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Killer whales (*Orcinus orca*) feeding on lumpfish (*Cyclopterus lumpus*) in northern Norway

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Abstract

Killer whales (*Orcinus orca*) in Norwegian waters have long been known to rely on Atlantic herring (*Clupea harengus*) as a main prey resource. However, research almost exclusively conducted at seasonal herring grounds may have biased studies away from detecting other potentially significant prey species. Since 2013, dedicated research efforts have focused on monitoring killer whale occurrence and foraging ecology throughout the year in northern Norway. This study presents results on site-fidelity of photographically identified individuals, predation records and behavioral patterns from five spring seasons (March–April) in 2014–2018 in Andfjord, northern Norway. A minimum number of 75 adult and subadult killer whales (out of a catalog of 971 individuals) returned seasonally to the study area for foraging and residency for up to six weeks. Lumpfish (or lumpsucker, *Cyclopterus lumpus*) was the only type of prey identified (based on molecular or visual identification) on 22 predation events from 2016 (n = 4), 2017 (n = 2) and 2018 (n = 16). Spatial group cohesion observed when foraging was a potential adaptation for efficiently hunting this prey species. These whales were also encountered at herring wintering grounds the same years, but with different group sizes. Such behavioral adaptations suggested intraannual switching between prey resources and foraging strategies.

KEYWORDS

feeding behavior, foraging, foraging strategy, killer whale, *Orcinus orca*, seasonality, site-fidelity

1 | INTRODUCTION

The killer whale (*Orcinus orca*) is found in all the world's oceans and as a species is generalist, with a wide range of prey documented including fish, marine mammals, cephalopods, reptiles and seabirds (Ford, 2009). However, populations have been shown to be prey specialists. For example, in the temperate coastal northeastern Pacific, killer whales feed exclusively on either marine mammals or fish, (Baird & Dill, 1995; Ford & Ellis, 2006; Ford et al., 1998). Such prey specialization, including underlying foraging behavior and knowledge about particular prolific feeding areas, are culturally transmitted in the form of learned behavior within groups and persist over time (Ford et al., 1998; Riesch et al., 2012). Resulting ecological and cultural divergences among social groups promote the formation of sympatric socially and genetically isolated ecotypes (Foote et al., 2016; Ford & Ellis, 2014). Divergent foraging strategies, by creating differences in occurrence and movement patterns as well as social organization, may further play a role in population structuring (Hoelzel et al., 2007; Morin et al., 2010; Parsons et al., 2013).

In the North Atlantic, two ecotypes of killer whales were proposed based on dietary specialization, Type 1 and Type 2, with nitrogen stable isotope values and tooth wear used as proxies to indicate key prey choice for each type (Foote, Newton, Piertney, Willerslev, & Gilbert, 2009; Foote, Vester, Vikingsson, & Newton, 2012). Type 1 refers to killer whales from Iceland, Norway, and the North Sea, which rely on the Atlantic herring (*Clupea harengus*) and/or the Atlantic mackerel (*Scomber scombrus)* as their main food source(s). In contrast, Type 2 primarily feeds on other cetaceans. However, this simplistic classification seems unlikely to encapsulate the broad-scale diversity of the diet of North Atlantic killer whales. In fact, there is strong evidence for interindividual variation in the relative proportions of prey types consumed within Type 1 killer whales. For example, some may also prey on pinnipeds, as evidenced by field observations (Foote, Similä, Vikingsson, & Stevick, 2010; Jourdain, Vongraven, Bisther, & Karoliussen, 2017; Samarra et al., 2018; Vongraven & Bisther, 2014). As such, different feeding specializations may exist within populations. Recent studies using ecological tracers were further supportive of interindividual variation in dietary habits among regions (e.g., Faroe Islands/Denmark vs. Greenland; Bourque et al., 2018), within regions (Samarra, Vighi, Aguilar, & Vikingsson, 2017), and within social groups (in Greenland, see Bourque et al., 2018). However, the lack of killer whale identification data and predation records for most regions has impeded our understanding of fine-scale seasonal and/or group-specific prey specializations so far. The potential occurrence of variable foraging strategies and dependence on main and alternative prey resources remains to be investigated further in the North Atlantic.

Between 1986 and 2005, Norwegian killer whale studies were mainly focused on wintering grounds of the Norwegian Spring Spawning (NSS) stock of the Atlantic herring. At that time these grounds were located in a fjord system (Vestfjord-Ofotfjord-Tysfjord) in the Lofoten region, northern Norway (68°13′N, 15°37′E). Research efforts were focused on photographic identification and investigation of feeding behavior, occurrence patterns, social ecology, and acoustics (Domenici, Batty, Similä, & Ogam, 2000; Similä, 1997; Similä & Ugarte, 1993; Similä, Holst, & Christensen, 1996; Van Opzeeland, Corkeron, Leyssen, Similä, & Van Parijs, 2005; Van Parijs, Leyssen, & Similä, 2004). These studies highlighted killer whales as efficient herring predators using specialized feeding strategies (e.g., Similä & Ugarte, 1993). Photo-identification surveys conducted on both wintering and spawning grounds of the NSS herring, combined with satellite tracking of six individual whales tagged in 2000 and 2001, further suggested that some groups may follow the herring's movements for most of the year (Bisther & Vongraven, 1995; Stenersen & Similä, 2004; Similä et al., 1996), though effective herring foraging offshore remained largely inconclusive. As a result, and due to lack of evidence for additional prey items, herring has been regarded as the main prey for killer whales in Norwegian waters. This conclusion was further supported by a lack of intrapopulation variation in stable isotope values from skin samples collected from whales in the NSS wintering grounds (Foote et al., 2012).

However, focusing research efforts on seasonal herring grounds may have biased studies away from detecting other potentially significant prey species. In fact, recent studies conducted outside seasonal herring grounds documented predation on Atlantic salmon (*Salmo salar*; Vester & Hammerschmidt, 2013), Atlantic mackerel (Nøttestad et al., 2014), harbor porpoise (*Phocoena phocoena*; Cosentino, 2015), and on pinnipeds (Jourdain et al., 2017; Vongraven &

Bisther, 2014), suggesting intrapopulation ecological variation. Combining sighting and predation records of individuals over time would help in assessing prey specializations of killer whales in this region.

Longitudinal photo-identification studies, as initiated by colleagues three decades ago, have been reestablished in 2013 at current herring wintering (November–February) grounds (see Huse, Fernö, & Holst, 2010; Jourdain and Vongraven, 2017). From mid-January to mid-February, the herring migrate to the main spawning area located 800–1,000 km south, off the central coast of Norway (Dragesund, Johannessen, & Ulltang, 1997), leading to the departure of the winter aggregating killer whales. Research efforts yet maintained throughout the rest of the year in the study area aimed at collecting photo-identification data and predation records.

Here, we report on a subset of known herring-feeding killer whales showing site-fidelity in a northern Norwegian fjord in spring (March–April), after the herring has departed, for the period 2014–2018. Behavior and predation records were collected over multiple years in order to assess foraging as a predominant function for seasonal use of the area in spring, and to identify the target prey. Group cohesion was investigated with reference to the focal prey and group sizes were compared to winter observations for insights into behavioral adaptations and therefore, indication of seasonal prey switching and specialization for these whales.

2 | MATERIALS AND METHODS

2.1 | Data collection

Data were collected in March–April of 2015–2018 east of Andøya (Andfjord, 69°19′N, 16°08′E; Figure 1), in Vesterålen region, northern Norway. Because killer whale presence was not known to be regular in the study area at this specific time of year, surveys were largely opportunistic, and effort varied considerably across years. In 2015, surveys were always conducted in response to sightings being reported by locals. In the following years, and based on the 2015 sighting records, land-based watches searched for killer whales on good weather days, as did opportunistic boat surveys, in addition to relying on sighting reports. Supplementary photographs of individual killer whales within the study area with associated date and time data were provided by local wildlife photographers for April–March of 2014–2017, and those of high enough quality were accepted for use in the analyses.

Surveys were conducted on a 20-ft-long (6 m) aluminum research vessel in sea conditions of Beaufort scale 4 or less. We defined an encounter as a sighting of a group of killer whales. A group was defined as all individuals observed in apparent association, acting in a coordinated manner during the observation period and which were within the visual range of the observers (as per Baird & Dill, 1995). For each encounter, the geographic position (GPS Garmin) was recorded and the whales were systematically photographed using a digital reflex camera and a mounted lens of 70–200 mm in focal length. Predominant behavioral pattern, group size estimate and cohesion index (see below) were also recorded at 5-min intervals for the majority of surveys. Surveys terminated when the group was lost from sight, traveled away from the study site, or if light and/or sea conditions deteriorated.

Behavior was divided into five categories (adapted from Ford, 1989): (1) *Foraging*—erratic swimming in varying directions, sudden lunges and high-speed swimming, presence of prey fragments and seabirds; (2) *Traveling*—consistent movement with all group members, in a tight group formation, following the same course at the same speed, while displaying synchronous dives and surfacings; (3) *Milling*—low speed movement with individuals engaged in frequent changes in direction leading to no directional movement by the group; (4) *Resting*—low level activity with individuals being stationary lined-up and floating motionless at the surface while displaying coordinated breathings; (5) *Socializing*—high energy activity in which individuals may physically interact with one another and/or perform aerial displays such as leaps, tail slaps, and spy-hops (defined as vertical half-rise of the body out of the water). Activities displayed by the majority of the whales were considered as the main behavioral pattern for the group.

Spatial cohesion of the group, often variable throughout encounters, was characterized using a cohesion index (CI) (adapted from Daura-Jorge, Wedekin, Piacentini, & Simões-Lopes, 2005). Within a group, individuals scattered over distances (visually assessed) greater than 200 m were classified as low cohesion (CI = 1), individuals occupying a

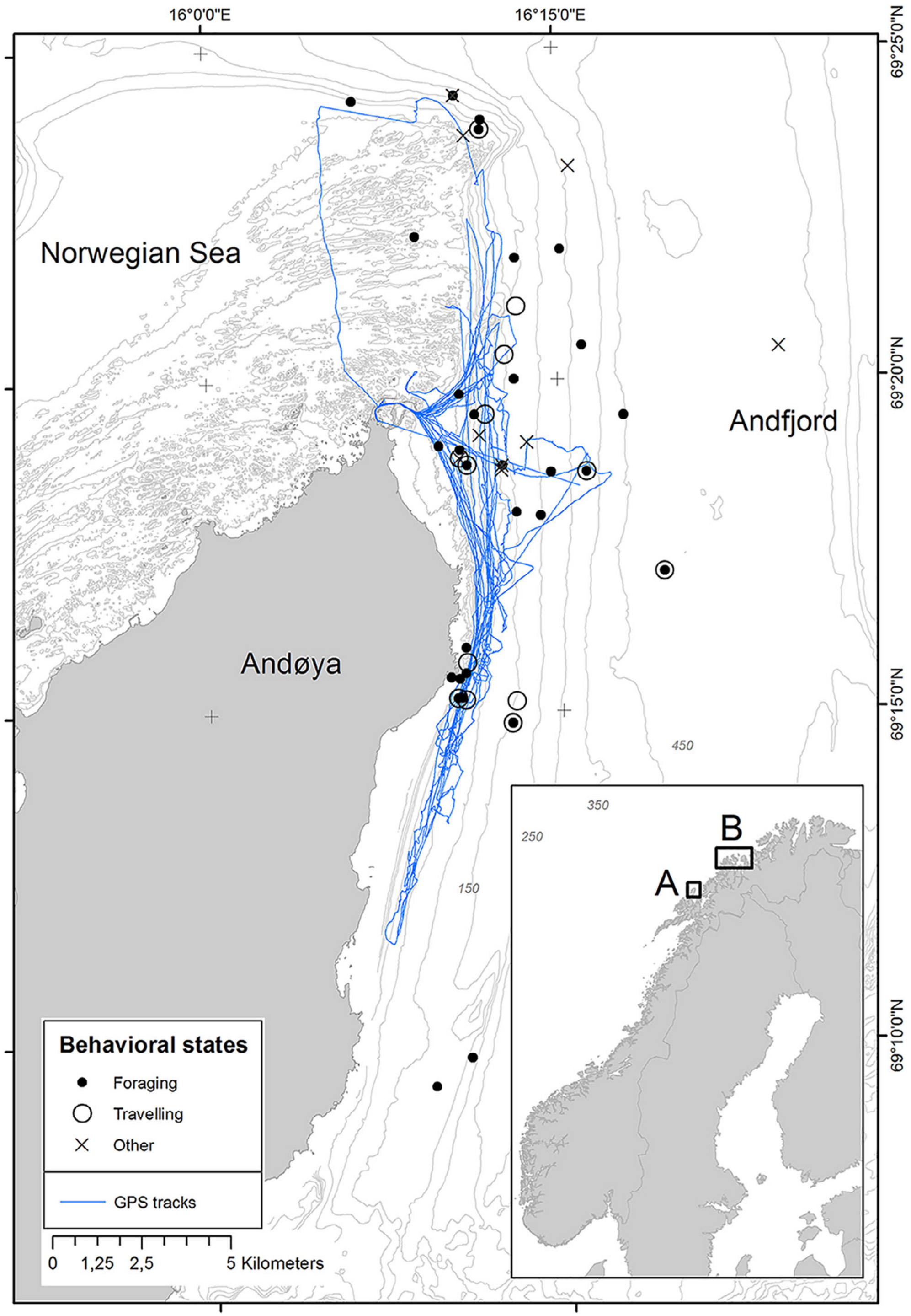

FIGURE 1 Location of the study area in northern Norway. Box A corresponds to Andfjord where the data presented in this study were collected. Box B locates the wintering herring grounds where the whales identified in this study were encountered in November–February in 2015–2018 while feeding on herring. Spatial distribution of killer whale encounters during March–April in 2014–2018, with corresponding behavioral patterns are plotted. Depth contours (m), as well as GPS tracks (blue plots) of the opportunistic surveys conducted in 2018 are also shown.

60–200 m area were classified as intermediate cohesion (CI = 2) and individuals aggregated within 50 m were classified as high cohesion (CI = 3). Smaller subgroups, often composed of adult female(s) with offspring(s), were considered as part of the main group. Classifications were made by the same observer throughout the study, reducing potential observer-related bias.

From 2016 onwards, collection of tissue fragments from prey killed and consumed by killer whales was also attempted. Based on the methods developed by Ford et al. (1998), we used speed bursts, directional chases, fast and sharp turns, and head-nodding movements of surfacing whales along with scavenging seabirds as clues to feeding events. Upon detection of such events, the research vessel slowly approached the focal whale, stopped in the fluke print (glassy area visible at the surface as the whale dives and its tail creates an upwelling, as defined by Ford & Ellis, 2006) and observers assessed potential presence of prey remains in the water column. Using a long-handled (3 m) fine-mesh net, one observer onboard collected any accessible prey fragments. Because collection was challenged by fast-sinking prey parts and common rough sea state, a professional free-diver assisted in collection of prey remains in April 2018. Upon collection, fragments were placed in a plastic bag and stored in a cooling box while in the field. Ashore, fragments were stored in 1.5 ml vials containing 95% ethanol at −20°C until analysis.

Whenever a focal whale was observed feeding at close range to the vessel, photographs were also taken in an attempt to visually-identify target prey species. An unmanned aircraft DJI Phantom IV carrying a DJI 1/2.3” CMOS camera was used on three days in 2018 to capture still images and video footage of prey capture events.

2.2 | Data processing

Killer whales were individually identified based on location and number of notches in the leading and/or trailing edge of the dorsal fin, along with pigmentation pattern of and natural markings occurring on the saddle patch (Bigg, 1982). Only individuals displaying one or several unique features were considered as distinctive and effectively catalogd. Calves and other individuals lacking persistent identifying markings were excluded. Individuals with distinctly taller dorsal fins were classified as “Male” (Olesiuk, Bigg, & Ellis, 1990), adult female-sized individuals repeatedly seen with one calf or older offspring(s) swimming in echelon position throughout the study period were qualified as “Female” and individuals for which sex was uncertain were qualified as “Unknown.” Photographs were scored for quality ($0 < Q < 2$) based upon sharpness, contrast and angle. To minimize misidentification, only excellent quality (Q2) photographic records of distinctive cataloged killer whales were considered in this study. Both left- and right-side identification photos were used for ID, but only whales cataloged from the left side were retained for analysis.

2.3 | Data analysis

2.3.1 | Sighting and behavioral patterns

To assess site-fidelity patterns, individual sighting records were compared across days and years. Despite sampling biases due to uneven effort throughout seasons and across years, we considered minimum residency to be informative of individuals' site-fidelity periods within seasons. Therefore, the number of days elapsed from the first to the last sighting within each season was calculated for each individual, as compared to the total length of survey period for each given season (as per Weinrich, Martin, Griffiths, Bove, & Schilling, 1997). Mean residency values were calculated across individuals per season, excluding individuals not seen, and averaged for the entire study period.

To investigate seasonal usage of the study area, relative predominance of observed behavioral states was calculated. Further seasonal behavioral characteristics, assumed to be adaptive to the target prey, were tested as follows. A chi-squared test was used to test the relationship between behavior and cohesion index (CI). Due to low occurrence, records of resting and socializing behaviors were not included in the test. Records of group size collected for this study were compared to group sizes recorded at herring wintering grounds for these same whales in 2015–2018 using a Mann–Whitney-Wilcoxon test. Statistical tests were performed using R software (R Core Team, 2016).

2.3.2 | Molecular and visual prey identification

Molecular analyses were conducted on prey tissue samples for identification of target species. Total DNA from 11 samples was extracted from ethanol-preserved samples following standard procedures (Sambrook, Fritsch, & Maniatis, 1989). A fragment of the cytochrome *c* oxidase I gene (COI) was PCR-amplified using the GoTaq G2 Hot Start Colorless Master Mix (Promega) and the primers Pros1Fwd and Pros2Rev (Sparks & Smith, 2004) with an annealing step at 46°C. Direct sequencing was carried out in both directions at the technical facilities of the Genotyping and Sequencing Platform of the Institut des Sciences de l'Evolution de Montpellier (ISEM). Sequences were then aligned in MEGA v7 (Kumar, Stecher, & Tamura, 2016) and blasted (https://blast.ncbi.nlm.nih.gov/Blast.cgi) against sequences from the GenBank database (https://www.ncbi.nlm.nih.gov/genbank/). Photographs and video footages of predation events were scanned for visual identification of prey species.

3 | RESULTS

3.1 | Effort

From 2015 to 2018, 42 days at sea in March–April resulted in 123.2 hr spent with killer whales and 14,170 photographs taken over 51 encounters from a dedicated research vessel. Photographic contributions from wildlife photographers led to 11 additional encounter days for the period 2014–2017. Behavior and CI were recorded for 62 hr from 48 encounters. Molecular (*n* = 11) and photographic (*n* = 11) evidence enabled positive identification of prey species for 22 predation events from 11 encounter days in 2016–2018. For the period 2014–2018, photographs resulted in 276 identifications of 75 distinctively marked individuals (Figure 2). The number of identified individuals per season varied from a minimum of six (in 2014) to a maximum of 42 (in 2018), with a mean of 27 (standard deviation *SD* = 13.3). Poor weather conditions in 2015 and 2017 resulted in lower numbers of encounter days and identifications for these years. Sampling effort is summarized in Table 1.

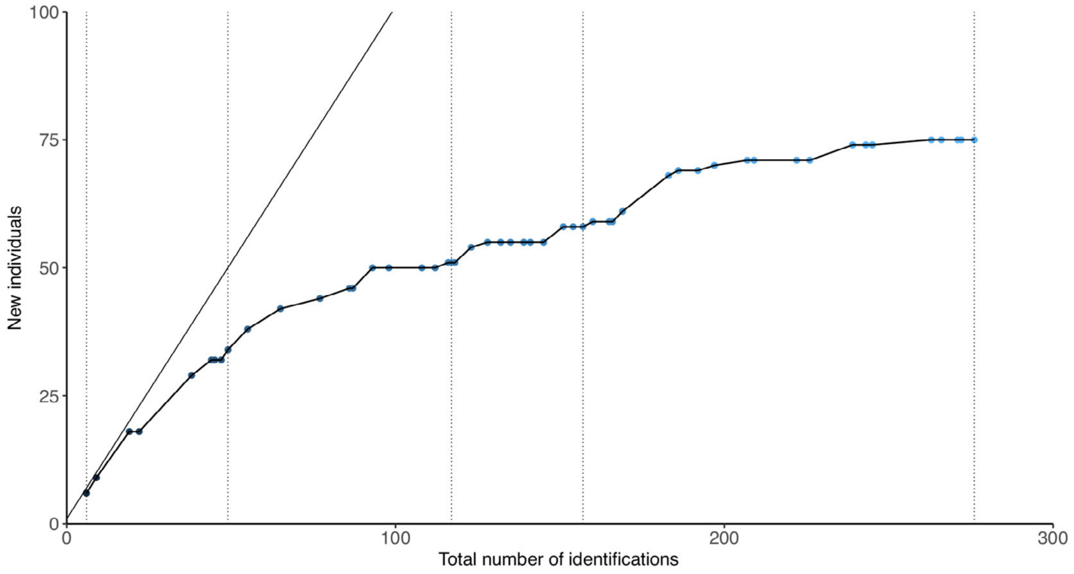

FIGURE 2 Cumulative number of identified individual killer whales in Andfjord in March–April plotted against cumulative identifications. Each data point represents a survey. The 1:1 plot is shown for reference. Dashed lines separate the five calendar years (2014–2018).

TABLE 1 Sampling effort for the period March–April in 2014–2018 in Andfjord.

	2014	2015	2016	2017	2018	Total
Dedicated effort by researchers						
Effort days	0	7	11	6	20	44
Encounter days	0	7	11	4	20	42
Killer whale encounters	0	7	15	4	25	51
Hours spent with whales	0	11.7	22.8	8.1	80.6	123.2
Hours of behavioral sampling	0	6.0	13.7	4.3	38.0	62.0
Photographs taken	0	2,480	5,080	990	5,620	14,170
Predation events for which prey remains were collected	0	0	2	0	9	11
Predation events for which prey were visually identified	0	0	2	2	7	11
Additional photographic contributions						
Encounter days	1	0	3	7	0	11
Photographs provided	300	0	127	1,280	0	1,707
Total						
Encounter days	1	7	14	11	20	53
Identifications	6	41	70	40	119	276
Distinct individuals	6	29	33	25	42	—

3.2 | Characterization of individual killer whales

The 75 identified individuals represent 7.7% of the 971 killer whales identified in the study area (Jourdain & Karoliussen, 2018). Of these, 34 (45.3%) were adult males, 21 (28%) were adult females and 20 (26.7%) were of unknown sex; 61 (81.3%) were encountered at herring wintering grounds on one or multiple years between 2013 and 2018 (unpublished data). Social associations appeared highly variable across encounters, and thus we considered individuals independently. Plotting the cumulative number of newly identified individuals in the period March–April from 2014 to 2018 revealed a steadily decreasing identification rate, suggesting that most distinctive whales using Andfjord in spring had been identified during the study (Figure 2).

3.3 | Sighting frequencies

Of 75 individuals, 20 (26.7%) were sighted only once, while 55 (73.3%) were sighted during two or more encounters in March–April from 2014 to 2018. Of these, 40 were seen in multiple years (range = 2–4; Figure 3). Averaging all five spring seasons, individuals were sighted during a mean of 1.8 seasons (*SD* = 0.9, range = 1–4) and on 3.7 d (*SD* = 2.7, range = 1–12). For individuals sighted on a minimum of two encounter days within each spring season (Figure 3), mean (minimum) residency varied from 8.3 days (in 2015) to 16 days (in 2018) leading to a mean of 11.3 days (*SD* = 6.2, range = 2–39; Table 2) throughout the study period.

3.4 | Behavioral patterns

Foraging (70.3%) and traveling (23.9%) represented the most frequently observed behavioral states, while milling, resting, and socializing accounted for less than 6% of the observations. Group cohesion varied with behavior (χ^2 = 3,940, *df* = 4, *p* < .001). Individuals adopted a tighter group formation when traveling as opposed to scattered over several hundred meters and up to 1 km when foraging. Groups encountered were significantly smaller (Mann–

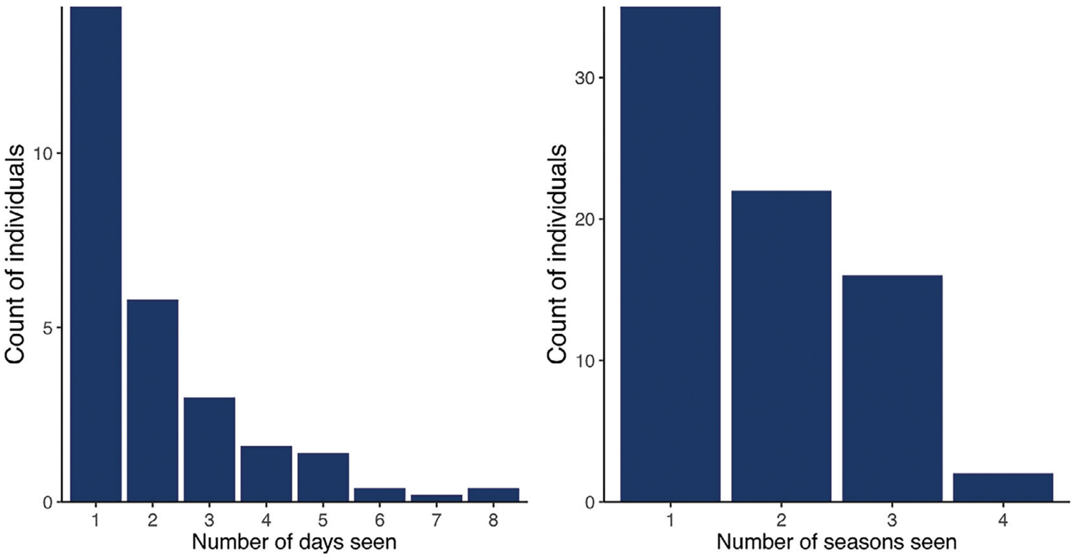

FIGURE 3 (a) Distribution of individual sighting frequencies within season (March–April), averaged over the entire study period 2014–2018; (b) Distribution of individual sighting frequencies across years, that is, number of seasons (March–April) in which individuals were photographed from 2014 to 2018.

TABLE 2 Summary of the parameters used to assess minimum residency of killer whales in Andfjord during March–April in 2014–2018. Calculated residency should be considered as minimum values due to opportunistic data collection.

	2014	2015	2016	2017	2018
Number of encounter days	1	7	14	11	20
First-to-last encounter period (days)	—	19	32	42	44
Individuals resighted	—	9	21	8	26
Residency mean ± *SD* (min–max)	—	8.3 ± 3.7 (2–14)	10.6 ± 4.8 (3–20)	10.3 ± 6.2 (4–16)	16 ± 10.3 (4–39)

Whitney-Wilcoxon: W = 297, p = .001) in spring (median = 8, range = 1–30, n = 49) than in winter (median = 14, range = 1–40, n = 23; Figure 4).

3.5 | Prey identification

Prey fragments from all 11 predation events sampled were identified to be from lumpfish (*Cyclopterus lumpus*; Table 3). The alignment of the COI fragment was 587 nucleotides long. From the 11 sequences obtained for molecular identification, all BLAST queries resulted in the identification of the lumpfish with 99% to 100% of similarity with the sequence JN311799 (Knebelsberger et al., 2014). The new sequences were deposited in GenBank under the accession numbers MF688049 and MH922998-MH923009.

Photo and aerial video material enabled unambiguous identification of the lumpfish as the consumed prey for seven and four additional predation events, respectively (Figure 5, Table 3).

Thirteen individual killer whales were confirmed feeding on lumpfish from these 22 predation events, of which five were adult males, three were adult females and five were of unknown sex including three subadults (Table 3). Five individuals (NKW-0004, NKW-0572, NKW-0712, NKW-0715, and Y093) fed on lumpfish on multiple occasions (range = 2–4) during the same encounter. Adult male NKW-0004 was further confirmed to be feeding on lumpfish over two different days, five days apart, in April 2018.

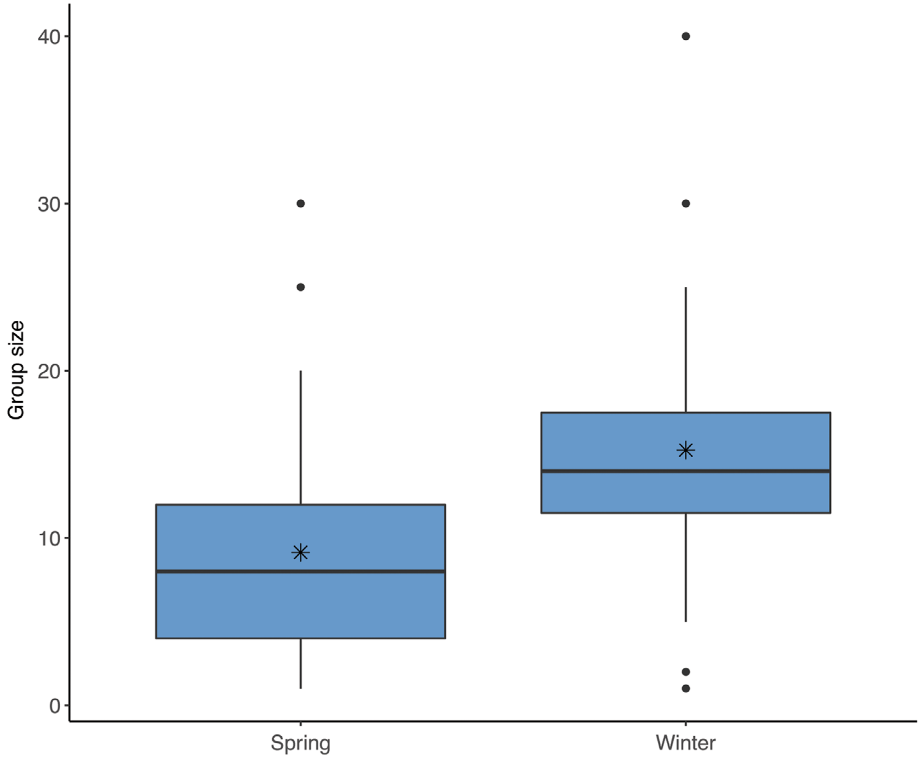

FIGURE 4 Distribution of group size adopted by the lumpfish-feeding killer whales when encountered at the lumpfish spawning grounds (*n* = 49) vs. herring wintering grounds (*n* = 23) in 2015–2018. Data distribution is displayed as second and third quartiles (box plot), median (vertical crossing line) and mean (star symbol) values for spring and winter seasons.

TABLE 3 Summary of predation events for which evidence was collected for identification of the target prey. All resulted in identification of the lumpfish as prey species.

Events	Date	Evidence	ID
1, 2	April 30, 2016	Prey fragments	NKW-0712
3, 4	April 30, 2016	Photographs	NKW-0712
5, 6	April 12, 2017	Photograph	NKW-0572
7	April 5, 2018	Prey fragments	NKW-0004
8–10	April 9, 2018	Prey fragments	NKW-0004
11	April 9, 2018	Photographs	NKW-0912
12	April 11, 2018	Photographs	NKW-0079
13	April 12, 2018	Prey fragments	NKW-0910
14	April 13, 2018	Aerial footage	Unidentified subadult
15	April 13, 2018	Aerial footage	NKW-0998
16	April 14, 2018	Aerial footage	NKW-0908
17	April 15, 2018	Aerial footage	Unidentified subadult
18, 19	April 22, 2018	Prey fragments	NKW-0715
20	April 22, 2018	Prey fragments	NKW-0716
21	April 24, 2018	Prey fragments	Y093
22	April 24, 2018	Photographs	Y093

4 | DISCUSSION

We have shown that a subset of killer whales seasonally visited Andfjord in March–April of 2014–2018 and remained in the area for several days and up to several weeks. Most of these whales were also encountered at herring wintering grounds in the same years. This further supports the idea that killer whales make adaptive seasonal movements in response to spatial and temporal changes in prey availability in this region (Similä et al., 1996). Marked seasonality and predominance of foraging in spring suggests the use of a seasonally reliable food source. All 22 predation events where the prey was identified revealed lumpfish to be the target prey species in March and April.

The lumpfish is widely distributed throughout the Norwegian Sea (Holst, 1993). It remains offshore often at abyssal depths most of the year and migrates to coastal breeding areas from April to July (Davenport, 1985). Due to dorsal muscles allowing only limited locomotory abilities (Davenport & Kjørsvik, 1986), the lumpfish travels at low swimming speeds (i.e., 0.72 km/hr in Mitamura et al., 2012). Spawning male and female lumpfish are about 28–30 and 40–45 cm in length, respectively (Albert et al., 2002). Spent females may complete spawning over a period of a few weeks and then return to the open ocean, or alternatively may visit adjacent fjords to lay eggs at multiple locations (Goulet, Green, & Shears, 1986; Mitamura et al., 2012). Males then guard the nest until the eggs hatch 6–10 weeks later (Davenport 1985). These movement patterns suggest seasonal increased availability of the lumpfish nearshore in spring, as supported by exclusive seasonal fishery from April through mid-June for this species (Bertelsen, 1994).

To the best of our knowledge, the lumpfish has not hitherto been reported as a prey species of Norwegian killer whales, despite previous analysis of 95 stomach contents (Christensen, 1982) and observational studies (e.g., Similä & Ugarte, 1993; Similä et al., 1996). However, the lumpfish was listed as prey of killer whales off West Greenland, where stomachs of 30 harvested killer whales contained only lumpfish (Laidre, Heide-Jørgensen, & Orr, 2006), and off Iceland from sporadic predation records (Samarra et al., 2018). Our results list the lumpfish as prey for killer whales in an additional region of the North Atlantic. Lumpfish repeatedly recorded as prey within single season (*n* = 16 records in 2018) and across years (2016–2018; Figure 5, Table 3) in this study suggests consistency of this seasonal dietary pattern, likely in response to the increased availability of lumpfish when migrating horizontally towards spawning areas.

In spring, not only were encountered killer whales and predation records consistent across seasons, but observed foraging behavior was in striking contrast to cooperative herring feeding strategies observed from November to February in the same region (Jourdain & Vongraven, 2017). When feeding on herring, killer whales aggregate in a tight group formation for coordinated school-herding, prior to slapping the fish with the underside of their flukes and then individually consuming stunned fish (Similä, 1997; Similä & Ugarte, 1993). Similar hunting behavior of killer whales feeding on schooling mackerel in the Norwegian Sea in July–August has also been observed (Nøttestad et al., 2014). In contrast, killer whales foraging on solitary lumpfish (Davenport, 1985) were spread over several hundred meters and aerial footage supported individual rather than group-based foraging. This behavior appears more similar to that of killer whales feeding on loose patches of Atlantic salmon in the Lofoten region, Norway (Vester & Hammerschmidt, 2013). This is in further support of killer whales adapting feeding strategies to behavioral traits of target prey (e.g., Baird & Dill, 1995; Samarra & Miller, 2015; Similä & Ugarte, 1993). Lumpfish-feeding killer whales also adopted smaller group sizes in spring than when observed at herring wintering grounds (Figure 4). By maximizing energetic gain, smaller groups could be adaptive to foraging on a scattered prey resource as opposed to highly concentrated wintering herring, where a more cooperative foraging strategy is required (Nøttestad & Axelsen, 1999; Nøttestad, Ferno, & Axelsen, 2002). Our results bring the first robust evidence, featuring individual records of site fidelity, behavior, and predation over several years, for seasonal adaptation and switching between alternative prey resources in Norwegian waters.

The NSS herring is found in most dense aggregations on its wintering grounds, compared to lower densities due to looser schools on spawning and feeding grounds (Nøttestad et al., 1996). The NSS herring is also subject to important changes in fat content throughout its life cycle with the highest rate of energy depletion occurring during the

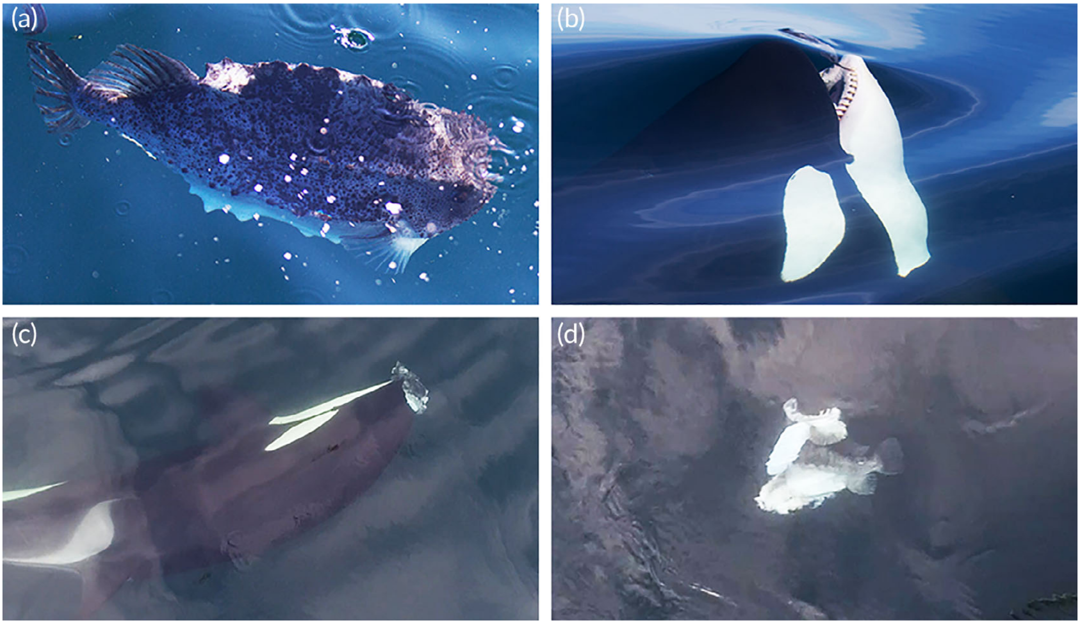

FIGURE 5 Sample of photographs used as evidence supportive of killer whale predation on lumpfish in Andfjord. All photos were taken in April 2016–2018; (a) Lumpfish observed below the surface prior to capture and consumption by adult male killer whale NKW-0572; (b) Adult male killer whale NKW-0712 catching a lumpfish; (c) Adult female-sized killer whale feeding on the carcass of a lumpfish; (d) A subadult killer whale consumed the inner part of a lumpfish before discarding the carcass.

spawning migration. As such, herring fat content is about 22% when entering the wintering area in September and is reduced to eight to 10% after spawning in February–April (Slotte, 1999). As herring both loses fat content and becomes more dispersed in spring, lumpfish with fat content ranging from >8% for gravid females to 20% for males (Davenport & Kjørsvik, 1986) enters the coastal waters to spawn. Some killer whale groups may have diversified their diet and be able to switch to foraging on this alternative, seasonally abundant and apparently relatively nutritious, prey.

Our results showed that at least 75 different killer whales have adapted to the seasonality of spawning lumpfish in Andfjord, returning year after year for temporary residence and foraging (Figures 2 and 3, Table 2). This represents 7.7% of the total number of marked individuals identified in the study area between 2007 and 2018 (Jourdain & Karoliussen, 2018). This number should be considered as a baseline minimum since it does not include unmarked individuals and calves also observed feeding on lumpfish during this study. Additionally, because this study was entirely based on opportunistic efforts and covered a relatively small area, and because killer whales may temporarily travel away from feeding sites or display group-specific preferences in habitat use, individuals or entire groups may have been undetected (Kuningas, Similä, & Hammond, 2014). While the lumpfish is a common species along the Norwegian coast with spawning grounds found in multiple regions (Davenport, 1985; Holst, 1993) it could very well be part of the diet of killer whales elsewhere and this feeding behavior could be important at the population level.

Although the NSS herring has long been assumed to be the main prey of killer whales in Norway, recent year-round data collection efforts uncovered persistent dietary specializations on pinnipeds (Jourdain et al., 2017) and on lumpfish (present study) in northern Norway. This highlights the likelihood that killer whale research conducted on a seasonal basis can miss seasonal specialized feeding behaviors and underestimating important prey resources. Our results further emphasize the importance of individual-focused studies, allowing for the detection of interindividual variations in dietary habits and prey specializations.

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