Norwegian killer whale movements reflect their different prey types

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Abstract

Norwegian killer whales (*Orcinus orca*) are thought to be generalists that feed primarily on fish, but some individuals have been observed targeting pinnipeds. In the study reported here, field observations of foraging behaviours formed the basis of a priori classification as either *seal-eaters* or *fish-eaters*. Concurrent collection of photographic identification and biopsies for stable isotope analysis were used to validate prey choice classification. We found through satellite tracking that whales classified as *seal-eaters* took different paths south after leaving the northern fjords seemingly optimized for pinniped predation. Specifically, we found that *seal-eaters* took paths that tightly followed the coastline, remaining on average 6.9 ± 10.7 km (mean $\pm$ SD, $n = 315$) from the coast, whereas *fish-eaters* moved offshore along the continental shelf, travelling on average 45.1 ± 30.2 km ($n = 1534$) from the coast. We also found that, compared to *fish-eaters*, *seal-eaters* displayed more movements directed towards harbour seal haul-outs ($p = 0.001$). As expected, our data suggest that the *fish-eaters* feed primarily on fish, whilst *seal-eaters* appear to opportunistically use diverse foraging strategies optimized for either fish or seals based on availability and preference. Our findings demonstrate that tracking data can elucidate Norwegian killer whale movements associated with different prey types and selection.

To access the supplementary material, please visit the article landing page

Introduction

Killer whales, as a species, are generalist opportunistic foragers that feed on available prey in their local environment. Globally, over 150 species have been recorded as potential killer whale prey, including squid, fish, other marine mammals, and even seabirds (Foster 2019). Generalist predator populations typically comprise sub-populations that often display a spectrum of foraging specialties (Bolnick et al. 2003; Ford & Ellis 2014). This might reflect the local prey availability at a specific time or place or individual preferences that may vary seasonally (Krahn et al. 2008; de Bryun et al. 2013; Jourdain, Andvik et al. 2020). For example, killer whales of the north-east Pacific are categorized in three distinct ecotypes: 'residents', specializing on fish and squid; 'transients', feeding solely on marine mammals, and 'offshores', feeding on both bony and cartilaginous fishes (Bigg et al. 1987; Ford et al. 2000).

Differentiating between prey preference and food availability is a fundamental challenge for understanding the feeding behaviours of wild animals. Stomach contents and stable isotopes analysis have been used to examine killer whale dietary ecology (Ford et al. 1998; Wijnsma et al. 1999; Saulitis et al. 2000; Pitman & Ensor 2003; Jourdain, Andvik et al. 2020). Measured ratios of stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) reflect foraging habitats and trophic positions, respectively (Hobson 1999; Newsome et al. 2007; Newsome et al. 2010). The $\delta^{13}C$ of a predator reflects the origin of its food sources, indicating the sources of primary production in the food consumed. Coastal ecosystems are typically characterized by higher $\delta^{13}C$ than offshore waters (Søreide et al. 2006; Newsome et al. 2010). The

isotope $\delta^{15}N$ is commonly used as an indicator of the trophic level of a consumer (Hobson & Welch 1992; Hobson et al. 1994; Hobson 1999; Kelly 2000; Hobson et al. 2002). Recent studies using $\delta^{13}C$ and $\delta^{15}N$ as dietary tracers highlighted differences in prey specialization (fish-eating versus seal-eating) in killer whales in Norway (Jourdain, Andvik et al. 2020; Bories et al. 2021). Specifically, Jourdain, Andvik et al. (2020) found that $\delta^{15}N$ values were significantly higher (12.6 ± 0.3) among *seal-eaters* than they were for *fish-eaters* (*herring-eaters*: 11.7 ± 0.2‰ and *lumpfish-eaters*:11.6 ± 0.2‰). A comparison of field observations, with the results of stomach content and stable isotopes analyses, can reveal either consistent prey choice or prey switching over time (Jourdain, Andvik et al. 2020). While these approaches can identify prey diversity, they often cannot differentiate between prey preference and seasonal changes in prey availability and/or declining abundance of prey.

While much is known about how prey choice influences the movements of killer whales in the Antarctic and North Pacific, less is known about NKW behaviours (Ford 1998; Pitman & Ensor 2003; Andrews et al. 2008; Ford & Ellis 2014; Reisinger et al. 2015). Field observations suggest that killer whales off the Norwegian coast feed almost exclusively on herring (*Clupea harengus*; Similä et al. 1996; Similä 1997; Simon et al. 2007; Mul et al. 2020; Vogel et al. 2021). However, recent investigations using stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and lipidomic fingerprints as dietary tracers indicate that NKWs feed on a wide spectrum of prey. Some individuals display specialization on fish while others seem more flexible, feeding on both fish and marine mammals (Jourdain, Andvik et al. 2020; Bories et al. 2021). Recent observations of NKWs preying upon harbour seals (*Phoca vitulina*) and other marine mammals, such as harbour porpoises (*Phocoena phocoena*; Cosentino 2015; Jourdain et al. 2017; Jourdain, Andvik et al. 2020) are consistent with these dietary studies. Studies on NKWs have primarily been conducted in the winter, when they are readily found, associated with overwintering herring along the coast of Norway. The perception that NKWs primarily feed on herring might therefore be influenced by sampling bias (Jourdain et al. 2019; Lennox et al. 2022). Indeed, field studies conducted at other locations and periods reported NKWs feeding on a wide variety of prey items, such as Atlantic salmon (*Salmo salar*), mackerel (*Scomber scombrus*), harbour porpoise (*Phocoena phocoena*), harbour seals and lumpfish (*Cyclopterus lumpus*; Vester & Hammerschmidt 2013; Nøttestad et al. 2014; Vongraven & Bisther 2014; Cosentino 2015; Jourdain et al. 2017; Jourdain et al. 2019; Jourdain, Karoliussen et al. 2020). Similar observations of populations of killer whales broadening their diets have been reported in the northeast Pacific (Hanson et al. 2021).

Unlike many other cetacean species that undertake seasonal migrations in response to critical life history stages, killer whales are thought to move primarily in search of feeding opportunities (Corkeron & Connor 1999). Field observations (Jourdain et al. 2017; Jourdain et al. 2019) and recent satellite-tag tracking studies (Mul et al. 2020; Vogel et al. 2021) show that NKWs persistently feed on overwintering herring, and frequently exhibit area-restricted foraging behaviours in dense herring aggregations along their offshore routes. Satellite tagging studies in the Antarctic have revealed similar localized foraging behaviours for fish-eating killer whales (Andrews et al. 2008). Strikingly, Antarctic killer whales targeting pinnipeds (such as the killer whales known as Antarctic type B) were found to display nomadic and far-ranging movements (Andrews et al. 2008). Similar nomadic movements have been described for NKWs on the basis of opportunistic field observations of whales targeting seals, where individuals were occasionally observed transiting between seal colonies (Jourdain et al. 2017). A detailed satellite tracking study of the long-term continuous movement behaviour of NKWs feeding on pinnipeds has not been reported. Tracking studies could help define how different prey might influence NKWs movements.

Here, we describe the movements of NKWs equipped with satellite transmitters to determine if the movements of killer whales observed targeting seals differed from those targeting fish. We used photo-identification and stable isotopes ratio analysis of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) to better understand if these differences were driven by prey preferences.

Materials and methods

Fieldwork

Fieldwork took place in Troms County fjord areas (2015–2021) between October and January. Individual killer whales were characterized a priori as either *seal-eater* or *fish-eater* on the basis of observed behaviours at the time of tagging. Specifically, whales that were observed feeding on seals or making fast and directed movements towards seals were deemed *seal-eaters*. *Fish-eaters* were those observed to make more tortuous movements concentrated in areas of overwintering herring; their proximity to purse-seine herring fishing boats was also taken into consideration (Mul et al. 2020).

Our procedures for satellite tagging and tag programming have been described in detail in previous articles (Mul et al. 2019; Dietz et al. 2020; Vogel et al. 2021). In short,

an aerial rocket tagging system (Kleivane et al. 2022) was used to deploy either SPOT5 or SPOT6 Limpet Argos transmitters (Wildlife Computers) onto the dorsal fin of killer whales. This placement maximized both tag retention and the accuracy of positions determined from the satellite-based Argos system (Mul et al. 2019). Tags were set to transmit 14–15 times every hour during the first 45 days, after which the transmission rate was reduced to 8–10 times per hour for the next 45 days, and finally 2–3 times per hour after 90 days. More detailed descriptions of tag programming is provided by Dietz et al. (2020). Following satellite tag deployment, whales were reapproached, and a skin/blubber biopsy—4 cm long and 0.5 cm thick—was subsequently collected also using the aerial rocket tagging system. The skin was separated from the blubber in each biopsy sample and kept frozen at -20°C within a few hours after sampling. In total, 13 killer whales were both tagged and biopsied. Photographs of the dorsal fins were acquired when light and weather conditions allowed ($n = 2$, IDs 182231 and 22065). Sampling and tagging were conducted in accordance with permits (8165 and 24075) issued through the *Forsøksdyrforvaltningens Tilsyns- og Søknadsystem* of the Norwegian national animal research authority.

Tag data processing and movement analysis

We used the pre-processed location data provided by Argos-CLS through their Kalman filter routine (Lopez et al. 2013). All further data processing and statistical analyses were performed using R software (version 3.6.1; R Core Team 2019). To compensate for the irregular nature of time series sampling using Argos positions, while accounting for the corresponding Argos location error, a continuous-time correlated random walk state-space model from the R package 'foieGras' (Jonsen & Patterson 2019; Jonsen et al. 2020) was applied. Using this model, we estimated locations at three-hour intervals. Of the 13 whales that were tagged and biopsied concomitantly in this study, eight had tracking durations that were greater than 12 days; only these were included for further analysis. Among these eight whales, two were a priori categorized *seal-eaters* (Table 1; individual tag IDs 182231 and 22065) and six as *fish-eaters* (Table 1; individual tag IDs 54011, 83760, 83768, 153483, 180318 and 196729). Previously published satellite tag data from whales categorized as *fish-eaters* ($n = 25$) were used to visualize and compare movements but are not detailed in this study. A detailed description of these whales has been previously published (Vogel et al. 2021).

One of the *fish-eaters* (153483) was tagged and biopsied in the Kaldfjord area outside Tromsø in November 2015, when herring was still overwintering within this

Table 1 Tagging information from eight killer whales tagged and biopsied between 2015 and 2021 utilized in this study.

ID	Initial tagging/biopsy					Out-of-fjord[a]					Stable isotope analysis[b]	
	Date	Latitude	Longitude	Tag longevity (days)	Extracted positions[c]	Start date	Latitude	Longitude	Tag longevity (days)	Extracted positions[b]	$\delta^{13}C$	$\delta^{15}N$
Seal-eaters												
182231	9 Oct 2019	69°51'N	18°3'E	82	1310	4 Dec 2019	70°4'N	21°9'E	26	212	-19.06	13.78
220657	9 Oct 2021	69°41'N	18°41'E	12	208	9 Oct 2019	69°47'N	18°32'E	12	103	-19.89	12.04
Fish-eaters												
54011[d]	6 Nov 2018	70°14'N	21°6'E	64	514	1 Jan 2019	70°3'N	20°55'E	8	65	-19.29	11.59
83760[d]	16 Nov 2018	70°14'N	21°4'E	40	323	16 Dec 2018	70°4'N	21°5'E	10	86	-18.6	11.94
83768[d]	23 Jan 2019	70°5'N	21°19'E	70	567	27 Jan 2019	70°1'N	20°52'E	67	539	-19.3	11.93
153483[e]	25 Nov 2015	69°5'N	18°35'E	106	850	24 Feb 2016	69°42'N	18°29'E	13	107	-19.41	11.03
180318	20 Nov 2019	70°2'N	20°58'E	14	117	30 Nov 2019	70°0'N	21°4'E	3	30	-19.13	11.75
196729	23 Nov 2020	70°52'N	20°55'E	110	881	15 Dec 2020	69°58'N	21°6'E	88	707	-18.31	12.13

[a]Portion of the track after each whale left the fjord in which it was tagged. [b]Isotopic values refer to $\delta^{13}C$ and $\delta^{15}N$ from skin samples. [c]The number of extracted positions are the raw Argos positions. [d]Data were concurrently used by Mul et al. (2020) and Vogel et al. (2021). [e]Tracking data were concurrently used by Dietz et al. (2020) and Vogel et al. (2021).

fjord. The rest of the *fish-eaters* (54011, 83760, 83768, 180318 and 196729) were tagged and biopsied in 2018–2020 (November and January) further north in the Kvænangen fjord at a time when herring had established overwintering areas there. It is worth observing that there are seal haul-outs in the areas of both Kaldfjord and Kvænangen fjords. The whales designated as *seal-eaters* (182231 and 22065) were both tagged and biopsied in the Kaldfjord area in October in 2019 and 2021. In these years, the herring had stopped using this area for overwintering.

The distance to the coast of each location was calculated using the 'dist2land' function in the R package ggOceanMaps (Vihtakari 2020).

It is not uncommon for NKWs to leave the herring overwintering areas within the northern fjords on transient round-trip offshore excursions (Van Ruiten 2021). This behaviour was hypothesized to be related to scouting for either alternative prey or more abundant prey patches. In this study we were primarily interested in determining the paths whales take after leaving the northern fjords and how prey preference might influence their paths. For this reason, we used only tracking data occurring after each whale permanently left the northern fjords (i.e., without returning in that season). Fjord boundaries were determined using spatial data from the Fjord Catalog published by the Norwegian Ministry of Climate and Environment (The Norwegian Enviroment Agency 2020), as previously described by Vogel et al. (2021). These truncated tracks are hereafter referred to as "out-of-fjord".

The direction of whale travel between two consecutive points, the "heading", was calculated using the bearingRhumb function from the geosphere R package (Hijmans 2021). The locations of harbour seal haul-outs ($n = 93$) were obtained from the time series of annual counting surveys along the Norwegian coast carried out by the Institute of Marine Research. We calculated the heading between each whale location and the closest seal haul-out. Using these two bearings—the whale heading and the heading to the nearest haul-out area—we calculated the absolute difference between these two headings as the delta-bearing (Δ-bearing). *Δ-bearing* values ranged from 0° (directly towards the nearest haul-out) to 180° (directly away from the nearest haul-out). We considered Δ-bearing values between 0° and 45° to indicate movements towards the nearest seal haul-out area, values between 135° and 180° to indicate whales moving away from the nearest haul-out area, and Δ-bearing values between 45° and 135° were considered non-directed. Delta-bearing values were also grouped into two categories: haul-out directed (0°< Δ-bearing < 45° or 135°< Δ-bearing < 180°) versus non-directed (45°< Δ-bearing <

135°). The inclusion of 135°–180° as directed movements related to seal predation might seem counterintuitive; however, these movements presumably reflect specific movements away from a haul-out after predation or after discovering the absence of prey at that location. The proportion of haul-out directed movements was calculated as the fraction of haul-out directed points divided by the sum of haul-out directed + non-directed points. Statistical comparisons between *seal-* and *fish-eaters* Δ-bearing proportions were calculated using a double-tailed two-proportion Z-test.

To test if the Δ-bearing proportions of the whales actually reflected the locations of the specific seal haul-outs and not simply the coastline, we also calculated Δ-bearing in relation to 93 randomly generated points along the coast within the geographical limits of the distribution of the known haul-out areas. Points were randomly selected from the coastline defined by Natural Earth (2023). This detailed coastline includes both the Norwegian mainland as well as its offshore islands. We then followed the same protocol that we used for calculating Δ-bearing of each point, but this time in relation to these random coastal points.

Photo identifications

Dorsal fin photographs were compared to the *Photo-identification catalogue of Norwegian killer whales 2007–2021* (Jourdain & Karoliussen 2021) to determine if prior feeding history could be ascertained to support a priori categorization for dietary preferences of tracked individuals. Only the two a priori categorized *seal-eaters* were concurrently photographed since they were the only whales tagged within daylight hours and prior to the complete onset of polar night.

Stable isotope analysis

Stable isotope analyses were conducted on freeze-dried skin samples ($n = 8$). Between 1.5 and 2.0 mg of sample was weighed into tin cups and placed in a Flash EA connected to a Delta V Advantage Thermo Scientific Continuous Flow Mass Spectrometer , which determined the values of $\delta^{13}C$ and $\delta^{15}N$ and the weight % of N and C. Lipid-extracted samples were used to determine $\delta^{13}C$ to control for the low $\delta^{13}C$ found in the lipid fraction of an organism that can lead to bias (Yurkowski et al. 2015; Jourdain, Andvik et al. 2020), whereas $\delta^{15}N$ values were obtained from non-lipid-extracted samples because of the unpredictable changes in $\delta^{15}N$ values of cetacean skin following lipid extraction (Lesage et al. 2010; Ryan et al. 2012; Jourdain, Andvik et al. 2020). Lipids were removed by using a solution of 7% methanol in dichloromethane.

The accuracy and precision of $\delta^{13}C$ and $\delta^{15}N$ analyses were measured by replicate analysis of B2155 Protein Reference material from Elemental Microanalysis Ltd. (Okehampton, UK) plotted on the calibration line made from the results of analyses of USGS64 and USGS66 Glycine reference material from US Geological Survey. On average, the values for B2155 for these analyses were $\delta^{15}N_{AIR}$ = 6.07‰ ± 0.18 and $\delta^{13}C_{VPDB}$= -27.11‰ ± 0.05, while the certified values of the reference material B2155 were $\delta^{15}N_{AIR}$= 5.94‰ ± 0.08 and $\delta^{13}C_{VPDB}$: -26.98‰ ± 0.13.

Results

Killer whale movements

In this study, both *seal-eaters* (182231 and 220657; Fig. 1b) and all *fish-eaters* (54011, 83760, 83768, 153483, 180318 and 196729; Fig. 1c) eventually travelled south, albeit following different paths (Supplementary Fig. S1). Upon tagging in October 2021, *seal-eater* 220657 subsequently began its coastal southward route (Fig. 1). In contrast, the other *seal-eater*, 182231, tagged in October 2019, first moved north to a fjord associated with herring overwintering and remained near there for an additional two months before travelling south. While *seal-eater* 182231 was in this fjord that was known to be associated with overwintering herring, it moved differently from the fish-eating whales who exhibited typical herring associated restricted movements towards the centre of the fjords. In contrast, *seal-eater* 182231 frequently travelled close to the perimeter of the fjords (Supplementary Fig. S1). During this time, killer whale 182231 was also observed taking an offshore excursion north-west out of the fjords. It next travelled north-east along the coastline before returning to the fjord it was tagged in (Fig. 1; Supplementary Fig. S1). This whale was photographed feeding on herring (image not
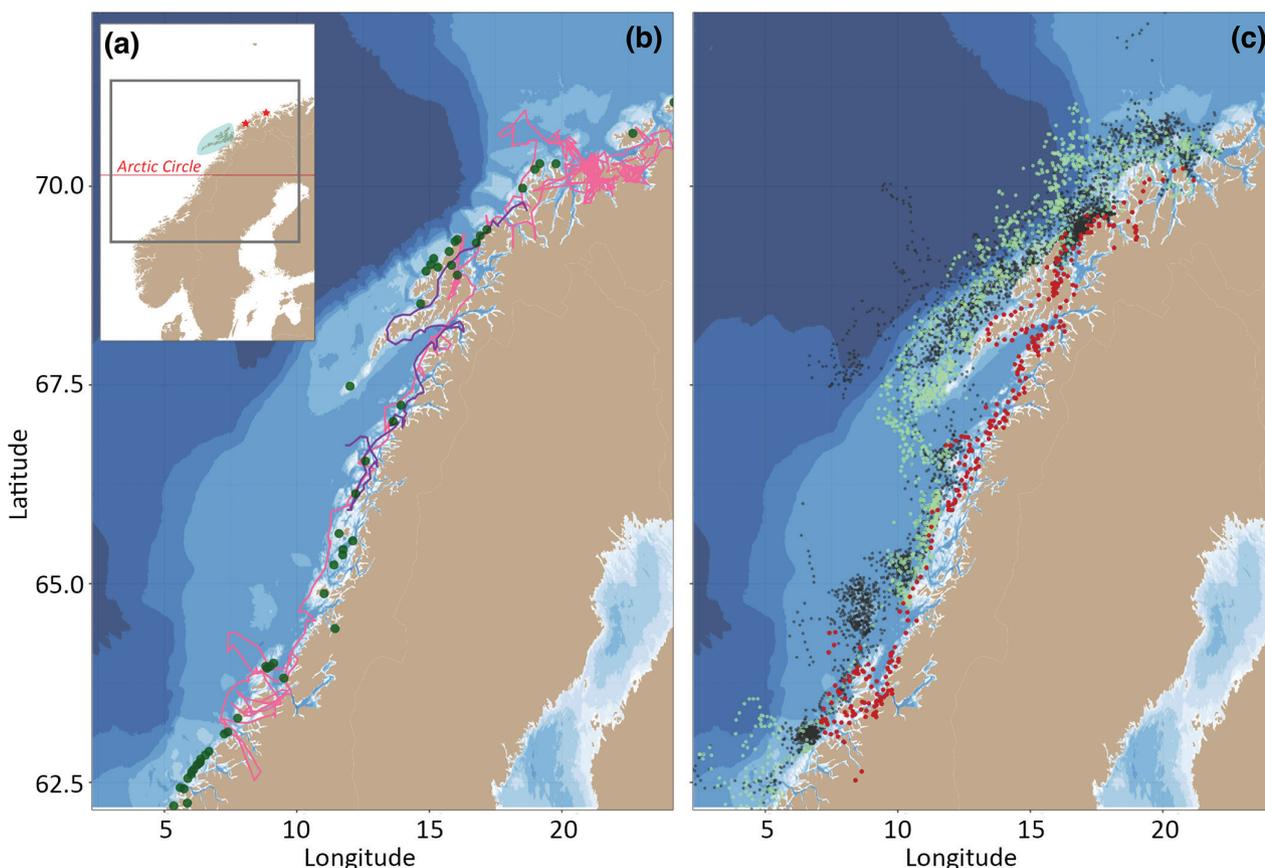

Fig. 1 (a) The positions of Lofoten and Versterålen (blue shading) along the Norwegian coast, as well as the tagging locations in the fjords (stars). (b) The full reconstructed paths of *seal-eaters* 182231 (pink lines) and 220657 (purple lines). Green dots indicate known harbour seal haul-outs. (c) The locations of the six *fish-eaters* (light green dots) and the two *seal-eaters* (red dots) after they left the fjords where they were tagged. These data are superimposed over data points from 25 additional killer whale tracks (grey dots) previously described by Vogel et al. (2021). These whales have a similar distribution to the six fish-eating whales but are distinct from our two seal-eating individuals. Bathymetry is depicted in shades of blues: darker is deeper water.
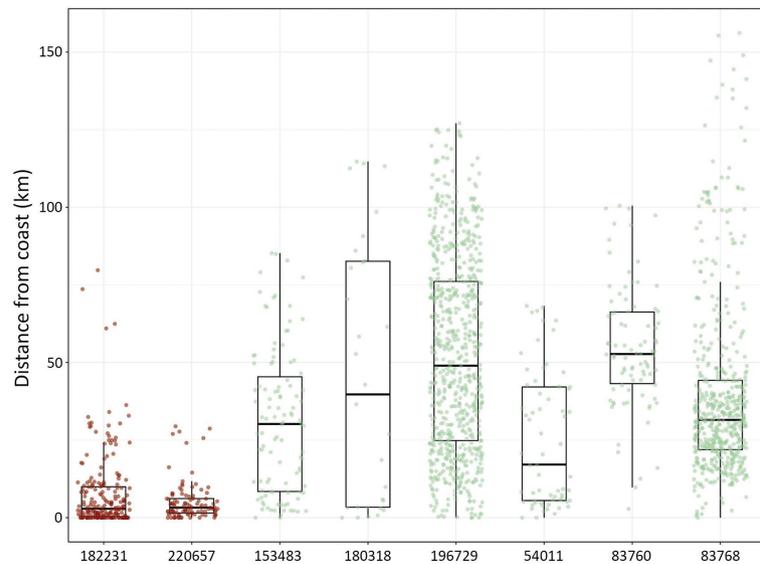
Fig. 2 Box plots of distance from the coast for individual whales. Individual tracking points for *seal-eaters* are shown in red, whereas *fish-eaters* are shown in green.

included). *Seal-eater* 182231 began its southern coastal route in early December. After leaving the herring overwintering areas, all *fish-eaters* initially headed offshore, west of Lofoten and Vesterålen, broadly following the known herring spawning migration paths (see Vogel et al. 2021 for details). The route taken by the six *fish-eaters* in this study (Fig. 1c) were similar to routes taken by the 25 killer whales—described in detail by Vogel et al. (2021)—that were all also a priori categorized as *fish-eaters* (compare light green and grey points in Fig. 1c). The *seal-eaters* followed a coastal path southward, staying typically within 6.9 ± 10.7 km (mean ± SD, n = 315, maximum = 79.7 km) from the shore (Fig. 2), while the six *fish-eaters* were routinely further offshore (45.1 ± 30.2 km, n =1534, maximum = 156.18 km). *Seal-eaters* generally explored fjords along their predominantly southward route (see tracks in Fig. 1b) and are the only whales tagged by our group to have been observed travelling in between the Lofoten/Vesterålen islands and the mainland (Fig. 1).

A significant fraction of the two *seal-eaters'* movements were seal haul-out directed, (Fig. 3a). The fraction of haul-out directed movements for *seal-eaters* 182231 and 220657 was 0.55 (n = 211) and 0.51 (n = 102), respectively. On average, the fraction of haul-out directed movements for both *seal-eaters* was 0.53. The six *fish-eaters* had a mean fraction of haul-out directed movements of 0.43 (range 0.34–0.48, n =1528 directed points). The differences in the fraction of haul-out directed movements between *seal-* and *fish-eaters*, while small, were statistically significant (Z-test; p value = 0.001, χ^2 = 10.573;

Fig. 3b). These results indicate that the movements of the *seal-eaters*, either towards or away from the nearest seal haul-out, were more frequently directed than the *fish-eaters*.

In contrast, when randomly generated coastal points (Fig. 3a) were substituted for seal haul-out areas, a difference between the *seal-* and *fish-eaters* was not observed (Fig. 3b). The fraction of randomly generated coastal points directed movements for *seal-eaters* 182231 and 220657 was 0.50 (n = 211) and 0.51 (n = 102), respectively. On average, the fraction of randomly generated coastal points directed movements for the *seal-eaters* and *fish-eaters* was, respectively, 0.50 (n = 313) and 0.44 (n = 1528, ranging from 0.26 to 0.54). These proportions were not statistically different (Z-test; p value = 0.073, χ^2 = 3.205; Fig. 3b). These results indicate that there was no significant difference in directional movements between *seal-* and *fish-eaters* relative to the randomly generated coastal points.

Photographic identification

Only one whale (220657) was successfully matched to a known individual (NKW-702) in the catalogue (Jourdain & Karoliussen 2021). Based on photographic associations with other conspecifics, it was determined that this whale is a member of a group with an observed history of feeding on both fish and seals (E. Jourdain, pers. comm.). The other putative *seal-eater*, 182231, could not be matched photographically to a whale in this database.
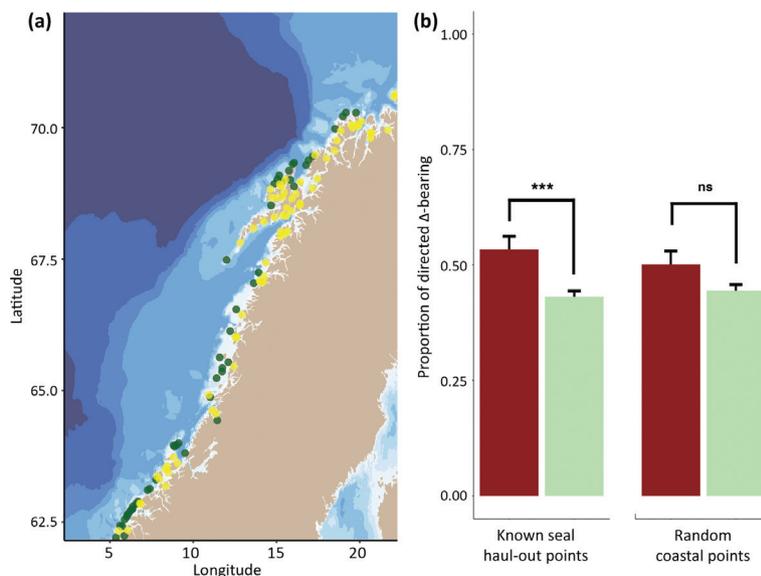
Fig. 3 (a) Known seal haul-out areas (green dots) and randomly generated coastal points (yellow dots) along the Norwegian coast. (a) A bar graph of the proportions of directed Δ-bearing to nearest known seal haul-out or nearest randomly generated coastal point. Bars are coloured in accordance with putative feeding grouping, where red indicates *seal-eaters* and light green indicates *fish-eaters*. Results from the two double-tailed two-proportion *Z*-test indicated by black brackets, where three asterisks indicate a significant *p* value of 0.001 and ns indicates a non-significant *p* value of 0.073.

Stable isotopes analysis

The highest $\delta^{15}N$ value (13.78‰, Table 1) was measured in one of the a priori categorized *seal-eaters* (182231), an individual that could not be matched to the catalogue. In contrast, we found a lower $\delta^{15}N$ value (12.04‰; Table 1) for the second a *seal-eater* (220657), whose photographic identification revealed a prior history of feeding on both seal and herring. This individual had a $\delta^{15}N$ ratio slightly below the values for seal-eating killer whales reported by (Jourdain, Andvik et al. 2020; 12.6 ± 0.3‰). The $\delta^{15}N$ values of the six whales a priori designated as *fish-eaters* (11.7 ± 0.35‰) were, on average, in line with values for herring-eating killer whales reported by Jourdain, Andvik et al. (2020; 1.7 ± 0.2 ‰).

Discussion

Based on our a priori classification of individual NKWs as either *seal-eaters* or *fish-eaters*, our tracking results indicate that these two groupings of whales take different paths, seemingly optimized for their preferred prey, after leaving the northern fjords. To the best of our knowledge, this study is the first to describe the satellite tracks of NKWs thought to be foraging on seals along the Norwegian coast. Our classification was further supported by $\delta^{15}N$ signatures and prior photo-identification history, when available. Together with our tracking data, these data suggest that the *fish-eaters* appear to specialize in fish, while *seal-eaters* may opportunistically use diverse foraging strategies optimized for fish and seals based on availability and preference. While all whales eventually travelled southward after leaving the northern fjords where the tagging was conducted, *fish-eaters* continued to follow the offshore herring spawning migration pathway along the continental shelf off the Norwegian coast, their movements appearing to respond to local herring aggregations (Hjøllo et al. 2012; Utne et al. 2012; Slotte et al. 2016; Vogel et al. 2021; Salthaug et al. 2022). In contrast, *seal-eaters* closely followed the coast, seemingly targeting known harbour seal haul-outs.

The offshore southward movements of *fish-eaters* were expected, as they reflected the movements and distributions of herring when they migrate south to their offshore spring spawning grounds (Dragesund et al. 1997). In contrast, the *seal-eaters* followed a coast-hugging path, traversing shallow coastal waters that are typically associated with harbour seal habitats (Nilssen et al. 2010). Seals tend to remain close to their coastal haul-outs throughout the year (Carter et al. 2020). We therefore speculate that the coastal paths taken by the *seal-eaters* were optimized for preying on pinnipeds near their haul-outs. This might also explain their southward travel direction, since most of the known seal haul-outs are south of the whales' tagging locations. Nonetheless, before leaving the fjords, *seal-eater* 182231 was photographed near herring fishing boats. Furthermore, tracking data for *seal-eater* 182231 indicated that, before

leaving of the northern fjords for the final time of the season (the criteria for inclusion for analysis in this study), this whale took an offshore excursion out of the fjords, presumably to feed on pelagic fish.

We found two aspects of movement that differentiated the *fish-eaters* and *seal-eaters*: (1) differences in the route taken as reflected by their average distance from shore and (2) differences in the proportion of directed movements towards or away from known harbour seal haul-out areas. These differences might reflect individual prey specialization (i.e., fish versus seals), preference or diversifying feeding strategies. In our previous studies we also found evidence consistent with prey switching behaviour among NKWs (Dietz et al. 2020; Vogel et al. 2021). In these studies, all individuals followed offshore herring aggregations (Vogel et al. 2021), but two individuals later deviated from the herring aggregations and switched to migrating northwards into the north-eastern Barents Sea, likely in search of alternative prey along the marginal ice zone (Dietz et al. 2020).

The movement patterns of the *seal-* and *fish-eaters* were strikingly different, suggesting that these groups utilized different foraging strategies, at least on a seasonal basis. We found that the *seal-eaters* (as compared to the *fish-eaters*) had a slightly higher propensity for directed movements relative to seal haul-out areas. This difference was not observed for the negative control using randomly generated coastal points. This suggests that while a coastal route might improve the chances of encountering a seal, a coastal route directed towards seal haul-out areas enhances the efficiency of that strategy. Since the fractions of directed movements towards the randomly generated coastal points were similar to those of haul-out directed points for the *fish-eater* and for one *seal-eater* (220657), it suggests that *seal-eater* 182231 drives the difference between haul-out-directed and random. This is consistent with the stable isotope data for this individual indicating that it was feeding at a higher trophic level. Regardless, the low number of *seal-eaters* in this study warrants caution in interpreting these results.

We cannot rule out the possibility that the whales designated as *seal-eaters* in our study could have also been feeding on porpoises. Norwegian killer whales have been observed to feed on harbour porpoises (Cosentino 2015), a coastal species whose spatial distribution frequently overlaps with that of harbour seals in Norwegian waters (Bjørge & Øien 1996; Cosentino 2015). Foraging on porpoises would result in elevated δ^{15}N ratios. The combination of stable isotope analysis, photo-identification records and visual observations (some of the most reliable methods for understanding individual killer whale diet) suggests that the *seal-eaters* in this study were generalists primarily preying on pinnipeds, but occasionally also

preying on fish. While one *seal-eater* (182231) had an isotopic signature consistent with feeding at a high trophic level four to seven weeks prior to tagging, the second *seal-eater* (220657) had a lower δ^{15}N ratio indicative of feeding at an intermediate trophic level, likely reflecting a mixed diet. Inter-individual variations in δ^{15}N are not surprising because of the proportion of marine mammal prey items in the diet of NKWs is known to vary considerably between individuals and across seasons (Jourdain, Andvik et al. 2020). Identified in the whale catalogue, Whale 220657 is part of a group that has been known to prey upon both seals and fish (E. Jourdain, pers. comm.). Although 182231 was observed pursuing seals at the time of tagging and had a δ^{15}N ratio that clearly indicates high trophic level feeding, it is likely that this individual also utilized a range of foraging strategies, since it remained near the main herring overwintering fjords for two months and was observed feeding on herring like the *fish-eaters* in this study. Although not included in the formal analysis of this study, since these movements occurred before the whale left the fjords for the season, it was noticed that that the in-fjord movements of *seal-eater* 182231 appeared to differ subtly from those of the typical *fish-eaters*. Specifically, this individual sometimes seemed to closely follow the perimeter of the fjords, presumably searching the edges for seals, while *fish-eaters* had more tortuous and concentrated movements associated with herring predation.

Prey-switching between fish and pinnipeds might reflect diverse feeding strategies influenced by the relative abundance and availability of prey types. It could also result from individual prey preferences. Demonstrating prey preference is challenging because it requires documenting predation on a certain species in the context of alternate available prey that are available. Since the availability of different prey types will vary seasonally and geographically, this type of information can potentially be leveraged to identify a prey preference. Both *seal-eaters* in this study were tagged in October, while the whales categorized as *fish-eaters* were tagged between November and January. It is therefore important to consider seasonal variations in herring abundance when attempting to differentiate between a preference for pinnipeds versus diversifying feeding strategies due to a diminished abundance of herring. *Seal-eater* 220657 left the fjords in October, at the very onset the herring overwintering aggregation. Herring may have been at relatively low concentrations when this individual left the fjords, making it is unclear if this individual had a preference for seals. In contrast, *seal-eater* 182231, which was also tagged in October, remained in the northern fjords for two more months, presumably feeding on high concentrations herring. In early December, when herring was still abundant,

this whale began its southward coastal journey thought to be optimized for seal predation. Displaying movements associated with seal predation when herring was still abundant suggests that *seal-eater* 182231 has a preference for seals.

One possible criticism of our study is that there were only two whales categorized a priori as *seal-eaters*, limiting the statistical power of our study. Nonetheless, the two seal-eating individuals in our study took clearly unique paths, presumably optimized for seal predation, as compared to the more commonly studied fish-eating NKWs. Future tagging efforts should prioritize seal-eating NKWs to increase the statistical power of the observations reported here. Additionally, it should be noticed that the validity of the discrete characterization of north-east Atlantic killer whales has been questioned (Foote 2023). Our tracking, stable isotope analyses and photo-identification results support recent studies that NKWs are opportunistic generalists with varying degrees of prey preference and specialization (Jourdain, Andvik et al. 2020). Our movement results based on a priori categorization suggest some level of prey specialization or preference. Future long-term studies investigating the diversity of feeding strategies are needed to determine the range of diverse feeding strategies. We conclude that the characterization of these whales as being either *seal-eaters* or *fish-eaters* has some value but should only be considered a reflection of their current prey selection (of undetermined duration), rather than a fixed specialization.

Conclusion

Horizontal movements and spatial use acquired using satellite telemetry can provide additional evidence for prey preference and may be specifically useful to differentiate individuals targeting fish from those targeting pinnipeds. While killer whales have been observed and photographed along the Norwegian coast, between the Lofoten and Versterålen archipelagos and the mainland, the seal-eating killer whale satellite tracking information presented in this study is the first to document the tracks and movement behaviours of these mixed-diet whales as they leave the northern herring overwintering areas and travel southward. Using satellite tracking, we identified geographical areas along the Norwegian coast that were uniquely used by killer whales targeting seals. Although based on only two individuals, it is striking how similar the coastal routes were for the *seal-eaters*. This area could be targeted in future tagging studies to balance against past *fish-eater* bias. Furthermore, predation at higher trophic levels (i.e., seals) is associated with greater exposure to toxic pollutants (Andvik et al. 2020; Andvik et al. 2021; Remili et al. 2022). It is therefore important to assess the proportion of the population that targets high trophic level prey, specifically, to understand the frequency, seasonality and geographical occurrence of NKW prey selection so that the drivers of this behaviour can be identified. Furthermore, understanding the nuances of killer whale feeding behaviour can help us better understand population demographic trends (Tixier et al. 2017).

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