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Emma F. Vogel
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Supervisors:
Audun Rikardsen: UiT - The Arctic University of Norway
Marie-Anne Blanchet: UiT - The Arctic University of Norway
Martin Biuw: The Institute of Marine Research

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1 Abstract

Killer whales *(Orcinus orca)* have a cosmopolitan distribution with a broad diet ranging from fish to marine mammals. Regional populations show local prey specialization and their movements are tightly linked to those of their prey. Norwegian killer whales are known to feed extensively on Norwegian spring spawning (NSS) herring (*Clupea harengus)*. Over the last decade, killer whales have begun to readily been observed feeding on high concentrations of overwintering herring in some fjords of northern Norway. Killer whale offshore behavior is less well understood, specifically their reliance on herring as a prey resource outside of the fjord systems. We used movement parameters extracted from 29 killer whale satellite tracks on the Norwegian shelf and related their movements to herring biomass and distribution. Two techniques were used to estimate herring biomass, one based on survey data, and the other based on a simulated ecosystem model. Mixed effects modeling was then used to estimate the effect of herring biomass and diel variations in light levels, on the whales' movement parameters. We found that killer whales tend to follow the herring when they leave their coastal overwintering areas for their spawning grounds. Individual whale movement characteristics changed from fast directed travel in areas of low herring biomass towards slower non-directed travel when relative herring biomass increased. This suggests that whales feed on herring when they encounter dense concentrations on the Norwegian shelf. Relationships between killer whale movement patterns and herring biomass were consistent for both survey- and simulation-based herring fields. This highlights the potential for using model-based estimates of prey distribution when interpreting predator behavior. We conclude that NSS herring constitutes an important prey resource for killer whales, both during the overwintering and subsequently until the end of the spawning events. Killer whale movements can potentially assist in identifying previously unknown NSS herring aggregations.

Keywords: move persistence; foraging; habitat; spatial ecology; Orcinus orca; Clupea harengus

2 Introduction

Prey distribution, abundance, and behavior all play a major role in shaping marine predator behaviors (Womble et al., 2014; Goldbogen et al., 2015; Hays et al., 2016). Predators adapt the way they forage in response to changes in such prey characteristics to optimize the efficiency of their foraging efforts. Behavioral changes in response to prey distribution may shape both horizontal and vertical movements of marine predators (Thums et al., 2011; Bestley et al., 2015; Joy et al., 2015). Heterogeneity of marine environments, such as physical oceanographic features and areas of high primary productivity, can result in patchy spatiotemporal distributions of prey (Boyd, 1996; Sims et al., 2008; Bestley et al., 2010). Optimal foraging theory predicts that predators will exploit areas with high prey densities to optimize their energy efficiency, thus, maximizing their fitness (Hedenström & Alerstam, 1997; Houston & McNamara, 2014). When predators forage or search for prey within a confined area, they frequently exhibit area-restricted search (ARS) (Kareiva & Odell, 1987; Witteveen et al., 2008; Hazen et al., 2009; Silva et al., 2013). This behavior is characterized by decreased travel speeds and increased turning rates (Jonsen et al., 2005; Breed et al., 2009; McClintock et al., 2012). Furthermore, when a foraging predator finds itself in an area where prey density has fallen below a specific threshold value, the predator will either leave the area in search of locations with higher prey densities or begin feeding on an alternate prey type (Murdoch, 1969; Baalen et al., 2001). Foraging theory also predicts that predators will minimize the time spent moving between desirable foraging areas, or hotspots. When moving between prey patches, predators will switch to a transiting behavior, characterized by elevated and consistent speeds with lower turning rates, presumably to minimize the time spent transiting between hotspots (Fauchald & Tveraa, 2003).

Killer whales are one of the most widely distributed marine mammals, inhabiting all the world's oceans. These odontocetes are top predators that have been observed consuming many different prey types, including fish, other cetaceans, pinnipeds and seabirds (Baird, 2000). Killer whales can be considered generalists predators at the species level, however, when focusing on a more local level, populations of killer whales have been identified with specialized diet (Ford & Ellis, 2014) that may vary seasonally (Jourdain et al., 2020). It is theorized that evolutionary selection will favor diet and foraging specializations, since specialists typically employ more efficient foraging strategies than their generalist counterparts (MacArthur & Pianka, 1966; Stephens & Krebs, 1986; Futuyma & Moreno, 1988; Ford & Ellis, 2014).

Multiple killer whale ecotypes have been defined for the North Pacific and Antarctic killer whale populations (Bigg et al., 1987; Ford et al., 2006; Pitman & Ensor, 2003; Pitman et al., 2007; Dalheim et al., 2008). These ecotypes are defined using a set of criteria. Differences in ecotype behaviors and habitat use are thought to be linked to prey preference (Bigg, 1982; Heimlich-Boran, 1988; Bigg et al., 1990; Jefferson, Stacey & Baird, 1991; Ford et al., 1996; Baird, 2000; Yurk et al., 2002; Pitman & Ensor, 2003; Jones, 2006; Krahn et al., 2008; Visser et al., 2008). For example, the long daily distances traveled by Type B whales in Antarctic waters, an ecotype specialized on pinnipeds, are thought to increase their chances of successfully finding their preferred prey. Their extensive range is thought to maximize foraging efficiency by compensating for seal's anti-predator response and more patchy nature of their distribution (Andrews et al., 2008). In contrast, Type C whales, who specialize on fish, do not need to travel far to feed, since their main prey, silverfish (*Pleuragramma antarctica*), are abundant in Eastern Antarctic waters.

In the North Atlantic, three populations of killer whales have been identified based on genetic data (Foote et al., 2011; 2013). The first is primarily localized to waters off of Gibraltar and the Canary Islands. The second group is found in British waters, the North Sea and around Iceland. The last and largest group is found primarily in waters off Norway as well as in Greenlandic waters (Leonard & Øien, in press). Several studies indicate that North Atlantic killer whales may be broadly divided into two ecotypes; generalists (feeding primarily on herring, mackerel, and seals) and specialists (feeding on baleen whales) (Foote et al., 2009; Foote et al., 2010). However, these studies were based on a limited sample size and thus might not accurately represent the entire population. Norwegian and Icelandic whales are thought to feed primarily on herring (Similä et al., 1996; Foote et al., 2010; 2013), while killer whales around the British Isles are thought to feed predominantly on mackerel (*Scomber scombrus*) (Foote et al., 2013) whereas off the coast of Greenland they preferentially feed on pinnipeds (Foote et al., 2013). Unlike whales in the North Pacific and Antarctica, clear ecotypes for North Atlantic killer whales have not yet been established (Foote et al., 2013).

Norwegian killer whales are known to be present year-round along the Norwegian coast and inside fjords, but are also frequently encountered in the Barents Sea, and have been shown to be strongly associated with Norwegian Spring-Spawning (NSS) herring (Similä et al., 1996; Similä, 1997; Simon, McGregor & Ugarte, 2007). These studies were based on killer whale photo-ids taken both in fjords and on the Norwegian shelf, and vocalization identifications recorded in fjords, and all clearly demonstrate that Norwegian killer whales frequently feed on herring. These observations were conducted in areas where whales were able to be visually

observed feeding on herring. Since these studies were conducted in the winter in easily accessible coastal areas known to be associated with NSS herring overwintering aggregations, our understanding of Norwegian killer whale ecology may be biased. Norwegian killer whales have also been observed feeding on a wide variety of other prey, such as other fishes, marine mammals, and seabirds (Similä et al., 1996; Foote et al., 2009; Vester & Hammerschmidt, 2013; Vongraven & Bisther, 2014; Jourdain et al., 2017; 2020). In theory, if Norwegian killer whales are herring specialists, we would expect them to tightly follow the NSS herring. In contrast, if the whales are generalists, some might follow the NSS herring until their density falls below a specific threshold, or until more profitable prey aggregations are encountered. Of course, it is plausible that more complicated intermediate responses could occur. It is not known if Norwegian killer whales observed feeding on overwintering herring follow the migration to the spawning grounds, and if so, how herring biomass and distribution during spawning influences whale movements and behavior.

Norwegian spring-spawning herring exhibit extensive seasonal migrations between their wintering, spawning and feeding grounds (Huse et al., 2002). Dense concentrations of overwintering herring form in late autumn, typically remaining in their wintering areas until the spawning migration begins, usually in mid-January (Røttingen et al., 1994; Huse et al., 2010). Herring migration pathways can differ both spatially and temporally between years (Huse et al., 2010; Toresen et al., 2019). Similarly, the location of spawning and wintering grounds can also change over time and often these location shifts are abrupt due to changes in herring population demographics. Specifically, this variability in herring overwintering and spawning distributions is thought to be influenced by the recruitment of dominant age classes into the adult stock (Huse et al., 2010). The first mass-aggregation overwintering event following the herring stock collapse in the 1970s occurred in Tysfjord and Vestfjorden during the 1990s and early 2000s (Huse et al., 2010). This was followed by a period of offshore overwintering along the shelf edge northwest of Vesterålen before eventually moving closer to the Vesterålen coast in 2010 (Rikardsen, 2019). Northerly shifts of NSS herring overwintering sites continued to progress to more coastal and inshore waters each year. By winter 2012/2013 overwintering aggregations were occurring in the Troms area fjords. This area became the herring hotspot until winter of 2016/2017 when the northward shifts continued. By 2017 overwintering hotspots were in northern Troms (Kvænangen fjord) and western Finnmark (Rikardsen, 2019). During this period, the majority of the herring stock overwintered offshore in the Norwegian Sea, and still do, but in the last years a considerable fraction have also overwintered in Kvænangen fjord (Rikardsen, 2019).

In addition to large-scale seasonal horizontal movements between wintering and spawning grounds, NSS herring also exhibit shorter-scale diel vertical migration in the water column, where they are typically observed concentrating at depth during the day, then dispersing upward in the water column at night between dusk and dawn (Huse & Korneliussen, 2000). This diurnal pattern is expected to be correlated with daily changes in light intensity and is attributed to avoiding predation and to conserving energy (Huse & Korneliussen, 2000). Herring vertical migrations may also influence the foraging decisions by whales, such that foraging efforts might increase at night when herring approach shallower waters, and decrease when herring move deeper into the water column. If so, diel variations in foraging effort may, in turn, affect killer whale horizontal movement patterns.

The main objective of this study was to use satellite telemetry to examine if Norwegian killer whales continue to feed on NSS herring once herring leave their overwintering areas, move offshore and migrate to their spawning grounds on the Norwegian shelf. Our sub-goals were to examine: (1) the extent to which NSS herring distribution influences offshore killer whale movements, (2) if killer whale movements are influenced by diel variations in light levels, and (3) if there is individual variation in whales' behavioral responses to herring biomass. Additionally, we evaluated the impacts of using two different methods for estimating herring biomass and distribution on killer whale movement.

3 Materials and Methods

3.1 Study area

The fieldwork for this study was conducted over three winter field seasons in northern Norway. The majority of tagging occurring between late October through February in the fjords around Tromsø (2015-2016) and then over two seasons in the Kvænangen fjord (2017-2019, Fig. 1 a). From late February-early March 2019, additional tagging occurred in southern Norwegian coastal waters off the coast of Møre in collaboration with the Norwegian Coast Guard. Recently, when NSS herring overwinter in northern fjords and coastal waters, their spawning grounds have been located south of the overwintering areas, along the Norwegian shelf, reaching to the southwestern waters off Møre (Fig. 1 b). After hatching, larva will drift with the northward North Atlantic current to the Barents Sea, where they feed until they reach sexual maturity (Toresen et al., 2019).
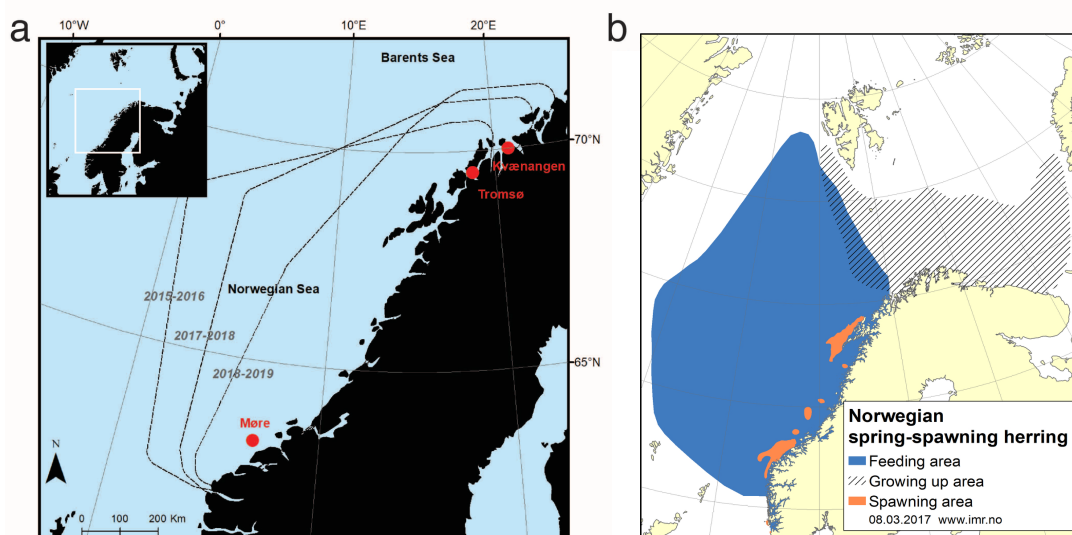
Figure 1 Maps of the northern Norwegian study area. In panel (a), the tagging sites are indicated with red circles. NSS Herring survey spatial extent for 2015-2016, 2017-2018 and 2018-2019 seasons are indicated by dashed lines. The insert shows the Norwegian coast in a larger geographic context. Panel (b) is taken from www.imr.no (2017) and depicts the distribution and general migration pathways of Norwegian spring-spawning herring.

3.2 Tagging

A 26-ft open RIB (Rigid inflatable boat) was used to slowly approach the whales and a Aerial Rocket Tag System (ARTs launcher), crossbow or Dan-inject CO_2 systems were used to deploy either SPOT5 or SPOT6 Limpet Argos transmitters (Wildlife Computers, Redmond, WA). Given that tag placement can influence the quality of data (Mul et al., 2019), we aimed

for tag placement in the center of the dorsal fin (Andrews et al., 2008). Tags were anchored in place using two 68-mm titanium sub-dermal darts protruding from the base of tag (Andrews et al., 2013; Mul et al., 2019). These barbed darts penetrate through the skin and anchor in the dense connective tissue (collagen) in the center of the dorsal fin (Andrews et al., 2008; Andrews et al., 2019). Darts were sterilized with 70% ethanol before deployment to decrease risk of infection. Tags were programed to transmit 14-15 times every hour for the first 45 days to obtain high temporal resolution early in the tagging period. In the following 35-45 days the transmission rate was reduced to 8-10 per hour to extend battery life. Finally, the transmission rate was further reduced to 55 transmissions per day until the tag detached from the whale or the battery failed.

3.3 Tagging data acquisition and analysis

Tag location estimates were calculated by the CLS-ARGOS service and pre-filtered using a Kalman filter in a state-space framework. All subsequent data processing and statistical analyses were performed using 'R' software (R Core Team, 2019). If a large gap in tracking data occurred near the very end of a track, the end of the track was trimmed to remove the gap and any subsequent data points. Three whales with gaps greater than ~16 hours in their transmission rates were not included for further analysis. To convert the irregular and relatively noisy time series of Argos position estimates to a time regularized path, we used a Correlated Random Walk (CRW) state-space model to fit the satellite data, using the 'fit_ssm' function from the 'foieGras' package (Jonsen & Patterson, 2019). This algorithm assumes that the movement characteristics at a given location are related to that of movements at previous locations (Johnson et al., 2008; Jonsen et al., 2019), and takes location error and irregular transmissions into account to produce a time-regularized model of the most probable path a whale may have taken (including uncertainty estimates). The model used was set to interpolate whale locations at three-hour intervals. Since our objective was to study behaviors occurring after whales leave fjords with overwintering herring for offshore waters, here referred to as the *Norwegian shelf*, all whale location points were designated as being either in fjord or on the Norwegian shelf. This study is based on tracking data obtained from twenty-nine (out of 37) whales that had at least 20 total locations outside of the fjords.

3.3.1 Move persistence

Move persistence (g_t) is a theoretical concept that can be used as a continuous index of an animal's movement behavior (Breed et al., 2012). Move persistence values were estimated

using the positional displacement of consecutive tracking points. These values are sensitive to how often an animal changes direction and speed along their trajectory (Jonsen, 2016; Jonsen et al., 2019). Move persistence values can range from 0 to 1, where 0 designates highly variable and restricted movement behaviors, and 1 denotes more consistent and directed movements (Jonson et al., 2019). In this study we used low move persistence values as a proxy for area restricted search (ARS) and high values for transiting behavior. Move persistence values were measured using the 'fit_mpm' function from the 'foieGras' package (Jonsen & Patterson, 2019). A joint move persistence model ('jmpm') was used in these calculations to normalize the move persistence of all whales in this study to the same scale. While there are many other algorithms to parametrize movement behavior, we selected move persistence because it gives a continuous scale of behavioral state, instead of discrete and somewhat arbitrary behavioral states (Breed et al., 2012; Auger-Méthé et al., 2017; Jonsen et al., 2019; Eisaguirre et al., 2019).

3.4 Environmental Variables

3.4.1 Observed herring biomass – INLA field

The Norwegian Institute of Marine Research (IMR) has conducted regular herring surveys since 1988 from the Møre coastline in south-western Norway to Troms in the north (Slotte et al., 2019), in order to estimate spawning stock biomass in support for regular stock assessments. Acoustic and biotic data were collected throughout these surveys and were used to estimate herring geographical trends of abundance, distribution and life stages. These annual standardized NSS herring surveys were conducted in February when NSS herring migrate from their wintering areas towards their southerly spawning grounds (Slotte et al., 2019). A multi-boat systematic survey design was used to collect acoustic Nautical Area Scattering Coefficient (NASC) values along pre-allotted survey tracks (Fig. 2). Survey areas were stratified prior to the start of the survey, according to projected herring density and age distribution, utilizing the standard stratified design (Jolly & Hampton, 1990). The survey paths and methods used for each of the three seasons considered in this study can be found in the corresponding survey reports (Slotte et al., 2016; Slotte, et al., 2018; Slotte et al., 2019). Survey design and data processing all utilized StoX opensource software (Johnsen et al., 2019) and 'RStoX' package (Holmin, 2019).

Biotic stations, where herring samples were collected via trawling, occurred throughout the survey track (Fig. 2 a). Weight and length data were collected from up to 100 individuals from each trawl. These data were used to calibrate the acoustic NASC distribution observations

in order to estimate numerical abundance and biomass (Fig. 2 b). While NASC values could be used as a proxy for biomass, estimates of actual herring biomass were obtained by integrating herring length and weight values, acquired from trawling data, with the acoustic NASC values. A script written with the 'RstoX' package was used to integrate these data and calculate herring biomass along the survey transects (see Appendix 2).

In order to obtain an interpolated surface of estimated relative biomass based on the NASC-derived point estimates along transects, we used Integrated Nested Laplace Approximations (INLA), that utilize stochastic partial differential equations (SPDE) and Gaussian Markov Random Fields (GMRF) to account for autocorrelation across space (Lindgren & Rue, 2015; Rue, Martino, & Chopen, 2009), using the 'INLA' package (Rue, Martino, & Chopen, 2009; Lindgren et al., 2011; Martins et al., 2013; Lindgren & Rue 2015). Supporting barrier models were used to account for the barrier effect caused by the Norwegian coastline (Bakka et al., 2016; Bakka et al., 2018; Bakka et al., 2019). A detailed description of INLA and the barrier model can be found in Lindgren & Rue (2015) and Bakka et al. (2016), respectively. A script adapted from Lindgren & Rue (2015) and Bakka (2016) was used to transform point biomass values into the interpolated 2-dimentional spatial biomass field (see Appendix 2). This interpolated field is hereafter referred to as the "INLA" field.
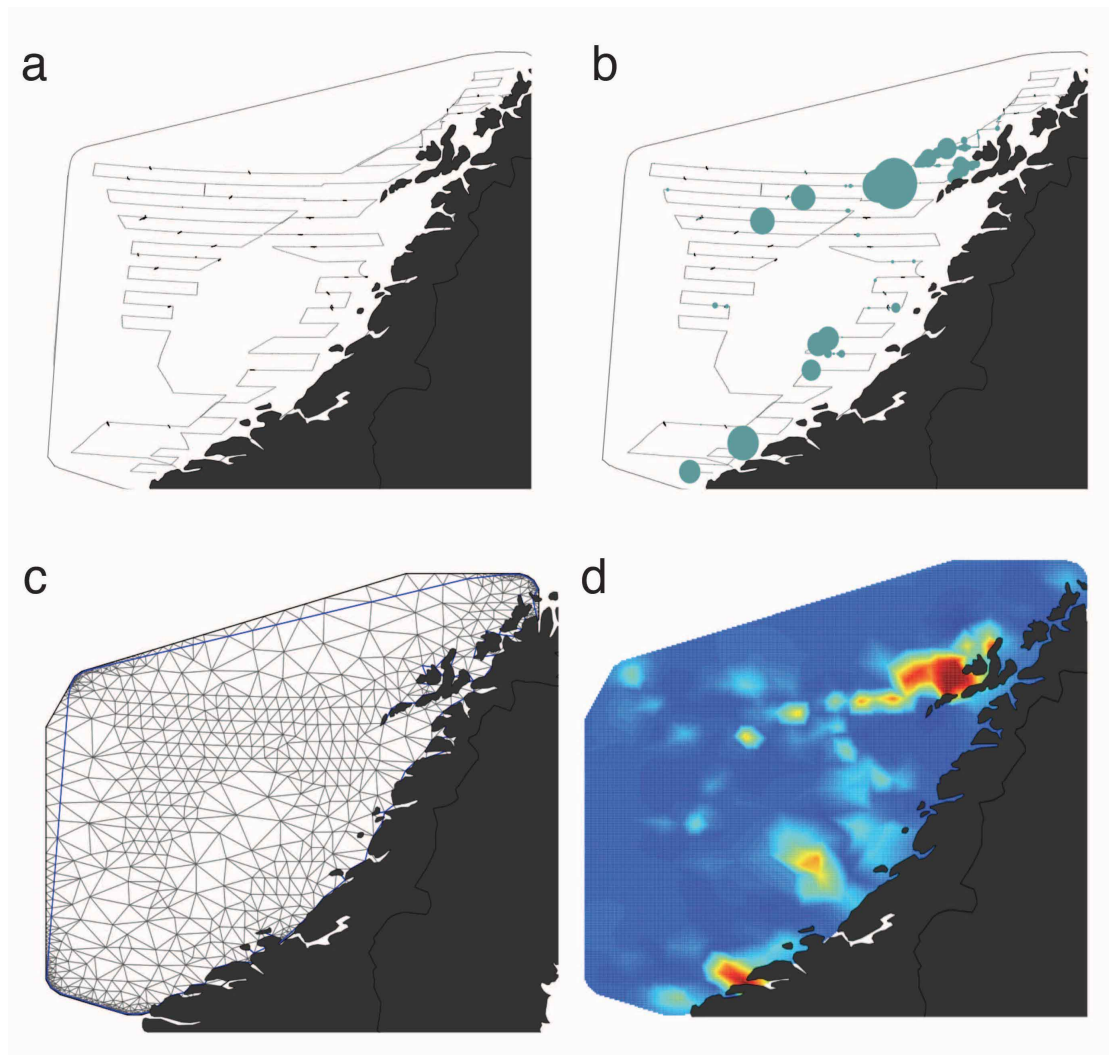
Figure 2 Schematic illustration showing analytical approach for using INLA to interpolate relative herring biomass point values over a portion of Norwegian coast. Panel (a) depicts the paths of 2016 NSS herring survey vessels, these vessels continuously collected NASC values as an indicator of herring distribution. Clusters of points along the path indicate biological trawl stations. Together with the NASC values, the biological data was used to characterize the herring spawning stock. In panel (b) survey paths are superimposed with teal circles whose diameter represents the magnitude of NASC values. Panel (c) shows the triangle mesh for INLA interpolations. Cell size was determined using the 'meshbuilder' function and allows the INLA model to compensate for different survey track densities in the region. Panel (d) depicts the 2016 NSS relative herring biomass distribution generated by INLA. Red indicates areas of high relative biomass.

3.4.2 Simulated herring biomass- E2E field

The Norwegian ecological end-to end model (NORWECOM.E2E) is a fully coupled model system consisting of a nutrient-phytoplankton-zooplankton-detritus (NPZD) model for lower trophic levels, and individual based models (IBMs) for *Calanus finmarchicus* and pelagic fish (Hjøllo et al., 2012; Utne et al., 2012; ClimeFish D3.3-report; Hjøllo et al., 2019). NORWECOM.E2E is one of very few bottom-up models world-wide where IBMs for different

trophic levels are two-way coupled and used to simulate food web dynamics of a large regional sea. NORWECOM.E2E is the only model system of this type for the Norwegian Sea. In this model, herring fish stocks were initiated based on the total number of individuals of each age class (and these age groups' corresponding weights) based on the 2012 analytic assessments (ICES, 2017). The model considers migration patterns' dependence on water temperature, prey availability and stock biomass (Fig. 3) Thus, changing environmental conditions will cause interannual variation. Hereafter, we refer to the herring data from NORWECOM as the "E2E" field.
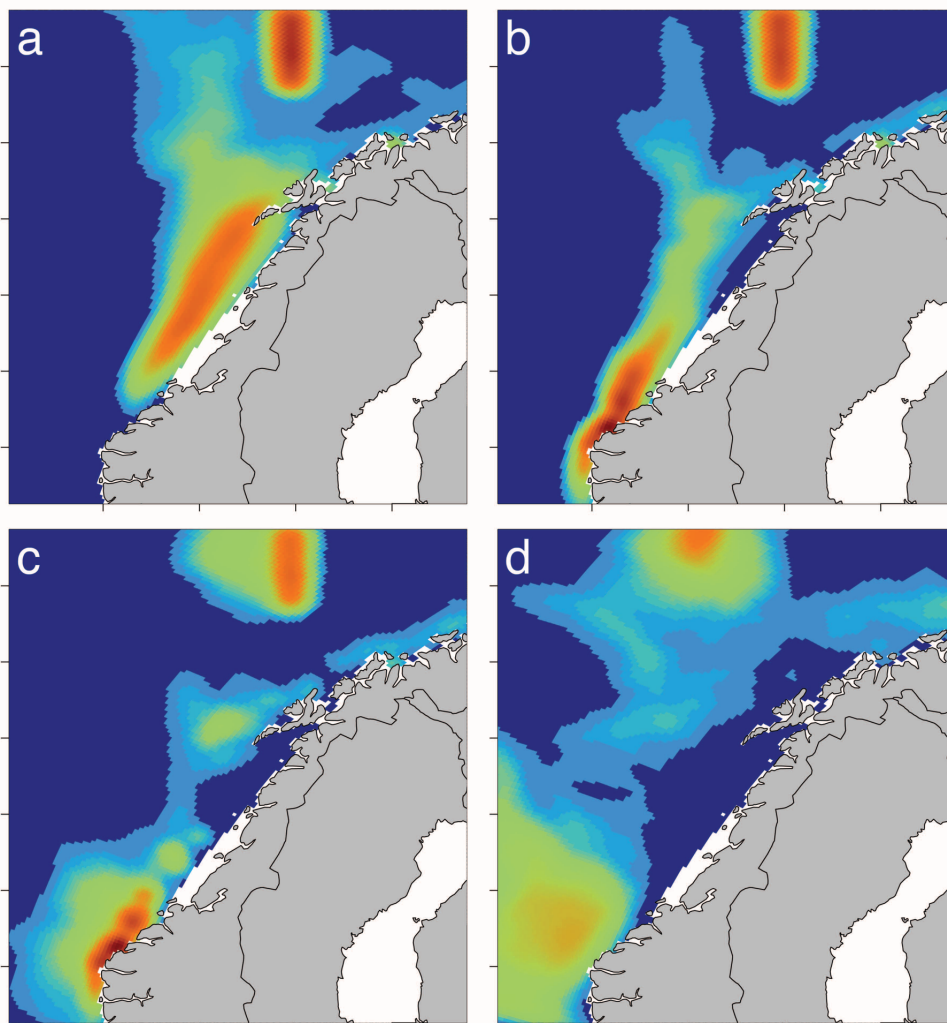
Figure 3 Maps of average E2E daily herring biomass distributions over 30-day periods (centered on the 1st of each month) as approximated by NORWECOM model. Panels represent (a) Mid-December – Mid-January, (b) Mid-January – Mid-February, (c) Mid-February – Mid-March, and (d) Mid-March – Mid-April. Red indicates high relative herring biomass.

3.4.3 Light intensity

Daily variations of light intensity are thought to drive daily vertical movements of herring (Huse & Korneliussen, 2000). To investigate if diurnal variations in light intensity influence

killer whale movement behavior, sun angle values for each whale location and time were obtained using the 'solarpos' function from the 'maptools' package (Bivand & Nicholas Lewin-Koh, 2019).

3.5 Modelling approach

We used a mixed effects modeling approach developed especially for animal movement data to investigate how killer whale movement characteristics (represented by the move persistence index g_t) is influenced by three environmental variables: (1) observed INLA herring biomass, (2) simulated E2E herring biomass, and (3) light intensity. This method can evaluate both individual and population level responses to the covariates such as environmental variables, and is implemented in the 'mpmm' package (Jonsen, 2020), based on the approach described by Jonsen et al. (2019). INLA herring biomass values were extracted from INLA generated distributions for the appropriate year based on whale track coordinates. E2E herring biomass values were extracted from the NORWECOM model distribution based on both Julian day and coordinates for individual whale track points. Sun angle values were calculated at each whale track location as described above. We evaluated nine candidate models for each biomass field (INLA and E2E): (1) ~ biomass + sun angle + (biomass + sun angle | id), (2) ~ biomass + sun angle + (biomass | id), (3) ~ biomass + sun angle + (sun angle | id), (4) biomass + sun angle + (1 | id), (5) biomass + (biomass | id), (6) ~ biomass + (1 | id), (7) ~ sun angle + (sun angle | id), (8) ~sun angle + (1 | id), and (9) ~ 1 + (1 | id). Since the observed herring biomass distributions covered a limited geographic range, only whale track location points within the interpolated field (whether INLA or E2E) were considered in each model. Each of the nine models, corresponding to either observed or simulated herring biomass, were ranked based on changes in the Akaike information criterion (ΔAIC) and on likelihood ratio (LR) tests. Individual models that failed to converge were not included in the ranking.

4 Results

4.1 Tracking

Average satellite tag longevity was 37 days, ranging from 3 to 105 days (Figs. 4 and 5). The earliest we observed a tagged whale finally leaving the fjords was on December 4th (ID 54013) and the latest was on February 25th (ID 153483). Tag retention after the whales left the fjords averaged 20 days, varying from 0 to 65 days. In total, 743 days of data were recorded while whales were on the Norwegian shelf. Upon exiting the fjords, all whales initially traveled southwards along the Norwegian Sea shelf (Fig. 4).
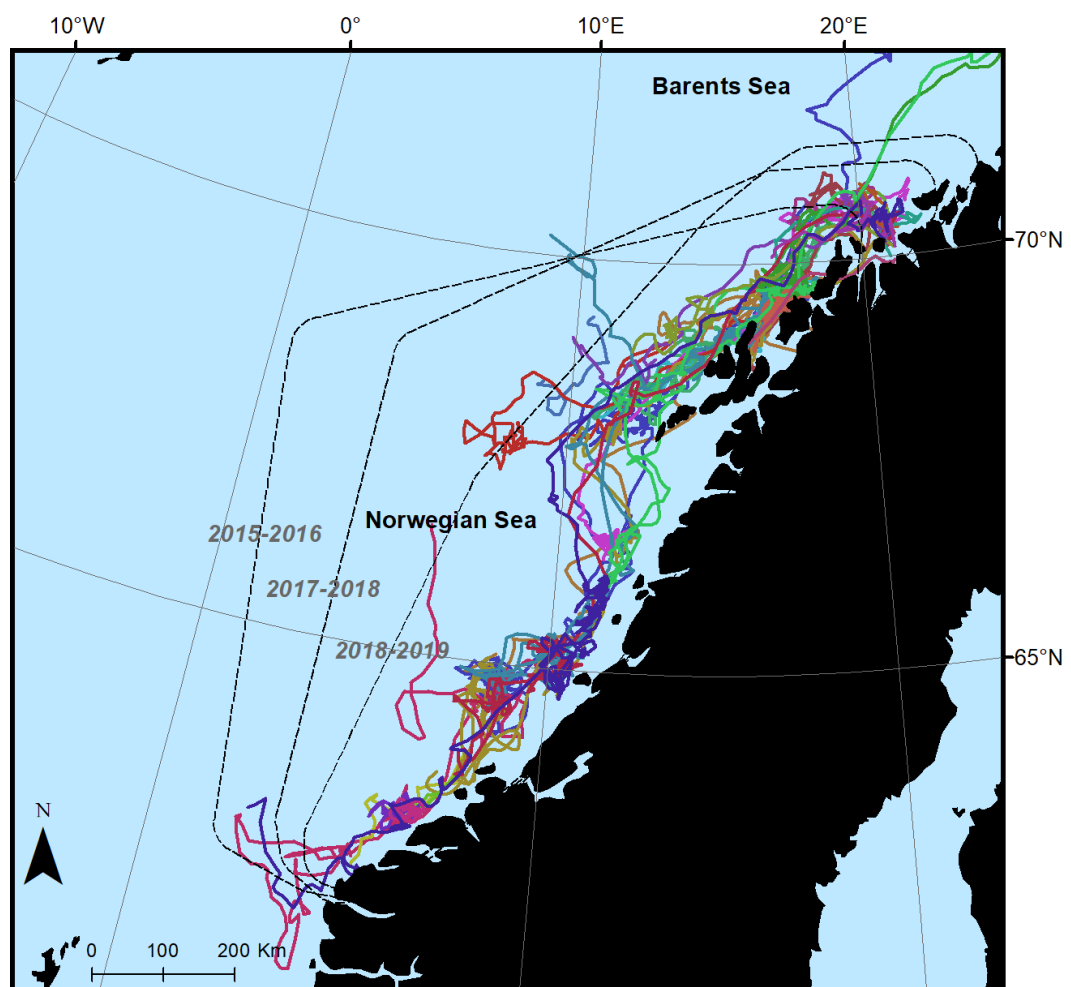
Figure 4 Map of killer whale tracks on the Norwegian shelf. Tracking data from individual whales collected over three field seasons are depicted and color coded by unique tag ID numbers. NSS Herring survey spatial extent for 2015-2016, 2017-2018, and 2018-2019 seasons are indicated by dashed lines.
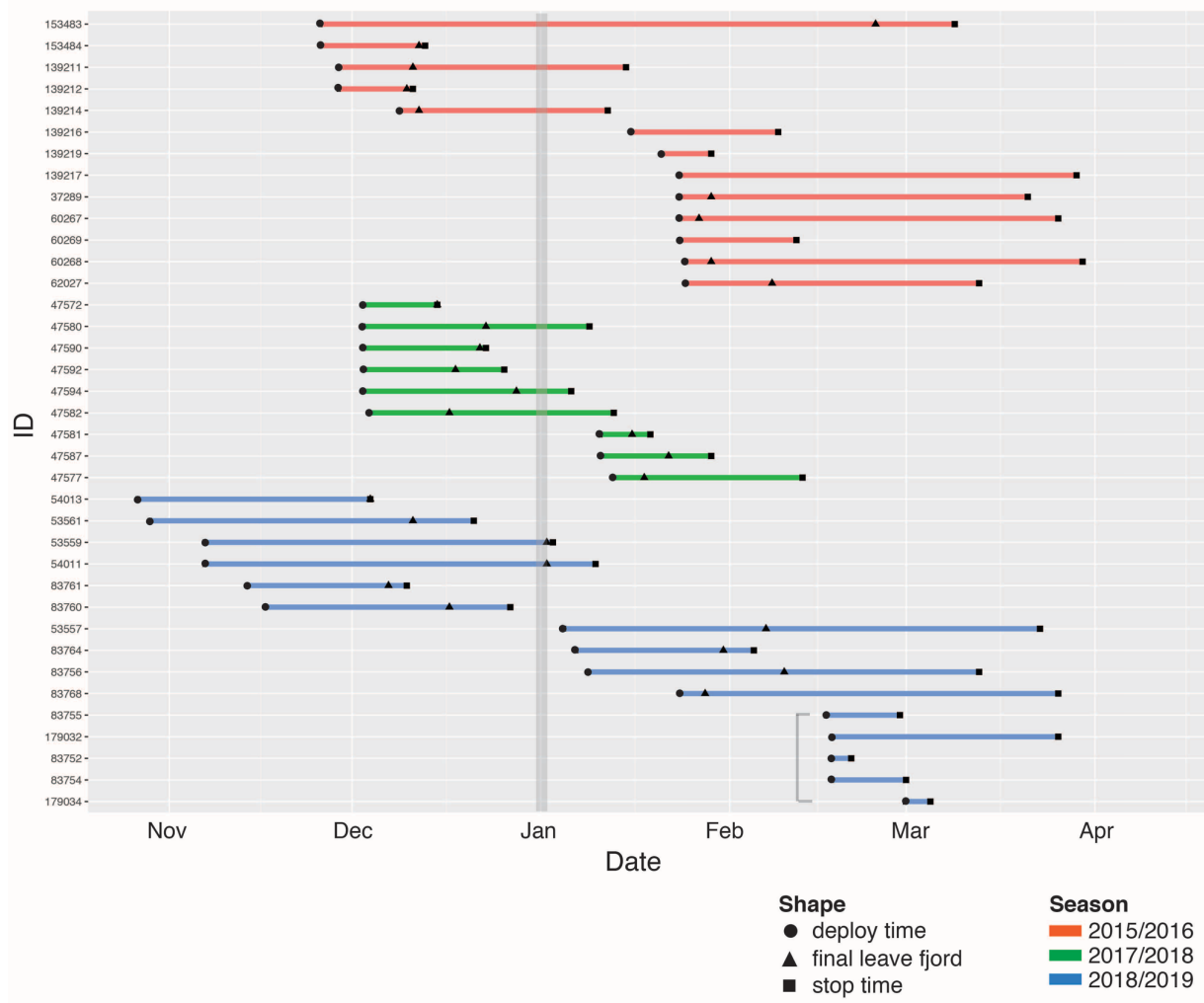
Figure 5 Tagging retention timelines obtained from 37 killer whales over three field seasons. Circles denote the date the tag was deployed, triangles denote the final leave fjord date of each whale, and squares denote last signal received from tag. For this study we focus on tracking data after whales left fjords. Note that whales that were tagged outside of fjords can be identified by the absence of a triangle in their timeline and were also included in this study. Grey bracket highlights individuals tagged off Møre in the southern herring spawning grounds.

4.2 Movement characteristics

The movement index g_t for all whales shows several discrete clusters of low move persistence values (purple) distributed along the Norwegian coast (Fig. 6). Transiting corridors of high move persistence (light green) connect these low move persistence zones. An example of a transiting corridor can be observed south of Lofoten, connecting two notable low move persistence clusters (one north of Andøya and the other along the coast of Norland County).
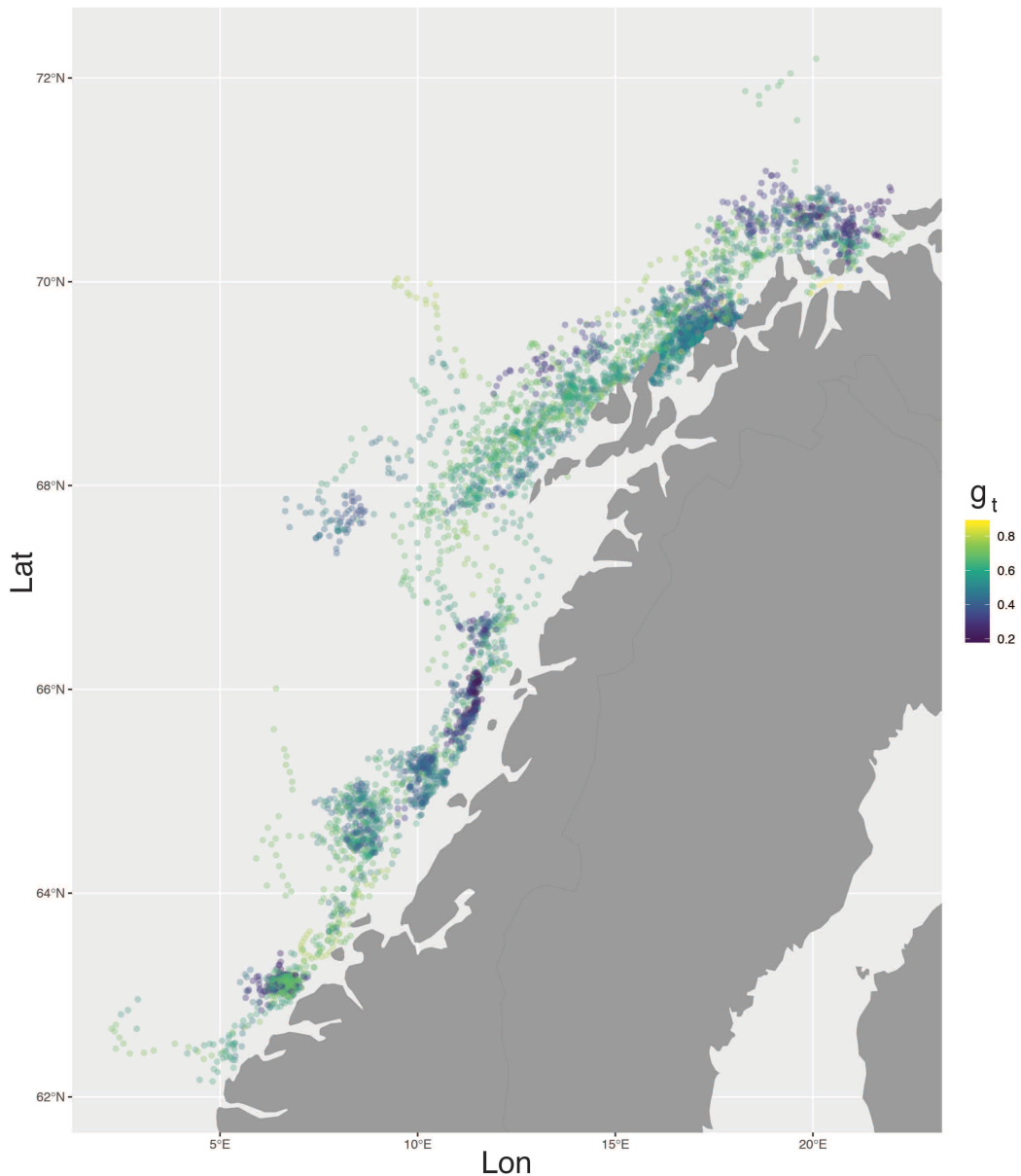
Figure 6 Combined map of three seasons of killer whale tracking locations on the Norwegian shelf with corresponding move persistence values, g_t (color coded). Low move persistence values (purple) indicate restricted behaviors, and high values (yellow) indicate directed movement.

4.3 Environmental variables

4.3.1 Spatial analysis of observed herring biomass- INLA

While there were substantial annual variations in the herring distribution, a few notable high biomass concentrations, or hotspots, were consistently observed at similar locations in all three years (Fig. 7 a-c). In 2016 most of the area surveyed had relatively low observed herring biomass, with a few patches of substantially higher biomass, whereas in 2018 and 2019 herring biomass was generally higher and more evenly distributed throughout the entire survey area.

For 2016, the main location where low move persistence was observed was to the northeast of Lofoten off the islands of Senja and Kvaløya (Fig. 7 a), and generally coincided with patches of high herring biomass. A few minor patches of low move persistence were also observed in association with locally elevated patches of herring biomass further south along the Nordland coast and in particular, off Nord-Trøndelag. In contrast, the 2018 and 2019 seasons had multiple patches of low move persistence west of Lofoten and in the south in addition to the patch off Senja and Kvaløya northeast of Lofoten (Fig. 7 b-c). Again, low move persistence generally coincided with elevated herring biomass.

Density plots of move persistence (g_t) values for whales of each season are depicted in Figure 7 (panels d-f). The move persistence values for 2015-2016 showed an overall unimodal distribution around relatively intermediate move persistence values (Fig. 7 d). Whereas 2017-2018 move persistence values had a broader distribution (Fig. 7 e). Move persistence values for 2018-2019 had a more bimodal distribution (Fig. 7 f). The distributions observed in individual move persistence density curves did not always follow the distributions observed in their corresponding seasons density plot (Fig. 7 d-f, colored by unique whale ID). Whales with unimodal, bimodal, and more variable distributions were observed, illustrating a high degree of individual variation in movement characteristics.
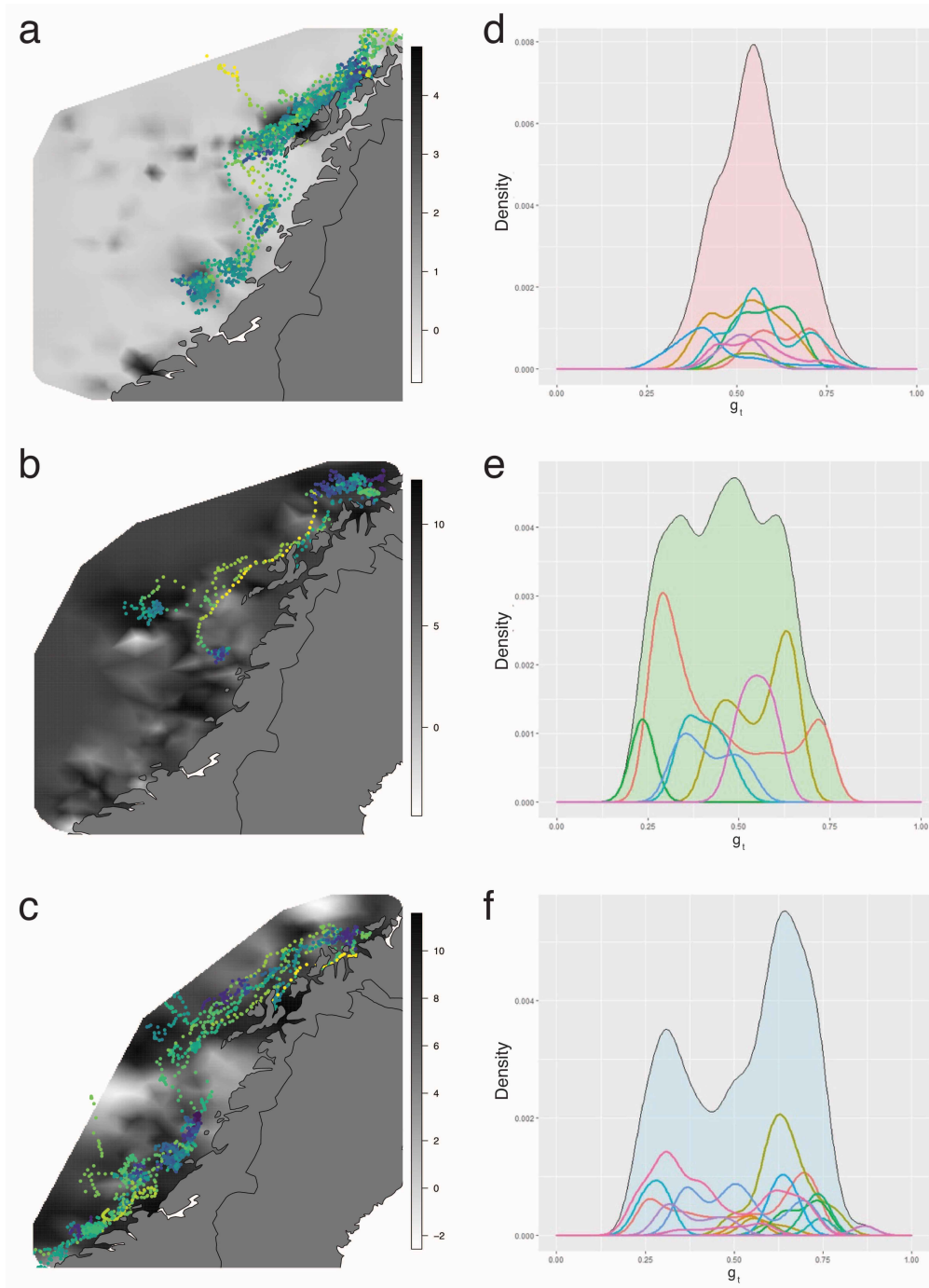
Figure 7 Overlay of relative observed herring biomass and killer whale move persistence (g_t) values. Maps of (a) 2016, (b) 2018, and (c) 2019 relative INLA herring biomass distributions (greyscale where darker values indicate higher relative biomass). Note that the relative observed herring biomass scales differ. Absolute biomass values cannot be compared across years, but relative values and distribution patters can. Move persistence values for the corresponding season are superimposed over the observed relative herring biomass distributions. Each point is colored by the corresponding move persistence value g_t, ranging from light green, indicating transiting behavior with high speeds and consistent directionality, to dark purple indicating foraging behavior with reduced speeds and frequently changing directionality. To the right of the maps are density plots of move persistence value distributions for (d) 2015-2016 (pink), (e) 2017-2018 (green), and (f) 2018-2019 (blue). Within each season's collective density plot, individual whale g_t density plots are shown (colored by whale ID).

4.4 Mixed effects modeling

Results from the mixed effects models indicate that the most parsimonious model, $g_t \sim$ biomass + (1|id), included a fixed effect for biomass and a random intercept term for individual whales (Tab. 1). This model was found to be the best fit for explaining killer whale move persistence using both observed INLA herring biomass and simulated E2E herring biomass values, see Table 1 and Figure 8 a-b. All individuals responded to herring biomass (both INLA and E2E) with a negative slope. This indicates an inverse relationship between whale move persistence and herring biomass. There was a consistently negative response in g_t with increasing relative herring abundance (Fig. 8), further supported by the fact that a model including individual random slope effects did not improve the fit. Including individual intercept terms did however improve the fit, suggesting that there are individual differences in overall movement characteristics. Of the nine models evaluated using observed herring biomass values (based on INLA estimates), seven converged, whereas for the simulated herring biomass values (based on E2E estimates), six converged. The most parsimonious model did not include light intensity as an environmental covariate that influences killer whale move persistence.

Table 1 Model rank table. Ranked lists of models using either relative observed herring biomass acquired from the INLA field or models using relative simulated herring biomass acquired from the E2E field. Model order was based on the change in Akaike information criterion (ΔAIC) and likelihood ratios (LR).

Biomass method	Model formula	df	ΔAIC	LR
INLA herring biomass	~biomass + (1 | id)	6	6310.46	6298.461
	~biomass + sun angle + (sun angle | id)	9	.64	-5.360
	~biomass + sun angle + (1 | id)	7	2.00	0.000
	~biomass + sun angle + (biomass| id)	9	6.00	0.000
	~1+ (1 | id)	5	12.07	14.070
	~sun angle + (1 | id)	6	14.07	14.070
	~sun angle + (sun angle | id)	8	15.46	11.460
E2E herring biomass	~biomass + (1 | id)	6	6306.46	6294.457
	~biomass + sun angle + (1 | id)	7	1.57	-0.430
	~1+ (1 | id)	5	16.08	18.080
	~ sun angle + (1 | id)	6	18.08	18.080
	~sun angle + (sun angle | id)	8	19.46	15.460
	~biomass + sun angle + (biomass| id)	9	NA	97.790
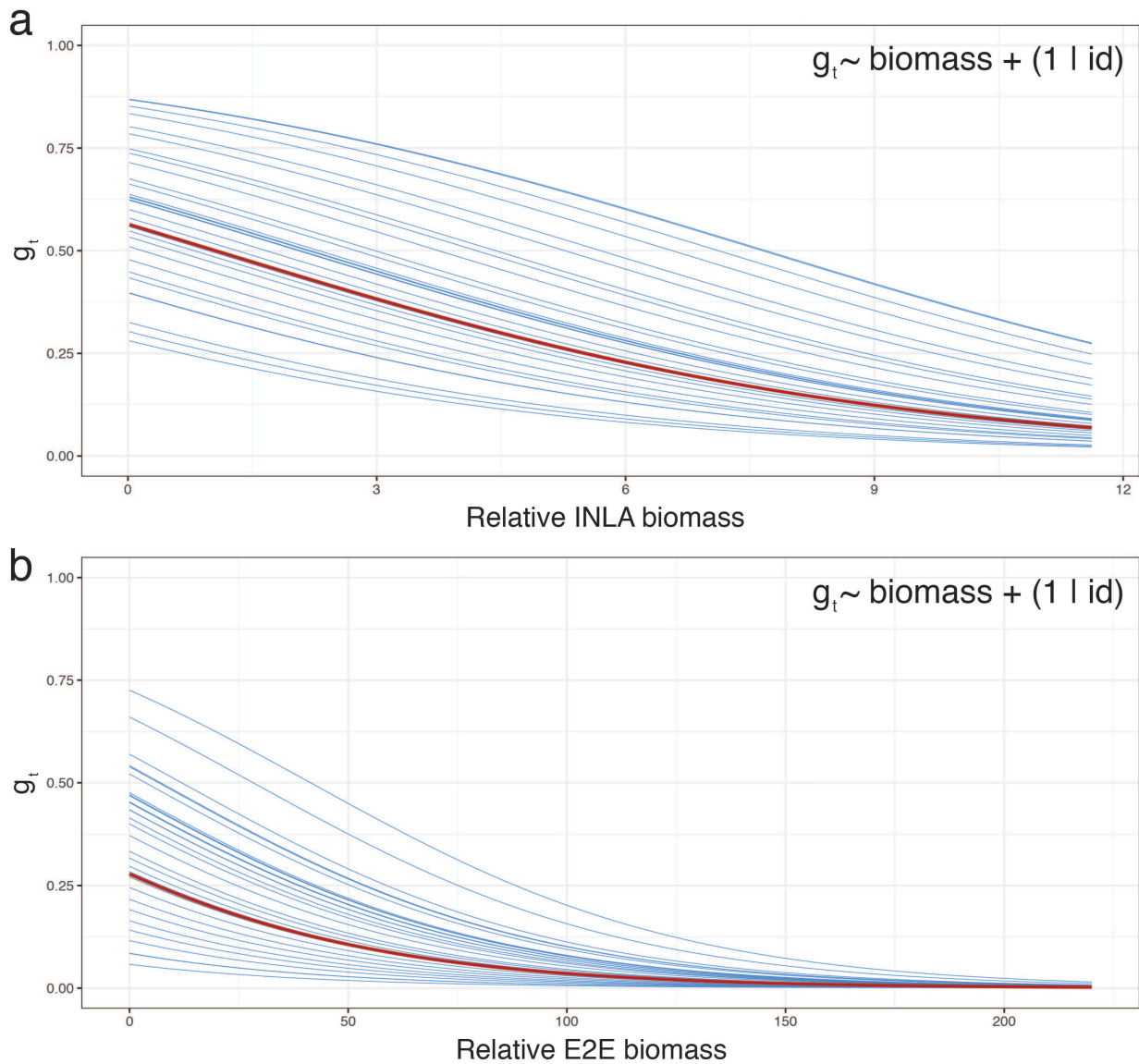
Figure 8 Most parsimonious model from mixed effect analysis. Panels a and b display individual (blue lines) random effects relationships and group (red line) fixed effects responses when using either (a) relative observed INLA herring biomass values or (b) relative simulated E2E herring biomass values. For both cases the most parsimonious model was ($g_t \sim$ biomass + (1|id)). Note that the relative INLA and E2E biomass scales are different and not directly comparable.

5 Discussion

5.1 Herring biomass and its influence on killer whale movements

This is the first study that describes the movement behavior patterns of Norwegian killer whales in relation to a key food resource, NSS herring. We found that after leaving the herring overwintering areas, killer whales tend to broadly follow the herring's migration south towards spawning grounds on the Norwegian shelf (between Troms and Møre). It was confirmed that relative herring biomass distribution patterns are an important driver of killer whale movements when on the Norwegian shelf. Furthermore, it was found that individual whales consistently reduce both the speed and directionality of their movements when encountering areas with increased relative herring biomass. Whale locations associated with low move persistence, were strongly associated with areas of high relative herring biomass. This inverse relationship suggests that whales respond to elevated herring biomass by reducing speed and directionality.

5.2 Light intensity and movement characteristics

Interestingly, including light intensity in models did not improve the fit, suggesting that killer whale movement characteristics do not display diel variations. Accordingly, the most parsimonious model included only biomass as a fixed effect suggesting that daily vertical changes in herring biomass distribution do not significantly influence the relationship between killer whale move persistence and herring biomass. Given that sun angle can be thought of as a proxy for both daylight and vertical herring distribution, there are at least three plausible explanations for why including sun angle in models did not improve the fit. First, whale behavior might not be influenced by variations in light intensity. This seems unlikely because herring are known to exhibit diel vertical migration throughout the water column (Huse & Korneliussen, 2000) concentrating at depth in the light hours and moving closer to the surface at night. The second possible explanation is that these diurnal patters do influence whale move persistence, but our reconstructed three-hour step intervals had insufficient resolution to detect these variations. The time scale used for path reconstruction is limited by the Argos location frequencies and accuracies, and thus may not fully capture changes over finer timescales. A third explanation could be that the diurnal migration of herring in the water column does not influence lateral whale movements (factors considered in calculating move persistence), but primarily influence changes in depth and dive patterns of killer whales. Future studies utilizing biologging techniques that record depth data and/or more frequent sampling rates might allow us to address more detailed questions regarding fine-scale behavioral variations, such as diel patterns in dive behavior and foraging intensity.

5.3 Individual whale move persistence distributions

Density distributions of move persistence (g_t) variation yielded insight into the observed variability of Norwegian killer whale movement behaviors, at both the population and individual level. Population density distributions across different years were compared for each of the three seasons. A unimodal peak, with intermediate move persistence values, as observed in the 2015-2016 season, suggest that the whales moved at a relatively intermediate speed and do not change this pattern in response to variations in herring biomass. This might be related to the relatively lower biomass and fewer high-density patches seen in the 2015-2016 season's INLA biomass distributions. It is important to note that characteristics of movement distribution patterns may be artifacts of smoothing. The broader and more variable movement distribution pattern from 2017-2018 suggests greater variability in move persistence due to either a) greater variation between individuals or b) more variable behavior within individuals. The distinctly bimodal movement pattern distribution of 2018-2019 suggests either a) individuals tend to switch regularly between ARS and directed travel or b) some individuals tend to be slower and others faster overall. Variations across individual whale move persistence distributions can be seen across all seasons, with some whales displaying distinct bimodal distributions, while others displayed unimodal or more variable distributions. Variability observed across all the individual whale movement patterns can be explained in numerous ways, such as differing environmental and prey field factors. For example, whale directionality and speed might differ when foraging on different prey types, or reflect changes in the whale's movements associated with efficient foraging at different prey densities and/or distributions. Similarly, variation among distributions for individual whales could be explained by different subcategories of transiting behavior, such as transiting between prey patches versus transiting from the fjords to the herring spawning grounds on the Norwegian shelf. Individual movement pattern variability can also be explained by variations in individual's propensity towards movement. Regardless, a high degree of movement variation was observed across individual whales.

5.4 Comparing methods for estimating herring biomass

In our study, killer whale move persistence was found to be strongly influenced by both observed (INLA) and simulated (E2E) herring biomass distributions. Each approach for modeling herring biomass has its strengths and weaknesses. The observed INLA herring biomass extrapolation was limited in geographical range and provided only yearly static snapshots of herring biomass distribution. It was, however, based on actual acoustic and biotic herring observations from yearly surveys. This limits the spatial range that can be modeled to

the geographical areas that were surveyed given the differences in yearly herring survey extents. Thus, this method results in a static snapshot of the biomass distribution that is thought to be representative of the NSS herring distribution of that year. In contrast, the simulated E2E herring biomass distributions, generated from a bottom-up ecosystem model, covered daily changes over a much broader geographical range. While this method predicts dynamic day-to-day changes in herring biomass distribution, it does not predict yearly changes. Together, these two methods can be thought of as complementary, where the strength of each method compensates for the weakness in the other. The most parsimonious model was the same for both herring datasets, suggesting that there is good overall correspondence between the two herring datasets.

5.5 Prey preference

Our findings show that when the herring leave their overwintering areas for their southern spawning grounds, killer whales tend to follow them at least for an initial period, and their movement behavior is clearly influenced by herring distribution along the migration corridors. This suggests that the Norwegian killer whales tagged in this study might be herring specialists, consistent with earlier studies conducted on former NSS herring overwintering areas (Similä et al., 1996; Simon, McGregor & Ugarte, 2007). Jourdain et al. (2017) identified two groups of Norwegian killer whales that repeatedly fed on seals, and suggested that it might indicate a degree of pinniped specialization. Together this might indicate that Norwegian killer whale populations are made up of subsections of herring specialists and seal specialists. It is also unclear if these pinniped specialized whales feed on seals year-round, or if they switch between different prey types depending on other factors such as season or prey distributions. Similarly, we cannot rule out the possibility that our study could have had bias, since we may have selected a subpopulation of whales with a preference for herring, given that we primarily tagged whales in known overwintering herring areas. Furthermore, our tracking period occurred when Norwegian herring were migrating to their spawning grounds and spawning, and thus herring were predictably available in high concentrations. Accordingly, we cannot rule out the possibility that the tagged whales are generalists, that were simply feeding on the most available and highly abundant prey species along the coast at this time of year (as seen among some Antarctic killer whales, e.g., Krahn et al., 2008; de Bruyn, Tosh & Terauds, 2013). This generalist classification of Norwegian killer whales is consistent with recent studies on Norwegian killer whale dietary variations (using stable isotope analysis) (Jourdain et al., 2020). In these studies, considerable heterogeneity between individuals' dietary patterns was observed.

While individual diversity in diet patterns suggests prey specialization within the Norwegian killer whale population, it is unclear if prey specialization is induced by an individual's affinity to specific prey types, variations in prey distribution and abundance, or a combination of both factors (Jourdain et al., 2020). Our observation that all killer whales in our study responded in the same way to changes in herring biomass, is consistent with this population specializing on herring at least for the period over which they were tagged. However, we cannot rule out the possibility that they are opportunistic generalists (in terms of their overall annual diet) that all respond to herring in the same way during the period of high herring biomass along the coast.

Two whales in our study (ID 60268 and 62027) displayed interesting tracks that might shed light on whether Norwegian killer whales are generalists or specialists. These whales were tagged in a fjord where herring were overwintering, exited the fjord and traveled south towards the herring spawning grounds, before changing course and ultimately traveling northward away from the herring spawning grounds and towards Novaya Zemlya (see Appendix 1 Figure S1). While we do not know what prey these whales may have targeted after leaving the southern herring spawning grounds, it is plausible that they switched from feeding on herring to a more ice-associated species of marine mammal or perhaps capelin (*Mallotus villosus*) in the Barents Sea. Individual Norwegian killer whales have occasionally been observed foraging on both pinnipeds and herring (Bisther & Vongraven, 2001; Jourdain et al., 2017). It is worth noting that the two individuals from our study, prior to traversing into the Barents Sea, showed the same negative relationship between their move persistence and herring biomass as all the other whales in the study. Further support for Norwegian killer whales being generalists comes from capture-recapture studies of naturally marked Icelandic killer whales. Similarly, Icelandic killer whale's long-term displacement patterns appear to be influenced by Icelandic herring stocks, but examples of individual Icelandic whales moving between herring grounds and known harbor seal pupping areas have also been documented (Foote et al., 2010).

If Norwegian killer whales are generalists, it is of particular importance to consider the timing of tracking data in relation to the abundance of various potential alternative prey species. Extensive research supports the idea that Norwegian killer whales feed primarily on herring during the herring overwintering period (Similä et al., 1996; Simon, McGregor & Ugarte, 2007). After the overwintering period, when herring leave the fjords for their southern spring spawning grounds, our study shows that killer whales also leave the fjords for the southern herring spawning grounds. It is striking that each of these 29 tagged whales relocated south to the NSS herring grounds, at least for an initial period, and in most cases until tags stopped transmitting. Throughout the spawning grounds, high relative herring biomass values were

correlated with low killer whale move persistence, suggesting that the whales were still feeding on herring. Reports of killer whales frequently being observed in the vicinity of herring fishing boats at the herring spawning grounds further support the continued relationship between these whales and NSS herring spawning events (Pers. Com. The Norwegian Coast Guard). Thus, at least during this time period, killer whale move persistence might be useful for potentially identifying previously unknown areas of high NSS herring biomass. New herring aggregation locations can in turn be used to inform future survey designs, and ultimately expand our understanding of their dynamic distribution.

It is not known if the relationship between Norwegian killer whales and herring persists beyond the herring spawning period. In our study, all but two of the whales remained on the Norwegian shelf where the herring summer feeding areas (Fig. 1 b) are after the NSS herring spawning. Thus, it is possible that most of the whales tagged in our study continue to associate with herring even after the spawning events. Determining if the relationship between killer whales and herring persists across all seasons would resolve whether these killer whales are mainly herring specialists or generalists. If (and the extent to which) Norwegian killer whales preferential prey shifts after the spawning event ends is not known. This question can be investigated by either extending tag retention time over periods that would eventually cover the full year, or tagging whales at multiple periods throughout the year and at different locations. Either way, extended tracking data could then be correlated with the simulated E2E herring distribution model over the full year. It is important to note that Norwegian killer whales have also been reported to aggregate around the mackerel fishing boats in late summer/early autumn (pers. com The Norwegian Coast Guard and fishermen). Alternatively, extended killer whale tracking data could be compared with the relative biomass distributions of other potential prey species to investigate their respective influence on whale move persistence. Understanding how other prey influences Norwegian killer whale movements is needed to determine if Norwegian killer whales are generalists, specialists or opportunistic generalists. Additionally, stable isotope analysis could help determine what trophic level whales had been feeding on during the period of time before a biopsy sample (Krahn et al., 2007; Caut et al., 2011).

It is uncertain if and how climate change, or other environmental factors, will affect the distribution patterns of NSS herring (Sissener & Bjørndal, 2004), it has been observed that herring feeding grounds have been shifting further north with increased water temperatures (ICES, 2013). While it was previously documented that warming ocean temperatures positively correlated with increasing herring biomass (Toresen and Østvedt, 2000), more recent studies found that that around 2005, ocean temperatures continued to increase, however herring

biomass plateaued and then began to decrease (Toresen et al., 2019), affecting both herring abundance and migration patterns. If herring distribution patterns continue to change, Norwegian killer whale distributions might also be expected to change (Nøttestad et al., 2015) particularly if they follow shifts in herring biomass, as would be expected for herring specialists. Alternatively, if most Norwegian killer whales are generalists, they may be less affected if alternative prey types are available. Our study examined how the spatial distribution of herring biomass influenced killer whale movement behavior between 2015-2019, and can serve as a baseline for future comparative studies, if and when the NSS herring distribution shifts.

5.6 Killer whale movements and ecosystem management

Marine megafauna, such as killer whales, can influence marine ecosystems both as predators, as well as by redistributing nutrients (Hays et al., 2016). Thus, killer whale movement and habitat use data obtained through satellite telemetry studies might play an important role in informing policy makers for protecting these pelagic systems. The data obtained through studies like ours has the potential to (1) identify previously unknown foraging areas, (2) uncover unknown or poorly studied ecological hotspots to be targeted by future surveys, (3) validate and inform ecosystem models, and (4) identify locations to be considered for Marine Protected Areas where killer whale and anthropogenic activity might overlap (Hooker & Gerver, 2004; Crowder et al., 2008).

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Appendix 1
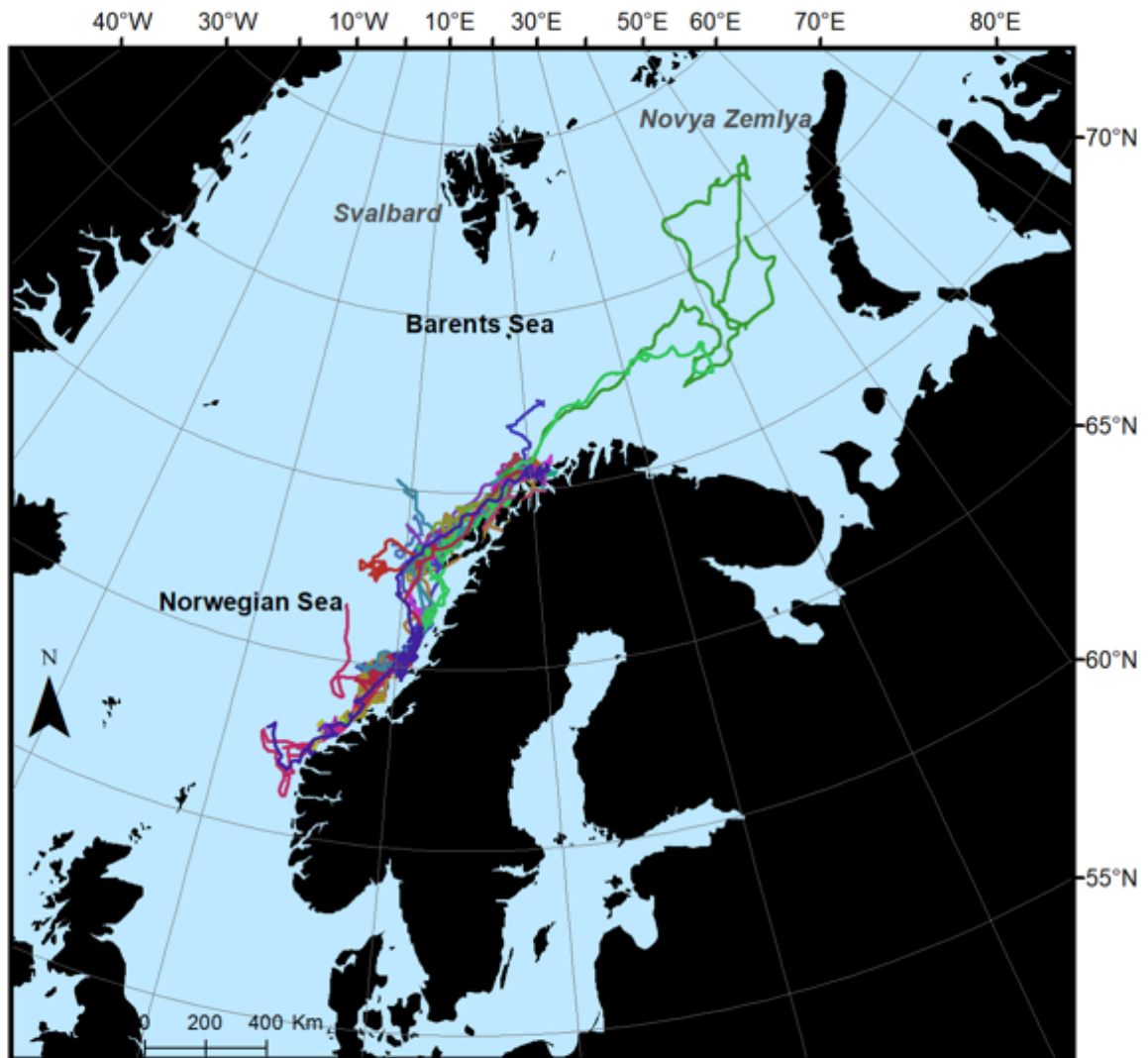
Figure S1 Map of complete whale paths of the Norwegian killer whale tracks along the coast of Norway. Paths were reconstructed with continuous-time correlated random walks (CRW). Note that two whales (light and dark green tracks) first went south to the NSS herring grounds before traveling north into the Barents Sea.

Table S1 Tagging information from 37 killer whales over three field seasons, tracked between November 25th, 2015 and April 11th, 2019 in Norway. Whales tagged outside of fjords received NA values for 'leave fjord date' and for 'out of fjord longevity'. Field seasons are partitioned by grey lines. Tracks from 29 whales used in move persistence analysis are denoted by '+'.

ID	Tagging position	Deployment date	Leave Fjord Date	Last Date	Total tag longevity (days)	Total extracted positions	Out of fjord longevity (days)	Out of fjord extracted positions	Used in analysis
153483	69.81,18.47	2015-11-25 07:08:47	2016-02-24 16:28:45	2016-03-08 11:20:17	105	3300	13	433	+
153484	69.83,18.65	2015-11-25 07:10:30	2015-12-11 09:10:46	2015-12-11 23:30:52	17	436	1	17	
139211	69.75,18.63	2015-11-28 15:35:45	2015-12-10 11:47:45	2016-01-14 08:31:39	47	936	35	690	+
139212	69.9,18.54	2015-11-28 12:55:19	2015-12-09 09:54:55	2015-12-10 10:21:11	12	172	2	19	
139214	69.75,18.53	2015-12-08 18:38:01	2015-12-11 13:06:02	2016-01-11 10:58:55	34	652	31	587	
139216	69.46,16.9	2016-01-15 11:26:07	NA	2016-02-08 11:24:49	24	191	NA	191	
139219	69.43,17.08	2016-01-20 10:25:22	NA	2016-01-28 12:39:59	9	143	NA	143	+
139217	69.54,17.89	2016-01-23 13:01:29	NA	2016-03-28 09:28:22	65	1101	NA	1101	+
37289	69.67,18.21	2016-01-23 12:47:45	2016-01-28 16:35:58	2016-03-20 17:47:18	58	910	53	817	+
60267	69.72,18.08	2016-01-23 20:09:17	2016-01-26 09:31:17	2016-03-25 12:05:27	62	894	60	855	+
60269	69.64,18.19	2016-01-23 13:24:22	NA	2016-02-11 09:50:52	19	269	NA	269	+
60268	69.81,18.64	2016-01-24 13:06:49	2016-01-28 17:37:10	2016-03-29 17:58:37	66	1282	62	1213	+
62027	69.81,18.66	2016-01-24 13:13:57	2016-02-07 17:24:15	2016-03-12 12:41:50	48	953	34	691	+
47572	70.09,21.26	2017-12-02 15:55:04	2017-12-14 14:16:49	2017-12-14 14:16:49	12	240	0	1	
47580	70.09,21.23	2017-12-02 15:54:53	2017-12-22 10:00:30	2018-01-08 08:09:21	37	1269	17	557	+
47590	70.08,21.23	2017-12-02 15:36:17	2017-12-21 19:23:32	2017-12-22 03:23:45	20	404	1	2	
47592	70.11,21.12	2017-12-02 17:13:56	2017-12-17 07:03:09	2017-12-25 20:13:13	24	523	9	228	+
47594	70.15,21.19	2017-12-02 11:14:09	2017-12-27 11:23:12	2018-01-05 21:18:55	35	680	10	145	+
47582	70.2,20.95	2017-12-03 11:02:09	2017-12-16 08:27:21	2018-01-12 04:06:27	40	317	27	144	
47581	70.06,21.09	2018-01-10 21:04:05	2018-01-15 08:18:18	2018-01-18 18:03:12	8	213	4	102	+
47587	70.04,21.04	2018-01-10 17:01:52	2018-01-21 00:14:49	2018-01-28 15:08:34	18	542	8	232	+
47577	70.11,21.07	2018-01-12 00:18:39	2018-01-17 09:27:20	2018-02-12 06:20:53	32	811	26	659	+
54013	70.07,21.09	2018-10-26 16:02:43	2018-12-03 17:14:19	2018-12-03 17:14:19	39	681	0	1	
53561	70,21.12	2018-10-28 14:08:07	2018-12-10 20:03:10	2018-12-20 19:01:23	54	1041	10	157	+
53559	70.24,21.03	2018-11-06 21:03:50	2019-01-01 04:07:16	2019-01-02 18:06:37	57	1112	2	28	+
54011	70.25,21.1	2018-11-06 19:05:03	2019-01-01 18:13:57	2019-01-09 21:08:20	65	1267	9	142	+
83761	70,21.07	2018-11-13 11:03:36	2018-12-06 05:14:43	2018-12-09 15:17:19	27	557	4	59	+
83760	70.24,21.08	2018-11-16 17:04:38	2018-12-16 10:02:24	2018-12-26 21:02:51	41	866	11	243	+
53557	69.98,21.12	2019-01-04 16:01:18	2019-02-06 11:12:09	2019-03-23 22:08:55	79	1594	46	884	+
83764	69.93,21.17	2019-01-06 13:54:28	2019-01-30 09:01:49	2019-02-04 06:00:46	29	498	5	100	+
83756	69.99,21.66	2019-01-08 11:06:33	2019-02-09 11:06:42	2019-03-13 06:06:03	64	1301	32	627	+
83768	70,21.17	2019-01-23 16:22:03	2019-01-27 04:06:43	2019-03-26 22:08:16	63	1271	59	1197	+
83755	63.13,6.74	2019-02-16 15:18:02	NA	2019-02-28 20:14:02	13	109	NA	109	+
83752	63.12,6.7	2019-02-17 15:07:26	NA	2019-02-20 04:02:29	3	46	NA	46	+
83754	63.12,6.62	2019-02-17 15:05:05	NA	2019-03-01 13:08:46	12	176	NA	176	+
179034	63.13,6.95	2019-03-01 13:10:00	NA	2019-03-05 19:16:38	5	69	NA	69	+
179032	63.2,6.75	2019-02-17 17:14:36	NA	2019-03-26 22:02:02	38	754	NA	754	+

Appendix 2

```r
###########################################################################
# Transforming survey results to biomass in Kg/sqNM in RstoX
# Get Rstox 2.11 Official release
library(Rstox)
# Run StoX project
pr <- "/workspace/stox/project/project1"
g <- getBaseline(pr)
# Inspection of available output/parameters
names(g)
names(g$outputData)
# Get your density by EDSU (as requested)
densByEDSU <- g$outputData$AcousticDensity
head(densByEDSU)
# Merge EDSU with posision data
# Get EDSU_PSU
edsu_psu <- g$processData$edsupsu
# Get acoustic posision
acoPos <- g$outputData$FilterAcoustic$FilterAcoustic_AcousticData_DistanceFrequency.txt
tmp <- strsplit(acoPos$start_time," ")
acoPos$start_Date <- sapply(tmp, "[", 1)
acoPos$start_Time <- sapply(tmp, "[", 2)
acoPos$EDSU <- paste(acoPos$cruise,acoPos$log_start,acoPos$start_Date,acoPos$start_Time,sep="/")
# Merge EDSU_PSU with acoPos
ans <- merge(acoPos, edsu_psu,by="EDSU",all.x=T)
# Merge ans with Acoustic density
ans1 <- merge(ans,densByEDSU, ans, by.x="PSU", by.y="SampleUnit",all.x=T)
# histogram showing frequency of LengthGroups
hist(ans1$LengthGroup)

lm.m <- lm(log(weight)~log(length), data=g$outputData$SuperIndAbundance)
ans1$weight <- exp(predict(lm.m, newdata=data.frame(length=ans1$LengthGroup)))
## biomass in g/sqNM...?
ans1$biomass <- (ans1$weight * ans1$Density)
ans1$biomassKG <- ((ans1$biomass)/1000)
ans2 <- ans1[match(unique(ans1$EDSU), ans1$EDSU),]
ans2$totbiomassKG <- aggregate(ans2$biomassKG, list(ans2$EDSU), sum, na.rm=T)$x
saveRDS(ans2, "/Desktop/Thesis/R/nss1.rds")

###########################################################################
#Extrapolating survey point value Kg/sqNM biomass across spatial area
# load libraries
require(tidyverse)
require(sf)
require(sp)
require(mapr)
require(INLA)
require(inlabru)
require(lubridate)
require(foieGras)
require(lattice)
require(adehabitatLT)
nss1 <- readRDS("~/Desktop/Thesis/R/nss1.rds")
prj = "+proj=laea +lat_0=66 +lon_0=10 +x_0=0 +y_0=0 +datum=WGS84 +units=m +no_defs"
# load data
dat <- nss1 [,match(c('start_time', 'lon_start', 'lat_start', 'totbiomassKG'), names(nss1))]
names(dat) <- gsub('_start', '', names(dat))
# Format date time
dat <- dat %>% mutate(start_time = ymd_hms(start_time, tz = "UTC"))
# Convert to sf object and project to get xy
dat_sf <- dat %>% st_as_sf(coords = c("lon", "lat")) %>% st_set_crs(4326)
dat_sf <- dat_sf %>% st_transform(crs = prj)

# Append coordinates to dat
dat <- dat %>% mutate(x = st_coordinates(dat_sf)[,1],
                      y = st_coordinates(dat_sf)[,2])
# Convert the projected locations from metres to kilometres
dat <- dat %>% mutate(x = x/1000,
                      y = y/1000)
# redefine projection
prj = "+proj=laea +lat_0=66 +lon_0=10 +x_0=0 +y_0=0 +datum=WGS84 +units=km +no_defs"
# Generate shapefile for plots
land <- mapr::mapr(dat,
                   prj,
                   buff = 200)
# Generate boundary for INLA mesh
b <- mapr::meshr(dat = dat,
                 prj = prj,
                 buff = 20,
                 keep = 0.9,
                 Neuman = F)
# Define the parameters of the boundary
max.edge = max(c(diff(range(dat$x)), diff(range(dat$y))))/10
bound.outer = 1
```

```r
# Use the boundary to generate the INLA mesh and pass the same projection
mesh = inla.mesh.2d(loc = cbind(dat$x, dat$y),
                    boundary = b,
                    max.edge = c(1, 5) * max.edge,
                    cutoff = 20, # Minimum allowed triangle edge length
                    offset = c(max.edge, bound.outer), #
                    crs = CRS(prj))
# Follow Haakon's example script to set up inla model
# Remove points on land
in.water = sp::over(b, SpatialPoints(cbind(dat$x, dat$y), proj4string = CRS(prj)), returnList = T)[[1]]
print(paste("There are", nrow(dat)-length(in.water), "points on land in the original polygon"))
dat <- dat[in.water,]
# Set up boundary matern model
tl = length(mesh$graph$tv[,1]) # the number of triangles in the mesh
# Compute triangle positions
posTri = matrix(0, tl, 2)
for (t in 1:tl){
  temp = mesh$loc[mesh$graph$tv[t, ], ]
  posTri[t,] = colMeans(temp)[c(1,2)]
}
posTri = SpatialPoints(posTri, proj4string = CRS(prj))
normal = over(b, posTri, returnList = T) # check which mesh triangles are inside the normal area
normal = unlist(normal)
barrier.triangles = setdiff(1:tl, normal)
poly.barrier = inla.barrier.polygon(mesh, barrier.triangles)
# Create the barrier Matern object
barrier.model = inla.barrier.pcmatern(mesh,
                                      barrier.triangles = barrier.triangles,
                                      prior.range = c(20, .1),
                                      prior.sigma = c(5, 0.01))

# Plot
ggplot() +
  inlabru::gg(mesh) +
  geom_sf(aes(), data = land) +
  geom_sf(aes(), data = dat_sf) +
  xlab("") + ylab("")
barrier.mat <- INLA:::inla.barrier.fem(mesh, barrier.triangles)
A.i.s = inla.spde.make.A(mesh, loc=cbind(dat$x, dat$y))
stk <- inla.stack(data=list(y=dat$totbiomassKG),
                  effects=list(s=1:mesh$n,
                               data.frame(m=1, dat$totbiomassKG),
                               # - m is the intercept
                               iidx=1:nrow(dat)),
                  A=list(A.i.s, 1, 1),
                  remove.unused = FALSE, tag='est')
hyper.iid = list(prec = list(prior = 'pc.prec', param = c(5, 0.01)))
m.formula = y~ -1+m + f(s, model=barrier.model) + f(iidx, model="iid", hyper=hyper.iid)
res <- inla(m.formula,
            data=inla.stack.data(stk),
            control.predictor=list(A=inla.stack.A(stk)),
            family="nbinomial",
            control.inla= list(int.strategy = "eb"),
            control.mode=list(restart=T, theta=NULL),
            verbose=TRUE)
local.plot.field = function(field, mesh, xlim, ylim, ...){
  require(fields)
  stopifnot(length(field) == mesh$n)
  # - error when using the wrong mesh
  if (missing(xlim)) xlim = bbox(b)[1, ]
  if (missing(ylim)) ylim = bbox(b)[2, ]
  # - choose plotting region to be the same as the study area polygon
  proj = inla.mesh.projector(mesh, xlim = xlim,
                             ylim = ylim, dims=c(300, 300))
  # - Can project from the mesh onto a 300x300 grid
  #   for plots
  field.proj = inla.mesh.project(proj, field)
  # - Do the projection
  image.plot(list(x = proj$x, y=proj$y, z = field.proj),
             xlim = xlim, ylim = ylim, col = tim.colors(17), ...)
  list(proj=proj, field.proj=field.proj)
}
field <- res$summary.random$s$mean + res$summary.fixed['m', 'mean']
res.mat <- local.plot.field(field, mesh, zlim=range(res$summary.random$s$mean + res$summary.fixed['m',
'mean']))
plot(land, add=T, col="grey"
```