

## Intergroup interactions among killer whales in Norwegian coastal waters; tolerance vs. aggression at feeding grounds

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### Abstract

Killer whales reside seasonally in two areas along the Norwegian coast. Different pods were commonly observed to feed on herring independently of each other within close range. Deviations from intergroup tolerance occasionally occurred as agonistic interactions, where one pod became displaced from its feeding patch by another pod. The interactions were rare events; only seven of 79 observations of killer whale pods feeding in the vicinity of other pods during 1990 to 2000 ended with a displacement. Because of their relative rareness, it was hypothesized that the killer whales refrain from interfering with neighbours, but agonistic interactions would occur if killer whales from other areas in the Northeast Atlantic provisionally entered the feeding grounds of Norwegian killer whales. The population identity of four interacting pods was tested with acoustic analyses of their sounds, and compared with calls produced by killer whales repeatedly photo-identified along the Norwegian coast from 1987 to 2000. The main conclusion of the analyses was that intergroup competition, expressed as cooperative resource defence, occasionally occurs within the local killer whale population off Norway.

**Key words:** social behaviour, mammals, group defence, aggression, cooperative feeding, killer whale, *Orcinus orca*.

### Introduction

The social and cooperative nature of killer whales (*Orcinus orca*) has been observed and documented from all parts of the world's oceans. Killer whales are consistently described as traveling in groups and coordinating their hunting techniques when feeding on fish and attacking mammalian prey (Smith *et al.*, 1981; Heyning & Dahlheim, 1988; Silberger *et al.*, 1990; Felleman *et al.*, 1991; Hoelzel, 1991; Frost *et al.*, 1992; Similä & Ugarte, 1993; Saulitis *et al.*,

2000; Visser *et al.*, 2000). The social lives of killer whales also include meetings of groups in areas with high quality food resources, such as breeding sites of pinnipeds (Condy *et al.*, 1978; Baird & Dill, 1995) and spawning grounds of fish (Christensen, 1988).

Territorial resource defence has not been reported for killer whales, or any whale species (Connor, 2000), but killer whale pods in the local population off British Columbia and Washington State avoid excessive overlaps in habitat use and separate their feeding areas in both time and space. The population consists of two resident, parapatric sub-populations feeding mainly on salmon. Whales from one community rarely enter the seasonal home range of the other (Ford *et al.*, 1994) and some temporal separation was found among pods within the same community (Nichol & Shackleton, 1996). The home ranges of the 'resident' killer whales are shared with a population of mammal-eating ('transient') killer whales, and both avoidance and aggression have been reported between these two forms (Baird & Dill, 1995). The killer whales in this area have been studied for more than twenty years, but no agonistic interaction has been observed between pods sharing the same food resource (Baird, 2000).

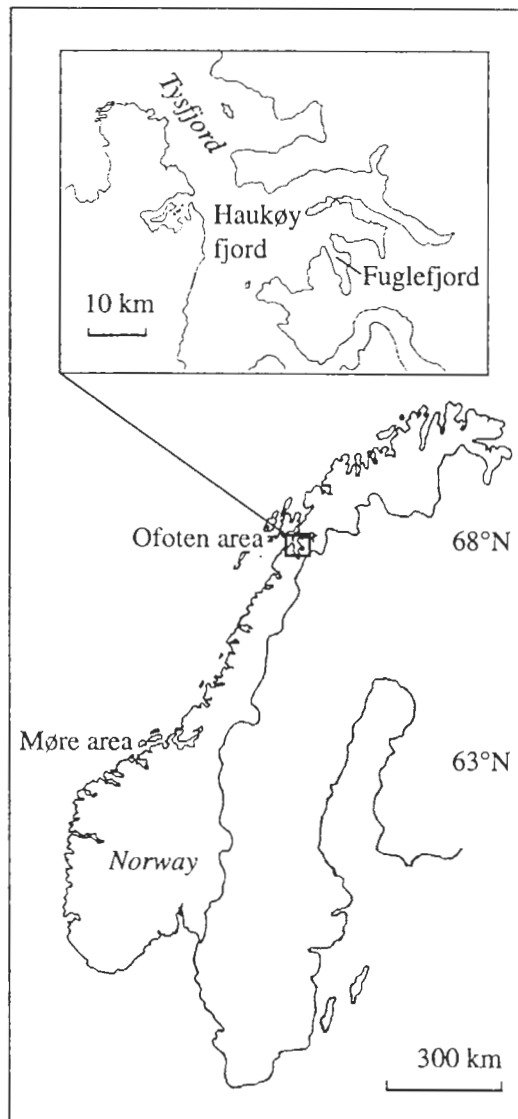
Killer whales in Norwegian coastal waters follow the occurrence of herring (*Clupea harengus*), a major prey for killer whales in this area (Christensen, 1988). Photo-identification studies of Norwegian killer whales were initiated in 1983, and due to re-sighted whales over a time period of >10 years, the population was considered to be local (Lyrholm, 1988; Similä *et al.*, 1996). All identified groups contain adult males and female with young and the social system of the whales seems to resemble the one described for the resident killer whales in the Northeast Pacific i.e., organization into stable pods where neither sex disperses from the natal group (Bigg *et al.*, 1990; Similä, 1997; Bisther & Vongraven, 1994). Norwegian killer whales also have pod-specific sound repertoires or

'dialects' (Strager, 1995; Bisther, 1991). Similarities in dialects is suggested to reflect a common ancestry, and different populations can be distinguished by the sounds of the whales (Moore *et al.*, 1988; Ford, 1991; Ford *et al.*, 1994). There is a small chance of mimicry and random convergence in call usage, but the probability decreases with increasing similarity in call repertoires.

The present study was conducted in two core areas where killer whales reside seasonally in Norway; the wintering fjords of the herring where 445 killer whales in 30 pods have been identified (Similä, 1997) and the spawning grounds of the same herring 700 km farther south where an additionally 63 killer whales have been identified (Bisther & Vongraven, 1994). Since the acoustic signals of killer whales are described to range 10 km under water (Ford *et al.*, 1994), it was assumed that feeding pods were aware of each other. The pods had the option to interact either by cooperation, mutual tolerance, or aggression, analogous to intergroup encounters described for primates (Harrison, 1983). The outcome of interactions among feeding killer whale pods are here described, with definitions of aggressive and submissive behaviour adopted from studies of bottlenose dolphins (*Tursiops truncatus*) (Samuels & Gifford, 1997). It generally included a forceful approach of one pod, resulting in an immediate retreat of another pod from its feeding patch. Because of their relative rareness, and because of the absence of agonism among the resident killer whale pods with defined home ranges in the Northeast Pacific, it was hypothesized that the whales refrain from interfering with neighbours, but agonistic interactions would occur if killer whales from other areas provisionally entered the feeding grounds of Norwegian killer whales.

### Materials and Methods

Killer whales were encountered off the coast of Møre, southwest part of Norway, and during late fall in the fjords of Ofoten, northern Norway (Fig. 1). Behavioural observations and acoustic recordings were made during 1990 to 1993, as part of a study of the population ecology and social behaviour of Norwegian killer whales (Bisther & Vongraven, 1994). Additional fieldwork was undertaken during 1987–88, 1994–97, and 1999–2000. Whenever feasible, photo-identification of whales was made following the method described by Bigg *et al.* (1990). The relative body size and the height of the dorsal fin were used to determine the age/sex of the whales, but these morphological characters can not distinguish between adult females and subadult males (Bigg *et al.*, 1990). Identified individuals were given alpha-numeric codes and



**Figure 1.** Map of Norway showing areas where killer whales were encountered; the spawning grounds of herring (Møre), and the wintering fjords of herring (Ofoten).

synchronized with other photo-identification studies in the areas (Lyrholm, 1988; Similä, 1997).

### Behavioural observations

Focal group sampling (Mann, 2000) was used to record rates and duration of feeding. Only established, cooperative feeding of groups were included; stationary whales circling and controlling a school of herring either at the surface or down to about a 20 m depth (details in Similä, 1997). Fish, stunned by underwater tail-slaps by the whales, could be

observed at the surface. Sea birds (e.g. common gulls, *Larus camus*) were at all times attracted to feeding whales, taking fish at the surface. The behaviour could be observed from a distance of ~4 km because of the accumulation of birds and because of the highly active, milling movements of the whales in a small spot. The occurrence of other pods within visual range was noted. Possible interactions among pods were formulated as: (1) approach and mixing of pods into cooperative feeding, (2) non-approach, representing tolerance, or (3) agonistic interactions.

Agonistic interactions involved pods behaving aggressively and submissively in response to each others. Behavioural definitions followed descriptions of agonism expressed in dolphins; *aggression* typified by threats and forceful attempts to inflict harm or *submission* typified by behaviours associated with avoidance, withdrawal, or escape. A submissive behaviour (i.e. to 'back-down') without the aggressive behaviour of a counterpart, also was considered as an agonistic interaction and defined dominance relationships (Samuels & Gifford, 1997). In this study, submissive behaviour referred to single contests (Drews, 1993).

#### Acoustic analyses

Acoustic recordings were made with Brül & Kjaer hydrophones (model 8103 and 8106) connected to a Sony TC-D5 tape recorder (30 Hz to 15 kHz  $\pm$  3 dB) or a Sony TCD-D10 (20 Hz to 22 kHz  $\pm$  1 dB). Recordings were analyzed on a Kay Elemetric DSP Sona-Graph model 5500, set at 10 kHz with 59 Hz filter bandwidth. A killer whale dialect consists of a limited and stable number of discrete calls (Ford, 1991). Classification of discrete calls were done with a combination of aural and visual examinations of spectrograms, following the methods described by Ford (1987, 1989). A call was defined as discrete when it occurred in an identical form twice or more, thereby constituting a call type. Aberrant renditions of calls that occurred just once were classified as variable and not analyzed. The structural differences between variable and discrete calls are shown in Figure 2. The majority of the 7 to 17 different call types within the dialects of killer whales off British Columbia were heard in one or two 10-min samples, and produced by the whales regardless of behavioural context (Ford, 1989). Norwegian killer whales had a similar pattern of call usage (Strager, 1995). A large part of the call repertoires of killer whales can then be expected to be heard in relatively short recordings of their sounds.

Calls recorded from killer whales repeatedly identified in Norway between years were considered as representative of the local population. These were compared with calls produced by un-identified

whales involved in agonistic interactions. Similarity indexes, ranging between 0 (totally different) and 1 (identical), were used for this comparison (Morgan *et al.*, 1976).

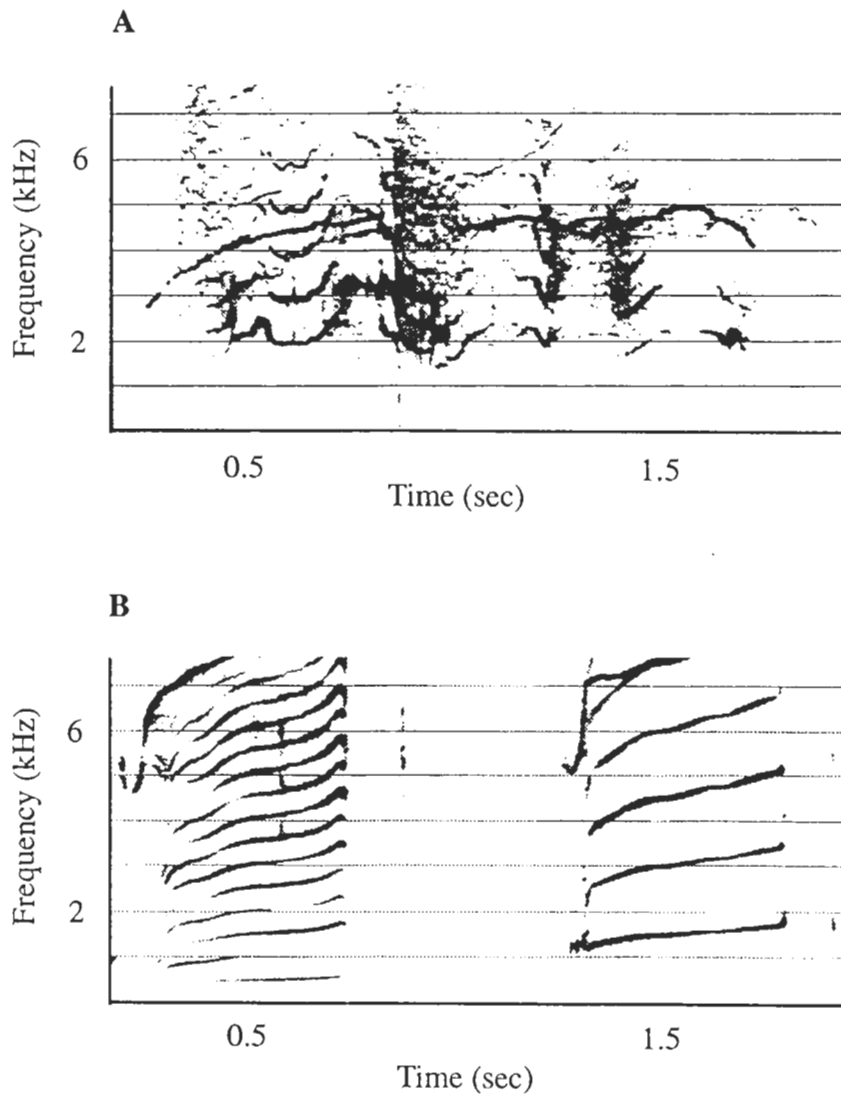
## Results

Killer whales were encountered 1089 h during 370 days of fieldwork during 1987–2000. A majority of whale encounters (92%) were made at the spawning grounds and wintering areas of herring. Most observations were made when more than one pod was sighted (Table 1). Feeding pods were recorded 72 times without any observed approach from other pod(s) nearby. This is considered as a minimum estimate. Pods were not observed to mix and cooperate during feeding. The whales were feeding on a herring school for an average time of 26.5 min when other pods were in the area, and 32.2 min when no other pod was sighted (Table 1). It did not seem to be a dramatic change in feeding durations when other pods were nearby.

#### Agonistic interactions

A total of seven agonistic interactions, where one pod became displaced from its feeding patch by another pod, was observed in the years 1991, 1992, 1993, 1995, 1996 and 2000. One observation was made at the spawning grounds, the rest in the wintering areas of the herring (one in Haukøysfjord, two within and three outside Tysfjord, Fig. 1). The interactions were similar at all instances: (1) one pod was feeding, (2) another pod approached from a distance (>1 km) at very high speed, porpoising with complete leaps through the water, (3) at the same time the approaching pod reached the feeding patch, the first pod immediately (within seconds) interrupted its feeding (contrasting the gradual termination (minutes) of undisturbed feeding), made a short, collective dive and left in a cohesive formation, and (4) the approaching pod spread-out in the former feeding patch of the other whales, payed no obvious attention to the pod who left and were twice observed to continue to feed on the herring. The behaviour of the pods seemed to include a threat from an aggressive part and a withdrawal of a submissive part, thereby defined as agonism.

The interactions were transitory and occasional events, and few demographic/photo-identification data are available; one photo-identified, but previously unknown, pod ('H-small') with eight whales (including one young male and four juveniles) had been feeding in Haukøysfjord for 23 min when it became displaced by a pod ('H-large') of about 12 whales (including two adult males). In November 2000, an approaching pod was identified as NP, known to belong to the Norwegian population.



**Figure 2.** Spectrograms illustrating the structural differences between a variable call (A) and two discrete call types (B).

NP-pod has been identified several times in the years 1990 1997 and 2000, and observed among other feeding pods without interfering.

One interaction differed from the others described here since it did not include any feeding behaviour, and since pronounced aggression was absent. However, submissive behaviour was both repeated and in response to the behaviour of another pod. It occurred in October 1993 and started with one pod ('F-small') in Fuglefjord, a fjord with a narrow entrance of about 450 m (Fig. 1). The pod consisted of seven whales, including one male, two calves and four females/subadults.

By the time a second pod ('F-large') with twice as many whales (including three males) entered the fjord, the small pod lined-up side-by-side against the rocks. When they began to advance outwards, all whales in the large pod simultaneously rotated at the surface, facing the small one. As a result, these whales turned 180 degrees within some seconds, went back and again lined-up against the rocks. The entering pod then moved around slowly in the fjord while the other pod held its position. After 31 min, another attempt to move outwards was made by the small pod. The other whales responded by again interrupting their activities and rotated

**Table 1.** Summary of field observations of feeding killer whales 1987–2000 in areas with at least two pods within visual range ('multipod occurrence') or only one pod visible ('single pod occurrence').

	Multipod occurrence	Single pod occurrence
Hours of observation	754	335
No. of observed feeding events	79	22
No. of agonistic pod interactions	7	N/A
No. of cooperative pod interactions	0	N/A
Duration (min) of feeding events	mean=26.5 (SD: 13.5) n=34, range: 4–49	mean=32.2 (SD: 23.3) n=4, range: 13–60

**Table 2.** Acoustic analyses of discrete calls produced by three killer whale pods repeatedly photo-identified in Norway, and by four pods involved in agonistic group interactions. Similarity index:  $2N/(R1+R2)$ . N=no. of shared call types, R=no. of call types produced by each pod.

Pod	Photo-ID in Norway	No. of calls	No. of call types	Similarity index between pods		
KA	1987, 1990, 1993	184	10	NP	KA	KB
KB	1988, 1990, 1993	217	8	0.4	0.6	
NP	1990, 1997, 2000	353	10		0.5	
H-small	1992	51	8	0.1	0.2	0.3
H-large	—	11	1	0	0.2	0
F-small	—	181	15	0.7	0.6	0.5
F-large	—	149*	6**	0.1	0.1	0.1

\*Discrete calls analyzed in recordings with both F-large and F-small present.

\*\*No. of call types when the variants produced by F-small alone are excluded.

simultaneously with their heads forward of the small pod, which retreated back to the rocks. After another 28 min, the large pod started to leave the fjord and 5 min later the whales in the small pod were spread-out in the middle of the fjord.

Distance between the two pods was approximately 600 m during the whole event. The large pod had a loose spatial arrangement compared to the small pod, which was tightly organized when the large one was present in the fjord.

#### Acoustic analyses

The acoustic recordings contained six sequences; three from single pods (KA, KB and NP) repeatedly identified in Norway (Table 2) and recorded 30–35 min while feeding on herring, one from a 'displacement' pods (H-small and H-large), and two sequences from the interaction in Fuglefjord where the first pod was recorded alone (F-small) and together with the second pod (F-large). Two hours and 39 min of acoustic recordings with sufficient signal-to-noise ratios were analyzed, and 1146 calls were found to be stereotyped renditions of 28 different call types. Frequency of different call types

ranged considerably in the analyses. Two call types occurred only twice, while four call types were each recorded more than a 100 times.

The Norwegian pods shared about half their repertoires of call types, the similarity indexes between KA, KB and NP pods were 0.4, 0.5, and 0.6, respectively (Table 2). The pod that left the feeding patch during 'displacement' (H-small) had eight different call types. Two of these were common calls among the Norwegian pods. At the end of the 'displacement' sequence, weak signals with increasing intensity could be heard from the approaching pod (H-large). The signals were identical with a call type also found in the recording of KA. The whales that repeatedly retreated and lined-up in Fuglefjord (F-small) had 15 call types in a 31-min recording. Twelve of these were call types also produced by the Norwegian pods. Sixteen call types were defined in the 17-min recording of both pods in Fuglefjord. Six call types might be attributed to the entering pod (F-large) when all the 15 call types found in the sequence from F-small were excluded. Two of these six call types were shared with the Norwegian pods.

Interacting whales had 1–12 call types in common with Norwegian killer whales, and the similarity indexes between H- and F-pods and any of KA, KB or NP ranged between 0.1 and 0.7 (Table 2). Three pods involved in agonistic interactions were considered to belong to the local population because of the presence of two or more Norwegian killer whale calls in their repertoires. Only one call type could be identified from the fourth pod, which weakens the analysis, even if the call was shared with the Norwegian whales.

### Discussion

Killer whales were frequently observed to feed undisturbed by other pods; the prevailing outcome of pod encounters seemed to be tolerance. Agonistic interactions occasionally occurred when a pod became displaced from its feeding patch. Aggression seemed to be at a low level, since displacing pods paid no obvious attention to the displaced pods, but concentrated on the food source. In that respect, the behaviour resembled interactions described for primates where encounters ended with one group supplanting another, which retreated without resistance (Harrison, 1983; Cheney, 1987).

The interaction where one pod seemed to be trapped in a fjord, unable to leave without crossing the larger pod, did not include an overt conflict about a food patch. Instead, the behaviour of the pods indicates the presence of a dominance system, defined by the repeated yielding response of a subordinate pod instead of escalation (Drew, 1993; Samuels & Gifford, 1997). Three of four pods in agonistic interactions had at least two call types in common with Norwegian killer whales, and one pod was visually identified as Norwegian while displacing another pod. The hypothesis that killer whales refrain from interfering with pods from their own population did not hold.

#### *Interactions between killer whale pods*

Categorization of killer whale behaviour usually involves single pod activity (Similä, 1997; Saulitis *et al.*, 2000), individuals acting within pods (Heimlich-Boran, 1986; Hoelzel, 1993) or the association pattern of pods occupying the same area (Ford, 1991; Baird & Dill, 1996). Coordinated pod activities directed towards other pods are rarely described.

There are two observations resembling the displacements observed in Norway. In a study of killer whales feeding on pinnipeds at the coast of Argentina, Hoelzel (1991) mentioned the behaviour of one pod with two adult females and five sub-adults actively displacing another pod of two adult males from a productive foraging area. This behaviour was observed twice during a 4-month study

period. The males were also observed to be hunting nearby when the other pod was hunting in the favoured area. In the Crozet Archipelago, a group of seven killer whales appeared to take a seal pup that had been killed by a smaller group of whales (F. Guinet, cited in Baird, 2000).

One instance of aggression, but not likely to include a conflict about a food resource, was observed off British Columbia when a large pod of 17 resident killer whales chased and apparently attacked a small pod of three transient killer whales (Ellis, 1994). These two forms of killer whales range in the same geographic area, but differ in feeding preferences and other behavioural characteristics. Transients feed mainly on other marine mammals, while residents feed on fish, and they are known to avoid each other when sighted together (Baird & Dill, 1995; Ford *et al.*, 1998). The interactions described from Argentina, British Columbia and two of the observations in this study, have the common feature of one small pod being displaced by a larger pod. Differences in pod size might influence the competitive ability of the whales (Bain, 1989; Baird, 2000), and create the asymmetric resource holding capacity described for other animals like primates (Wrangham, 1980; Parker & Sutherland 1986).

Osborne (1986) described non-aggressive interactions between killer whale pods off Washington State, which he referred to as 'greeting ceremonies' and 'intermingling sessions'. They appear to be 'friendly' activities that follow the meeting of two pods from the same community. During 'greeting', the two pods line-up and approach each other head-on, submerge, and surface as one group. The approach and line-up resembles the interaction observed in the Norwegian Fuglefjord, but with an opposite result. Instead of resulting in one intermingled group, the behaviour seemed to be regulated by dominance and reinforced distance between two pods.

A crucial definition in this study was the submissive behaviour of pods. It was assumed that the whales were forced to leave their feeding patch, and forced to retreat when there was not enough space to pass. An alternative to displacement could be that they by coincidence ended feeding when another pod came by. This does not seem to be the case, as feeding terminated abruptly and coincided with the high speed swimming of the approaching pods. Whales swimming at such speed (twice estimated to >15 knots) were only observed to precede a displacement.

Another alternative could be that it was a form of cooperation, that a pod voluntarily turned over its feeding patch to another. The rapid approach and the immediate departure could then be a functional way to prevent the herring escaping downwards. An

argument against this, is how the whales departed. Instead of the normal interindividual distance of one or two whale lengths, the whales were tightly grouped. A similar formation was video-filmed in 1992 when a large group of pilot whales (*Globicephalus melanaea*) entered the Tysfjord area. The killer whales moved away arranged in a tight group where the whales almost had physical contact. The immediate reorganization into cohesive pods was described in a similar way by Christensen (1978). The killer whales were then responding to attempts to shoot plastic tags into their backs and dorsal fins. Christensen (1978) also referred to similar observations made by Norwegian whalers, that frightened killer whales will gather into a school before attempting to escape. Spotted dolphins (*Stenella attenuata*) and bottlenose dolphins 'bunch' into a tight group when agitated (Pryor & Schallenberg, 1991; Schneider *et al.*, 1998), and this behaviour is known from captive animals to be signs of fear, stress, excitement, or frustration (Norris and Döhl, 1980).

#### *Inter-group competition*

Interference competition is described to occur when animals secure access to resources by excluding others from using them, either by setting-up territories or by displacing them at the resource (van Hooff & van Schaik, 1992). It can depend on a dominance system, where the identity or properties of the animals modify the interaction (Huntingford & Turner, 1987). Inter-group dominance is not often seen in nature, and Wilson (1980) suggested it depends on well-organized societies developed among social animals, and that dominance appears in overlapping home ranges. Social primates with no territorial defence can have extensive overlaps of home ranges, but the groups avoid each other at long distance. Aggressive interactions are rare because subordinate groups avoid dominant ones, and neighbouring groups tend to have stable dominance relationships (Wrangham, 1980).

Some whale populations seem to have a stable distribution where the whales avoid interfering with conspecifics sharing the same food source; the killer whales off British Columbia and Washington State with their seasonal home ranges and preferred feeding areas (Ford, 1991; Baird & Dill, 1995; Nichol & Shackleton, 1996) and the bottlenose dolphins in the Moray Firth (Wilson *et al.*, 1997). Stratified movements of the dolphins suggests that individuals do not move freely in the area, and that competition among individuals or social groupings shapes the spatial distribution of the population. Seven killer whale pods in Norway were suggested to have preferred areas within the wintering fjords of herring. They were frequently encountered (47% of all pod encounters) and seemed to favour the two

most surveyed subareas (Similä *et al.*, 1996). Other pods may have avoided the favoured areas of these pods.

Even if territorial behaviour is not an option in a three-dimensional sea with mobile prey, certain food patches might still be worth defending, also for whales (Connor, 2000). For the killer whales in Argentina, the pinniped breeding site contains areas with high success rates of attacks, and the agonistic interactions among whales occurred in the most profitable area (Hoelzel, 1993). Norwegian killer whales have been found to ignore large concentrations of herring distributed at 150–350 m depth during daytime, and preferentially feed on smaller patches close to the surface (Similä, 1997; Nøttestad & Axelsen, 1999). Even if killer whales are able to dive to the range of the major herring concentrations (Baird, 1994), it was suggested by Similä (1997) that herring patches close to the surface might be easier to control for the whales. A decreased handling time of certain herring patches might make them more attractive for the whales, similar to the preferred hunting area on the coast of Argentina. However, it is not clear why a food patch would be worth defending at some rare occasions, while most of the time other pods are left undisturbed while feeding. For killer whales in Norway, one contributing factor could be a history of unstable ecological conditions.

#### *Norwegian killer whale population*

Killer whales along the coast of Norway have been described for a long time to follow the migration of herring (Collet, 1912; Christensen, 1988). Norwegian spring spawning herring collapsed to 1% of its original biomass in the early 1970s due to human over exploitation. As a consequence, the herring altered its migrational routes and stayed along the Norwegian coast year-round, with main seasonal concentrations at the spawning grounds off Møre and in wintering areas farther north. These areas were previously found at several localities in the Norwegian Sea (Hamre, 1989; Røttingen, 1990). With the aim to protect the depleted herring stock, killer whale catches became intensified in the late 1960s, and 753 killer whales were taken in the coastal waters of Norway in the period 1968–1981 (Øien 1988). In 1987, the increasing herring stock began to spend the winter months in two fjords in Ofoten, followed by 551 killer whales (Dragesund *et al.*, 1997; Similä, 1997).

Considering the long lives of killer whales, 80–90 years for females and 50–60 years for males (Olesiuk *et al.*, 1990), our study population has experienced a temporary, but severe reduction in an important food resource, a changed migrational route of the prey, and a sudden decrease in population density. The well-organized society,

described by Wilson (1980) to reduce intergroup dominance, might for the Norwegian killer whales have been affected by two factors: the accumulation of the herring into one small area during winter months and the possibility for immigrating pods of killer whales to become established in the coastal areas of Norway.

The nearest known local population of killer whales outside Norway is found around Iceland (Sigurjónsson *et al.*, 1988). The sounds of killer whales recorded off Iceland and Norway were analyzed by Moore *et al.* (1988), who suggested population-specific calls for the whales in each area. However, Strager (1995) described the Norwegian killer whale call N25 to match the Icelandic call I32i, and pointed-out that the only Norwegian killer whale pod found to have this call (NN3) also was the most socially isolated pod identified in the Ofoten area. It arrives late in the season, and stays until long after the other pods have left the area. The pod still shares one call type with all the other Norwegian pods analyzed.

One other finding in the acoustic analyses by Strager (1995) relates to this study: the adult female in the H-small pod, identified as one of the whales who became displaced from their feeding patch, belongs to a pod suggested to have a similar call type as killer whales in Alaska (photo-analyses by F. Ugarte & D. Vongraven). The possibility of the same call type evolving independently in two separate areas is acknowledged, but also the prospect of a call type common among killer whales north of Siberia. The distributional range of killer whales having the same call types in their repertoires can be considerable, since killer whales recorded in southern California and northern southeast Alaska shared the same basic dialect (Ford, 1995). Killer whales are also known to have moved between these areas, a distance of 2700 km (Goley & Straley, 1994).

The killer whale population off Norway is recognized as local, because of the seasonal occurrence of the same whales who share the same discrete calls in their acoustic repertoires, indicating a common ancestral origin. However, ecological events, such as prolonged periods of food shortage, and whaling, might have affected the distribution of the whales on time scales not comparable with social or geographic isolation, leading to repertoire divergence. The rate of dialectal formations in killer whales was tentatively estimated by Ford (1991), using an acoustic recording from 1958 and the longevity of a 'cultural generation'; the time which individuals may have an influence on the vocal development of others in the pod. Ford (1990) concluded that if it is advantageous for killer whales to have pod-specific dialects, it may persist in a similar form for several centuries.

Considering the social isolation described for the Norwegian pod with an Icelandic call in its repertoire (Similä *et al.*, 1996; Strager, 1995) and the displacement of a Norwegian pod having a presumably Arctic call in its repertoire, any further acoustic analyses of pods involved in agonistic interactions should include the sounds of killer whales from a wide area in the North Atlantic. It is emphasized that it requires a higher degree of call sharing with distant whales than has been demonstrated for these two Norwegian pods, to reveal if the present distribution of whales conceals a common ancestry.

This study concludes that killer whale pods in Norwegian waters may cooperatively defend food resources against other pods by displacing them at their feeding patch and that population-specific calls did not prevent such agonistic interactions. The population itself, however, might have a history of instability, resulting in potential founding pods from the Northeast Atlantic having a variable degree of call sharing with killer whales established in Norwegian coastal waters.

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