ARTICLE





Seasonal changes in the feeding aggregation structure of male sperm whales (*Physeter macrocephalus*) in Northern Norway

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Abstract

The sperm whale (Physeter macrocephalus) is one of the most widely distributed cetaceans. Adult males commonly occupy high latitudes, whereas females and juveniles occupy lower latitudes. In Northern Norway, previous studies focused on the summer period limiting our understanding of the seasonal dynamics of male foraging aggregations. We used year-round capture-mark-recapture data based on photo identification between 2009 and 2023 to examine seasonal patterns within a male aggregation off Andøya, Northern Norway. Our analysis encompassed 426 days of data, 111 days in winter (October-April) and 315 days in summer (May-September). Among 365 identified individuals, 29% were encountered across multiple years. A higher number of individuals could be identified in winter compared to summer. The mean estimated residency time was shorter in winter (13 days) than in summer (18 days). We identified four groups with distinct seasonal preferences in occurrence and residency, suggesting seasonal and individual foraging and social patterns. Despite the marked

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seasonal patterns, the relatively short residency times imply this area constitutes only a fraction of the broader foraging range of sperm whales in the Northeast Atlantic. This study highlights the year-round presence of sperm whales in the area, emphasizing their individual seasonal preferences.

KEYWORDS

foraging ground, male aggregation, Northeast Atlantic, residency time, seasonal occurrence, seasonal preferences, submarine canyon

1 | INTRODUCTION

The sperm whale (*Physeter macrocephalus*) is a cosmopolitan species found in all oceans, from the ice edges to the equator (Gosho et al., 1984; Jaquet, 1996). However, their distribution is characterized by a strong sexual geographic segregation (Gosho et al., 1984; Rice, 1989; Whitehead, 2018). Adult females and juveniles live at low latitudes in tight family groups, while adult males are commonly found at higher latitudes when not breeding. This sexual geographic segregation is thought to be driven by the higher nutritional requirements of adult males, due to their large size and weight (up to three times heavier than an adult female), and to decreased intraspecific competition (Teloni et al., 2008; Whitehead, 2018). Young males leave their natal group before reaching sexual maturity, forming "bachelor groups" when moving to the rich foraging grounds at higher latitudes (Best, 1979; Gaskin, 1970; Gero et al., 2014; Ijsseldijk et al., 2018; Ohsumi, 1971; Whitehead & Weilgart, 1991). Once at the high latitude foraging grounds, adult males have been described as becoming more and more solitary as they grow older (Best, 1979; H. Whitehead, 2003).

High latitude foraging grounds of male sperm whales are usually characterized by steep bathymetric features often at the continental shelf edge where the primary and secondary productions are high (Jaquet et al., 1996). Although long-term photo-identification studies on male sperm whales have been conducted at different foraging grounds such as Kaikoura (New Zealand), Gulf of Alaska (US), Nemuro Strait (Japan), and the Bleik Canyon (Norway) (Childerhouse et al., 1995; Ciano & Huele, 2001; Jaquet et al., 2000; Kobayashi & Amano, 2020; Lettevall et al., 2002; Mellinger et al., 2004; Rødland & Bjørge, 2015; Whitehead et al., 1992), relatively little is known about their behavior compared to adult females and juveniles. Previous long-term studies at high-latitude foraging grounds describe loose aggregations of adult male sperm whales, defined as several individuals within areas of 30 km in diameter over deep waters, with short residency times of a few days (Ciano & Huele, 2001; Jaquet et al., 2000; Lettevall et al., 2002; Rice, 1989), and a seemingly lack of social interactions between individuals. However, Kobayashi et al. (2020) were the first to report adult male sperm whales observed in pairs over several years in the Nemuro Strait (Japan). This highlights the lack of understanding of the social structure among adult male sperm whales, which have mostly been described as solitary animals outside the breeding grounds (Lettevall et al., 2002; Oliveira et al., 2013; H. Whitehead, 2003).

In the Northeast Atlantic, male sperm whales occur in the Norwegian and Greenland Seas, mainly over deep water and along the continental shelf break. The number of male sperm whales in the Northeast Atlantic was estimated to be 5704 individuals (CV = 0.26, 95% CI: 3374–9643) over a 5-year period between 2014 and 2018 (Leonard & Øien, 2019).

In Northern Norway, the deep-water Bleik canyon is located only 15 km off the coast of Andenes, in the Vesterålen islands. This area of steep bathymetry is regarded as a hotspot for marine life and is a known foraging ground for male sperm whales (Ciano & Huele, 2001; Lettevall et al., 2002; Rødland & Bjørge, 2015). Previous studies have shown that the aggregation of male sperm whales observed in this area likely consists of individuals with residency times ranging from about 3 days to about 30 days and with a constant inflow of new individuals (Ciano & Huele, 2001; Lettevall et al., 2002). However, these studies were conducted only during summer, from May to

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September, offering no insight on potential seasonal changes within the aggregation. In other high-latitude areas, such as New Zealand, the Gulf of Alaska, and along the continental slope in the western North Atlantic Ocean (United States), significant seasonal patterns in the abundance, distribution, and diving behavior exist (Childerhouse et al., 1995; Guerra et al., 2020; Mellinger et al., 2004; Stanistreet et al., 2018). Childerhouse et al. (1995) showed a difference of residency time among individuals, with animals more transient than others that remain in the feeding area for a short period ranging from a few hours to a few days. In addition, the study showed that some individuals seem to occupy the waters off Kaikoura (New Zealand) only in certain seasons. Thus, the structure of male aggregations seems to vary seasonally.

Using a long-term photo-identification data set collected on whale-watching boats, covering the area off Andenes, including Bleik canyon and Andfjord, throughout the year between 2009 and 2023, we aim to (1) describe the aggregation of male sperm whales observed in the study area throughout the year and (2) to explore potential seasonal patterns in the number of identified sperm whales, residency time, and individual occurrence.

2 | METHODS

2.1 | Study area

Our study area was defined by the maximum distance covered by the whale-watching boats (45 km). The study area covered two deep-underwater systems on either side of the island of Andøya: Andfjord and the Bleik Canyon (Figure 1). Andfjord, a deep fjord system down to 500 m, which has not been studied for sperm whales, is located on the east side of the island while the Bleik Canyon is located on the west side towards the open Northern Atlantic

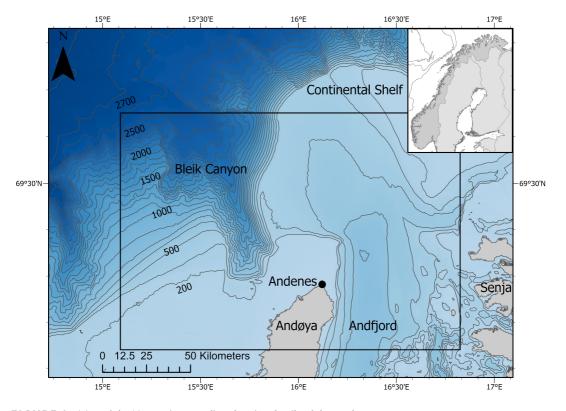


FIGURE 1 Map of the Norwegian coastline showing details of the study area.

Sea and is characterized by a steep bathymetry down to 3000 m. The canyon is 50 km long and 20 km wide at its mouth (Laberg et al., 1999). The effect of the North Atlantic stream combined with the steep bathymetry of the canyon creates a mixing of three main water masses (the Atlantic water from the surface, the Arctic intermediate water, and the Arctic deep water) leading to upwellings and a high primary production (Blindheim, 1990; Sundby, 1984).

2.2 | Data collection

The aggregation observed in the Bleik canyon and Andfjord consisted of male sperm whales only (Ciano & Huele, 2001; Lettevall et al., 2002; Rødland & Bjørge, 2015). We used a photo-identification data set based on photographs collected onboard whale-watching rigid inflatable boats (RIBs – Whale2Sea), between 2009 and 2023. Photographs and data were collected on one boat per trip. Each trip lasted between 2 and 3 h. Between May and September, one to four trips per day were conducted between 9:00 a.m. and 24:00 p.m. Between October and April, one to two trips per day were conducted between 12:00 p.m. and 17:00 p.m. The number of trips conducted per day varied depending on the wind speed and direction. A trip was undertaken only at Beaufort scale <5. Sperm whales were detected acoustically and tracked underwater using a directional hydrophone.

Between 2009 and 2019, photographs, date, and time were collected without location. The trip path and the number of trips per day were not recorded preventing us from being able to make any estimations of effort. From 2020 to 2023, more complete information per observation was recorded. We collected photographs, date, location, number of individuals in group, their surface behavior, and the number of trips conducted per day. Photographs were taken using Digital SLR cameras with 70–200 mm lenses. We refer to the entire data set when using data collected over the period 2009–2023, and to the partial dataset when using data collected over the period 2020–2023.

In this study, we defined a group as a set of two or more individuals at the surface within 500 m from each other. A sighting refers to a first encounter with an identified individual, and re-sighting as an encounter that occurred at least 1 day later. The term transient referred to individuals that were observed in 1 year only.

2.3 | Photo-identification

Sperm whale individuals were identified from photographs of the ventral side of the fluke using markings on the trailing edges and pigmentation patches. Each photograph was given a quality rating (Q) from 1 to 5 based on the focus, the angle of the fluke relative to the camera, and the visible proportion of the fluke within the frame (Table 1).

TABLE 1 Quality and distinctiveness rating of photographs and ventral side of the flukes.

Rating	Quality	Distinctiveness
1	Out of focus, the angle of the fluke respective to the camera at $0^{\circ}/180^{\circ}$, not all fluke edges visible	Lack of pigmentation and no markings
2	Focus, angle of the fluke outside of 45–135 $^{\circ}$ range, fluke edge partly visible	Few markings (nicks) hardly visible without a good-quality photograph and/or pigmentation
3	Focus, angle of the fluke respective to the camera between 45° and 135°, fluke edge visible	Markings occupying at least 30% of the fluke
4	Focus, angle of the fluke respective to the camera between 45° and 135° , all fluke visible	Markings occupying at least 50% of the fluke
5	Focus, angle of the fluke perpendicular respective to the camera, all fluke visible	Markings occupying at least 75% of the fluke

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Photographs with $Q \ge 3$ were used to identify individuals. Each photograph was given a distinctiveness rating (*D*) from 1 to 5 based on the proportion of markings on the trailing edges and/or pigmentation patches (Table 1) (Arnbom, 1987; Dufault & Whitehead, 1995). To minimize misidentification, only photographs with $D \ge 3$ were used to identify individuals. Identification and matching were done manually by the same person to avoid any identification biases linked to the observer. We used the Discovery software (Gailey & Karczmarski, 2012) to organize the sightings history.

2.4 | Statistical analysis

Numerical and statistical analyses were performed using R version 2.1.4 (R core Team, 2023). Model selection was done using the Akaike Information Criterion (AIC) or quasi-AIC (QAIC), if count data were overdispersed, and the percentage of deviance explained was provided in the model selection tables.

2.4.1 | Seasonal trend in the number of identified sperm whales

To investigate seasonal trends in the number of identified individuals, we used the partial data set (2020–2023). Summer was defined from May 1 to September 30 following previous studies in the same area (Ciano & Huele, 2001; Lettevall et al., 2002; Rødland & Bjørge, 2015); winter was defined from October 1 to April 30. We used generalized linear models (GLMs) using the Rpackage "stats" (version 4.4.0) to test whether the number of identified individuals depends on the effort and month as a categorical variable and their interaction.

2.4.2 | Estimated seasonal residency

We used the lagged identification rate (LIR — probability of identifying an individual over a time lag) to estimate a mean residency time using the entire dataset (2009–2023). We calculated a seasonal LIR in Socprog 2.8 (Whitehead, 2015) separately for individuals observed for only 1 year and for individuals observed over multiple years. We set a maximum time lag at 155 days for individuals observed for only 1 year and at 365 days for the individuals observed over multiple years. Thus, we regarded mortality rate as negligible at this time scale considering that sperm whale is a long-lived species (Chivers, 2009). Following Whitehead (2001), we fitted three models of residency with different assumptions:

a. "Closed": There is neither temporal change in the composition of the aggregation due to emigration nor immigration.

$$R(\tau) = \left(\frac{1}{N}\right) \tag{1}$$

b. "Emigration": The temporal change in the composition of the aggregation can be linked to individuals leaving the study area

$$R(\tau) = \left(\frac{1}{N}\right)e^{-\tau/l} \tag{2}$$

 c. "Temporary emigration": The temporal change in the composition of the aggregation can be linked to individuals entering, leaving, and returning in the study area.

$$R(\tau) = \frac{O * e^{-\tau(\frac{1}{O} + \frac{1}{I})} + I}{(I + O) * N}$$
 (3)

Where τ is the time lag in days, $R(\tau)$ is the lagged identification rate, N is the number of individuals in the area; I is the mean time spent within the area; and O is the mean time spent outside of the area (Whitehead, 2009). We calculated 95% confidence intervals and standard errors for each model parameter using bootstrap (1000 bootstrap replicates) (Whitehead, 2007).

2.5 | Seasonal occurrence of individuals

To explore the seasonality in occurrence of individuals, we calculated two metrics using the entire data set (2009-2023) using the whole database: The yearly sighting rate, which is the ratio between the number of years a sperm whale, was identified and the total number of study years (n = 14) in summer and n = 10 in winter). The site fidelity index, which is the ratio between the number of days an individual, was re-sighted and the number of days with at least one identified whale (n = 270) in summer, (n = 91) in winter) (Simpfendorfer et al., 2011; White et al., 2014; Zanardo et al., 2016). These metrics were calculated separately for each season (yearly resighting rate in winter (WYSR) and summer (SYSR); site fidelity index in winter (WSFI) and summer (SSFI)). A WYSR of zero indicated that an individual was sighted only in summer and vice versa.

To investigate whether individuals could be grouped based on their re-sighting history, we used individuals that were sighted over multiple years in either season WYSR >0 or SYSR >0. The resighting metrics were centered and standardized, and we built an Agglomerative Hierarchical Cluster with the package "cluster" (Maechler et al., 2023) based on a Euclidean distance (Gere, 2023; Legendre & Legendre, 2012; Schleimer et al., 2019). Following the AGNES (AGglomerative NESting) clustering method and the silhouette visualization method, we determined the optimum number of clusters (Rousseeuw, 1987). We calculated a cophenetic correlation coefficient to assess whether the clustering solution reflects the structure in the data (Carvalho et al., 2019; Gere, 2023). Wilcoxon tests were used to test whether the average metrics for each cluster were statistically different. Tukey post hoc tests were used for each pairwise combination of clusters to assess the difference between the metrics.

3 | RESULTS

3.1 | Overview of the data

Over the 14 years of the study (June 2009 to September 2023) we collected and analysed 3365 photographs. We used 1373 photographs of the ventral side of the flukes, with a quality $Q \ge 3$ and a distinctiveness $D \ge 3$, to identify 365 individuals over 426 days (Table 2). A hundred and six individuals (29%) were encountered on multiple years ranging from 2 to 10 years (Figure 2).

Between 2020 and 2023, 685 trips occurred over 374 days. During this period, sperm whales were observed on 87% of these days (325 days, 505 trips) and were identified on 63% of the days (235 days) (Table 2). The number of individuals identified per year varied, ranging from seven in 2009 to 125 in 2022 (Figure 3). The proportion of resighted individuals per year varied throughout the years, between 0 to 51% (Table 2). From 2021 to 2023, the proportion of resighted individuals decreased (from 51% in 2020 to 38% in 2023) even though the number of days with identifications was the highest.

TABLE 2 Summary of the photo-identification dataset from 2009 to 2023.

year) of	Number of trips	Number of days w/ trips	days w/ trips (number of trips) In winter	days w/ trips (number of trips) In summer	Number of days w/identifications	New individuals	Resighted individuals	Proportion of resighted individuals	Total number of individuals
2009					8	7	0	0.00	7
2010					9	7	ო	0.30	10
2011					2	2	0	0.00	2
2012					7	က	2	0.40	5
2013					80	6	2	0.18	11
2014					11	23	6	0.28	32
2015					11	31	7	0.18	38
2016					26	17	9	0.26	23
2017					24	35	14	0.29	49
2018					55	34	22	0.39	56
2019					33	14	13	0.48	27
2020 11	117	09	9 (11)	51 (106)	39	24	25	0.51	49
2021 13	128	73	19 (19)	54 (109)	53	37	30	0.45	29
2022 23	222	125	41 (59)	84 (163)	82	84	41	0.33	125
2023 21	218	116	33 (41)	83 (177)	61	49	30	0.38	79
Total 14 years 68	685	374	102 (130)	272 (555)	426	376	204	0.32	580

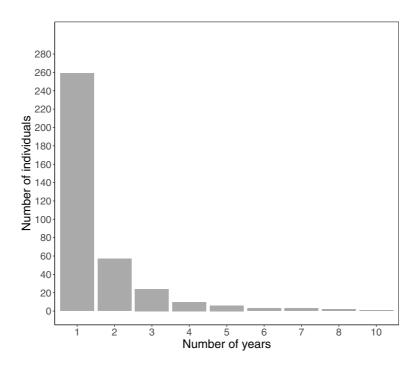


FIGURE 2 Frequency of re-sightings (number of years in which individual sperm whales were observed) for the 365 individual male sperm whales identified between 2009 and 2023.

3.2 | Seasonal trend in the number of identified sperm whales

Based on the data from 2020 to 2023, sperm whales could be observed alone as well as in groups. Male sperm whales seemed to be more solitary in summer, especially in June, July, and August, than in winter, especially in February and March, when groups of up to 12 individuals were encountered (Figure 4).

The GLM with the best support included the interaction between effort and month (Table 3). The number of identified individuals per month increased with the number of trips. The more trips were conducted, the more individuals were identified. However, it also depended on the month. To show the effect of month only, we divided the number of identified individual sperm whales by the number of trips per month for each year. The lowest relative number of identified individuals was in July, while the highest relative number of identified individuals was in March (Figure 5). Comparing both seasons, winter and summer, more individuals were identified in the winter, especially in March and April, than in summer, especially in June, July, and August, when more trips took place.

3.3 | Residency in the study area

For individuals observed over multiple years, the best model for lagged identification rate selected was the "Temporary emigration" model, based on the lowest quasi-AIC (QAIC), for winter and summer (Table 4). The estimated mean residency was 13 days (SE = 9, 95% CI: 1-32) in winter, while it was 18 days (SE = 6, 95% CI: 6-33) in summer. For individuals observed in only 1 year, the best model for the lagged identification rate selected was the "Emigration" model, based on the lowest QAIC, for winter and summer (Table 4). The mean estimated residency time was 11 days (SE = 1, 95%CI: 7-13) in winter, while it was 14 days (SE = 4, 95%CI: 9-26) in summer.

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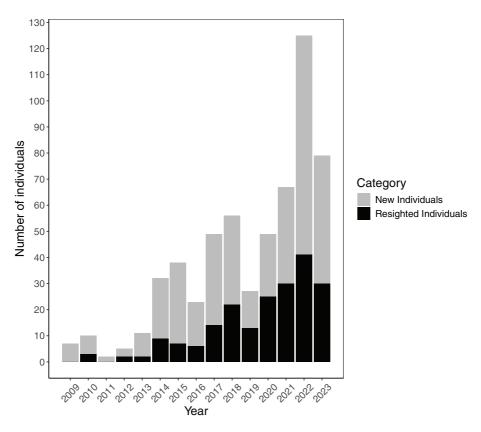


FIGURE 3 Number of male sperm whales identified for the first time (new individuals, in gray) and previously identified individuals (re-sighted individuals, in black) from 2009 to 2023.

For both models in summer (temporary emigration and emigration), the lagged identification rate starts to strongly decrease from the 11th day (temporary emigration LIR = 0.093 ± 0.011 ; emigration LIR = 0.038 ± 0.014) until 85 days after the first encounter (Figure 6a,b), whereas, in winter and for both models, the lagged identification rate starts to strongly decrease from the sixth day (temporary emigration LIR = 0.044 ± 0.015 ; emigration LIR = 0.025 ± 0.006) until 45 days after the first encounter (Figure 6c,d). Thus, the residency time range was greater in summer than in winter; individual sperm whales could be re-identified over a longer period in summer. The models also gave an estimation of the number of individuals present in the area at any time. Between 13 (temporary emigration SE = 9) and 15 (emigration SE = 3), individuals could be present at any time in summer (Table 4). These results highlight the presence of more individual sperm whales in the area in winter than in summer.

3.4 | Seasonal occurrence of individuals

Over the 14 years of study, both the Summer Yearly Sighting Rate (SYSR) and Winter Yearly Sighting Rate (WYSR) ranged from 0 to 0.6 (individuals sighted in eight different summers, and individuals sighted in six different winters). We then looked at the seasonal Site Fidelity Index (SFI) corresponding to the number of days an individual was observed over the number of survey days. The Summer Site Fidelity Index (SSFI) varied from 0 (individuals that were

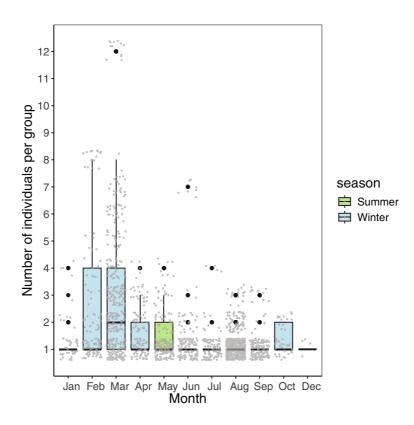


FIGURE 4 Number of sperm whales observed at the surface at the same time within 500 m of each other per month, from 2020 to 2023. The black horizontal line corresponds to the median, the black vertical line (whisker) corresponds to the last quartile of the data, and the black dots to the number of individuals observed together at the surface for each encounter of sperm whales between 2020 and 2023.

TABLE 3 Summary of generalized linear models for the number of identified individuals. Models were built using two explanatory variables, the number of trips per month and the month as a categorical variable. We tested the effect of each explanatory variable, alone, additive (+), and interactive (*). The most optimum model was chosen based on the lowest AIC.

Model	DF	AIC	Delta AIC	Deviance explained (%)
Number of individuals \sim number of trips * month	21	195	0	95
Number of individuals \sim number of trips $+$ month	12	238	43	67
Number of individuals \sim month	11	266	71	52
Number of individuals \sim number of trips	2	327	132	15
Number of individuals ${\sim}1$	1	356	161	0

never sighted in summer) to 0.148 (individuals that were sighted 40 days out of 270 days), while the Winter Site Fidelity Index (WSFI) varied from 0 to 0.132 (individuals that were sighted 12 days out of 91 days).

The optimum number of clusters was four, based on the differences between the four metrics (SYSR, WYSR, SSFI, and WSFI) for each individual (Figure 7). The clustering solution was confirmed by a cophenetic correlation coefficient of 0.68 and by significant differences in mean SYSR, WYSR, SSFI, and WSFI (Wilcoxon tests p < 0.05).

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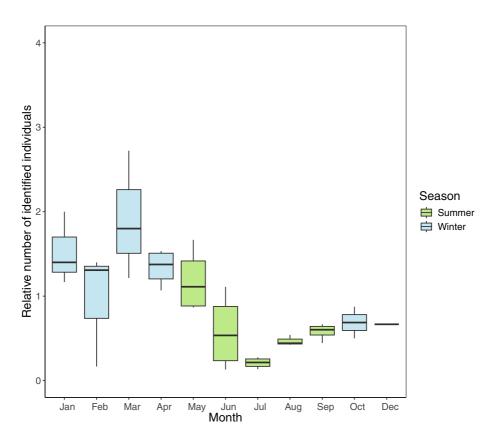


FIGURE 5 Relative number of identified individuals per trip in each month, from 2020 to 2023.

The four clusters were defined as (1) Visitor summer whales (N = 67) regrouping individuals observed mainly in summer (WYSR < SYSR and WSFI < SSFI), for an average SYSR of 2 years and an average SSFI of 4.5 days; (2) summer whales (N = 7) regrouping individuals observed mostly in summer (WYSR < SYSR and WSFI < SSFI) for an average SYSR of 6 years and an average SSFI of 20 days; (3) visitor winter whales (N = 25) regrouping individuals observed mainly in winter (WSYR > SYSR and WSFI > SSFI), for an average WYSR of 3 years and an average WSFI of 3 days; and (4) winter whales (N = 7) regrouping individuals observed mostly in winter (WSYR > SYSR and WSFI > SSFI), for an average WYSR of 5 years and an average WSFI of 8 days. The results from the Tukey post hoc tests highlighted differences and similarities between clusters (Figure 8).

4 | DISCUSSION

This study provides new knowledge on male sperm whales at a high-latitude foraging ground in arctic Norway, using whale-watching boats as opportunistic observation platforms. We show that male sperm whales are present throughout the year in the study area, highlight seasonal patterns in the occurrence of known individuals, and confirm previous studies documenting that some individuals use this foraging ground more frequently than others (Lettevall et al., 2002; Rødland & Bjørge, 2015). The majority of the individuals (71%) were observed only for 1 year in the area, whereas some occurred more regularly (29%) and were re-sighted for multiple years with seasonal preference in their occurrence. This indicates that the area is highly dynamic and constitutes an important area for male sperm whales.

TABLE 4 Estimated residency parameters (±SE) for all individuals in all years.

Estimated residency parameters (252) for an individuals in an years.						
	Estimated	Mean stay time (
Model	number of individuals	In the study area	Outside the study area	AIC	QAIC	Inflation factor c
SUMMER						
Individuals observed over m	ultiple years					
Closed	19 ± 3	-	-	8383	3368	6.14
Emigration	13 ± 2	386 ± 103	-	8247	3314	4.77
Temporary emigration ^a	5 ± 1	18 ± 6	83 ± 24	7974	3206	2.49
Individuals observed for 1 y	ear					
Closed	0 ± 0	-	-	534	154	29.82
Emigration ^b	6 ± 3	14 ± 4	-	435	127	2.30
Temporary emigration	6 ± 3	14 ± 5	$6.3*10^{14} \pm 1.7*10^{15}$	437	129	3.45
WINTER						
Individuals observed over m	ultiple years					
Closed	33 ± 4	-	-	1293	519	5.48
Emigration	25 ± 5	$525 \pm 1.7^*10^{14}$	-	1286	518	5.00
Temporary emigration ^a	10 ± 4	13 ± 9	44 ± 31	1263	509	2.49
Individuals observed for 1 year						
Closed	59 ± 9	-	-	610	365	17.03
Emigration ^b	16 ± 3	11 ± 1	-	543	326	1.25
Temporary emigration	16 ± 3	11 ± 2	$1.4*10^{15} \pm 7.6*10^{14}$	545	328	1.67

^aModels, for individuals observed in more than onyear, with best support based on quasi-Akaike information criterion (QAIC).

4.1 | Seasonality

Our study area, especially Bleik canyon, is a known feeding ground for male sperm whales based on whaling records, ship-based surveys, and tourism activities (Christensen et al., 1992; Leonard & Øien, 2019; Lettevall et al., 2002; Rødland & Bjørge, 2015). However, these previous studies only covered the summer period from May through September. We included observations from the entire year and showed that male sperm whales use the area as a foraging ground throughout the year, most likely more intensively during winter than summer. In fact, based on the period 2020–2023 when the effort was reliably documented, more individuals were likely to be identified during the winter months, especially from February to April, although less trips were conducted due to challenging weather conditions and limited daylight. Our results even suggest that more individuals are present in winter than in summer. Thus, the area constitutes an important part of the foraging ground for male sperm whales in Norwegian waters throughout the year and not mostly during summer as previously stated (Christensen et al., 1992; Lettevall et al., 2002; Rødland & Bjørge, 2015).

Seasonal differences in the abundance and/or presence of male sperm whales within feeding aggregations have also been described in Kaikoura, the Gulf of Alaska, off Antarctica, and off Svalbard, related either to polar ice extent and/or prey availability (Mellinger et al., 2004; Miller & Miller, 2018; Pöyhönen et al., 2024; Stanistreet et al., 2018). Although based on limited data material, male sperm whales found off the coast of Northern Norway, have a mixed diet, consisting of cephalopods, as well as meso- and bathypelagic fish (Simila et al., 2022; Teloni et al., 2008).

^bModels, for individuals observed in 1 year, with best support based on quasi-Akaike information criterion (QAIC).

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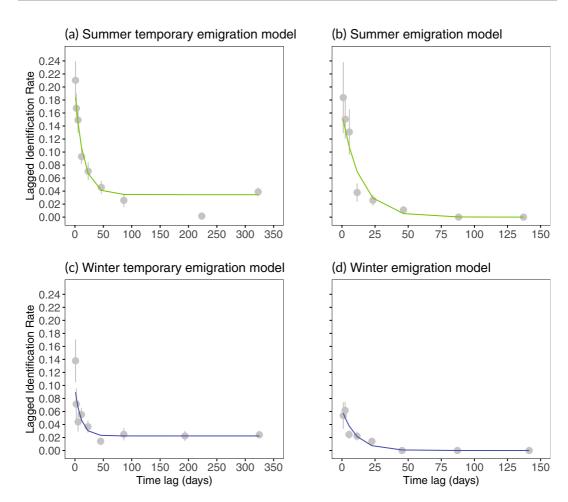


FIGURE 6 Lagged identification rate (probability of reidentifying an animal after a certain time lag) of male sperm whales in Bleik Canyon and its surroundings over the whole study period with a time lag of 365 days for individuals observed over multiple years during summer (a), with a time lag of 155 days (about one full summer) for individuals observed in 1 year during summer (b), with a time lag of 365 days for individuals observed over multiple years during winter (c), with a time lag of 155 days for individuals observed in 1 year during winter (about one full winter) (d). Error bars represent standard error estimated using 1000 bootstrap replicates.

Depending on the time of the year, male sperm whales might target different preys, thus, adapting their foraging in response to fluctuations in prey availability and abundance (Jaquet et al., 2000; Mellinger et al., 2004). This potential difference in foraging behavior and prey availability could influence the number of individual male sperm whales in the area, attracting more individuals during specific times of the year. Future studies on seasonal variation in their migration, diving patterns, habitat use, and diet could explain the seasonal difference in the number of individuals found in the study area.

Furthermore, our data from 2020 to 2023 showed that male sperm whales tend to be observed in groups of up to 12 individuals in winter, especially between February and March, and are relatively solitary at the surface in summer as showed in previous studies (Lettevall et al., 2002; Oliveira et al., 2013; Rødland & Bjørge, 2015). The presence of groups during winter might give a higher chance of observing a larger number of individuals even though there are fewer trips conducted per month than in summer. The seasonal occurrence of groups could be related to seasonal changes in foraging strategies or social behavior, or both, of the male sperm whales within the study area.



FIGURE 7 Dendrogram showing the four clusters obtained from the best solution of the Agglomerative Hierarchical Cluster analysis conducted on individuals observed in at least two different years, between 2009 and 2023. The clustering solution was based on the dissimilarity between yearly sighting rates in winter (WYSR) and summer (SYSR) for each individual and between site fidelity indices in winter (WSFI) and summer (SSFI) for each individual.

Male sperm whales have been described to occur in groups when young males form so-called "bachelor groups" while migrating from lower latitudes towards the arctic foraging grounds (Best, 1979; Gaskin, 1970; Ijsseldijk et al., 2018; Ohsumi, 1971; H. Whitehead & Weilgart, 1991). Although no seasonality has been documented in the formation and migration of bachelor groups towards the Arctic, the higher occurrence of groups and number of newly identified individuals during winter could be due to a higher presence of young males arriving from the lower latitudes during this time of the year in our study area.

4.2 | Estimated residency in the study area

During winter and summer, the mean residency time of male sperm whales ranged between a few days to a few weeks. This result was similar to what has been described in previous studies conducted in the area during the summer months (Lettevall et al., 2002; Rødland & Bjørge, 2015). The short mean residency time found for both seasons in our study supports Rødland and Bjørge (2015) who suggested that male sperm whales use the area as a part of a bigger feeding ground. The lagged identification rates tend to show that the residency time of individual sperm whales is greater in summer than in winter. However, this result could be due to a gap in effort with too few days out at sea in winter compared to summer, leading to an underestimation of the days individuals spent in the area.

4.3 | Site fidelity and seasonality

Among the individuals who were sighted over multiple years, we found seasonal patterns in their occurrence and site fidelity with individuals who had preferred seasons of occurrence (higher yearly sighting rate and site fidelity indices in either season). We obtained four clusters based on the differences between seasonal yearly resighting rates and site fidelity indices. We defined as "visitor winter whales" and "visitor summer whales" the individuals that were observed for an average of two to 3 years, with low site fidelity indices. The individuals defined as "winter whales" or "summer whales" were observed for an average of 5–7 years, with greater site fidelity indices.

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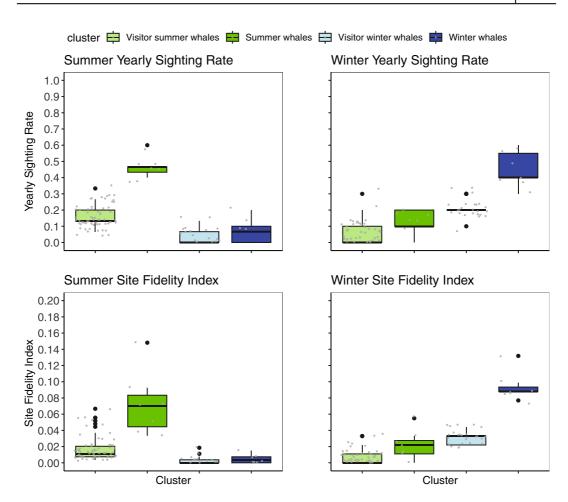


FIGURE 8 Variability of the four metrics (Summer Yearly Sighting Rate, Winter Yearly Sighting Rate, Summer Site Fidelity Index, Winter Site Fidelity Index) within each cluster. SYSR and SSFI between Visitor winter whales and Winter whales were not found to differ significantly (p > .05). SSFI between Visitor summer whales and Winter whales were not found to differ significantly (p > .05). WSFI between Summer whales and Visitor winter whales were not found to differ significantly (p > .05).

A similar seasonal pattern in the occurrence of individual male sperm whales in a foraging ground has also been described by Childerhouse et al. (1995) in New Zealand. This seasonal pattern can potentially highlight the existence of subgroups of individuals, either driven by specific foraging strategies, migration strategies, or by age classes or kinship associations. Sperm whales and African elephants (*Laxodonta africana*) have a similar social system, with males leaving the family groups when reaching puberty (Best, 1979; Charif et al., 2005; Connor et al., 1998; Gaskin, 1970; Moss & Poole, 1983). Young adult male elephants tend to follow mature males to learn from them, thus influencing their habitat choices (Allen et al., 2020; Evans & Harris, 2012). The mix of transient and recurrent sperm whale individuals observed in winter, most likely in groups, could be explained by young adults learning from older adults, affecting their seasonal occurrence and behavior. Future work in our study area should focus on group composition, identifying which individuals are observed gathered. In addition, combining these observations with acoustic recordings could give insights into the social and foraging behavior of these groups.

Previous studies mentioned the presence of transient and resident sperm whales (Ciano & Huele, 2001; Lettevall et al., 2002; Rødland & Bjørge, 2015) with individuals that were observed only once in the area while other

individuals were observed in summer over multiple years. Our results were similar, most of the individuals were transients (71%), while others were observed over multiple years. However, it also shows that individual sperm whales stay for a short period of time in the area, regardless of the season or if the individual was sighted in only 1 year or over multiple years. Re-sightings over multiple years were often nonconsecutive, meaning either that individuals were present in the area and not observed, or that they were indeed not present, potentially using foraging area beyond our range of observation.

5 | CONCLUSION

Our study highlights how long-term photo-identification data collected from whale-watching platforms can offer valuable insights into the behavioral ecology of cetaceans. Our results reveal that male sperm whales are found year-round in a high-latitude foraging area, with seasonal variation in the individual composition of the foraging aggregation and generally short residency times. The seasonal pattern of large gatherings of male sperm whales observed during winter is another previously nondocumented aspect of the behavioral ecology of male sperm whales in their arctic foraging grounds. Our study suggests that the Bleik Canyon, previously described as a "main foraging ground" for male sperm whales (Ciano & Huele, 2001; Lettevall et al., 2002; Rødland & Bjørge, 2015), and the adjoining Andfjord are part of a larger foraging area.

AUTHOR CONTRIBUTIONS

Zoë Morange: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. Tiu Similä: Conceptualization; data curation; funding acquisition; methodology; project administration; resources; supervision; validation; writing – review and editing. Marie-Anne Blanchet: Formal analysis; investigation; supervision; validation; visualization; writing – review and editing. Audun H. Rikardsen: Funding acquisition; project administration; resources; supervision; validation; writing – review and editing.

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