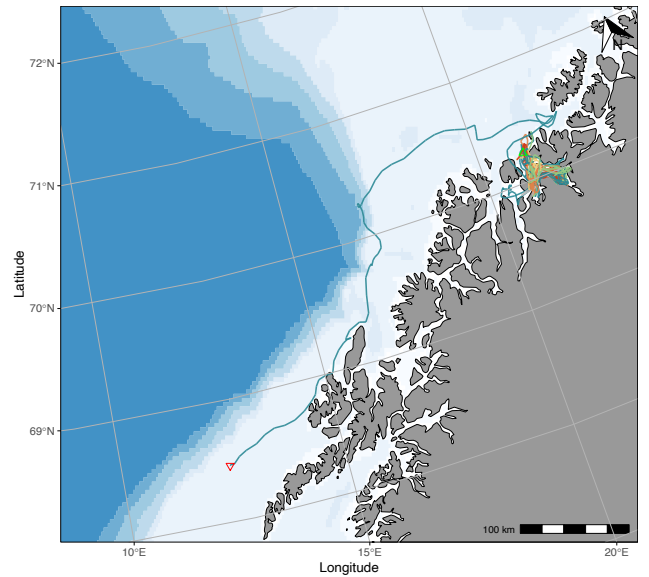
ID 53559



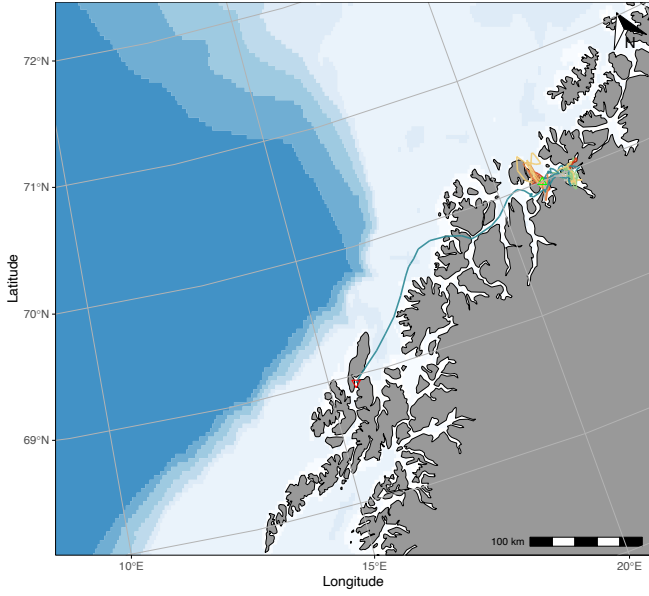
ID 53561



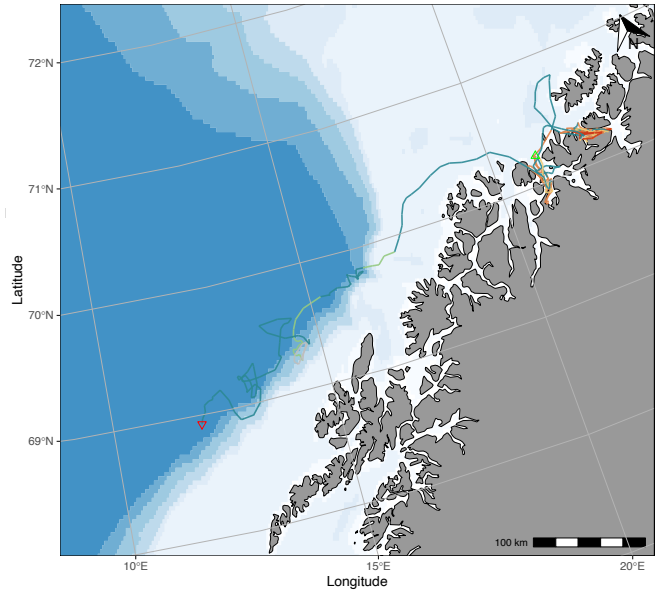
ID 54011



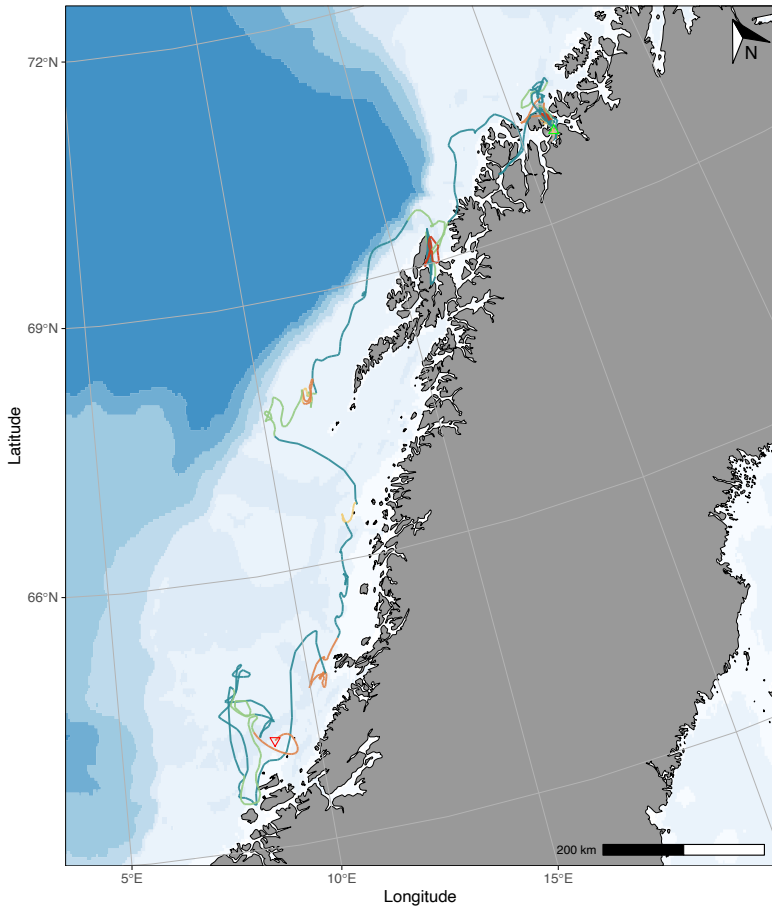
ID 83761



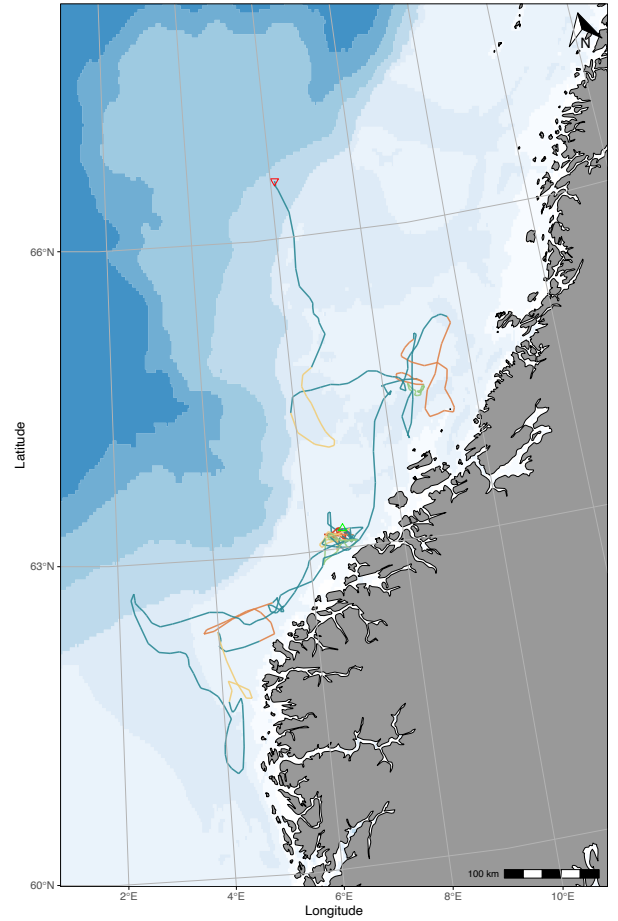
ID 83760



ID 53557



ID 179032



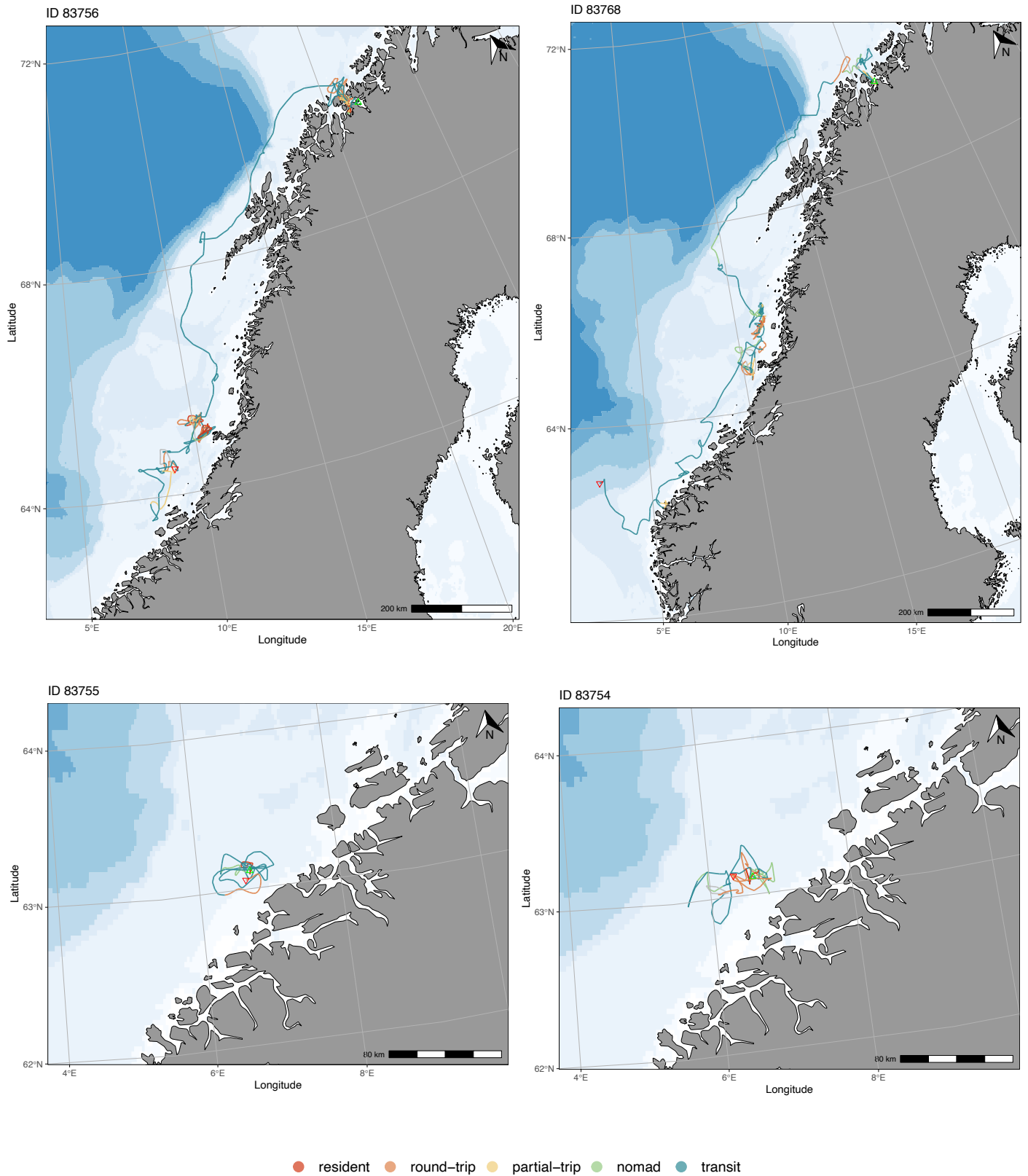


Figure 1S Maps of 13 satellite tagged killer whale tracks along the Norwegian coast during the winter and spring of 2018/2019. Tracks are segmented and colored by the corresponding movement mode classified. Green triangle indicates start of track and red triangle indicates end of track.

Appendix 2

```
#####
# load necessary packages
library(move)
library(adehabitatLT)
library(bcpa)
library(FlexParamCurve)
library(circular)
library(reshape)
##### FUNCTIONS #####
#----- Concordance Criteria function -----
CC<- function(nsd_data, fitted_val){
  cc<-1 - (sum((nsd_data - fitted_val)^2) /
    (sum((nsd_data - mean(nsd_data))^2) +
    sum((fitted_val - mean(fitted_val))^2) +
    length(nsd_data)*((mean(nsd_data)-
    mean(fitted_val))^2))) }
#####
# 1. GET THE DATA

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

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

#choose ID
kw<- subset(whales.crw, id == "179032")
kw<- kw[order(kw$date),]

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

#WINDOW SWEEP
Simp.ws <- WindowSweep(Simp.VT,"V*cos(Theta)", #log(V), V*cos(Theta)
  windowsize = 50,
  K = 3)
cps<-ChangePointSummary(Simp.ws,clusterwidth=3)
cps<- cps[[1]]

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

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

```

dataseg<- NULL

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

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

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

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

datansd<-NULL

for(n in 1:length(summary(d2)[,1])) {
  nsdall<-d2[[n]][,8]
  nsdtimeall<-d2[[n]][,3]
  nsdtimestartzero<-d2[[n]][,3]-d2[[n]][1,3]
  nsdid<-rep(as.vector(summary(d2)[n,1]),
            length.out=summary(d2)[n,3])
  nsdtrip<-rep(as.vector(summary(d2)[n,2]),length.out=summary(d2)[n,3])
  datansd1<-data.frame(nsdall,nsdtimeall,nsdtimestartzero,nsdid,nsdtrip)
  datansd<-rbind(datansd,datansd1)
}
head(datansd)

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

```

```

datansd1<-na.omit(datansd)

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

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

data1<-NULL

pdf("ID179032.pdf",height = 5, width = 5)

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

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

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

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

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

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

  ##### TRANSITING : MOD 32

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

  #derive starting parameters for fixed effects
  if(class(mod32) == "try-error") {
    CC_mod32 <- 0
  }
  if(class(mod32) != "try-error") {
    CC_mod32 <- CC(data_id$NSD,fitted(mod32))
  }
}

```

```

aic_mod32 <- AIC(mod32)
lines(data_id$zerostart, predict(mod32), col="blue")
}

##### ROUND-TRIP : MOD 2

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

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

##### PARTIAL-TRIP: MOD 22

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

#derive starting parameters for fixed effects
if(class(mod22) == "try-error") {
  CC_mod22 <- 0
}
if(class(mod22) != "try-error") {
  CC_mod22 <- CC(data_id$NSD,fitted(mod22))
  aic_mod22 <- AIC(mod22)
  lines(data_id$zerostart, predict(mod22), col="red")
  df22 <- data.frame(data_id$zerostart,predict(mod22))
  names(df22) <- c("x", "y")
}

##### RESIDENT

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

#derive starting parameters for fixed effects
if(class(hr) == "try-error") {

```

```

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

#### NOMADIC

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

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

data1$strip <- levels(trip)
data1$CC_mod32 <- CC_mod32
data1$CC_mod2 <- CC_mod2
data1$CC_mod22 <- CC_mod22
data1$CC_nom1 <- CC_nom1
data1$CC_hr <- CC_hr
data1$aic_mod32 <- aic_mod32
data1$aic_mod2 <- aic_mod2
data1$aic_mod22 <- aic_mod22
data1$aic_nom1 <- aic_nom1
data1$aic_hr <- aic_hr

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

if (names(best.aic)=="aic_hr" | (best.cc <.7 & CC_nom1 <.4)) { # | aic$aic_hr/min(aic) <
1.01 ...
  best.model<- hr

```

```

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

predW<- predict(best.model)
# add result on the plot
title(paste("kw.179032 trip n°", trip,"-",strategy, sep=""))
}

dev.off()

```