Occurrence and diet of killer whales in northern Norway: seasonal patterns relative to the distribution and abundance of Norwegian spring-spawning herring

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Abstract: Our objectives were to investigate the seasonal occurrence of photoidentified killer whale pods in relation to the distribution of Norwegian spring-spawning herring and whether or not pod-specific differences in the occurrence or diet of killer whales could be demonstrated. In a 4-year study, the killer whales occurred in different areas during the summer and the fall–winter, and these areas coincided with the distribution areas of herring. Killer whales were encountered most frequently during October–January when the whole adult and part of the adolescent stock of spring-spawning herring wintered in the study area. Thirty-nine killer whale pods were identified, and generally the same pods were encountered each year of the study. Differences in the timing and areas of occurrence of pods could be demonstrated. Adult and adolescent herring seemed to be the main prey of the killer whales during both fall–winter and summer. Six new species were added to the list of known prey species of Norwegian killer whales. The present pattern of seasonal occurrence of killer whales in the coastal waters of northern Norway is expected to change as a result of growth in the Norwegian spring-spawning herring stock.

Résumé : Nous avions comme objectifs d'étudier l'apparition saisonnière de groupes d'épaulards photo-identifiés relativement à la distribution des harengs norvégiens se reproduisant au printemps, et de déterminer s'il y avait des différences spécifiques aux groupes dans le nombre ou le régime alimentaire des épaulards. Lors d'une étude de 4 ans, les épaulards ont été observés à différents endroits à l'été et pendant la période automne–hiver, et ces endroits correspondaient à l'aire de distribution des harengs. On observait surtout des épaulards durant la période allant d'octobre à janvier lorsque la totalité du stock d'adultes et qu'une partie du stock des adolescents de harengs se reproduisant au printemps passaient l'hiver dans l'aire d'étude. Trente-neuf groupes d'épaulards ont été dénombrés, et ce sont surtout les mêmes groupes qui étaient observés chaque année de l'étude. On a fait état de différences dans les moments et les endroits où les groupes étaient observés. Les harengs adultes et adolescents semblaient constituer la principale proie des épaulards, tant pendant la période automne–hiver qu'à l'été. Six nouvelles espèces ont été ajoutées à la liste des proies connues des épaulards norvégiens. La distribution actuelle des épaulards dans les eaux côtières du nord de la Norvège changera, prévoit-on, à la suite de la croissance du stock de harengs norvégiens se reproduisant au printemps.
[Traduit par la Rédaction]

Introduction

Killer whales (*Orcinus orca*) are found in all oceans and feed on a variety of prey including several kinds of fish, cephalopods, pinnipeds, cetaceans, and birds (Matkin and Leatherwood 1986). Although a generalist as a species, killer whale populations behave as specialists, following seasonal movements of their preferred prey (Condy et al. 1978; Berzin and Vladimirov 1983; Sigurjonsson et al. 1988; Felleman et al. 1991; Guinet 1991; Ford et al. 1994). However, no killer whale population has been studied throughout the year and little is known about possible seasonal changes in their diet. Diet preferences of killer whales may vary within the same geographical area; for example, separate populations with differences in their diet and distribution pattern have been found off British Columbia and Washington state (Bigg et al. 1990; Felleman et al. 1991; Ford et al. 1994), Alaska (Ellis 1987), and the Antarctic (Berzin and Vladimirov 1983).

In Northeast Atlantic waters, the occurrence of killer whales is associated with the presence of herring (*Clupea harengus*) in Iceland (Sigurjonsson et al. 1988), of herring and salmon (*Salmo* spp.) in waters around the British Isles (Evans 1988), of herring and mackerel (*Scomber scombrus*) around the Faroe Islands (Bloch and Lockyer 1988), and of herring along the coast of Norway (Jonsgård and Lyshoel 1970; Christensen 1982, 1988; Øien 1988). Other known types of prey in Norwegian waters are cod (*Gadus morhua*), squid, seals (Christensen 1978), and bottlenose whales (*Hyperoodon ampullatus*) (Jonsgård 1968).

Christensen (1988) estimated that a minimum of 1500 killer whales might be present in Norwegian coastal waters when herring is abundant. Seasonal peaks in the abundance of herring

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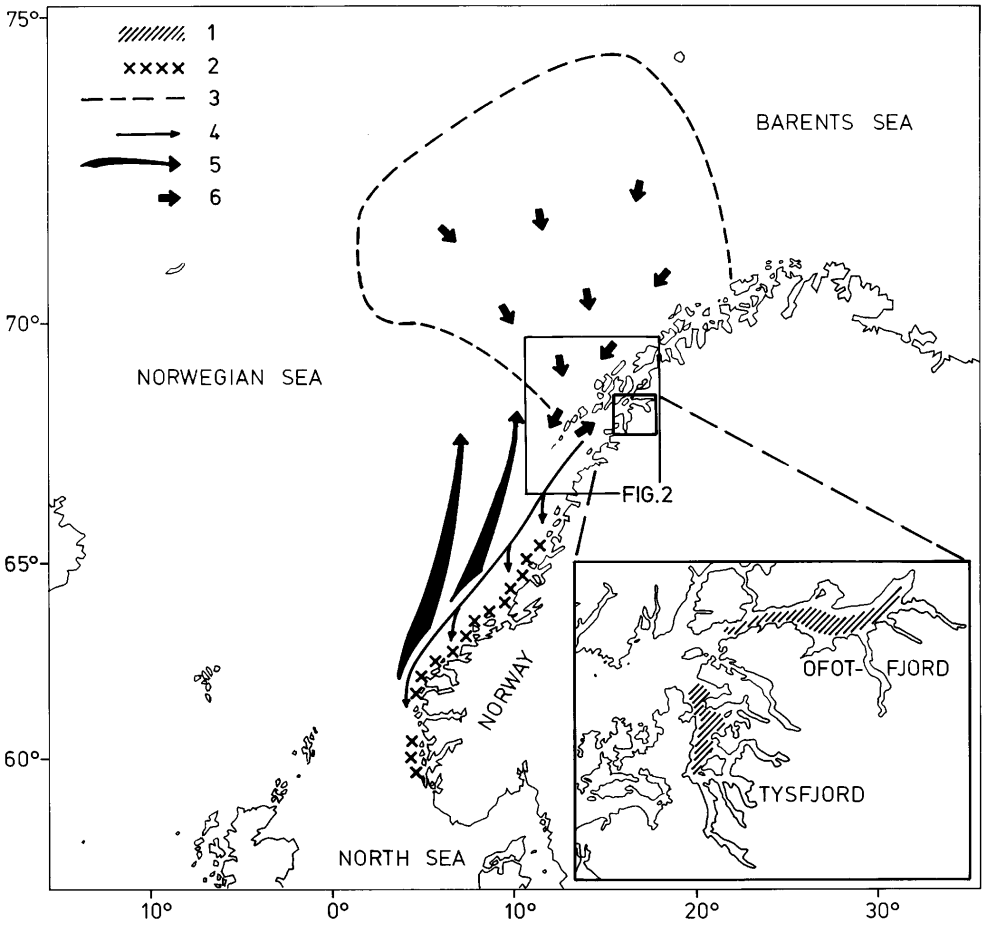
Fig. 1. The approximate yearly migration pattern of the adult fraction of the Norwegian spring-spawning herring stock during 1990–1993. 1, wintering area; 2, spawning area; 3, feeding area; 4, spawning migration; 5, feeding migration; 6, wintering migration. The area marked Fig. 2 covers the killer whale study area.



and killer whales occur in October to January in the Lofoten area (wintering grounds of herring) and in February and March off the coast of Møre (the spawning grounds of herring) (Christensen 1988; Øien 1988; Hamre 1990; Røttingen 1990). Lyrholm (1988) reported movements of photoidentified individual killer whales between Lofoten and Møre. The Lofoten area is the only area in Norwegian coastal waters where killer whales have been reported year-around (Christensen 1988).

The Norwegian spring-spawning herring performs large-scale seasonal migrations between the wintering, spawning, and feeding areas in Norwegian coastal waters and in the Norwegian Sea (Dragesund et al. 1980; Hamre 1990; Røttingen 1990) (Fig. 1). Following the major stock collapse in the late 1960s (Dragesund et al. 1980), the migratory pattern of the herring changed from oceanic to more coastal, and since 1987 the wintering area has been mainly in two fjords, Tysfjord and Ofotfjord, in northern Norway (Hamre 1990; Røttingen 1990; International Council for the Exploration of the Sea 1994) (Fig. 1). The concentration of the wintering grounds to a small area in coastal waters has offered a unique possibility for intensive studies on herring and on one of its predators, killer whales.

We present results from a 4-year (1990–1993) photoidentification study of killer whales in waters around the islands of Lofoten and Vesterålen in northern Norway (Fig. 1). Our main objective was to examine fall–winter and summer occurrence of photoidentified killer whale pods (groups) in relationship to the distribution of Norwegian spring-spawning herring. Furthermore, potential pod-specific differences in occurrence or diet were investigated.

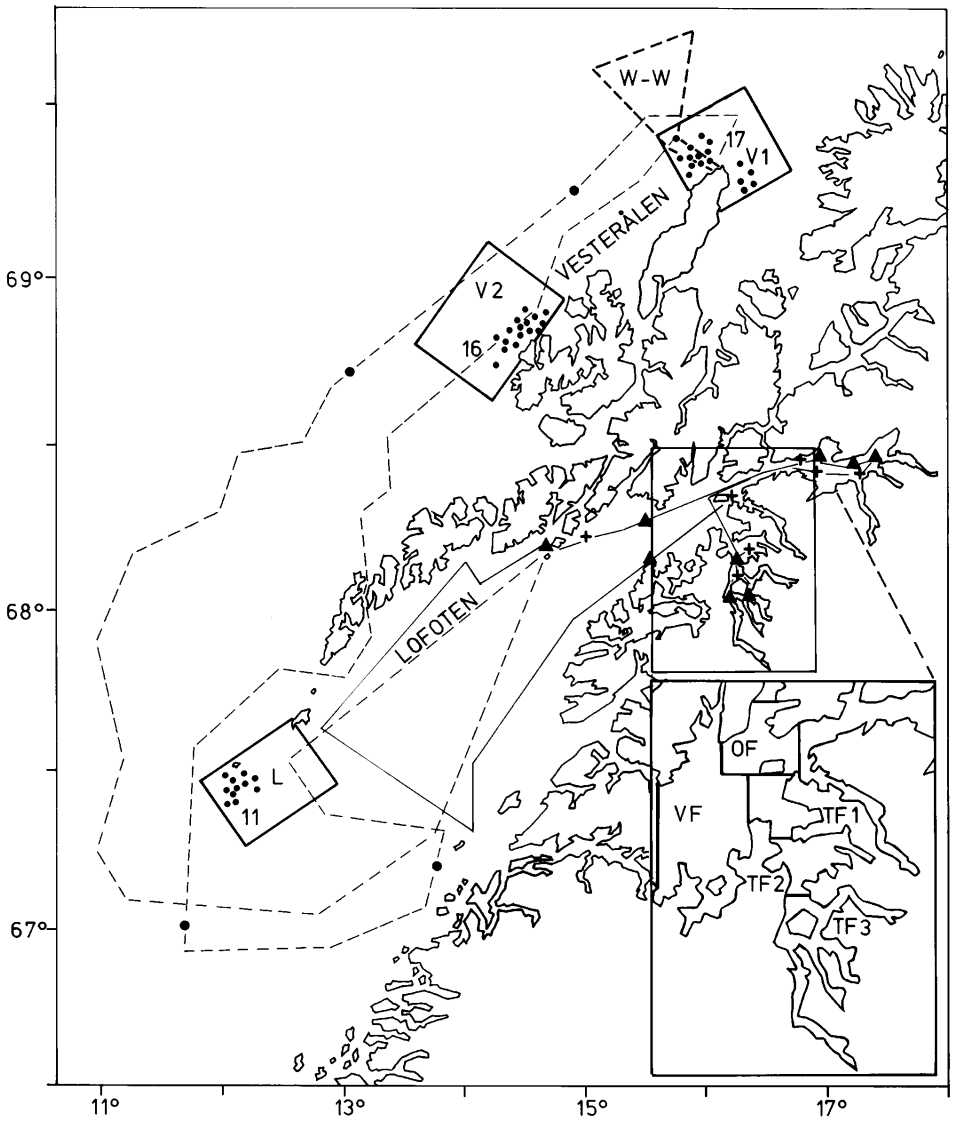
Material and methods

Study area and periods of fieldwork

The study area included the waters around Lofoten and Vesterålen islands and the Tysfjord–Ofotfjord area in northern Norway (Fig. 1). In a pilot study, photographs of killer whales were taken in this area in 1983–1986 (Lyrholm 1988) and in 1987–1989 (T. Similä, unpublished data). On the basis of the experience from the pilot study, core study areas were identified within the overall study area for potential occurrence of killer whales during different seasons (Fig. 2).

In the summers of 1990–1991 there were two core areas off the Vesterålen islands (V1 and V2), and in 1992–1993 an additional core area was found around the islands of Røst and Væröy in Lofoten (L). In fall–winter (1990 –1993) one large core study area was divided into five subareas: one in Vestfjord (VF), one in Vestfjord–Ofotfjord (OF), and three in Tysfjord (TF1, TF2, TF3). Two of these subareas

Fig. 2. Killer whale sighting surveys and locations of pod encounters in the summer core study areas V1, V2, and L. The solid line marks the sighting surveys on November 18–27 in 1990 and 1991, and the broken line marks the sighting survey on August 15–24 in 1992. ▲, areas where killer whales were sighted in November 1990; +, areas where killer whales were sighted in November 1991; ●, areas where killer whales were sighted in August 1992. The symbols VF, OF, and TF13 mark the fall–winter core study areas. W–W, the area where sperm whale watching trips operated during June–August.



(TF1, TF2) were visited more often than the others. Fieldwork was done in October to November and June to August and in 1991–1992 also in January to February (Table 1).

Methods used in obtaining observations of killer whales

Killer whales were searched using two different methods. (*i*) During the 300 days of fieldwork in the core study areas, we searched for killer whales by using a combination of land watch, telephone calls to pilot stations, ferries, and fishing boats and by searching in the area with the research vessel. (*ii*) Ten-day sighting surveys were conducted once in November 1990 and once in November 1991 on board RV *Johan Ruud* and in August 1992 on board MS *Leif Junior* (Fig. 2). The November sighting surveys covered the fall–winter core study areas (VF, OF, TF1–TF3) as well as Ofotfjord and a major part of Vestfjord. The summer sighting survey was done in coastal and offshore waters off the Lofoten and Vesterålen islands, including all three summer core areas (V1, V2, L). During sighting surveys whales were observed from crow's nests or flying bridges from vessels cruising along predetermined transect lines.

Methods used in estimating relative occurrence of killer whales

Relative occurrence of killer whales during October–November and January–February 1991–1992 was calculated on the basis of killer whale encounters in the core areas VF, OF, TF1-3 (not including data from sighting surveys). A killer whale encounter was an occasion where one or more individuals in a killer whale pod were photoidentified. The occurrence was calculated from ED/EFD where effort day (EFD) is a day spent searching for whales and encounter day (ED) is a day whales were encountered (one encounter per day regardless of the number of pods encountered). The number of pods encountered

Table 1. Dates and areas of killer whale fieldwork in the core study areas in 1990–1993 and the boats used.

Date	Area	Boat
1990		
June 8–13	V1	MS *Spekkulf* (9.3 m)
June 25–27	V1	MS *Spekkulf*
July 22–25	V2	MS *Spekkulf*
Aug. 1–2	V2	MS *Spekkulf*
Aug. 14–18	V1	MS *Spekkulf*
Sept. 9	V1	Zodiak (3.5 m)
Oct. 16 – Nov. 15	TF, OF, VF	MS *Spekkulf*
1991		
Jan. 15.1 Feb.15	TF, OF, VF	MS *Spekkulf*
June 11–15	V2	MS *Spekkulf*
July 18	V1	Zodiak
July 23	V1	Zodiak
July 25	V1	Zodiak
July 31	V1	Zodiak
Oct. 8 – Nov. 17	TF, OF, VF	MS *Spekkulf*
1992		
Jan. 5 – Feb. 3	TF, OF, VF	MS *Spekkulf*
Feb. 4–6	TF, OF, VF	MS *Øyprinsen* (13.5 m)
June 8–15	L	MS *Øyprinsen*
June 25 – July 4	V2	MS *Spekkulf*
July 10	V1	MS *Spekkulf*
July 19–21	V1	MS *Spekkulf*
Oct. 7 – Nov. 20	TF, OF, VF	MS *Spekkulf*
1993		
June 14–24	L	Zodiak
June 28 – July 7	V2	SY *Oda* (11.5 m)
July 15–19	L	MS *Øyprinsen*
July 14, 20, 21	VF	MS *Øyprinsen*
Oct. 13 – Nov. 18	TF, OF, VF	MS *Sandøy* (9.3 m)

Note: For the location of the core study areas, see Fig. 2.

per effort day (PEC/EFD) was also calculated for each season. Boat traffic in the fall study area increased from 1990 to 1993 (research vessels and whale-watching vessels searching for killer whales) and the assistance in finding the killer whales increased correspondingly.

During the summer months, killer whales were sought in the core study areas (L, V1, and V2) with variations in the methods used and areas covered, and therefore the data were not used for estimating relative occurrence. A more consistent data set consisted of sighting data received from whale-watching vessels, which operated outside Andenes, Vesterålen, in June–August. The whale-watching vessels took out tourists daily, weather permitting, for 5- to 8-h trips to see sperm whales (*Physeter macrocephalus*) in an area overlapping the core study area V1 (Fig. 2). All sightings of killer whales made during these trips were recorded.

Photoidentification of killer whales

Photographs taken of killer whales were used for studying the seasonal occurrence of different killer whale pods (groups). Killer whales were identified by natural markings on the dorsal fin and the grey saddle patch behind the fin (Bigg et al. 1990). The pictures were taken with 35-mm SLR cameras using 300-mm lenses and 400 ASA black and white film pushed to 1600 ASA. The films were analyzed for identifications with a stereoscopic microscope. Identification pictures were taken during sighting surveys, during field studies in the core areas, and occasionally from the whale-watching vessels.

Pod is a term used for groups of killer whales with stable membership (Bigg et al. 1990). In the study area, killer whales occur in groups that seem to have a stable structure (T. Similä and F. Ugarte, unpublished data). The analysis of seasonal occurrence of killer whales was not based on sightings and resightings of individuals but of pods (all individuals of a pod were assumed to be present even if only a few individuals were identified). This approach was chosen because there are substantial differences in the resightability of killer whale individuals (owing to differences in the recognizability of individuals) (Similä and Lindblom 1993), whereas the resightability of killer whale pods is more equal (well-marked individuals are present in all pods).

Each of the killer whale pods was given an alphabetic code, e.g., NA, where N is for Norway and A is the name of the pod. Once the capital letters from A to Ø had been used, the same letters were used again in lower case.

Killer whales were also photographed at the coast of Møre (Bisther and Vongraven 1995). Photographs from these two areas were compared for analyzing movements of killer whales between the spawning and wintering grounds of herring.

Species identification of killer whale prey

Prey species eaten by killer whales were identified during encounters with feeding whales by observing either the prey species or pieces of it at the surface. During clear-water conditions in the fall in 1991–1993, an underwater video camera with a view of the upper 15 m of the water column was used to observe feeding behavior (Similä and Ugarte 1993). When possible, the age of herring was determined as adult (≥29 cm) or adolescent (<29 cm) on the basis of length measurements from herring captured during the feeding bouts.

Distribution and abundance of herring

The distribution and abundance of Norwegian spring-spawning herring was monitored regularly in 1990–1993 by the Institute of Marine Research (IMR), Bergen, Norway, as part of the routine stock assessment programmes. The wintering area in Ofotfjord and Tysfjord was surveyed yearly in November–December and January, while the feeding areas off the Vesterålen and Lofoten islands and in the Norwegian Sea were surveyed in July–August 1991 and 1993.

Continuous echointegration of fish registrations was carried out with a Simrad EK-500 echointegrator and the abundance of herring was estimated according to the method described by Midtun and Nakken (1971) and Dalen and Nakken (1983). Samples of herring were obtained with a standard pelagic trawl hauled at about 4 kn (1 kn = 1.852 km/h) at depths that varied according to the observed concentrations of herring. Samples of up to 100 fish were taken randomly from the catches and individual fish were weighed, their total length was measured, and various parameters such as sex, maturation stage, and age were recorded.

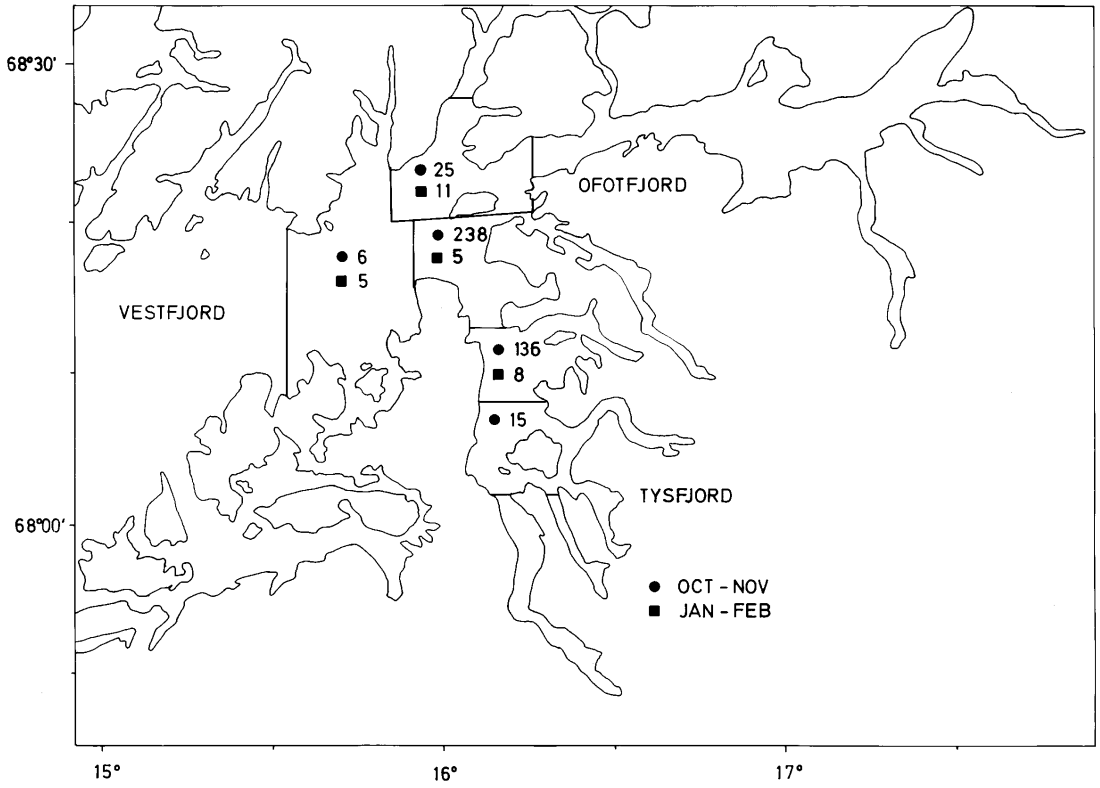
Most of the juvenile stock was distributed outside the study area during the period investigated, so only interactions between killer whales and adolescent and adult herring will be considered.

Results

Seasonal occurrence of killer whales

The majority of killer whale pod encounters were made in October and November in Vestfjord, Tysfjord, and Ofotfjord (core areas VF, OF, TF1–3) (Fig. 3). Most encounters were made in the two subareas (TF1, TF2) that were surveyed more often than the others. In October and November 1990–1992, killer whales were encountered on all effort days in the core study area (Table 2). In 1992, both the total number of pods identified and the number of pod encounters per effort day were higher than during the other years. In the fall of 1993, killer whales were not encountered on all effort days, and the number of different pods encountered was lower than in

Fig. 3. Locations of killer whale encounters in the fall–winter core study area (not including sighting surveys) during October and November 1990–1993 and January and February 1991–1992. The numbers represent the amount of pod encounters in the subareas of the core study area.



1990–1992 (Table 2). A total of 420 killer whale pod encounters were made in October and November 1990–1993 (data from sighting surveys not included) and 20–28 different killer whale pods were identified each fall.

During the sighting surveys in late November 1990 and 1991, killer whale pods were sighted within the core study area and in the Ofotfjord (Fig. 2). In 1990, 18 pods were sighted and 10 of these were identified; in 1991, 10 pods were sighted and 6 of these were identified. The pods identified in Ofotfjord (seven encounters) were all pods that had also been encountered in the core study area.

Killer whales started leaving the Tysfjord–Ofotfjord area during the first weeks of January, and both the encounters per effort day and the number of different pods identified were lower in January and February than in October and November (Table 2). A total of 29 pod encounters were made, and six different pods were identified in January and February 1991–1992. In 1991, the last killer whale encounter was made on February 11 and in 1992 on January 22.

In June–August, killer whales were encountered in all of the summer core study areas (L, V1, V2) in waters around the Vesterålen islands and around the outermost islands of Lofoten (Fig. 2). A total of 44 killer whale pod encounters were made in the core study areas in June–August, and each summer 4–9 different pods were identified. During the sighting survey in August 1992, killer whales were sighted throughout the study area (Fig. 2). Six killer whale pods were sighted and four of them were identified; one pod was encountered twice. The occurrence of killer whales varied between the summers;

Table 2. Relative occurrence of killer whales during October and November 1990–1993 and January and February 1991–1992.

Year	EFD	ED	ED/EFD	PEC	PEC/EFD	PODS
October–November						
1990	23	23	1.00	68	2.96	26
1991	32	32	1.00	127	3.97	27
1992	35	35	1.00	153	4.37	28
1993	24	22	0.92	72	3.00	20
January–February						
1991	22	14	0.63	20	0.91	5
1992	14	7	0.50	9	0.64	4

Note: EFD, effort day, day spent searching for whales; ED, encounter day, day killer whales were encountered; PEC, pod encounter; PODS, number of different pods encountered.

killer whales were sighted during 5–18% of the whale-watching trips (Table 3). In addition to sperm and killer whales, harbor porpoises (*Phocoena phocoena*) and minke whales (*Balaenoptera acutorostrata*) were often sighted from the whale-watching vessels.

Patterns in occurrence of photoidentified killer whale pods

A total of 408 killer whale individuals were identified in the study area in 1990–1993. The whales were provisionally divided into 39 different pods (Table 4). The sizes of the pods varied between 6 and 30 individuals, with a median size of 15 individuals.

Table 3. Sightings of killer whales made during sperm whale watching trips outside Andenes, Vesterålen, in June–August 1990–1993.

Year	Trips	Sightings	% of trips
1990	96	12	12
1991	128	11	9
1992	132	24	18
1993	154	8	5

Note: A sighting of killer whales was registered as one observation, regardless of the numbers of killer whales seen.

During the 4 years of study, 525 pod encounters were made (Table 4). Generally, the same pods were seen in the study area each year (Table 4). The number of resightings was high in 1991–1993, and the cumulative number of pods identified (27, 32, 38, and 39 in 1990, 1991, 1992, and 1993, respectively) suggests that the majority of killer whale pods occurring in the area have been identified. There were differences in the frequency of encounters of the different pods (Table 4; Fig.4); 81% of the pods were encountered 1–20 times during the study period. Seven pods (NA, NC, NE3, NG30, NO, NP, NY) were encountered 26–47 times and they made up 47% of all encounters. These seven pods and eight others (NB, NE15, NG11, NQ, NT, NV, NW, NÅ) were encountered in each of the study years, but only NP was seen each season and year. Each year there were several resightings of the seven most often encountered pods, except for 1992, when NE3 and NO were encountered only a few times (Table 4).

A total of 34 different pods were encountered during October–February and 23 different pods in June–August. Eighteen pods (47%) were encountered during both fall–winter and summer, and five pods (10%) were encountered only during summer (Table 4). Sixteen pods (42%) were encountered only during fall–winter (Table 4) and one of these, NN3, was seen only in the late winter when most of the other pods had left the study area.

Killer whales belonging to seven different pods (NA, NC, NG30, NP, NQ, NU, and KA) were identified both in the study area and in the spawning grounds of herring at the Møre coast (Lyrholm 1988; D. Vongraven, Institute of Zoology, University of Trondheim, 7055 Dragvoll, Norway, personal communication).

Prey species identified

The methods used in identifying prey were most suitable for detecting killer whales feeding on schooling fish, marine birds, or marine mammals near the surface and were less likely to detect solitary fish or squid being eaten.

In 99 out of the 105 occasions when the prey among feeding killer whales was identified, the prey was herring. However, most observations of feeding killer whales were made in October and November; herring was identified as prey on 89 occasions in the fall but only on 10 occasions in the summer. The pods observed feeding on herring during the summer were NA, NE5, NG30, NO, NP (three observations), NT, NØ, and NÆ.

The length of the herring preyed upon by killer whales was estimated on 35 occasions (Fig. 5). Adult herring dominated the diet in the fall (94%), whereas adolescent herring dominated the samples collected in the winter (100%) and the summer (70%).

In October 1993, a killer whale was observed eating a saithe (*Pollachius virens*) that was swimming close to a herring school on which the killer whale and its pod were feeding. In June 1990, a killer whale pod fed on mackerel. In October 1991, a group of unidentified killer whales were seen feeding on eider ducks (*Somateria molissima*). In October 1992, a juvenile from NW pod ate a little auk (*Alle alle*), and in July 1992 a juvenile from NP pod ate a northern fulmar (*Fulmarus glacialis*). The chasing of eider ducks appeared to be organized hunting in which several birds were taken, whereas the feeding on the two other birds looked like playing behavior. Once a young killer whale was observed eating a jellyfish, and the whales were often observed playing with jellyfishes. The three species of seabirds and jellyfish, mackerel, and saithe are all additions to the list of known prey of Norwegian killer whales.

In June 1993, the NØ pod was observed trying to catch a young harbor seal (*Phoca vitulina*) in Røst, Lofoten, without succeeding. On the following day, the same whales fed on herring in the same area.

Seasonal distribution and migratory pattern of herring

The adult part of the herring stock showed a rather stable migratory pattern throughout the period studied. At the end of the oceanic feeding season, the herring concentrated in large schools off the Vesterålen and Lofoten islands in late August, when herring schools also entered the Vestfjord basin. The herring concentrated in the two main wintering fjords, Tysfjord and Ofotfjord (an area covering approximately 680 km^2), from early October and remained in the area until about mid-January. The adult herring (which comprised 96–98% of the biomass) started the southbound spawning migration by mid-January (Fig. 1) while the adolescent herring remained in the fjords a bit longer. The estimated biomass of herring in the wintering area remained fairly stable throughout the period studied, with estimates ranging from about 2.2 to 3.4 million tonnes (International Council for the Exploration of the Sea 1993, 1994). Besides herring, cod and saithe were present in the trawl hauls in the wintering area of herring.

Throughout the period studied, the spawning grounds were situated between Egersund and Vesterålen, although the main spawning grounds were observed off Møre (Fig. 1). After the spawning season the herring started a northwestern migration in March and April towards the Norwegian Sea feeding area. The main feeding area was observed off Vesterålen and southern Troms, out to about 0° west, and from 68 to 75° north, in an area covering approximately 250 000 – 300 000 km^2 in July–August. A southwestward extension of the feeding area took place during 1991 to 1994 (International Council for the Exploration of the Sea 1995). In general, the adolescent herring fed closer to shore than the adult herring that were observed further west and north. Besides herring, significant concentrations of mackerel, horse mackerel (*Draculus draco*), lumpsucker (*Cyclopterus lumpus*), and saithe were present in the trawl catches within, or close to, the killer whale core study area during the summer.

Besides this general migratory pattern, immature herring originating from the Barents Sea enter the areas off Vesterålen and Troms, where they feed for 1 or 2 years before entering

Table 4. Killer whale pod encounters during 1990–1993 in October and November (F) and June to August (S).

	1990		1991		1992		1993		Total		
Pod	F	S	F	S	F	S	F	S	F	S	Sum
					Both seasons						
NA	8	—	10	—	8	—	4	4	30	4	34
NB	6	—	7	—	4	—	1	2	18	2	20
NE3	4	2	7	—	1	1	8	3	20	6	26
NE5	2	3	6		6	—	—		14	3	17
NE15	6	—	5	1	2	—	6	—	19	1	20
NG11	5	—	1	—	4	—	2	1	12	1	13
NG30	6	—	13	—	18	2	4	2	41	4	45
NL	4	—	1	1		—			5	1	6
NN17	5	—			1	1	1	1	7	2	9
NO	5	2	5	—	4	—	10	—	24	2	26
NP	2	3	10	5	12	4	4	2	28	14	42
NT	3	—		1	1	8	—	2	14	1	15
NU			3	—	4	—	—	1	7	1	8
NY	4	1	7	—	9	1	4	—	24	2	26
NÅ	2	—	1	—	4	1	2	—	9	1	10
NÆ					1	—	—	1	1	1	2
Nb	1	—			1	1			2	1	3
Nc			1	—	1	—	3	1	5	1	6
					Fall only						
NC	6	—	15	—	20	—	6	—	47	—	47
ND	2	—							2	—	2
NG8	6	—	3	—	3	—			12	—	12
NN3	9	—	3	—					12	—	12
NQ	3	—	4	—	10	—	1	—	18	—	18
NR	1	—	2	—	1	—			4	—	4
NS	1	—							1	—	1
NV	1	—	6	—	3	—	3	—	13	—	13
NW	1	—	7	—	5	—	4	—	17	—	17
NX			3	—	3	—			6	—	6
NZ			4	—	10	—	1	—	15	—	15
KA			8	—	5	—	5	—	18	—	18
Na	2	—	4	—					6	—	6
Ne					4	—			4	—	4
Nf	3	—	5	—			1	—	9	—	9
Ng					1	—			1	—	1
					Summer only						
NK	—	1	—	1	—	1			—	3	3
NG58					—	2			—	2	2
NØ					—	1	—	3	—	4	4
Nd					—	1	—	1	—	2	2
Nh							—	1	—	1	1
Totals											
No. enc.	98	13	142	9	153	16	72	23	465	61	525
No. pods	27		28		32		25				
Resightings			23		26		24				

Note: Fall 1990 includes January and February 1991, and fall 1991 includes January and February 1992. The data include all killer whale pod encounters (i.e., pods identified in the core study areas, during sighting surveys, and from the whale-watching boats).

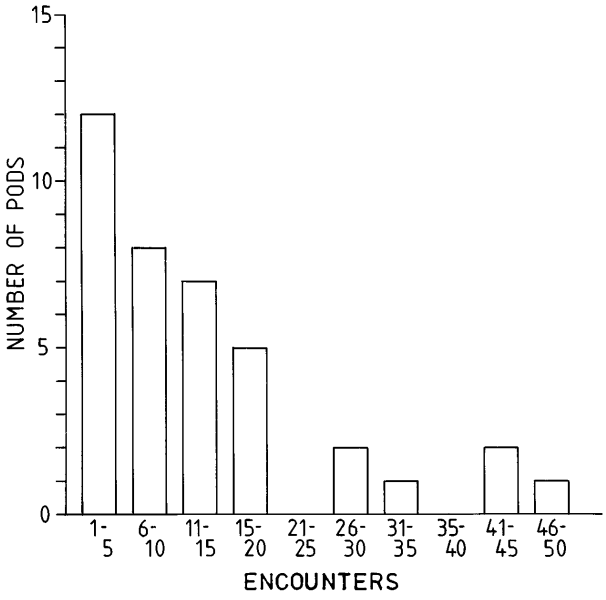
the spawning stock. During the period studied, the 1988 and 1989 year-classes left the Barents Sea and recruited to the spawning stock from 1992. Most of these herring adopted the migratory pattern of the older herring, although some of the 1989 year-class was observed spawning off Vesterålen in March and April 1993.

Discussion

Seasonal occurrence and diet of killer whales

Earlier studies demonstrated a connection between the occurrence of killer whales and herring off Lofoten and Vesterålen islands in northern Norway during the wintering period for

Fig. 4. Frequency distribution of encounters of the different killer whale pods photoidentified in northern Norway in 1990–1993. The data include all occasions when killer whale pods were identified in the core study areas during the sighting surveys and from the whale-watching boats in Andenes.



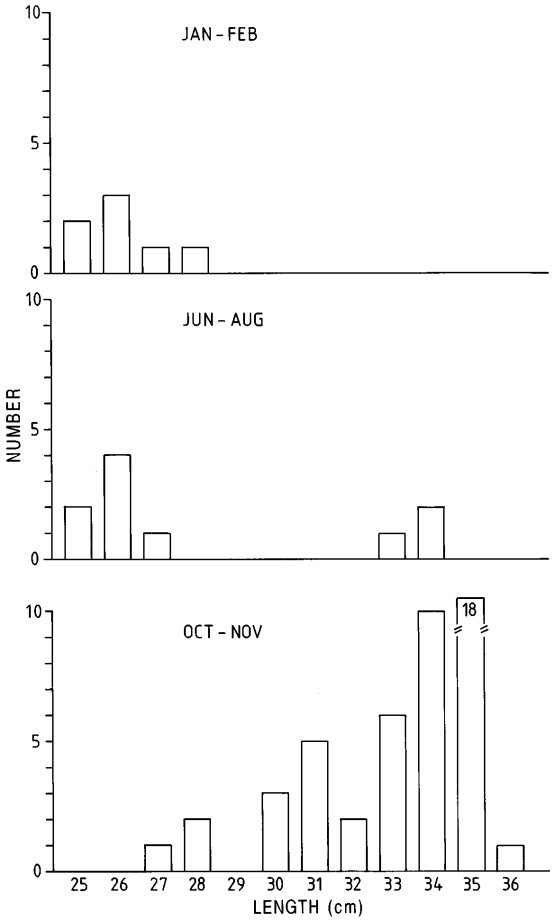
herring (Christensen 1988; Øien 1988). However, the identity of the killer whales occurring in these waters and their areas of occurrence and diet during summer months were not known.

This study shows that it was mainly the same killer whale pods that returned to the study area in northern Norway year after year; almost half of the pods were observed yearly and the number of resightings was high in 1991–1993. The cumulative number of pods identified suggests that the majority of killer whale pods occurring in the study area was identified.

There was a consistent pattern in the seasonal occurrence of killer whales in the study area: the whales occurred in different areas during October to January and June to August and were encountered most often in October and November. In the fall, killer whales occurred in the Tysfjord–Ofotfjord area, which was the wintering area for the whole adult stock and part of the adolescent stock of the spring-spawning herring. The adult herring dominated both the biomass of wintering herring and the diet of killer whales in October and November. Cod and saithe were present in the wintering area of herring and could have contributed to the diet of the killer whales, as indicated by the one observation of saithe being eaten by a killer whale in Tysfjord and by cod being found in the stomach contents of killer whales caught in the Lofoten area in winter (Christensen 1982).

The increase in the number of pod encounters from fall 1990 to 1992 could be related to an increased searching effort. However, in October and November 1993, the searching effort was considerably higher than in previous years, but fewer killer whale encounters were made. The estimated abundance of herring in the wintering area remained stable from 1992 to 1993, so diminished food resources do not explain this decrease in killer whale encounters. As this was a period of strong herring recruitment, it is possible that some killer whale

Fig. 5. The length distribution of herring caught among feeding killer whales in January and February (n = 7, caught during five different feeding occasions from January 20 to February 11, 1991), June to August (n = 10, caught during eight different feeding occasions in 1990–1993), and October and November (n = 48, caught during 22 different feeding occasions in 1990–1993). Adolescent herring are <29 cm, and adult herring are ≥29 cm long.



pods exploited the alternative resources of recruiting adolescent herring that wintered outside the study area.

Killer whales left the Tysfjord–Ofotfjord area in early winter when the adult herring started to migrate to the spawning grounds. The onset of the herring spawning migration was relatively abrupt, with almost complete desertion of the wintering area within a few weeks around mid-January. In winter 1992, no killer whale pods were observed after the 3rd week of January. In 1991, killer whales feeding on the adolescent herring still present in the fjords were encountered until the 2nd week of February.

During the summer, killer whales occurred off the Lofoten and Vesterålen islands and this area overlapped with the herring feeding area. Mostly adolescent herring occurred in these nearshore waters and dominated the few observations of killer whale diet. Mackerel and saithe were abundant in the summer study area and could have been included in the diet of killer whales to a larger degree than indicated by the one observation of killer whales feeding on mackerel.

The results of this study suggest that marine birds are not an important part of the diet of killer whales, either during the fall or in the summer. The unsuccessful attempt of killer whales to catch a young harbor seal was the only indication of killer whales feeding on marine mammals, although harbor seals, harbor porpoises, sperm whales, and minke whales were present in the summer study area and are known to be part of the diet of killer whales elsewhere (Jefferson et al. 1991).

During the summer months, herring fed in small schools over an area of several thousand square kilometres, which could explain the irregular occurrence of killer whales and the small number of different pods observed each summer in the coastal waters studied. According to Øien (1993), offshore waters in the Norwegian Sea are an important habitat for killer whales during the summer months and more observations of killer whales could probably have been obtained by doing surveys further off the coast.

Of the seven killer whale pods encountered in both the wintering and spawning grounds of herring, four (NA, NP, NG30, and NC (in 1989)) were also observed in the summer feeding grounds of herring, which indicates that at least these pods follow the main migration route of the Norwegian spring-spawning herring stock throughout the year.

In British Columbia and Washington state, the resident killer whales follow summer salmon runs to the coastal waters around Vancouver Island (Heimlich-Boran 1988; Nichol 1990). The locations and timing of these salmon runs have been generally the same over a long period of time, and the resident killer whales are highly familiar with their environment and have developed location-specific behavioral traditions (Heimlich-Boran 1988; Felleman et al. 1991). The size and the migration pattern of the Norwegian spring-spawning herring stock have varied considerably, often with abrupt changes in summer and winter distribution (Devold 1963; Dragesund et al. 1980; Røttingen 1990), and these changes seem to have been followed by killer whales (Christensen 1988; Øien 1988). Therefore, long-term seasonal occurrence of killer whales in the coastal waters of northern Norway is unpredictable and location-specific traditions are not likely to develop. The herring stock is expected to grow rapidly in the coming years (International Council for the Exploration of the Sea 1994), and as a consequence, major changes could be expected in the present seasonal distribution pattern of both herring and killer whales.

Differences in occurrence of killer whale pods

The stable social structure within killer whale populations creates the potential to form populations with distinct social and behavioral characteristics. Off British Columbia and Washington state, three different types of killer whales occur: transients, residents, and offshore killer whales (Bigg et al. 1990; Felleman et al. 1991; Ford et al. 1994). The transient killer whales have a wide home range, occur irregularly, and feed mainly on marine mammals. Resident killer whales occur regularly and feed on salmon (*Oncorhynchus* spp.) and other fish. Less is known about the offshore killer whales, but they probably feed on herring and other fish. Because of these findings and similar results from other parts of the world (Berzin and Vladimirov 1983; Ellis 1987), it was of interest to investigate if any differences could be found in the pattern of seasonal occurrence or diet of the killer whale pods occurring in northern Norway.

The majority of killer whale pods identified in this study seemed to share a similar pattern of occurrence and was encountered during both the fall and the summer. After each summer of field studies, more pods were added to the category observed during both seasons, and it is possible that all pods observed in the wintering area of herring may occur in the study area during the summer.

The seven most commonly encountered pods (NA, NC, NE3, NG30, NO, NP, and NY) could have been more stationary in the study area or simply favoured the two most often surveyed subareas of the fall study area (TF1 and TF2). In British Columbia, the resident killer whale pods show area preferences within their general summer home range (Ford et al. 1994).

The five pods (NG58, NK, NØ, Nd, and Nh) that were observed only during the summer may have a different pattern of seasonal occurrence and prey preference than the pods encountered in the wintering area of herring. It is interesting that the six pods identified in the area prior to 1990 (T. Similä, unpublished data) and not resighted during 1990–1993 were all encountered during the summer. When all of the pods identified in 1983–1993 are considered, as many as 24% (11 pods) were observed only during the summer. The single pod (NØ) observed only during the summer that was also observed feeding was trying to catch a young harbor seal in June 1993 and was seen feeding on herring the following day in the same area.

One of the pods (NN3) was encountered several times during both winter surveys but not earlier in the wintering season of herring. This pod was present when the adult herring and almost all other pods had left the study area and was exploiting adolescent herring still present in the fjords. The pattern of occurrence of this pod is difficult to explain by changes in the herring abundance because it entered the study area when herring biomass was starting to diminish.

Killer whale social groups and populations are known to differ from each other in their vocal repertoire (Ford 1991). In a comparison of call repertoires of 10 Norwegian and 4 Icelandic killer whale pods, Strager (1995) found that the NN3 pod was acoustically quite different from the other Norwegian pods and shared a call with Icelandic whales. Since the call is complex in structure, it is unlikely to have evolved independently in the two areas (Strager 1995). Jonsgård and Lyshoel (1970) suggested that killer whales might have moved between Icelandic and Norwegian waters during the earlier (prior to 1970) migration pattern of the Norwegian spring-spawning herring. The NN3 pod might represent a present or previous contact between the two areas.

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