

The relationship between the acoustic behaviour and surface activity of killer whales (*Orcinus orca*) that feed on herring (*Clupea harengus*)

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Abstract We describe the acoustic behaviour of piscivorous killer whales in Norwegian and Icelandic waters. Whales were assigned to one of three activities (feeding, travelling or other), and sound recordings were made in their proximity with a single hydrophone and a digital audiotape (DAT) recorder. A quantitative analysis of the production of pulsed calls, whistles and echolocation clicks in the three activities revealed that there was a significant effect of activity on the production of these sound types. Both killer whales in Icelandic and Norwegian waters produced high rates of clicks and calls during feeding and low rates of click, calls and whistles during travelling. The differences can be used as acoustical markers and provides new possibilities for acoustic monitoring of killer whales in these areas. Based on the similarity between their prey choice, hunting strategies, phenotype and acoustic behaviour, we suggest that the killer

whales in Icelandic and Norwegian waters belong to the same ecotype: Scandinavian herring-eating killer whales.

Keywords Acoustic behaviour · Killer whale · *Orcinus orca* · Scandinavian waters

Introduction

The relationship between acoustic behaviour and activity has been studied in several species of toothed whales (e.g. Sjare and Smith 1986; Ford 1989; Weilgart and Whitehead 1990; Janik 2000; Thomsen et al. 2002; Deecke et al. 2005; Van Opzeeland et al. 2005). All of these studies showed that the animals produce sounds at different rates and/or of different types depending on their activity.

The acoustic behaviour of killer whales (*Orcinus orca*) is especially interesting because killer whales worldwide specialise in different prey species and use a variety of hunting strategies (Baird 2000), and their rates of sound production are influenced by the type of prey (Barrett-Lennard et al. 1996; Deecke et al. 2005).

The acoustic behaviour of killer whales has been best studied in two sympatric ecotypes from the coastal waters of the northeast Pacific, known as transients and residents (Ford 1989; Morton 1990; Barrett-Lennard et al. 1996; Thomsen et al. 2002; Deecke et al. 2005), as well as in two apparently separated populations in Norway and Iceland (Moore et al. 1988; Strager 1995; Van Parijs et al. 2004; Simon et al. 2005–2007; Van Opzeeland et al. 2005). The northeast Pacific resident killer whales feed on salmon, *Oncorhynchus* sp., whose hearing is poor in the frequency range of killer whale sounds (Richardson et al. 1995). These whales are acoustically active during foraging (Ford 1989; Barrett-Lennard et al. 1996). Northeast Pacific

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transient killer whales feed on marine mammals, which have a well-developed sense of hearing. To avoid acoustic detection by their prey, transient killer whales are practically silent while foraging (Deecke et al. 2005). The majority of killer whales in Norway and Iceland feed on Atlantic herring, *Clupea harengus* (Christensen 1982; Sigurjónsson and Leatherwood 1988). Despite the fact that herring have a well-developed sense of hearing, it has been reported that killer whales in Norwegian and Icelandic waters are acoustically active during foraging (Similä and Ugarte 1993; Simon et al. 2005–2007). However, the sound production of killer whales in Norwegian and Icelandic waters has not yet been studied in detail in relation to activity other than feeding (Simon et al. 2005, 2006; Van Opzeeland et al. 2005).

Killer whales produce three types of sounds: echolocation clicks, whistles and pulsed calls (Ford 1989). Echolocation clicks are short-duration, broadband pulses used for navigation, location of prey and conspecifics, and possibly for communication (Evans 1973; Ford 1989; Au et al. 2004; Simon et al. 2007). Whistles are sinusoidal sounds (Ford 1989; Thomsen et al. 2001). Thomsen et al. (2002) suggested that northeast Pacific resident killer whales use whistles for short-range communication, mainly during socialising. Some whistles seem to be shared among killer whales of different groups that interact and interbreed (Riesch et al. 2006).

Pulsed calls (hereafter referred to as calls) are signals consisting of several short pulses emitted at such a high repetition rate that they sound tonal to humans. Northeast Pacific resident killer whales have group-specific repertoires of pulsed calls that reflect the maternal genetic relationship of the groups (Ford and Fisher 1982, 1983; Ford 1991). Killer whales in Norway and Iceland also seem to have group-specific call dialects (Moore et al. 1988; Strager 1995). In addition, the structure of some killer whale calls seems to be adapted to specific functions, such as maintaining the spatial geometry of travelling groups (Miller 2002) or herding prey (Simon et al. 2006).

Killer whales in Iceland and Norway use underwater tail-slaps to debilitate herring before eating them (Similä and Ugarte 1993; Domenici et al. 2000; Simon et al. 2005). The underwater tail-slaps produce a characteristic multi-pulsed broadband sound (Simon et al. 2005). These sounds are probably produced by cavitation and physical impact of the killer whale tail on herring, and the sound is, thus, a by-product of the tail-slap rather than a sound specifically produced by the killer whale (Domenici et al. 2000; Simon et al. 2005).

Although the acoustic repertoires of killer whale populations are not completely understood in functional terms, the use of the various sound types generally depends on activity. The aim of this study was to quantitatively

describe the relationship between sound production and the activity of herring-eating killer whales in Icelandic and Norwegian waters to investigate whether sounds can act as markers for different activities.

Materials and methods

We made recordings off southern Iceland for 17 days (19 June to 31 July 2002) using a custom-built hydrophone (Woods Hole Oceanographic Institute, frequency response flat within ± 4 dB up to 20 kHz). Sound recordings of Norwegian killer whales were made in Vestfjord and adjacent fjords from October to December 2000 and 2001, using a hydrophone produced by *Offshore Acoustics* (frequency response flat within ± 4 dB up to 14 kHz). In both areas, the hydrophones were deployed at depths of 2 to 5 m and connected to a Sony TCD-D8 digital audio tape (DAT) recorder (flat frequency response, 0.1–22 kHz). Water depths were 20–150 m in Iceland and 50–700 m in Norway. Recordings in Iceland were made from a 12-m gaff-rigged sloop and, in Norway, either from a 12-m ketch or from a 10-m cabin cruiser.

When a group of stationary killer whales had been located, the boat was placed approximately 30 m upwind and the engine switched off so that the boat could drift across the activity spot while recording. When a group of moving killer whales had been located, the boat was placed approximately 100 m ahead of the whales, and the engine was switched off while recording. These procedures resulted in minimal disturbance to the herring and whales.

Additional recordings of killer whales engaged in feeding activity in Norway were extracted from underwater videotapes obtained in 1992 (the methods are described in detail in Similä and Ugarte 1993; Domenici et al. 2000; Simon et al. 2005). During those recordings, an Offshore Acoustics hydrophone was placed at a depth of 1.5 m from a 3.7-m rubber boat. The hydrophone was connected to the audio channel of a video 8 recorder. When necessary, an electric engine was used to keep the boat in the proximity of killer whales. An underwater video camera was rigged beneath the boat and connected to a monitor and to the video channel of the video recorder.

To avoid pseudo-replication, we did not make two consecutive recordings of the same group of killer whales, unless it was engaged in a different behaviour. To avoid biases due to group-specific dialects, we attempted to spread the recordings across as many different killer whale groups as possible. A few individuals in most killer whale groups have conspicuous natural markings that allow the observer to distinguish between groups (Bigg et al. 1990).

The surface activity of the killer whales was identified as “feeding”, “travelling” or “other”. Feeding activity was

defined as whales facing in different directions when surfacing, seabirds taking fish close to the whales, herring or parts of herring visible on the surface, whales arching their body before diving, whales breaking the surface with the head up to the flippers when breathing or whales hitting the water surface with the underside of the fluke (Ugarte 2001). Ugarte (2001) concluded that killer whales travelling in Norway perform few individual behaviours, move in a straight line at a speed of 2–5 knots, with all the individuals usually facing in the same direction when surfacing and either arranged with no clear geometrical formation or in a line abreast. In this study, travelling activity was defined as whales swimming in a constant direction. We did not differentiate between travelling for the purpose of moving from place to place and travelling that incorporated activities such as searching for prey, resting or socialising. Other activity was defined as activities performed by stationary killer whales that were not feeding. Other activity included a range of different behaviours, such as resting, playing and socialising (Ugarte 2001).

The reproductive state of the herring influences their schooling behaviour (Nøttestad et al. 1996, 2002). At the time of the recordings in Norwegian waters, the Norwegian spring-spawning stock of herring was wintering in the fjords. The recordings in Icelandic waters were made during summer on the spawning grounds of the Icelandic summer-spawning herring stock. To examine their reproductive status, herring immobilised by the killer whales in Iceland were dissected and classified as (1) “ready to spawn/ejaculate” if the gonads were turgid with egg/sperm, in some cases, dripping from the opening; (2) “having recently spawned/ejaculated” if the gonads were still distended but flaccid and empty from egg/sperm or (3) “not ready”, if the fish was in a more “normal” state with no signs of recent or of imminent spawning or ejaculation.

Analysis

Sounds were digitised on a computer with a sampling rate of 48 kHz, using Adobe Audition (Adobe Systems) and a sound card with built-in anti-aliasing filter.

One 5-min section of each recording was randomly chosen for further analysis. Each 5-min section was divided into 60 5-s parts. Each 5-s part was analysed for the occurrence of echolocation clicks, calls and whistles. Due to the difficulty of separating overlapping sounds and to minimise biases due to recordings of different numbers of animals, we chose to rate the occurrence of sounds as presence/absence in each 5-s part, rather than to count the actual number of sounds.

We did not take intra-group variance in sound emission into account, which would require locating and following sound-producing individuals. For this, it is necessary to use

techniques that were out of the scope of this paper, such as recording devices attached to a number of individuals in the group.

The occurrence of echolocation clicks in each 5-s part was categorised into one of four classes: (0) no clicks; (1) separate clicks, no buzzes; (2) separate clicks and buzzes; and (3) constant clicks and buzzes. Two clicks were considered as “separate clicks” if there was >10-ms interval separating them. The influence of activity on the production of echolocation clicks was tested with Kruskal–Wallis test (Fowler and Cohen 1996).

The occurrence of calls and whistles was quantified by the number of 5-s parts in each 5-min section with calls or whistles. The influence of activity on the production of pulsed calls and whistles was tested with nonparametric two-way analysis of variance (ANOVA; Barnard et al. 2001).

Results

In Iceland, three to seven groups, each containing about ten killer whales, were regularly found feeding from the morning until midnight on a specific shallow ground. In Norway, killer whale groups were usually spread over larger distances, and it was difficult to predict where to find them. Various species of gulls (*Larus* sp.) took fish among foraging whales in both areas. Northern gannets (*Morus bassanus*) and fulmars (*Fulmarus glacialis*) were observed feeding among killer whales in Iceland, while in Norway, white-tailed eagles (*Haliaeetus albicilla*) and kittiwakes (*Rissa tridactyla*) were observed (although birds of the family Alcidae were abundant in Iceland, we did not observe them feeding among killer whales). In both areas, herring was the only prey species observed. Stunned herring collected from among feeding killer whales in Iceland ($N=8$) were either about to spawn/ejaculate or had just spawned/ejaculated.

Surface observations of travelling killer whales were similar in both areas. We observed two different patterns of travelling in Iceland: (a) relatively short displacements (<10 km) made between 6 A.M. and 10 P.M. and (b) long loops of up to 75 km that started in the feeding areas around 12 P.M. and ended in the same feeding areas before 10 A.M. Due to the short day lengths and difficulties of following whales in open waters during the winter in northern Norway, we were not able to follow travelling killer whales in Norway for long periods of time.

We analysed a total of 205 min of recordings of killer whales in Norway ($N=13$ recordings of feeding, 10 recordings of travelling and 18 recordings of other) and 210 min of recordings of killer whales in Iceland ($N=12$ recordings of feeding, 9 recordings of travelling and 21 recordings of other).

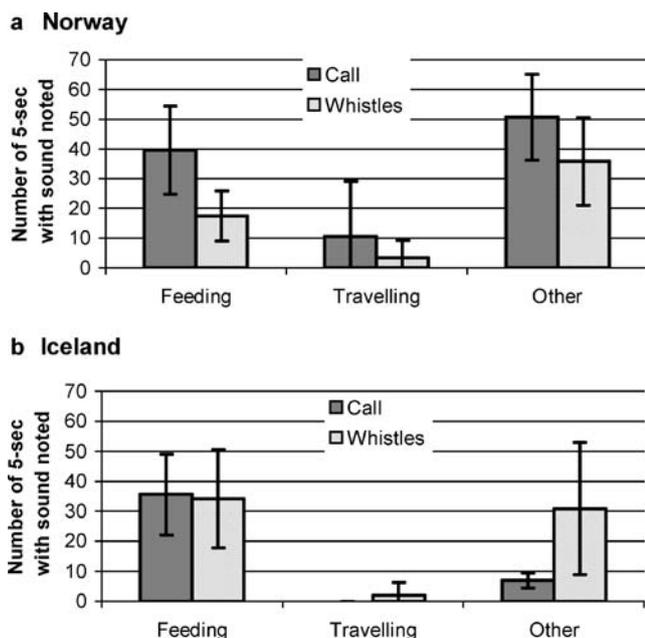


Fig. 1 Number of 5-s periods with calls and whistles in recordings of killer whales (+/- standard deviation). **a** In Norwegian waters. There was a significant effect of activity ($N=13$ recordings of feeding, 10 recordings of travelling and 18 recordings of other) on the production of calls and whistles (nonparametric two-way ANOVA test; calls, $H=29.71$, $P>0.01$; whistles, $H=20.19$, $P>0.01$). **b** In Icelandic waters. There was a significant effect of activity ($N=12$ recordings of feeding, 9 recordings of travelling and 21 recordings of other) on the production of calls and whistles (nonparametric two-way ANOVA test; calls, $H=16.38$, $P>0.01$; whistles, $H=24.97$, $P>0.01$)

There was a significant effect of activity on the production of calls and whistles (Fig. 1). Whales in Iceland and Norway produced fewer calls and whistles while travelling compared with feeding and other activities. Activity also had a significant effect on the category of echolocation clicks used by the killer whales both in Iceland and Norway (Table 1). The majority of the recordings of travelling killer whales in both Norwegian

and Icelandic waters were assigned to click categories 0 and 1. Most recordings of whales feeding were assigned to click category 3 in Norway and 2 in Iceland. The recordings of killer whales in other behaviours were assigned to click categories 1 and 2 in both areas. This means that the whales echolocated most while feeding and least while travelling, and other was intermediate (Table 1).

Discussion

One aim of this study was to investigate whether particular sounds were associated with the different activities of killer whales; if so, they could be considered acoustic markers. Simon et al. (2006) adopted this approach with underwater tail-slaps from the same recordings as analysed in this study. They found that feeding was the only activity where underwater tail-slaps were heard; they occurred during 80% of the recordings of killer whales feeding in Norwegian waters and in 100% of the recordings of killer whales feeding in Icelandic waters.

Besides being the only activity when underwater tail-slaps were heard, feeding activity was, in the present study, characterised acoustically, both in Iceland and in Norway, by being the only activity where echolocation clicks were heard constantly and at a high rate (Table 1). During this activity, calls were also produced at high rates (Fig. 1).

Travelling killer whales were silent in nearly all the recordings made in Norway and in all but two of the recordings made in Iceland. Other observations suggest that the two recordings in which sounds were recorded from travelling killer whales in Iceland were atypical. The first recording (30 July 2002) was of a group of killer whales shortly before they stopped travelling and engaged in other activity. The second recording made on the same date but at midnight was the only recording made in darkness (earlier and during most of the study, there was no real darkness at

Table 1 Category of echolocation clicks (0=no clicks; 1=separate clicks, no buzzes; 2=separate clicks and buzzes; 3=constant clicks and buzzes; for further details see “Materials and methods”) used by killer whales in relation to activity

Activity	Click category 0 (%)	Click category 1 (%)	Click category 2 (%)	Click category 3 (%)	Sum
Norway					
Feeding	0 (0)	0 (0)	0 (0)	13 (100)	13
Travelling	5 (50)	3 (30)	2 (20)	0 (0)	10
Other	0 (0)	6 (33)	11 (61)	1 (6)	18
Iceland					
Feeding	0 (0)	0 (0)	12 (100)	0 (0)	12
Travelling	5 (56)	3 (33)	1 (11)	0 (0)	9
Other	0 (0)	5 (24)	16 (76)	0 (0)	21

The activities had a significant effect on the category of echolocation clicks used by killer whales in Iceland (Kruskall–Wallis, $K=15.00$, $N=42$, $P<0.01$) and in Norway (Kruskall–Wallis, $K=28.12$, $N=41$, $P<0.01$).

night in Iceland). Travelling animals that are not in visual contact might produce more sounds to keep group cohesion. Echolocation clicks are highly directional and will only be recorded in front of the echolocating animal if the hydrophone is at a distance from the whale. This, however, does not explain the lack of echolocation found in this study from travelling killer whales, as the recordings were made in front of the whales (see “[Materials and methods](#)”).

In Norway, whistles were more common during other activity than during feeding and travelling. In contrast, the acoustic behaviour of killer whales in Icelandic waters engaged in other activity was difficult to distinguish acoustically from feeding based on the occurrence of clicks, calls and whistles. However, underwater tail-slap thuds were strongly associated with feeding behaviour (Simon et al. 2006); thus, the occurrence of clicks, calls and whistles coupled with the absence of underwater tail-slap thuds could be considered as an acoustic marker for other activity in Iceland. The variety in the occurrence of clicks, calls and whistles during other activity in Iceland could be explained by the fact that this category can include a broad variety of activities, such as sexual, aggressive and affiliative behaviours or resting.

The recordings in Iceland were made during summer where the dark hours are few and the visibility under water is poor. These whales feed upon herring, which were spawning in shallow areas. Schools of spawning herring settle on the bottom and have small vertical extent and low density compared to non-spawning schools (Nøttestad et al. 1996). In contrast, the recordings in Norway were made during winter when the light hours are very few and the underwater visibility is extremely good (>30 m). These killer whales were feeding on wintering herring, which are less predictable, school strongly and are often difficult to reach in the depths of the fjords (Nøttestad et al. 2002). Despite the differences in the environment, our study showed the acoustic behaviour of the whales recorded in Iceland and in Norway to be remarkably similar. Besides having similar acoustic behaviour, killer whales in Icelandic and Norwegian waters have a number of common traits: Both follow migrating herring throughout the year (Similä et al. 1996; Sigurjónsson and Leatherwood 1998) and use similar hunting techniques that include herding and debilitating herring schools with the help of bubbles and using underwater tail-slaps (Sigurjónsson et al. 1988; Similä and Ugarte 1993; Simon et al. 2005). Killer whales in Norwegian and Icelandic waters resemble each other more than northeast Pacific killer whales in their patterns of pigmentation (Visser and Mäkeläinen 2000), as well as in the structure of their calls (Strager and Ugarte 1995). Despite all these similarities, it is unlikely that killer whales in Icelandic and Norwegian waters belong to the same population for two

reasons. First, there have been no matches between killer whales photographically identified in both areas (Similä, personal communication; Ugarte and Simon, personal observation). Second, the migrations of Norwegian spring-spawning and Icelandic summer-spawning herring that the killer whales follow do not extensively overlap in space and time (Jakobsson and Østvedt 1999). We suggest that the herring-eating killer whales in Icelandic and Norwegian waters belong to two different populations of the same ecotype of “herring-eating Scandinavian killer whales”, a situation comparable to the three separate populations of northeast Pacific salmon-eating resident killer whales (Barrett-Lennard 2000).

Although the behavioural categories are defined somewhat differently, there are clear differences in the acoustic behaviour of herring-eating Scandinavian killer whales (this study) and northeast Pacific resident killer whales (Ford 1989; Thomsen et al. 2002). Northeast Pacific resident killer whales have very low click repetition rates and have long periods of silence interrupted by bouts of vocal activity while foraging (Ford 1989). Herring-eating Scandinavian killer whales had high rates of sound production during foraging, with intensive use of echolocation clicks, pulsed calls and tail-slaps, and no periods of silence. Salmon, the prey of northeast Pacific resident killer whales, have a poor sense of hearing and weak schooling behaviour (Hawkins and Johnstone 1978). Unlike salmon, herring have a well-developed sense of hearing and strong schooling behaviour (Enger 1967; Olsen 1990; Sharpe and Dill 1997; Mann et al. 2005). Herring-eating Scandinavian killer whales probably use sounds to herd the herring into tight schools close to the surface (Simon et al. 2006). Differences in the acoustic behaviour between foraging Pacific resident and herring-eating Scandinavian killer whales might be related to the differences in the schooling behaviour and hearing abilities of their respective prey species.

Except for occasional isolated calls and echolocation clicks, herring-eating Scandinavian killer whales travelled in silence both in compact and spread groups. In contrast, northeast Pacific resident killer whales produce high rates of vocalisations (Ford 1989; Miller 2002) when travelling and are only silent when travelling in compact groups (Ford 1989). While northeast Pacific resident killer whales might find it advantageous to acoustically coordinate their movements when travelling in turbid waters in search of a prey with low hearing sensitivity, there are at least two possible adaptive reasons for herring-eating Scandinavian killer whales to travel in silence. First, in an experiment with Pacific herring, Wilson and Dill (2002) showed that the fish react by increasing swimming speed and depth when they detect killer whale echolocation clicks. If Atlantic herring have a similar reaction, detection by the prey would have

serious energetic costs for herring-eating Scandinavian killer whales because they have difficulties herding herring at depths below 180 m (Nøttestad et al. 2002). Therefore, herring-eating Scandinavian killer whales might travel in silence in order to avoid early detection and evasive movement by their prey, just like the northeast Pacific mammal-eating killer whales (Barrett-Lennard et al. 1996; Deecke et al. 2005). Second, herring make sound by emitting air from the anal duct (Wahlberg and Westerberg 2003; Wilson et al. 2004). Scandinavian killer whales might travel in silence to facilitate the detection of their prey by passive listening, as northeast Pacific transient killer whales do when foraging on marine mammals (Barrett-Lennard et al. 1996).

As socialising was a common activity in the other category where whistles were frequently heard, our results are in accordance with the hypothesis that whistles are important for killer whales during close-range social interactions (Ford 1989; Thomsen et al. 2002).

Passive acoustic monitoring (PAM) of cetaceans is a developing field (e.g. Mellinger 2004). PAM studies rely on the identification of acoustic markers together with detailed information on the acoustical characteristic of the different sound types and sound emission rates per individual, including individual variations. In this study, we provide descriptions of acoustic markers that can serve as initial baseline information for PAM of killer whales.

We conclude that similarity in, e.g., colouration, prey choice, hunting strategies and acoustic behaviour suggests that killer whales in Icelandic and Norwegian waters belong to the same ecotype, herring-eating Scandinavian killer whales. The acoustic behaviour of herring-eating Scandinavian killer whales is different from the acoustic behaviour reported from other killer whale ecotypes, supporting the theory that the different choice of prey in killer whale ecotypes influence the acoustical behaviour of the whales. Finally, the surface activity of herring-eating Scandinavian killer whales has a significant influence on the acoustic behaviour, and each activity has its own acoustic markers enabling identification of activity through acoustic monitoring. Future work in this subject would require an increased sample size, extensive analysis of the acoustical characteristics of the different sounds and estimations of the sound emission rates per individual.

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