



Killer whale movements on the Norwegian shelf are associated with herring density

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ABSTRACT: Killer whales *Orcinus orca* have a cosmopolitan distribution with a broad diet ranging from fish to marine mammals. In Norway, killer whales are regularly observed feeding on overwintering Norwegian spring-spawning (NSS) herring *Clupea harengus* inside the fjords. However, their offshore foraging behavior and distribution are less well understood. In particular, it is not known to what degree they rely on the NSS herring stock when the herring move to deeper offshore waters. Satellite telemetry data from 29 male killer whales were analyzed to assess whether their offshore foraging behavior is linked to herring distribution. Unlike most marine predator–prey studies that use indirect proxies for prey abundance and distribution, our study utilized 2 herring density estimates based on (1) direct observations from acoustic trawl survey data and (2) simulations from a fully coupled ecosystem model. Mixed effects models were used to infer the effect of herring density and light intensity on whale movement patterns. Our results suggest that killer whales follow NSS herring over long distances along the coast from their inshore overwintering areas to offshore spawning grounds. All whales changed from fast, directed, to slow, non-directed movement when herring density increased, although individuals had different propensities towards movement. Our data indicated that whales continue to feed on herring along the Norwegian shelf. We conclude that NSS herring constitute an important prey resource for at least some killer whales in the northeastern Atlantic, not only during the herring overwintering period, but also subsequently throughout the herring spawning migration.

KEY WORDS: Move persistence · Foraging · Habitat · Spatial ecology · *Orcinus orca* · *Clupea harengus* · Predator–prey

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1. INTRODUCTION

The behavior of marine predators is influenced by the distribution, availability, abundance, and behavior of prey (Womble et al. 2014, Goldbogen et al.

2015, Hays et al. 2016). To optimize foraging efficiency, marine predators may respond to changes in prey distribution by modifying both their horizontal and vertical movements (Thums et al. 2011, Bestley et al. 2015, Joy et al. 2015). Patchy spatiotemporal

distributions of prey are related to the heterogeneous nature of the marine environment (Boyd 1996, Sims et al. 2008, Bestley et al. 2010). Optimal foraging theory predicts predators will exploit high prey density patches to maximize their energy efficiency, thus maximizing their fitness (Hedenström & Alerstam 1997, Houston & McNamara 2014).

When predators forage, they frequently exhibit area-restricted search (ARS) behavior (Kareiva & Odell 1987, Witteveen et al. 2008, Hazen et al. 2009, Silva et al. 2013), which is characterized by decreased speeds and increased turning rates, which should allow them to remain in a prey patch (Jonsen et al. 2005, Breed et al. 2009, McClintock et al. 2012). When a predator is in an area where prey density has fallen, they will either leave the area or switch to alternate prey species (Murdoch 1969, Van Baalen et al. 2001). Optimal foraging theory predicts that predators will minimize the time spent transiting between foraging areas (Jonsen et al. 2005, McClintock et al. 2012). Elevated consistent speeds and lower turning rates are characteristic of this transiting behavior (Fauchald & Tveraa 2003). Based on the predicted relationship between prey density and predator movement patterns, ARS behavior has been used to detect foraging areas for killer whales *Orcinus orca* and other odontocetes (e.g. Reisinger et al. 2015, Dietz et al. 2020, Stalder et al. 2020).

Killer whales are widely distributed odontocetes that are considered generalist top predators at the species level. However, some populations have specialized diets (Durban & Pitman 2012, Ford & Ellis 2014) that may vary seasonally (Jourdain et al. 2020a). Based on limited tissue samples, North Atlantic killer whales have been divided into 2 ecotypes; generalists (feeding primarily on herring *Clupea harengus*, mackerel *Scomber scombrus*, and seals) and specialists (feeding on baleen whales) (Foote et al. 2009, 2010). Nonetheless, an ecological gradient may exist. Specializations may only be beneficial in environments with a stable and predictable availability of the target prey, while a more generalist strategy may be favored under variable conditions.

Killer whales in Norwegian waters are thought to primarily feed on Norwegian spring-spawning (NSS) herring (Similä et al. 1996, Similä 1997, Simon et al. 2007). However, these whales have also been observed feeding on a wide variety of other prey types, such as harbor seals *Phoca vitulina*, salmon *Salmo salar*, mackerel, and lumpfish *Cyclopterus lumpus*, along the Norwegian coast (Similä et al. 1996, Foote et al. 2009, Vester & Hammerschmidt 2013, Nøttestad et al. 2014, Vongraven & Bisther 2014, Jourdain et al.

2017, 2020b). While overwintering herring have been identified as important prey for killer whales (Similä et al. 1996, Similä 1997, Simon et al. 2007), it is not known if this relationship persists after the herring leave the overwintering areas for their spawning grounds. It is plausible that the distribution of at least some killer whales will be tightly associated with the migration of NSS herring.

NSS herring migrate seasonally between their wintering, spawning, and feeding grounds (Dragesund et al. 1997). Although the spawning grounds of NSS herring are relatively well defined and constant, herring migration pathways can change, often abruptly, both spatially and temporally, presumably due to shifts in the overwintering areas (Dragesund et al. 1997, Huse et al. 2010, Toresen et al. 2019). Shifts in NSS herring overwintering areas have long been observed (Dragesund et al. 1997, Huse et al. 2010). Recent shifts in herring overwintering areas are thought to be initiated when strong cohorts of herring suddenly enter new fjords (Huse et al. 2010), thus influencing where Norwegian killer whales are feeding in the winter (Jourdain & Vongraven 2017).

In addition to seasonal horizontal movements between wintering and spawning grounds, NSS herring also exhibit 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 diel pattern is assumed to be correlated with changes in light intensity and is attributed to avoiding predation (Huse & Korneliussen 2000), but may also be involved in maintaining buoyancy (Blaxter & Batty 1984).

The main objective of this study was to assess if Norwegian killer whales that feed on NSS herring in northern Norwegian fjords during winter continue to do so as the fish move towards more southern offshore spawning grounds. Unlike the majority of marine animal studies (Pendleton et al. 2020) that correlate predator density, distribution, or movement to indirect proxies of prey distribution (Redfern et al. 2006, Sequeira et al. 2012, Becker et al. 2016), our study was designed to investigate how whale movements might be influenced by actual prey density distributions. Specifically, we examined: (1) the extent to which killer whale horizontal movement behavior is associated with NSS herring distribution during their spawning migration, (2) if killer whale horizontal movement behavior is associated with diel variations in light levels, and (3) if there is individual variation in the behavioral responses of whales to herring density.

2. MATERIALS AND METHODS

2.1. Killer whale tagging

2.1.1. Study site

Tagging occurred between late October through February in 2 northern Norwegian fjord systems: the Gryllefjord area (2015–2016) and the Kvænangen fjord area (2017–2019). This corresponds to the current high-usage overwintering areas and time periods for NSS herring prior to their migration towards more southerly spawning areas. Additional tag deployments were conducted in central Norwegian waters off the coast of Møre between late February and early March 2019 (see Table 1 and Fig. 1). This region corresponds to one of the main spawning areas along the Norwegian coast, and the timing also coincides with the onset of spawning.

2.1.2. Tagging methods

Anchored tags deployed by A. Rikardsen and colleagues followed best practices (Andrews et al. 2019), and data obtained from these whales were used in this and concurrent studies (Mul et al. 2019, 2020, Dietz et al. 2020, Vogel 2020). In brief, a 26 ft (~7.9 m) open rigid inflatable boat was used to slowly approach the killer whales, and an Aerial Rocket Tag System (ARTS launcher, LKARTS), crossbow, or Dan-inject CO₂ systems (DAN-INJECT) were used to deploy either SPOT5 or SPOT6 Limpet Argos transmitters (Wildlife Computers). Given that tag placement can influence data quality (Mul et al. 2019), we aimed for tag placement in the center of the large dorsal fin of males (Andrews et al. 2008, Dietz et al. 2020). Photo-IDs were made when possible and used to confirm that individuals were not double tagged. Furthermore, only a single individual was tagged from each group of whales on any day. Tags were anchored in place using 2 titanium, sub-dermal 68 mm darts protruding from the base of the tag (Andrews et al. 2013, Mul et al. 2019). These barbed darts penetrate the skin and anchor in the dense connective tissue (collagen) in the center of the dorsal fin (Andrews et al. 2008, 2019). Darts were sterilized with 70% ethanol before deployment. Tags were programmed to transmit 14–15 times every hour for the first 45 d to obtain high temporal resolution early in the tagging period. In the following 35–45 d, the transmission rate was reduced to 8–10 h⁻¹ to extend battery life. Finally, the transmission rate was further reduced to 55 d⁻¹

until the tag detached from the whale or the battery failed. A more detailed description of tag programming can be found in Dietz et al. (2020).

2.1.3. Tag data processing

Tag location data were calculated by the CLS-ARGOS service using their Kalman filter algorithm (Lopez et al. 2014). All subsequent data processing and statistical analyses were performed using 'R' language (version 3.6.1, R Core Team 2019). To account for location uncertainty and the irregular time series of Argos positions, we used the continuous-time, correlated random walk (CRW) state–space model in the R package 'foieGras' (Jonsen & Patterson 2019, Jonsen et al. 2020). Specifically, we used the CRW to estimate time-regularized (3 h) intervals to predict the most probable paths for each whale. Large gaps in tracking data, typically observed near the beginning or end of our tracking data sets, can be problematic when fitting CRW models, as the lack of data may lead to implausible predictions in these gaps. For this reason, prior to CRW modeling and statistical analysis, tracking data with a gap (here defined as ~18 h or longer) were trimmed to remove the gap and prior data, when near the start of a track, or subsequent data, when near the end. Additionally, since our objective was to study offshore (here referred to as the Norwegian Shelf) behaviors occurring after whales leave fjords with overwintering herring, all predicted whale locations were designated as being either inshore or on the Norwegian Shelf based on fjord spatial data from the Fjord Catalog provided by the Norwegian Ministry of Environment (Christensen 2020). Specifically, spatial data from Kvænangenfjord, Kaldfjord, Vengsøyfjord, Ersfjord, and Sessøyfjord were used. Based on tracking data, the final time that each individual whale crossed a fjord barrier was recorded. Only points after the final time crossing the fjord barrier were used for analysis in this study. Tracks were cut to only include points after the final time that each whale left the inshore area (the fjords). In this study, we only analyzed contiguous tracks with at least 20 locations on the Norwegian Shelf.

2.2. Herring density

2.2.1. Observed herring density

Data from the annual acoustic-trawl herring surveys carried out by the Norwegian Institute of Marine Re-

search (IMR) in February 2016, 2018, and 2019 (Slotte et al. 2016, 2018, 2019) were used to map the distribution and density of NSS herring off the Norwegian coast during the period of their spawning migration towards southerly spawning areas. Three vessels covered the survey area using a stratified systematic transect design (Slotte et al. 2019), where more effort was allocated in high-density strata (Slotte et al. 2019) (see Fig. S1a in the Supplement at www.int-res.com/articles/suppl/m665p217_supp.pdf). The echosounder data were recorded using SIMRAD EK60 or EK80 and post-processed with LSSS software (Korneliussen et al. 2016). Acoustic signal characteristics combined with pelagic trawl catches were used to classify and allocate the acoustic backscattering of fish to the acoustic categories 'herring' or 'others' (Saltaug et al. 2020). The acoustic density values were stored by acoustic category in nautical area scattering coefficient (NASC) units (MacLennan et al. 2002) with a horizontal resolution of 1 nautical mile and a vertical resolution of 10 m. If permitted by the size of the catch, weight and length data were collected from up to 100 individuals from each haul. StoX software (Johnsen et al. 2019) and the R-package 'RstoX' (Holmin et al. 2019) were used to convert to density of herring by combing the trawl samples and NASC values for herring as input (see Johnsen et al. 2019 for details).

To estimate interpolated surfaces of relative density based on the NASC-derived point values along transects, we used integrated nested Laplace approximations (INLAs) as implemented in the 'INLA' package (Rue et al. 2009, Lindgren et al. 2011, Martins et al. 2013, Lindgren & Rue 2015). Here, we assumed that the NASC-derived density values follow a negative binomial distribution. To model spatial point processes, INLA uses stochastic partial differential equations and Gaussian Markov random fields to account for autocorrelation across space (Rue et al. 2009, Lindgren & Rue 2015). This interpolated density surface is hereafter referred to as the 'observed' field (Fig. S1c,d). Supporting barrier models were used to account for the barrier effect caused by the Norwegian coastline (Bakka et al. 2016, 2018, 2019). A detailed description of INLA and the barrier model can be found in Lindgren & Rue (2015) and Bakka et al. (2016), respectively.

2.2.2. Simulated herring density

The observed method delivers a static distribution of the herring density, but is limited to the surveyed area and the specific time period. To overcome these

limitations and explore the potential of using predicted herring distributions from a model covering a greater spatial domain with a longer time period, we used the Norwegian ecological end-to-end model (NORWECOM.E2E). This is a fully coupled model system consisting of a nutrient–phytoplankton–zooplankton–detritus model for lower trophic levels, and individual-based models (IBMs) for the copepod *Calanus finmarchicus* and mackerel *Scomber scombrus*, herring, and blue whiting *Micromesistius poutassou* (Hjøllo et al. 2012, 2019, Utne et al. 2012a). NORWECOM.E2E is one of very few bottom-up models world-wide where IBMs for different trophic levels are 2-way coupled and are used to simulate food web dynamics of a large regional sea, and the only model system of this type for the Norwegian Sea. The model has been validated by comparison with field data in the Nordic and Barents Seas (Skogen et al. 2007, Hjøllo et al. 2012, Utne et al. 2012b, Skaret et al. 2014). The biogeochemical component is validated against observations of chlorophyll *a* measurements at an observation station in the Norwegian Sea (Skogen et al. 2007), and *C. finmarchicus* IBM fields are compared to density, abundance, and the annual production in the Norwegian Sea (Hjøllo et al. 2012). Movements and the resulting horizontal distribution of herring and mackerel are validated against observed distributions in the period 1995–2006 (Utne et al. 2012b), and for 2012, Holmin et al. (2020) found the modeled center of gravity (64.21° N, 7.35° E) for herring winter distribution to corresponds well with the observed center of gravity. Thus, the model provides distributions similar to those of the real population in the Norwegian Sea, although not for a specific year. The NORWECOM.E2E model considers wind, short-wave radiation, ocean currents, salinity, temperature, water level, and sea ice, all taken from a downscaling (10 km horizontal resolution using the ROMS model) of the Norwegian Earth System (NorESM1_ME) climate model under an RCP4.5 emission scenario (IPCC 2013, Skogen et al. 2018). The climate model represents the statistics of the climate in a period, and forcing is representative of present-day climate, not of a specific year.

In this model, herring fish stocks were initiated based on the total number of individuals of each age class (and the corresponding weights of these age groups) based on the 2012 analytic assessments (ICES 2017). Herring growth, feeding, spawning, and migration patterns depend on water temperature, prey availability, and stock density; thus, changing environmental conditions will cause interannual variation. With regard to this study, advantages of

the NORWECOM.E2E model are that the model has a much wider geographical range than the observed herring method, and accounts for daily changes in herring density distribution. Hereafter, we refer to the daily spatial herring density surface from NORWECOM.E2E as the ‘simulated’ field. Example fields are shown in Fig. S2. The simulation can be found in Hjøllø et al. (2019).

2.3. Killer whale move persistence

We inferred how killer whales alter their movement patterns in Norwegian waters by estimating their move persistence. Move persistence (γ_t) is a measure of the autocorrelation between successive displacements, accounting for variability in both speed and heading (Jonsen et al. 2019). Values range continuously between 0 and 1, where 0 designates highly variable movement typically in a restricted area, and 1 denotes consistent and directed movement (Jonsen et al. 2019). We selected this movement metric because it provides a continuous scale of movement behavior, instead of discrete and somewhat arbitrary behavioral states (Breed et al. 2012, Auger-Méthé et al. 2017, Eisaguirre et al. 2019, Jonsen et al. 2019) and because a continuous metric can reveal differing propensities towards movement across individual whales. Move persistence was estimated from the horizontal location data using the ‘fit_mpm’ function in the ‘foieGras’ R package (Jonsen & Patterson 2019).

2.4. Herring–killer whale interactions

We used mixed effects modeling (Jonsen et al. 2019) to investigate how killer whale movement characteristics (represented by the move persistence index, γ_t) may be influenced by 2 environmental variables: (1) herring density and (2) light intensity (more specifically sun angle, which influences herring diel vertical migration). This approach can evaluate both individual and population-level responses to e.g. environmental variables, and is implemented in the ‘mpmm’ R package (Jonsen 2020), based on the approach described by Jonsen et al. (2019). Observed herring density values were extracted from the INLA-generated distributions for the appropriate year based on whale track coordinates. Only 6.4% of all tracking locations fell outside of the INLA-interpolated observed field for the corresponding year, and therefore were excluded from the analyses. Simulated herring density values were extracted from

the NORWECOM.E2E model distribution based on both day of the year and coordinates for individual whale track points. Sun angle values, used as a proxy for light intensity, were calculated for each whale location using the ‘solarpos’ function in the ‘maptools’ package (Bivand & Lewin-Koh 2019).

We evaluated 9 candidate models for each density field (observed and simulated). These models reflected all possible combinations of the full model’s components. The full model was:

$$\text{logit}(\gamma_t) = \rho_t + \alpha_t + (\rho_t + \alpha_t | \text{id}) \quad (1)$$

where density and sun angle are denoted by ρ_t and α_t , respectively, and represent fixed effects. Terms in parentheses represent random slopes, with id denoting random intercepts for individual whales (see Jonsen et al. 2019 for details). Since the observed herring density distributions covered the most limited geographic range, only whale track location points within the interpolated observed herring density field were considered in each model (Fig. S3). The models, corresponding to either observed or simulated herring density, were ranked based on changes in Akaike’s information criterion (ΔAIC) and likelihood ratio (ΔLR). Individual models that failed to converge were not included in the ranking.

3. RESULTS

3.1. Killer whale tagging

Average satellite tag longevity was 40.8 ± 25.6 d (mean \pm SD, $n = 29$), ranging from 3 to 105 d (Table 1). The earliest we observed a tagged whale definitively leaving the fjords was on 4 December and the latest was on 25 February. In total, 1183 whale-days of data were recorded. Tag retention after the whales left inshore waters averaged 23.2 ± 20.6 d ($n = 29$), and ranged from 2 to 65 d, with a total of 673 whale-days of Norwegian Shelf data. Upon exiting the northern fjords, most tagged killer whales initially traveled southwards along the Norwegian Sea Shelf towards the herring spawning grounds (Fig. 1). Two of these whales eventually left the spawning grounds and traveled north of Norway (Dietz et al. 2020), into the Barents Sea (Fig. S4).

3.2. Herring density distributions

There were substantial annual variations in the observed relative herring density distributions (Fig. 2).

Table 1. Tagging information from 29 killer whales over 3 field seasons utilized in this study. Whales tagged outside of fjords are indicated by 'NA' for 'leave fjord date' and for 'out of fjord longevity'. Field seasons are partitioned by grey lines. Note that the number of extracted positions represents the number of ARGOS positions received before fitting the state-space model. Dates are given as yr-mo-d. * indicates that tracking data were concurrently used by Dietz et al. (2020); ** indicates that data were concurrently used by Mul et al. (2020); *** indicates that data were concurrently used by Mul et al. (2019) as well as Mul et al. (2020)

Tag ID	Tagging position	Tagging location	Deployment date	Leave fjord date	Last date	Total tag longevity (days)	Total extracted positions	Out of fjord longevity (days)	Out of fjord extracted positions
153483*	69° 48.6' N 18° 28.2' E	Kaldfjord (Tromsø area)	2015-11-25	2016-02-24	2016-03-08	105	3300	13	433
139211*	69° 45.0' N 18° 37.8' E	Kaldfjord (Tromsø area)	2015-11-28	2015-12-10	2016-01-14	47	936	35	690
139219*	69° 25.8' N 17° 04.8' E	North of Gryllefjord	2016-01-20	NA	2016-01-28	9	143	NA	143
139217*	69° 32.4' N 17° 53.4' E	West of Kaldifjord (Tromsø area)	2016-01-23	NA	2016-03-28	65	1101	NA	1101
37289*	69° 40.2' N 18° 12.6' E	West of Kaldifjord (Tromsø area)	2016-01-23	2016-01-28	2016-03-20	58	910	53	817
60267*	69° 43.2' N 18° 04.8' E	West of Kaldifjord (Tromsø area)	2016-01-23	2016-01-26	2016-03-25	62	894	60	855
60269*	69° 38.4' N 18° 11.4' E	West of Kaldifjord (Tromsø area)	2016-01-23	NA	2016-02-11	19	269	NA	269
60268*	69° 48.6' N 18° 38.4' E	South of Vengsøya (Tromsø Area)	2016-01-24	2016-01-28	2016-03-29	66	1282	62	1213
62027*	69° 48.6' N 18° 39.6' E	South of Vengsøya (Tromsø Area)	2016-01-24	2016-02-07	2016-03-12	48	953	34	691
47580**	70° 05.4' N 21° 13.8' E	Kvænanngen fjord system	2017-12-02	2017-12-22	2018-01-08	37	1269	17	557
47592**	70° 06.6' N 21° 07.2' E	Kvænanngen fjord system	2017-12-02	2017-12-17	2017-12-25	24	523	9	228
47594**	70° 09.0' N 21° 11.4' E	Kvænanngen fjord system	2017-12-02	2017-12-27	2018-01-05	35	680	10	145
47581**	70° 03.6' N 21° 05.4' E	Kvænanngen fjord system	2018-01-10	2018-01-15	2018-01-18	8	213	4	102
47587***	70° 02.4' N 21° 02.4' E	Kvænanngen fjord system	2018-01-10	2018-01-21	2018-01-28	18	542	8	232
47577**	70° 06.6' N 21° 04.2' E	Kvænanngen fjord system	2018-01-12	2018-01-17	2018-02-12	32	811	26	659
53561**	70° 00.0' N 21° 07.2' E	Kvænanngen fjord system	2018-10-28	2018-12-10	2018-12-20	54	1041	10	157
53559**	70° 14.4' N 21° 01.8' E	Kvænanngen fjord system	2018-11-06	2019-01-01	2019-01-02	57	1112	2	28
54011**	70° 15.0' N 21° 06.0' E	Kvænanngen fjord system	2018-11-06	2019-01-01	2019-01-09	65	1267	9	142
83761**	70° 00.0' N 21° 04.2' E	Kvænanngen fjord system	2018-11-13	2018-12-06	2018-12-09	27	557	4	59
83760**	70° 14.4' N 21° 04.8' E	Kvænanngen fjord system	2018-11-16	2018-12-16	2018-12-26	41	866	11	243
53557**	69° 58.8' N 21° 07.2' E	Kvænanngen fjord system	2019-01-04	2019-02-06	2019-03-23	79	1594	46	884
83764**	69° 55.8' N 21° 10.2' E	Kvænanngen fjord system	2019-01-06	2019-01-30	2019-02-04	29	498	5	100
83756**	69° 59.4' N 21° 39.6' E	Kvænanngen fjord system	2019-01-08	2019-02-09	2019-03-13	64	1301	32	627
83768**	70° 00.0' N 21° 10.2' E	Kvænanngen fjord system	2019-01-23	2019-01-27	2019-03-26	63	1271	59	1197
83755**	63° 07.8' N 06° 44.4' E	Møre	2019-02-16	NA	2019-02-28	13	109	NA	109
83752**	63° 07.2' N 06° 42.0' E	Møre	2019-02-17	NA	2019-02-20	3	46	NA	46
83754**	63° 07.2' N 06° 37.2' E	Møre	2019-02-17	NA	2019-03-01	12	176	NA	176
179034	63° 07.8' N 06° 57.0' E	Møre	2019-03-01	NA	2019-03-05	5	69	NA	69
179032**	63° 12.0' N 06° 45.0' E	Møre	2019-02-17	NA	2019-03-26	38	754	NA	754

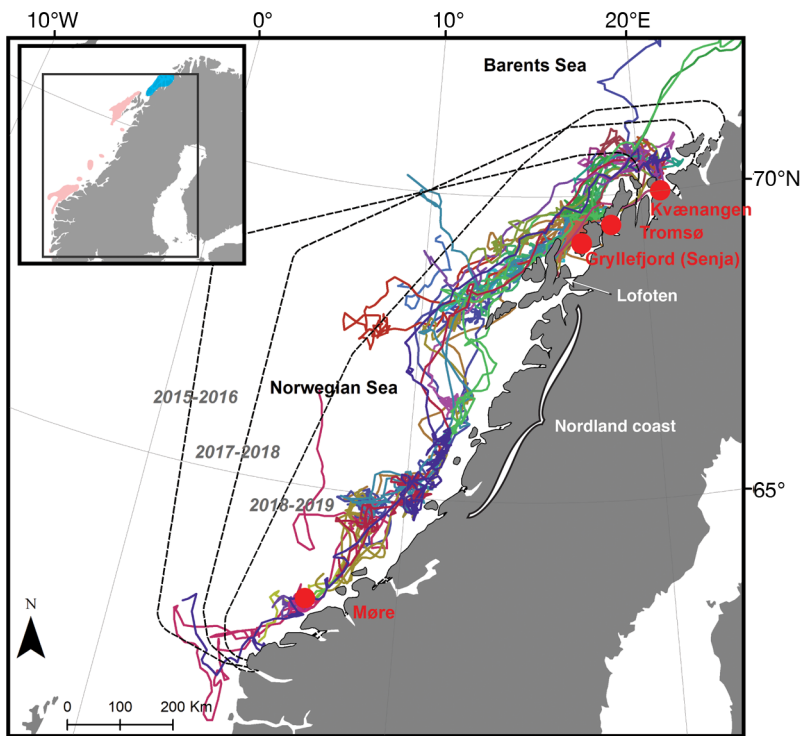


Fig. 1. Killer whale tracks on the Norwegian Shelf. The tagging sites are indicated with red circles. White text indicates places referred to in the text. Tracking data from individual whales collected over 3 field seasons are depicted and color coded by unique tag ID numbers. Norwegian spring-spawning (NSS) herring survey spatial extent for 2015–2016, 2017–2018, and 2018–2019 seasons are indicated by dashed lines. The inset shows the Norwegian coast in a larger geographic context, with pink shading representing general NSS herring spawning areas and blue indicating current coastal NNS herring overwintering areas

The relative density scales in these figures are normalized and therefore, not directly comparable in terms of absolute density. Nonetheless, a few consistently high-density concentrations, or hotspots, were observed at similar locations in all 3 years. In 2016, the observed relative herring density was predominantly low throughout most of the surveyed area, with a few patches of substantially higher relative density, whereas in 2018 and 2019, relative herring density was generally higher and more evenly distributed throughout the entire survey area.

3.3. Killer whale behavior

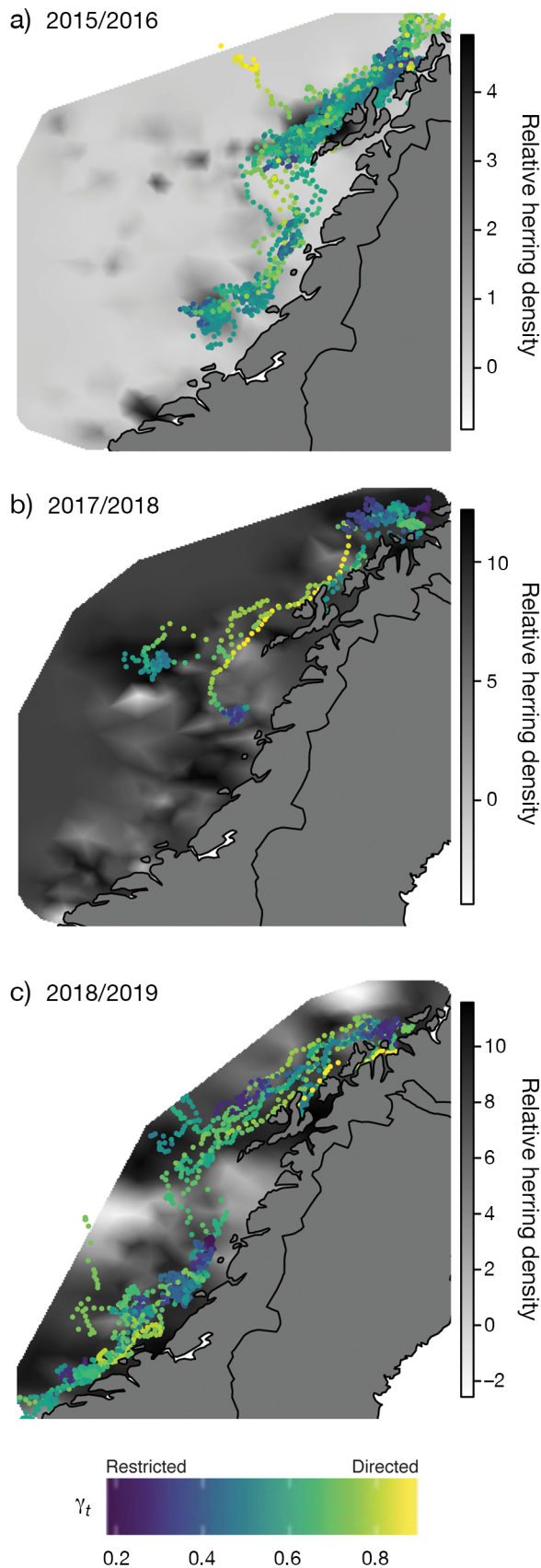
The move persistence values for all whales showed several discrete clusters of low move persistence behavior (blue/purple in Fig. 2), indicative of ARS, distributed along the Norwegian coast. Transiting corridors, consisting of higher move persistence (yellow/

light-green) connect these low move persistence zones. Because move persistence is a continuous index, and whales do not behave dichotomously, there will also be intermediate values (blue-green). This might be indicative of intermediate types of movements that do not correspond directly to the extremes of this continuous index. An example of a transiting corridor can be observed south of Lofoten, connecting 2 notable low move persistence clusters (one west of Senja and the other along the coast of Nordland County).

3.4. Herring–killer whale interactions

In 2015/2016, areas with low move persistence for killer whales overlapped with patches of high herring density (Fig. 2a). A few minor patches of low move persistence were also observed in association with locally elevated patches of herring density further south along the Nordland coast (see Fig. 1 for specific location names). In contrast, the 2017/2018 and 2018/2019 seasons had multiple patches of low killer whale move persistence including north of Tromsø, northwest of Lofoten, and in the south along the Møre coast (Fig. 2b,c), which generally coincided with elevated herring density.

Ranking the mixed effects models (Table 2) indicated that the most parsimonious model, $\text{logit}(\gamma_i) = \rho_i + (1\gamma_i | \text{id})$, included a fixed effect for density and a random intercept term for individual whales. This model had the best fit for explaining killer whale move persistence using both observed herring density and simulated herring density values (see Table 2 and Fig. 3). The move persistence of all individual killer whales was negatively correlated with herring density. Killer whales tended to exhibit ARS-type movement in areas of high herring densities, suggesting foraging behavior (Fig. 3). This model included individual intercept terms that did improve the fit, suggesting that there are individual differences in overall movement characteristics between killer whales. It is worth noting that in this most parsimonious model, light intensity (sun angle) was not considered as an environmental covariate that influ-



enced killer whale behavior. Nonetheless, the second ranked model $\text{logit}(\gamma_t) = \rho_t + \alpha_t + (1\gamma_t | \text{id})$ for simulated herring density was also considered based on its ΔAIC (<2.00) and its small LR. While this model did include sun angle as an environmental covariate, the fitting of this model indicated that move persistence did not vary with sun angle (Fig. S5). Based both on model ranking order, as well as the response curve of the second ranked model, it is unlikely that sun angle influenced whale movements. Additionally, based on the principle of parsimony, we can conclude that the simplest of these 2 models, $\text{logit}(\gamma_t) = \rho_t + (1\gamma_t | \text{id})$, best describes the behavior of the whales. Additional supplemental analysis was conducted to test how variations in relative simulated herring density data affect modeling results (Text S1, Figs. S6–S8, and Table S1).

4. DISCUSSION

This study describes the movement behavior patterns of killer whales along the Norwegian shelf in relation to a key food resource, NSS herring (Similä et al. 1996, Similä 1997, Simon et al. 2007). We found that after leaving the herring overwintering areas in northern Norway, killer whales broadly followed the herring migration south towards their spawning grounds on the Norwegian Shelf. Our results suggest that killer whales alter their behavior in response to herring biomass distribution patterns by reducing their speed and directionality in areas with elevated relative herring density on the Norwegian Shelf. This is consistent with previous studies on predator–prey interactions (Womble et al. 2014, Goldbogen et al. 2015, Hays et al. 2016). While performing our analysis, Mul et al. (2020) used much of the same 2017/2018 and 2018/2019 tracking data and found that

Fig. 2. Observed relative density of herring during the month of February with killer whale move persistence (γ_t) estimates overlaid, for (a) 2015/2016, (b) 2017/2018, and (c) 2018/2019 (greyscale, where darker values indicate higher relative herring density). Note that the relative observed herring density scales differ. Absolute density values cannot be compared across years, but relative values and distribution patterns can. Move persistence values for the corresponding season are superimposed over the observed relative herring density distributions. Each point is colored by the corresponding move persistence value γ_t , ranging from yellow, indicating transiting behavior with high speeds and consistent directionality, to dark purple indicating foraging behavior with reduced speeds and frequently changing directionality

Table 2. Model rank table. Ranked lists of models using either relative observed herring density acquired from the observed field or models using relative simulated herring density acquired from the simulated field. Model order was based on the change in Akaike's information criterion (ΔAIC) and change in likelihood ratios (ΔLR). The most parsimonious models, indicated in **bold**, show AIC (not ΔAIC) and LR (not ΔLR) values

Herring density method	Model formula	df	ΔAIC	ΔLR
Observed herring density	~density + (1 id)	6	6310.46	6298.461
	~density + sun angle + (1 id)	7	2.00	0.000
	~density + (density id)	8	4.00	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
Simulated herring density	~density + (1 id)	6	6306.46	6294.457
	~density + 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

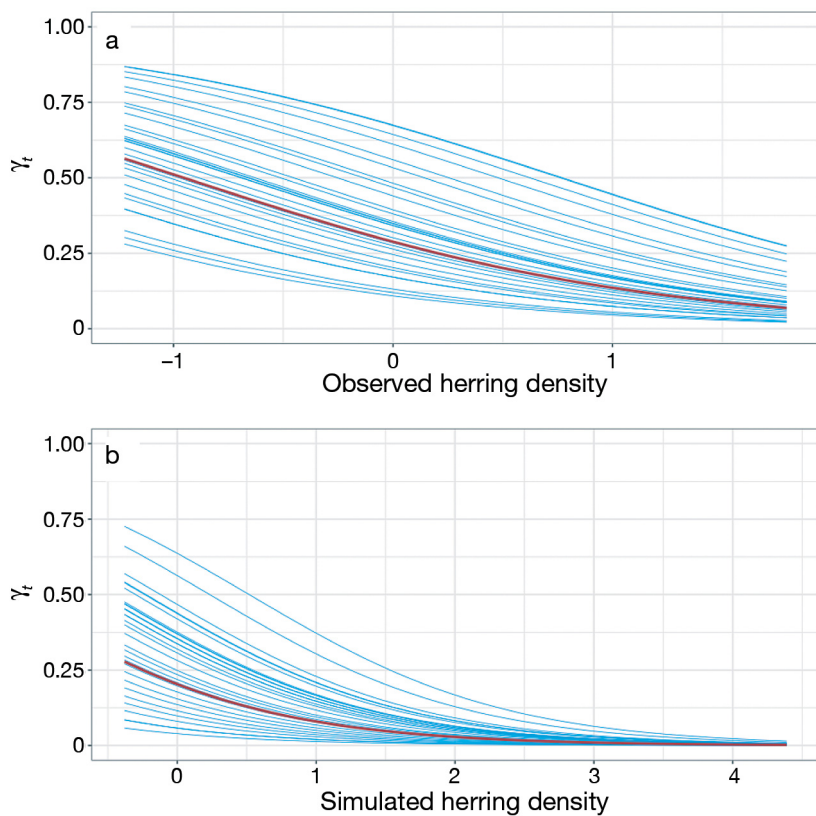


Fig. 3. Most parsimonious model from mixed effect analysis of killer whale move persistence and herring density. Panels display individual (blue lines) random effects relationships and group (red line) fixed effects responses when using either (a) relative observed herring density values or (b) relative simulated herring density values. For both cases, the most parsimonious model was $\text{logit}(\gamma_t) = \rho_t + (\rho_t | \text{id})$. Note that the relative observed and simulated density scales are different and not directly comparable

these Norwegian killer whales were frequently attracted to herring fishing vessels, especially within the fjords. Thus, we may consider herring fishing

boat locations as an indirect proxy of herring density. It is worth noting that a small number of tracks in this study were from whales tagged in Møre and therefore do not necessarily represent whale movements following the spawning migrations of NSS herring. Nonetheless, since these individuals also remained within the high-concentration herring areas for the majority of the tracking period, their behavior supports the notion that herring remain a key prey species for killer whales outside of the main overwintering areas, even though we do not know their behavior prior to arriving at the spawning grounds.

In our study, killer whale move persistence was inversely influenced by both observed and simulated relative herring density. Each approach for modeling relative herring density had its own strengths and weaknesses. The observed annual spatial fields based on NASC-derived herring density was limited in geographical range to the areas covered by the NSS herring surveys in each specific year and provided a static snapshot of herring density distribution during their spawning migration. A strong point of this method is that it was based on actual acoustic and biotic herring observa-

tions. In contrast, the simulated data provided dynamic predictions of variation in herring density distributions across a broader geographical range, but due

to the physical forcing applied, did not represent a specific year. The similarities in mixed effect modeling when using these different relative herring density estimates strongly suggest that in general, killer whale movements along the Norwegian Shelf are broadly associated with herring distribution during the period between overwintering and spawning. Since the most parsimonious model for explaining killer whale movement behavior was the same when each method of predicting herring density was used, we conclude that both approaches for modeling herring density capture the key elements of NSS herring density distributions related to killer whale movements. Furthermore, each of these methods validates the use of the other in future studies.

Light intensity did not improve the fit of the models tested, suggesting that killer whale movement characteristics do not display diel variations in this period. There are at least 3 plausible explanations for why including light intensity did not improve model 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, even in the winter in northern fjords (Huse & Korneliussen 2000). Nonetheless, the lack of relationship with sun angle could be attributed to different propensities in diurnal patterns based on sex of the whales (Beck et al. 2003). In that study, male grey seals *Halichoerus grypus* dove consistently throughout the day, whereas females had strong diurnal diving patterns. As our tagging protocol targeted only male killer whales, we cannot rule out a similar sexual bias. Second, the 3 h reconstructed step intervals used in this study might provide insufficient temporal resolution to detect variations in whale movements caused by herring diel vertical patterns (Sims et al. 2008, Postlethwaite & Dennis 2013). A third explanation may be that vertical migrations of herring in the water column only influence the dive patterns of killer whales, but not their horizontal movements. This explanation is consistent with pinniped studies that have recently questioned whether optimal foraging theory can be explained based solely on pinniped horizontal movements, and they suggest that both vertical and horizontal movements need to be considered since individuals may still forage while seeming to be exhibiting directed transiting behavior (Bestley et al. 2015, Carter et al. 2016). Future studies utilizing biologging techniques that record depth data and/or more frequent sampling rates might allow us to address more detailed fine-scale behavioral variations, such as diel patterns in dive behavior and for-

aging intensity. Fine-scale diving behavior pattern studies have been conducted extensively on killer whales in other regions (e.g. Baird et al. 1998, 2008, Reisinger et al. 2015, Wright et al. 2017, Tennessen et al. 2019). Reisinger et al. (2015) found clear diel variations in the dive behaviors of killer whales and related these variations to the diel vertical migration of species which this population of Marion Island killer whales are known or thought to prey upon. The influence of vertical diving on the interpretation of horizontal movement behavior has not been addressed in cetaceans.

After the overwintering period, when herrings leave the fjords for their southern spring spawning grounds, our study shows that killer whales also do so. Most tagged whales in our study 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 density values were correlated with restricted whale movement behaviors, suggesting that the whales continue to feed on herring along the shelf well into the spring. The fact that all killer whales in our study responded similarly to changes in herring density suggests that this population specialized on herring, at least for the period over which they were tagged. This is consistent with previous studies suggesting that Norwegian killer whales are largely herring specialists (Similä et al. 1996, Simon et al. 2007). However, numerous observation-based studies have reported Norwegian killer whales foraging on a variety of prey types in addition to herring, including other pelagic and benthic fish as well as marine mammals (Similä et al. 1996, Foote et al. 2009, Vester & Hammerschmidt 2013, Vongraven & Bisther 2014, Jourdain et al. 2017, 2020a,b). This is also supported by telemetry-based studies such as Dietz et al. (2020) which showed movements in to areas where they likely target other prey types. Since the whales in our study were primarily tagged in known overwintering herring areas, and our tracking period occurred when Norwegian herring were migrating to their spawning grounds and spawning, it is possible that our study was biased towards herring specialists.

Our data are also consistent with an alternative hypothesis, that Norwegian killer whales are opportunistic generalists (in terms of their overall annual diet) that all respond to herring in the same way when herring are abundant along the coast. As herring move offshore after the spawning period, killer whales may remain along the coast and switch to other prey types (Nøttestad et al. 2014), or they may

follow the herring migrations towards their summer and autumn feeding grounds. The former would suggest a more generalist strategy, while the latter would indicate stronger specialization towards herring. This seasonal shift in feeding is consistent with studies on Marion Island killer whales, where stable isotope analysis indicated seasonal shifts in foraging area for that population (Reisinger et al. 2016). One possibility is that some fraction of the population remains along the coast, while another follows the herring offshore. It is also possible that whales switch back and forth between coastal and offshore behavior. This would be consistent with previous studies that found killer whales exhibiting prey-switching behaviors depending on seasonality and/or prey availability (Bisther & Vongraven 2001, Krahn et al. 2008, Foote et al. 2010, de Bruyn et al. 2013, Jourdain et al. 2017). Furthermore, genetic data suggest a substantial degree of mixing between Norwegian, Icelandic, and Greenlandic waters (Foote et al. 2010, 2011, 2013, Jourdain et al. 2019), while killer whales are also observed along the Norwegian coast year-round (Similä et al. 1996). This suggests that there may be a mix of strategies operating simultaneously within this population. A generalist classification of Norwegian killer whales is consistent with recent studies on Norwegian killer whale dietary variations (using stable isotope analysis), where considerable heterogeneity between individual dietary patterns was observed (Jourdain et al. 2020a).

We noted that the population of whales tagged in the northern fjords left those fjords over a 3 mo period. Considering the clear relationship between the behavior of these killer whales and herring densities on the shelf, it is plausible that the heterogeneity observed when the whales left the fjords might reflect heterogeneity in the timing of the herring spawning migration. Similarly, not all herring actually enter the fjords to overwinter; some aggregate on the shelf instead. Thus, it is plausible that whales leaving the fjords early still associate with herring aggregations, and are simply switching to aggregations occurring outside the fjords.

Two whales in our study (ID 60268 and 62027), described by Dietz et al. (2020), displayed interesting tracks that might shed light on whether Norwegian killer whales are generalists or herring specialists. These whales were tagged in a fjord where herring were overwintering, exited the fjord, and traveled towards the herring spawning migration, before changing course and ultimately traveling northward away from the herring spawning grounds and towards Novaya Zemlya (see Fig. S4). 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 other fish species such as capelin *Mallotus villosus* or ice-associated species such as polar cod *Boreogadus saida*, or perhaps other marine mammals. It is worth noting that these 2 whales, prior to traversing into the Barents Sea, showed the same pattern of decreased move persistence in association with high herring density as all the other whales in the study. This is consistent with prey-switching behavior. Our study was designed to investigate the influence herring density has on killer whale move persistence. Future investigations to specifically evaluate prey-switching behavior among Norwegian killer whales, in agreement with the results of Jourdain et al. (2020a), could entail evaluating the influence of both proximity to known seal haulout areas, as well as herring density, on killer whale move persistence.

In conclusion, the main finding of our study was that killer whale movements are influenced by changes in herring density distributions on the Norwegian Shelf during the herring spawning period. Unlike most previous studies that correlate changes in marine predator behavior to indirect proxies of prey distribution (Redfern et al. 2006, Sequeira et al. 2012, Becker et al. 2016), our study provides compelling evidence based on whale telemetry data and herring density distributions. The use of actual prey density distributions to examine predator–prey relationships is rare for marine studies of this kind (Pendleton et al. 2020). Based on this approach, killer whale movement behaviors might be useful for potentially identifying previously unknown areas of high NSS herring density. Such locations can in turn be used to inform future herring survey designs, and ultimately expand our understanding of their dynamic distribution. It is uncertain if and how climate change, or other environmental factors, will affect the distribution patterns of NSS herring (Sissener & Bjørndal 2005); however, it is clear that changes in herring distributions could influence the distribution and behavior of killer whales. 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 density (Toresen & Østvedt 2000), more recent studies found that that around 2005, ocean temperatures continued to increase, whereas herring density 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, Jourdain & Vongraven 2017), particularly if they follow shifts in herring density, as demonstrated in our study. Regardless, our study, conducted between 2015 and 2019, can serve as a baseline for future comparative studies, if and when the NSS herring distribution shifts.

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