

Acoustic Behaviour of Norwegian Killer Whales, *Orcinus orca*, During Carousel and Seiner Foraging on Spring-Spawning Herring

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Abstract

Norwegian killer whales (*Orcinus orca*) use different techniques to forage on spring-spawning herring. Two of the commonly observed techniques are carousel feeding, a cooperative feeding method, and seiner feeding, a noncooperative method. During seiner foraging, large groups of whales forage on herring discards around the nets or on discarded by-catch of fishing boats. Very little is known about the acoustic behaviour during these foraging contexts. The aim of this study was to examine possible differences in killer whale acoustic behaviour during both foraging contexts using simple sound analysis techniques. Calling, echolocation, and tail-slap activities were measured and compared between foraging contexts. Of these, calling and tail-slap activities were higher during carousel feeding, whereas echolocation activity increased with the number of individuals, irrespective of foraging context. No call types were used exclusively during a particular foraging context. A difference in mean occurrence of one call type was detected; call type N21 occurred more often during seiner foraging than during carousel foraging contexts. We suggest that the sequence of call types, rather than the use of isolated call types, is of greater importance in the coordination of group movements during carousel foraging.

Key Words: killer whale, *Orcinus orca*, cooperative foraging, seiner foraging, carousel feeding, calling behaviour, Tysfjord, Norway

Introduction

Group feeding has been described for a wide range of animal species (D'Vincent, 1985; Elgar, 1986; Kruuk, 1975). Among the benefits of social

feeding are reduced risk of predation (Roberts, 1996) and reduced time spent in predator vigilance (Elcavage & Caraco, 1983; Elgar, 1989; Lima, 1995; Pulliam, 1973; Underwood 1982). When individuals in a group cooperate during foraging or hunting, this also may increase the effectiveness with which prey is caught (Brown et al., 1991; Caraco & Wolf, 1975; Creel & Creel, 1995; Kruuk, 1975).

For predators, the effectiveness of hunting in a group depends on the size of prey (Caraco & Wolf, 1975; Zimen 1976). In lions (*Panthera leo*), prey size and capture efficiencies determine the range of group sizes that can meet the energetic requirements of individual group members (Caraco & Wolf, 1975). Hyenas (*Crocuta crocuta*) hunt wildebeest (*Connochaetes taurinus*) and zebras (*Equus burchelli*) in groups of seven to eight individuals, whereas gazelles (e.g., *Gazella thomsoni*) are hunted by only one individual hyena (Kruuk, 1975). Similarly, when hunting for many small prey, cooperation improves the hunting success of all group members (Brown et al., 1991; D'Vincent et al., 1985; Norris & Dohl, 1980; Sharpe, 2000).

Several species of marine mammals hunt cooperatively. Humpback whales (*Megaptera novaeangliae*), for example, feed in groups (D'Vincent et al., 1985) by creating a bubble net, which forms an ascending curtain, to concentrate prey. Steller sea lions (*Eumetopias jubatus*) form foraging lines consisting of up to 300 individuals, foraging cooperatively on large fish schools (Gende et al., 2001).

Marine mammals are known to exhibit a wide variety of strategies when attacking schooling prey. Successful strategies are largely dependent on the size, shape, and behaviour of the prey school, as well as the number and type of predators (Parrish, 1992). In killer whales (*Orcinus orca*), social

determinants of group size are likely to be the result of optimizing foraging group sizes (Baird & Dill, 1996; Baird & Whitehead, 2000). Two sympatric populations occurring in the area around Vancouver Island, British Columbia, are known to exhibit markedly different foraging behaviour (Bigg et al., 1987). The transient form specializes on marine mammal prey and associates in groups that consist of one or two matrilineal generations. These long-term groupings are termed pods and are defined as groups of individuals that are observed together at least 50% of the time over a long period (Bigg et al., 1990). Transient killer whales have been found to maximize the per capita energy intake by foraging in small groups (Baird & Whitehead, 2000). Residents specialize on fish prey and form matrilineal pods comprising one to four generations (Bigg et al., 1990). For the resident population in the area around Vancouver Island, foraging in larger groups has been suggested to be beneficial during cooperative food searching (Hoelzel, 1993).

The Norwegian killer whale population has been observed to hunt cooperatively during carousel feeding (Christensen, 1978, 1982; Similá & Ugarte, 1993). Carousel feeding is a cooperative hunting technique that was first described (Bel'kovich et al., 1991) in bottlenose dolphins (*Tursiops truncatus*). In killer whales, whales cooperatively herd small fish into a tight ball close to the surface and subsequently stun them by hitting them with the underside of their flukes. The stunned fish are eaten one by one (Similá & Ugarte, 1993).

In many cooperatively foraging species, communication can be an important factor for alerting other individuals and coordinating the group's behaviour during hunting or foraging (Brown et al., 1991; D'Vincent, 1985; Dittus, 1984; Elgar, 1986). In humpback whales, the initiation of coordinated lunge behaviour and simultaneous surfacing are closely associated with a distinct type of call (D'Vincent et al., 1985); however, many species stop calling when the presence of conspecifics no longer confers any benefit. Individual house sparrows (*Passer domesticus*) do not elicit conspecific-recruitment calls when they feed from a nondivisible food source and by this means evade competitive interactions with flock mates (Elgar, 1986).

Killer whales produce a wide variety of underwater calls (Ford, 1987; Moore et al., 1988; Strager, 1993). Most of the information on killer whale calls to date has been derived from the studies that have been conducted around British Columbia, Canada, and in Washington State in the USA where killer whales exhibit pod-specific dialects (Ford, 1987, 1989, 1991; Yurk et al., 2002).

The Norwegian killer whale population has not been the subject of such intense study and less is known about their sound production and social system. The existence of pod-specific dialects has been reported for the Norwegian killer whale population (Strager, 1993, 1995), and a number of call types used during differing contexts have been described (Moore et al., 1988; Simon, 2004; Strager, 1993, 1995); however, whether calling behaviour of Norwegian killer whales differs when cooperative foraging occurs compared to calling behaviour when whales are not feeding cooperatively to date has not been studied.

In this study, killer whale calls during two different foraging contexts were compared: (1) carousel feeding, a cooperative foraging context, and (2) seiner foraging, a noncooperative foraging context. Our hypothesis was that killer whale schools used specific call types to coordinate different foraging contexts. Also, when comparing social to non-social foraging contexts, social foraging requires conspecifics to be alerted and the subsequent coordination of the group's behaviour; therefore, acoustic activity in general is hypothesised to be higher during social foraging compared to non-social foraging. To compare foraging activity between contexts, the activity of two foraging-associated sounds was measured during both contexts. First, tail slaps, which are used to stun herring once the shoal has been herded in a ball-shaped form and, secondly, echolocation clicks, which are used to localise prey. Tail-slap activity was expected to be higher during carousel foraging since during seiner foraging, the majority of fish in the nets are already stunned or dead. Echolocation activity was hypothesised not to differ between foraging contexts since in both situations prey items need to be localized.

Materials and Methods

This study was carried out in the Tysfjord area, near the Lofoten islands, Norway (Figure 1; 68° 17' N/16° 3.2' E) between 9 and 27 November 2002. Killer whales occur frequently in this area from October to January, following the Norwegian spring-spawning herring (*Clupea harengus*), which form the killer whales' primary prey in their wintering grounds.

Weather permitting, daily surveys were conducted throughout Tysfjord. Surveys were carried out in weather conditions of \leq Beaufort 3. Each time we found a school of killer whales, we classified this as a new encounter. A school was defined as a discrete group of animals coordinating behaviour over periods of minutes to hours (Chilvers & Corkeron, 2001; Conner et al., 1998). During each encounter, we determined group

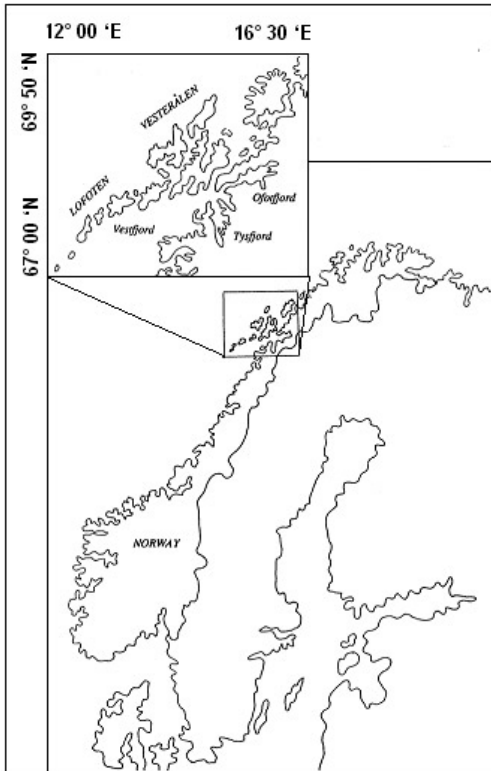


Figure 1. Underwater calls of feeding killer whales were recorded in the Tysfjord area of Norway; see insert.

composition and size. Behaviours were recorded (Chilvers & Corkeron, 2001) as (1) traveling defined as swimming in a consistent direction with regular surfacing intervals; (2) motionless defined as slow or minimal movements at the surface with a tendency for animals to remain or spend long periods of time within the same area; (3) active surface defined as behaviour that included interactions with other school members; and (4) foraging defined by dives of changeable duration, frequency, and length or by erratic movements at the surface, indicative of chasing fish.

Acoustic recordings were only made when a school was foraging. Frequently, fish scales, pieces of fish, or stunned fish were observed among feeding killer whales. We discriminated between the two predominant foraging contexts observed in Norwegian killer whales while foraging on spring-spawning herring. The first type was carousel foraging, a cooperative hunting method whereby whales herd herring into a tight ball close to the surface and then stun them by hitting the ball with their flukes. Whales subsequently eat the stunned fish one by one (Similä & Ugarte, 1993). Given that the killer whales follow the spring-

spawning stock of herring into the Tysfjord area, this foraging behaviour is the dominant form of foraging behaviour observed during this period of the year. The second type was seiner foraging wherein whales gather around fishing boats to forage on herring discards around the nets. See Fertl & Leatherwood (1997) for a review of the many ways in which cetaceans exploit fisheries to obtain food.

Other foraging contexts, which could not be classified as either carousel or seiner feeding but consisted, for example, of individual whales or loosely associated groups performing lunges, presumably chasing cod (*Gadus morhua*), saithe (*Pollachius virens*), or small patches of herring, were not included in this study. This category was too broad to use in the scope of this study.

The distance between the inflatable boat and a school during acoustic recordings varied between 5 m to approximately 70 m. During both carousel and seiner foraging contexts, whales concentrated in the area where the prey was. Given our proximity to the whales and the fact that the whales were not spread out over a large area during recordings, we are confident that calls, echolocation clicks, and tail-slap sounds were picked up by the recording equipment. Acoustic recordings were made using a High Tech Inc. hydrophone (model HTI-96-MIN, Gulfport, MI; sensitivity -170 dB, flat frequency response from 5 Hz to 30 kHz \pm 1.0 dB) connected to a Sony digital audiotape recorder (TCD-D8; linear frequency response from 5 Hz to 22 kHz). The hydrophone was hung from the side of the boat and was at an average depth of 2 to 3 m under water during recordings.

The acoustic recordings were played and then resampled (sampling frequency 22 kHz, dynamic range = 170 dB) using *Gram Version 5.0.6* software (Horne, 1998). Additionally, video-recordings made between 14 and 17 of November 1992 by Domenici et al. (2000) of encounters with carousel feeding killer whales were used for acoustic analysis (see Domenici et al., 2000, for technical details of the video-equipment). The sounds of carousel foraging killer whales were digitised from video (frequency range 80 Hz-8 kHz; sampling frequency 22 kHz; dynamic range 170 dB) using *Gram* software (Horne, 1998). Killer whale calls and foraging-associated sounds from video were treated in the same way as the acoustic recordings made in 2002 during subsequent analysis.

Spectrographic analyses of the sounds were conducted using *Batsound Version 2.0* software (Pettersson Elektronik, Uppsala, Sweden). All calls were separated into four different categories—very poor, poor, medium, and good—based on the quality of the spectrogram (Fast Fourier Transforms, time resolution [dt]: 10 ms,

frequency resolution [df]: 102 Hz, FFT size: 512). Only medium and good quality calls were used in these analyses.

Using overall spectrogram call-shape, discrete calls were type-identified using an existing catalogue on Norwegian killer whale calls developed by Strager (1993). Calls that were not identifiable from the catalogue, but were present twice or more were assigned a new catalogue number. To minimise observer error, all classifications were crossvalidated by a second observer. Discrete calls were composed of one distinct component or more, visually detectable by abrupt shifts in pulse repetition rate (Ford, 1989; Moore et al., 1988). For each component within a call (Figures 2A & 2B), two parameters were measured: the duration (s) and the frequency of most energy (kHz). Variable calls exhibit a great variety of forms, ranging from trills and squawks to buzzes (Ford, 1989). Because of the large variation within these call types, we only classified the buzz as a repeatedly observed pulsed call type. Whistles typically exhibit a nonpulsed waveform, which appears in the spectrogram as a narrow-band tone, with its primary energy above 5 kHz

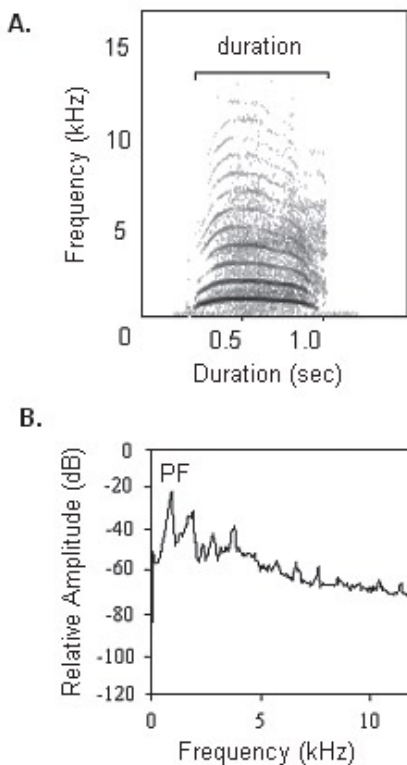


Figure 2. Measurements from (A) the spectrogram of a Norwegian killer whale call, showing duration in s; and (B) the power spectrum, showing the peak frequency (PF)

and little harmonic or side-band structure (Ford, 1989; Steiner et al., 1979; Thomsen & Frank, 2001; Thomsen et al., 2002). No classification within whistle types was made because of their extreme structural variability (Ford, 1989); however, for each whistle, duration (s) and frequency of most energy (kHz) was determined. Patterns in discrete call type usage during carousel and seiner foraging contexts were explored using *SPSS Version 11.0* software, discriminant function analysis, and two-tailed *t* tests.

To compare calling activity between both foraging contexts, calling activity was expressed as the number of calls per s. Subsequently, calling activity was related to the number of individuals present during the encounter. All visible calls on the spectrogram were included in the counting.

The number of different call types used during each encounter also was compared between both foraging contexts.

Tail-slap activity was compared for the two foraging contexts. Tail slaps are known to be used by killer whales during carousel foraging to stun herring once the shoal has been in herded in a tight, ball-shaped form (e.g., Similä & Ugarte, 1993). Tail slaps produce short banging sounds characterised by a slow onset, usually occurring during bouts of calling activity. They exhibit a “signature” power spectrum marked by a peak in the frequency of most energy around 0.25 kHz along with a typical curved shape (Marten et al., 1986). Tail-slap activity for each encounter was determined by counting the number of audible tail slaps using the signature power spectrum and subsequently relating the number to encounter duration and to the number of individuals present. Echolocation click activity was estimated by counting the number of echolocation clicks for each foraging encounter and subsequently relating the number to encounter duration and to the number of individuals present. Due to the limited frequency range of the video recordings, the echolocation clicks were counted from the spectrograms of the acoustic recordings only.

Results

Acoustic recordings of foraging killer whales were made during 18 encounters. The number of individuals during each encounter varied from 6 to 16 during carousel foraging ($n = 16$, total recording duration = 615 min) and 65 to 180 individuals during seiner feeding ($n = 2$, total recording duration = 78 min). The mean duration for encounters with carousel foraging killer whales was 2,309 s (SD = 2,143 s) and 2,336 s (SD = 793 s) for encounters with seiner foraging whales. After quality selection, a total of 1,922 calls were suitable for analyses. Of these, 1,721 were recorded

during carousel foraging and 201 were recorded during seiner foraging.

The discriminant analysis showed that 100% of the call types were correctly grouped according to foraging context ($\chi^2 = 26.16$, $DF = 15$, $p = 0.036$). This result suggested that there were categorical differences in call types between the two contexts. We found no discrete call types to be exclusively associated with one particular foraging context, however; therefore, the relationship between call types and foraging context was explored further by determining the occurrence of different call types during a given foraging context (Figure 3A-3E). At the start of the study, we hypothesised that if a call type was used specifically during a particular foraging context, it would occur at a higher rate compared to the other context. Therefore, we tested for differences in occurrence of the call types relative to the duration of the encounter for both foraging contexts, using two-tailed *t*-tests.

We found one call type (type N21; Strager, 1993) that occurred significantly more often during seiner foraging than during carousel foraging ($n = 58$, $t = -4.45$, $p < 0.001$).

Next, calling activity, measured as the number of calls per s, and the number of different call types used between foraging contexts was compared in relation to group size. It was possible to estimate group size during 10 of the 18 encounters. Of these, eight encounters were during carousel and two were during seiner foraging context. For carousel foraging whales, the number of calls per group member varied greatly with group size. For the two seiner foraging encounters, call rate was highest for the encounter with the smaller group (Figure 4). The number of different call types used per encounter followed a similar trend for both foraging contexts (Figure 5).

Tail-slap behaviour also was compared between foraging contexts. For most carousel encounters,

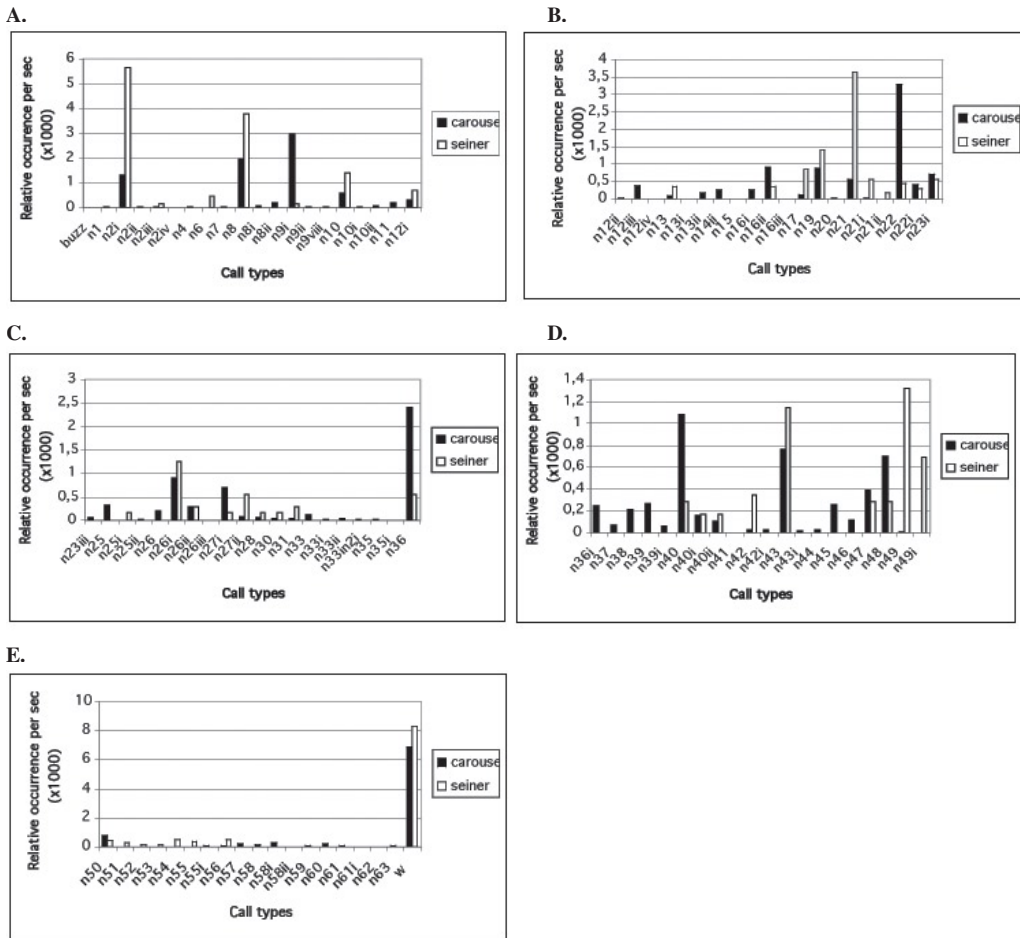


Figure 3. Relative occurrences of killer whale call types (A-E) per s ($\times 10^3$) for carousel and seiner foraging encounters

the number of tail slaps per s was higher compared to seiner foraging encounters (Figure 6).

For encounters with good quality spectrograms, the number of individual echolocation

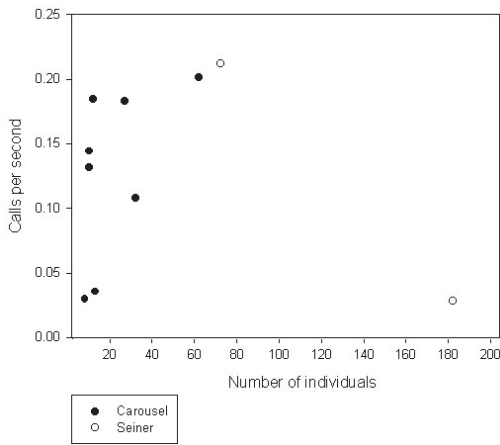


Figure 4. Calling activity measured as the number of calls per s of recording time in relation to the number of individual killer whales present during carousel ($n = 8$) and seiner ($n = 2$) feeding contexts

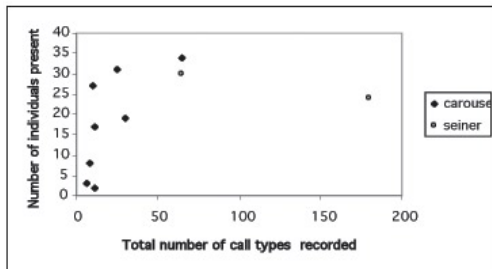


Figure 5. The total number of different call types recorded in relation to the number of individual killer whales present for carousel ($n = 8$) and seiner ($n = 2$) foraging context

clicks was counted to obtain a measure of foraging activity. This measurement was expressed as echolocation clicks per s of recording time. A total number of nine encounters were included of which seven were carousel and two were seiner foraging (Figure 7). For carousel and seiner foraging encounters, the number of echolocation clicks per s increased with the number of individuals in the group.

Acoustic properties of the call type that was found to occur more during seiner foraging than during carousel foraging were compared to the literature values of this call type (Table 1). The table shows this study's measurements of the duration

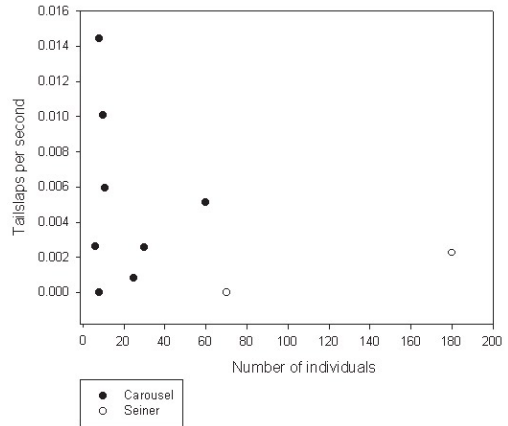


Figure 6. Average number of audible tail slaps per s of recording time in relation to the number of individual killer whales present during carousel ($n = 8$) and seiner ($n = 2$) feeding contexts

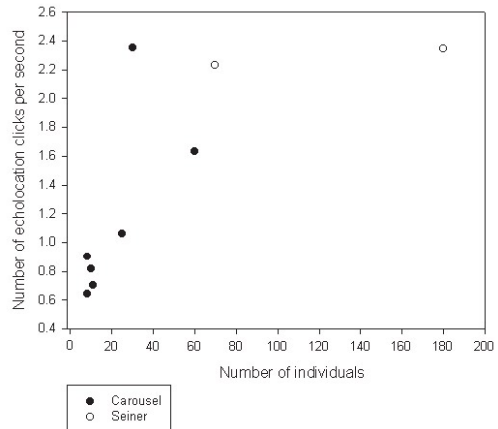


Figure 7. The number of echolocation clicks per s of recording time in relation to the number of individual killer whales present during carousel ($n = 7$) and seiner ($n = 2$) feeding contexts

of call type N21 differ from those reported in the literature (Strager, 1993).

Discussion

This study compared a cooperative to a noncooperative foraging context and aimed to determine whether there were specific call types used exclusively during carousel or seiner foraging contexts. The analyses identified no context that was associated exclusively with the occurrence of any particular call type; however, comparisons of call usage between foraging contexts did reveal a difference in the mean occurrence of one call

Table 1. Acoustic characteristics of call type N21; characteristics measured during this study are indicated with “2003,” and those derived from Strager (1993) are indicated with “1993.” Acoustic parameters compared are mean duration = mean duration in s, max duration = maximum duration in s, min duration = minimum duration in s, mean pf = mean peak frequency (kHz), max pf = maximum peak frequency (kHz), min pf = minimum peak frequency (kHz), *n* 2003 = the number of calls per call type recorded in 2003.

Call type	Mean duration	Max duration	Min duration	Mean pf	Max pf	Min pf	<i>n</i>
Year	2003	2003	2003	2003	2003	2003	2003
Year	1993	1993	1993				1993
N21	0.61	1.42	0.20	3.08	7.85	1.09	58
	1.36	1.63	1.02				19

type. These findings are comparable to those of Ford (1989) for resident killer whales in British Columbia, Canada. He found that no specific call types were linked exclusively to any of the analysed behavioural contexts, but that there was a difference in mean occurrence of call types when different behaviours were compared. This study found no call types exhibiting a higher mean occurrence during carousel than seiner foraging encounters. Isolated calls might therefore not be of major importance in the coordination of a carousel. Humpback whales use a specific sequence of calls during their coordinated foraging behaviour (D’Vincent, 1985), in which case coordination of a carousel might require detailed communication, which is only achieved through the use of a sequence of calls rather than isolated call types.

The Norwegian killer whale population is known to closely follow the movements of Norwegian spring-spawning herring, their primary prey (Similä et al., 1996). The herring moves seasonally between offshore and coastal waters. The adult and adolescent herring move in autumn into fjords to await spring to spawn (e.g., Huse et al., 2002). The large concentration of herring gathered in the Vestfjord-fjord complex attracts a large number of fishing boats during the autumn and winter season. Many marine mammal species have modified their foraging behaviour to take advantage of industrial fishing activities (Fertl & Leatherwood, 1997). Bottlenose dolphin communities specialise in foraging from prawn trawlers, anticipating their movements by using the sounds of the boats’ engines (Chilvers & Corkeron, 2001). Similarly, in the Norwegian situation, the sounds of the seining activities should be detectable by whales over several km, and whales often are observed gathering around the boats to forage from the fishing nets when these are drawn in (Tiu Similä, pers. comm.); however, foraging in a noisy environment may limit acoustic communication due to auditory masking (e.g., Richardson et al., 1995). This may have consequences for communication

and may be a possible explanation for the differences in duration of call type N21 found between this study’s measurements and those reported in literature (Strager, 1993). This call type might be thought to exhibit acoustic characteristics that prevent masking by engine noise. Many cetacean species—for example, gray whales (*Eschrichtius robustus*), belugas (*Delphinapterus leucas*), and bowhead whales (*Balaena mysticetus*)—respond to high background noise levels by modifying call types or the frequencies of the sounds they produce (Richardson et al., 1995); however, more data on acoustic behaviour of killer whales in situations where background noise is high, as well as during differing foraging contexts, is needed to explore these possibilities further.

Since noncooperative foraging requires little or no group coordination compared with social cooperative foraging, we hypothesised that the necessity to call frequently or use specific call types would be lower during seiner foraging compared to carousel foraging. This hypothesis agrees with our finding that there was a lower number of calls per individual during seiner foraging context. The number of different call types used per individual was also lower for seiner foraging encounters than for carousel encounters. The usage of specific sequences of call types when the whales are coordinating a carousel might cause the total number of calls and the number of different call types used per individual to be higher during carousel foraging than during seiner foraging.

Audible tail slaps were more frequently present in recordings made during carousel foraging when compared to seiner foraging encounters, irrespective of the number of whales in a school. During seiner foraging, the fish foraged upon by the whales were already dead, stunned, or crushed in the nets and so did not require the active use of tail slapping. The number of audible tail slaps might be argued not to be a representative measure for the actual number of tail slaps; however, when analysing the video recordings of carousel

foraging killer whales, very few tail slaps were visible but not audible. Since tail slapping was estimated in the same way for both foraging contexts, we believe that the number of audible tail slaps can function as a representative for the actual number of tail slaps and can be compared between both foraging contexts.

Prey detection was hypothesised not to differ between foraging contexts since all prey, whether stunned during catching in nets or stunned by tail slaps during carousel foraging, were detected by means of echolocation. This accounts for our finding that echolocation activity increased with the number of individuals, irrespective of foraging context. Barrett-Lennard et al. (1996) studied the echolocation activity of Alaskan resident and transient killer whales off British Columbia and found echolocation use per individual to decrease with increasing number of individuals for both populations. This finding suggests the sharing of information between foraging individuals. The difference in findings of the study by Barrett-Lennard et al. and the present study may reflect the difference in prey species and foraging strategy between the Alaskan and Norwegian resident populations.

The bandwidth of the video recordings was very narrow compared to the bandwidth of the acoustic recordings that were made in 2002. This biases which calls are detected and measurable acoustic properties; however, most killer whale calls occurred within the frequency range of the video recordings. The exception to this was that the average frequencies of echolocation clicks were found to be partly outside the frequency range and were therefore counted only from the spectrograms of the acoustic recordings.

The fact that the majority of call types recorded during this study could be classified using the catalogue by Strager (1993) shows that the two studies are comparable. Comparing Norwegian call types to the ones found by studies conducted in British Columbia, Canada, is less straightforward since both catalogues use different names for the same call types. In British Columbia, Ford (1989) reported call types N2, N4, N5, N7, and N9 to be most abundant when whales were foraging. These call types resemble other call types that also have been classified during this study but are not the call types found to occur most often during foraging behaviour in the Norwegian situation. None of the foraging events studied by Ford (1989) involve carousel foraging nor seiner foraging events, however. Instead, recordings were made during foraging behaviour that this study classified as "other" foraging behaviour, characterised by individual chases and lunging behaviour. If foraging behaviour is associated with specific call types, the difference in foraging context between the studies on killer

whales in British Columbia, Canada, might explain the difference found in predominant call types used. Yet, for these comparisons to be made, more data on calling behaviour of killer whales in comparable foraging contexts is needed.

This study found one call type that exhibited a higher mean occurrence during seiner foraging than during carousel foraging. It cannot be ruled out that this call type represents a pod-specific dialect call (Ford, 1989, 1991; Strager, 1995). A next step in the study of killer whale calling behaviour, therefore, is the analyses of foraging calls of known pods to determine to what extent differences in call types used during foraging reflect context-specific call types or pod-specific dialects. Identification of groups of killer whales also could investigate whether all groups of whales take part in either foraging contexts or whether communities have specialised on a particular foraging context. This would require a long-term study of killer whale calling behaviour in combination with photo-identification of groups of whales.

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