Vocal behaviour and feeding ecology of killer whales *Orcinus orca* around Shetland, UK

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ABSTRACT: Killer whales *Orcinus orca* are sighted regularly off Shetland, UK, but little is known about their numbers, diet and population identity. We aimed to relate vocal behaviour to diet of killer whales around Shetland in order to investigate population structure and differences in feeding strategies. Fieldwork was conducted in the summers of 2008 and 2009. We located killer whales through a sightings network and shore-based scans and collected photo-ID data, behavioural information, feeding data and acoustic recordings from a small boat. The majority of encounters (n = 14) were of small groups (1 to 15 individuals) travelling close to shore and feeding on marine mammals. Two encounters were with large groups (20+ individuals) feeding on herring *Clupea harengus* farther offshore. Seal-hunting groups vocalised rarely, producing pulsed calls, echolocation clicks and whistles almost exclusively when surface-active or milling after a kill. Herring-eating groups were largely silent during one encounter, but very vocal during the other. Analysis of pulsed calls identified 6 stereotyped call types for seal-hunting groups and 7 for herring-eating groups. No call types were shared between both kinds of groups. The vocal behaviour of seal-hunting groups showed striking parallels to that of Pacific marine mammal specialists and presumably evolved to decrease detection by acoustically sensitive prey. One call type produced by Shetland herring-eating killer whales matched a vocalisation that a previous study had described from Iceland and identified as a possible herding call that may function to concentrate herring during feeding. These findings point to behavioural and dietary specialisation among Shetland killer whales, which should be taken into account when making management decisions affecting these animals.

KEY WORDS: Dietary specialisation · Vocal behaviour · Feeding ecology · Killer whale · North Atlantic

INTRODUCTION

Killer whales *Orcinus orca* are top predators in the marine environment and, being homeotherms, have a high energetic requirement (Williams et al. 2004). It has therefore been suggested that predation by killer whales has a substantial structuring influence in marine ecosystems and could be largely responsible for large-scale declines in pinnipeds and sea otters in the North Pacific (Estes et al. 1998, Springer et al. 2003, Williams et al. 2004). A similar decline has been observed in Scottish waters: harbour seals *Phoca vitulina* in Shetland and Orkney declined by 40% between

2000 and 2006 (Lonergan et al. 2007). Harbour seals are a preferred prey of killer whales in the northeastern Pacific (Ford et al. 1998, Saulitis et al. 2000, Dahlheim & White 2010), and predation on harbour seals has also been reported from killer whales around Shetland and Orkney (Weir 2002, Bolt et al. 2009).

While predation by killer whales could be an important factor in the decline in harbour seals off northern Scotland (Bolt et al. 2009), assessing the impact of killer whale predation requires precise information on abundance, distribution, diet and population identity of local killer whales. Killer whales have been sighted regularly in Shetland waters since the 1970s (Evans

1988, Weir 2002). Published records include sightings of large groups offshore often associated with trawl fisheries for mackerel (Couperus 1994, Luque et al. 2006, Foote et al. 2010), as well as smaller groups close to shore reported to take marine mammals (Evans 1988, Weir 2002, Foote et al. 2010). However, information on the number, diet, social structure and population identity of killer whales around Shetland is currently limited.

As a species, killer whales feed on a wide range of prey including elasmobranchs, teleosts, marine reptiles, birds and mammals (e.g. Rice 1968, Jefferson et al. 1991, Pitman & Dutton 2004, Ford et al. 2011). Research in northeastern Pacific and Antarctic waters suggests a high degree of dietary specialisation, with different sympatric populations specialising on fish and sea mammals respectively (Ford et al. 1998, Saulitis et al. 2000, Pitman & Ensor 2003). The situation in the North Atlantic is less clear. While there is evidence that the diet of some populations is highly specialised, stable isotope analysis suggests that in others, individuals with the same mitochondrial haplotype feed at different trophic levels (Foote et al. 2009), which could point to a greater niche width for these populations.

Studies of the vocal behaviour of different killer whale populations have revealed quantitative and qualitative differences related to dietary specialisation. Like other delphinids, killer whales produce 3 types of vocalisations: echolocation clicks are thought to function primarily for orientation and prey detection, whereas pulsed calls and whistles are thought to be communicative signals (Ford 1989, Thomsen et al. 2002, Janik 2009). Many pulsed calls and some whistles are stereotyped, show population-specific and group-specific variation, and can thus be used to identify acoustic lineages (Ford & Fisher 1982, Yurk et al. 2002, Riesch et al. 2006). In addition, mammal-hunting killer whales in the northeastern Pacific produce echolocation clicks, pulsed calls and whistles at significantly lower rates compared to sympatric fish eaters (Barrett-Lennard et al. 1996, Riesch et al. 2006, Riesch & Deecke 2011). Whereas many fishes have poor hearing sensitivity at the frequencies of killer whale vocalisations, marine mammals can detect killer whale vocalisations at significant distances, and this eavesdropping makes vocal behaviour costly for mammal-hunting killer whales (Barrett-Lennard et al. 1996, Deecke et al. 2002, 2005). The overall amount of vocal behaviour may therefore also provide information about feeding specialisation in other populations.

The objective of the present study was to determine the diet and analyse the vocalisations of killer whales in relation to their foraging behaviour around Shetland. First, we investigated the frequency of occurrence of the different sound types (echolocation clicks, whistles and pulsed calls) to see if usage and behavioural context of vocal activity are more characteristic of mammal- or fish-eating killer whales. We would expect to see much reduced levels of vocal behaviour in groups hunting for acoustically sensitive marine mammals compared to those feeding on fish. Second, we described the stereotyped pulsed calls produced by different groups recorded in Shetland and investigated group-specific variation in call repertoires, which could indicate the presence of several different vocal traditions in Shetland waters.

MATERIALS AND METHODS

Dedicated fieldwork was conducted in Shetland between 22 May and 17 August 2008 and between 29 April and 11 July 2009. We searched for killer whales from elevated points on land and set up a sighting network to obtain information on killer whale movements from ferry personnel, fishing crews and members of the general public. Upon finding whales or receiving sighting information, we launched a 6 m rigid-hulled inflatable powered by two 40 hp outboard engines to approach the animals whenever sea state, weather conditions and daylight permitted.

Identification photographs were taken using digital SLR cameras (Canon EOS 20D, Canon EOS 40D, Nikon D100 or Nikon D700) with telephoto lenses (Canon EF 70–200 mm F2.8 zoom lens, Sigma 100–300 mm F4 EX DG APO HSM zoom lens or Nikkor 300 mm F4 AF-S fixed lens). Whales were assigned 3-digit identification numbers in the order they were first identified. Once sufficient photographs of all group members had been obtained, we followed the animals at a distance of 100 to 500 m for a maximum of 4 h or as long as conditions permitted and used focal group sampling (Altmann 1974) to quantify behaviour and vocal activity. At every surfacing, we noted our distance to the group and its behavioural state. We also recorded any evidence of feeding and collected prey remains whenever possible. We divided behaviour into 'travel', 'slow travel', 'milling', 'surface-active' and 'after kill' using the method of Deecke et al. (2005), which classifies behavioural states depending on the animals' swim speed, surface behaviour and synchronicity. This classification does not make assumptions about whether animals are actively foraging, but in Pacific transient killer whales, confirmed kills are typically preceded by travel, slow travel or milling (Deecke et al. 2005). Distances were estimated and confirmed using laser range finders (Leica Geovid 7×42 BDA) whenever possible. At distances <500 m, estimates typically have an average error of ±11% (Deecke et al. 2005).

Acoustic recordings were made using a towable hydrophone array consisting of 2 AQ-4 transducers (Benthos) with HP-02 pre-amplifiers (Magrec) towed 60 m behind the boat at a depth of approximately 5 to 20 m. Sound was recorded on a Marantz PMD671 solid-state recorder (D&M Professional) with a sampling rate of 96 kHz. The system's frequency response was flat (±3 dB) from 0.1 to 40 kHz. When analysing the context of vocal behaviour, we only included sections when the animals were within 500 m of the boat to minimise the number of faint vocalisations missed. These sections were analysed with Adobe Audition 2.0 (Adobe Systems) using real-time spectral analysis to determine the number of detectable pulsed calls, whistles and echolocation click trains. We also examined any vocalisations for signs of strong multi-pathing, which would suggest that they came from distant animals rather than the focal group. To establish vocal repertoires, quality of pulsed calls was then scored by the first author on a scale from 1 (poor) to 5 (excellent), taking into account the call's signal-to-noise ratio, clarity and overlap with other vocalisations. Frequency contours (fundamental frequency as a function of time) were extracted from calls with a quality rating of 3 and higher using a combination of algorithms (Buck & Tyack 1993, Deecke et al. 1999), and contours were divided into call types using the automated ARTwarp categorisation method of Deecke & Janik (2006). Any categories represented by a single example were not retained, and categories that only differed in 1 part of the call were labelled as sub-types of a common call type.

Only predation events where prey remains were clearly seen, photographed or recovered were listed as confirmed kills. Species identity of the prey was established visually from photographs or through molecular analysis of prey remains. Prey remains were wrapped in aluminium foil and frozen at −20°C without preservative within 10 h after collection. For the molecular identification, DNA was extracted from prey remains using a Qiagen DNeasy kit following the manufacturer's guidelines. The mitochondrial DNA (mtDNA) control region of mammalian samples was amplified with 2 sets of primers, first using universal primers MTCRf and MTCRr (Hoelzel et al. 1998) and secondly using primers L16371 and HI6571 (Lamont et al. 1996) specifically designed for harbour seals. For DNA extracted from fish samples, a 682 bp fragment of the mtDNA control region was amplified using primers Q and B (Lee et al. 1995).

Each 25 µl PCR contained 1 µl extracted DNA, 1× PCR buffer, 1 mM $MgCl_2$, 400 nM of each primer, 0.1 mM mixed dNTPs and 0.1 µl AmpliTaq Gold enzyme (Applied Biosystems). PCR amplifications were performed using an MJ Thermocycler with a 4 min activation step at 95°C, followed by 50 cycles of 95°C for 20 s, 54°C for 20 s, 72°C for 20 s and a final extension period of 72°C for 7 min. The amplified PCR products were purified using the Invitek PCRapace purification kit. Purified products were sequenced in both directions using the PCR primers and ABI sequencing chemistry by a commercial sequencing service (Macrogen, Seoul, South Korea). Sequences were compared with sequences in GenBank using the BLAST algorithm (Altschul et al. 1990).

RESULTS

We sighted killer whales on 22 occasions and obtained usable photo-identification data on 18 of these. Two encounters involved animals for which we had neither feeding data nor acoustic recordings, and these were removed from the analysis. The majority (n = 14) of the remaining encounters were of small groups (1 to 15 individuals) travelling close to shore (often within a few body lengths of the shoreline). The high number of resightings of individuals between the 2 field seasons (Table 1) suggests a small assemblage of animals with a high degree of site fidelity. We confirmed successful predation of marine mammals during 4 encounters (Table 1): prey remains were recovered on 4 July 2008 and 24 May 2009, and both samples were identified as harbour seals by the BLAST algorithm (see the supplement; www.int-res.com/articles/suppl/b013p079_supp.pdf). On 2 July 2008, we photographed a harbour seal being attacked and killed, and on 28 June 2009, we observed a large section of mammalian intestine floating at the surface following an attack. In 2 additional encounters, we observed unsuccessful attacks on seals (1 grey seal *Halichoerus grypus* and 1 unidentified seal). On 20 May 2009, a large blood plume in the water near a milling group indicated a predation event. This is listed as a probable kill of an unidentified marine mammal in Table 1. All individuals recorded travelling close to shore were either involved in a confirmed kill of a marine mammal or were encountered in close association with individuals that were involved in a confirmed marine mammal kill (Table 1). We did not detect any evidence that these animals targeted fish. Two additional encounters were with large groups (20+ individuals) more than 3 nautical miles off Unst. We recovered fish swim bladders around feeding whales in both encounters (2 swim bladders on 29 June 2009 and 4 on 1 July 2009). We were unable to obtain a sequence from 1 swim bladder collected on 1 July 2009; all others were identified as Atlantic herring *Clupea harengus* (see the supplement for details). The sampling location implies that these herring were from the North Sea stock (Mariani et al. 2005, Ruzzante et al. 2006).

Table 1. *Orcinus orca*. Summaries of encounters of killer whales around Shetland in the summers of 2008 and 2009. All encounters with individuals for which diet and/or acoustic data are available are shown. For focal follows, observed behavioural states and any sounds recorded are also listed. Details on pulsed call types given in Fig. 3

Date	Time (h)	Individuals present	Predation	Behavioural states	Acoustic behaviour
12 Jun 08	14:59	032, 064, 065, 066, 067	–	Not monitored	Not monitored
12 Jun 08	17:45	014	–	Not monitored	Not monitored
22 Jun 08	11:06	032, 064, 065, 066, 067	–	Not monitored	Not monitored
30 Jun 08	20:48	032, 064, 065, 066, 067	–	Milling, slow travel, travel	Echolocation
02 Jul 08[a]	10:25	014	Confirmed kill of harbour seal	Not monitored	Not monitored
04 Jul 08	15:31	032, 064, 065, 066, 067	Confirmed kill of harbour seal	After kill	Pulsed calls (NASh05, variable), echolocation, whistles
14 Jul 08	15:51	064, 066, 067 +2	–	Not monitored	Not monitored
18 Jul 08	15:38	032, 064, 065, 066, 067	–	Surface-active, travel	Pulsed calls (variable)
15 Aug 08	15:17	027, 034, 072, 073	–	Not monitored	Not monitored
20 May 09	13:15	032, 064, 065, 066, 067	Probable kill of unidentified marine mammal	After kill, travel	Pulsed calls (variable), echolocation, whistles
24 May 09	20:57	032, 064, 065, 066, 067	Confirmed kill of harbour seal	After kill, surface-active, travel	Silent
31 May 09	15:12	032, 064, 065, 066, 067	Possible attack on unidentified seal	Milling, slow travel, travel	Pulsed calls (variable), whistles
20 Jun 09	15:07	027, 034, 072, 073	Probable attack on grey seal	Milling, travel	Echolocation
28 Jun 09	15:20	014, 018, 024, 025, 027, 028, 029, 030, 031, 034, 035, 072, 073 +~0–4	Confirmed kill of unidentified marine mammal	After kill, milling, surface-active, slow travel, travel	Pulsed calls (NASh01, NASh02, NASh03i, NASh03ii, NASh04i, NASh04ii, NASh05, NASh06, variable), echolocation, whistles
29 Jun 09	15:08	044, 050, 104, 105, 106, 107, 108, 109, 110, 111, 112, 113, 114, 115, 116, 117, 118, 119, 120, 121, 140, 141, 142, 143 +~5–30	Confirmed feeding on Atlantic herring	Slow travel	Whistles
01 Jul 09	14:24	122, 123, 124, 125, 126, 127, 128, 129, 131, 132, 133, 134, 138, 139, 145, 146, 148, 149, 150, 151 +~0–2	Confirmed feeding on Atlantic herring	Milling, slow travel, travel	Pulsed calls (NASh07, NASh08, NASh09, NASh10, NASh11, NASh12, variable), echolocation, whistles, underwater tail slaps

[a]Animal photographed and followed from shore. The attack was photographed and clearly showed the prey

We conducted 10 focal follows (8 with seal-hunting groups and 2 with fish-eating groups), which lasted between 29 min and 2 h 36 min with an average of 1 h 37 min and we spent between 10 min and 1 h 40 min (average: 45 min) recording sounds within 500 m of the animals. Group composition as well as feeding and acoustic behaviour recorded during focal follows, are given in Table 1. The 2 focal follows of fish-eating groups involved different individuals (although both encounters contained unidentified individuals), and we found no photographic matches with seal-hunting groups. Focal follows of seal-hunting groups involved 18 individuals (likely a significant proportion of the

seal-hunting assemblage seen around Shetland), although the majority of follows were of the same group of 5 individuals. Fish-eating killer whales were largely silent during one encounter (29 June 2009), but frequently produced pulsed calls, click trains, whistles and underwater tail slaps during the other (1 July 2009). Vocal rates (vocalisations ind.$^{-1}$ min^{-1} given as median and quartile range) were 0.48 (0.24–0.74) for pulsed calls, 0.13 (0.07–0.20) for click trains and 0.04 (0.02–0.05) for whistles (Fig. 1). Seal-hunting groups showed lower vocal rates for all vocalisation types: 0.01 (0.00–0.14) for pulsed calls, 0.02 (0.00–0.06) for click trains and 0.00 (0.00–0.01) for whistles (Fig. 1). Seal-
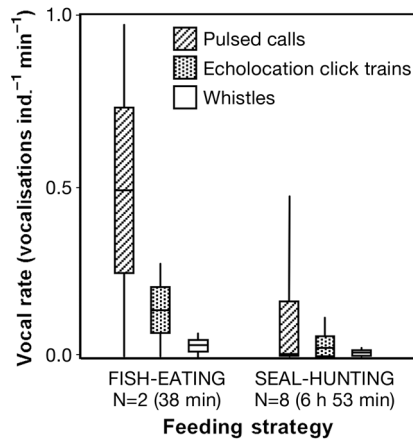
Fig. 1. *Orcinus orca*. Rates of vocal behaviour (vocalisations ind.$^{-1}$ min^{-1}) for fish-eating and seal-hunting groups of killer whales around Shetland, UK. Rates of pulsed calls, echolocation click trains and whistles are plotted separately. Boxes indicate median and quartile ranges; whiskers delineate full ranges. N gives the number of encounters with each type of group and the total recording time analysed in parentheses

hunting groups primarily vocalised when milling after a kill or engaged in surface-active behaviour. During behavioural states typically associated with active hunting in other populations (travel, slow-travel or milling; Deecke et al. 2005), the animals were largely silent (Fig. 2).

In total, 469 pulsed calls were recorded from seal-hunting groups around Shetland (421 on 28 June 2009), and of these, 85 (83 from 28 June 2009 and 2 from 4 July 2008) were of sufficient quality to extract frequency contours for categorisation. We recorded 656 pulsed calls from herring-eating groups (all on 1 July 2009), of which 35 were good enough to be included in the analysis. The relatively small number of high quality calls for the herring-eating groups is due to frequent overlapping calls and almost constant echolocation and suggests that we have probably only identified a small portion of the total group repertoire
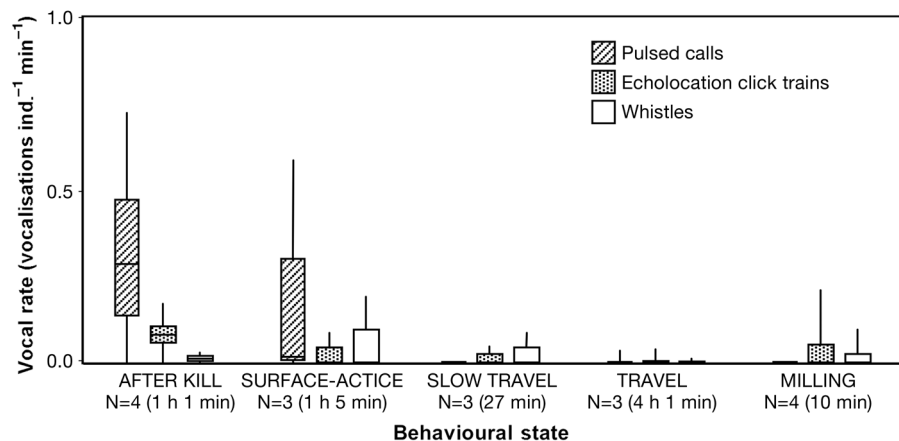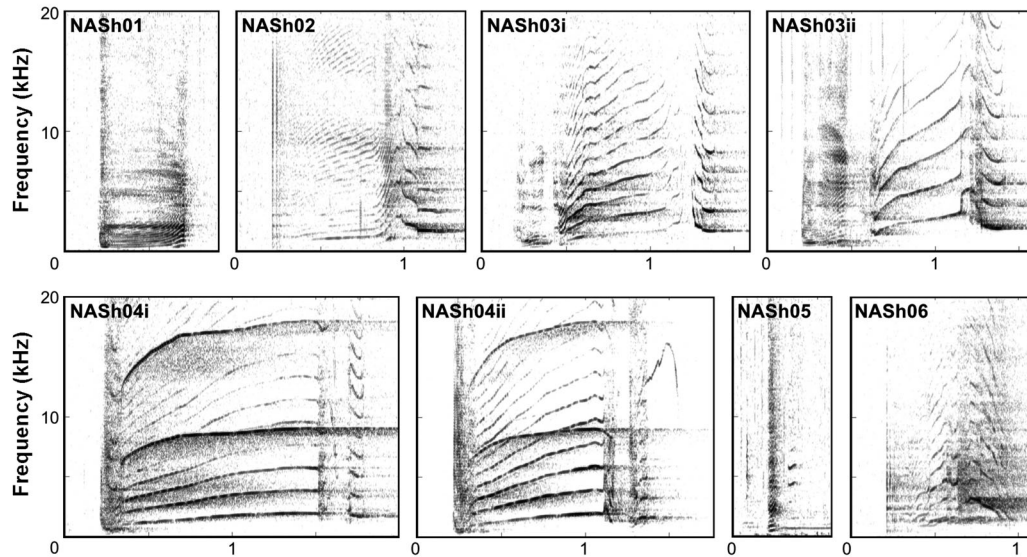
of call types. The ARTwarp categorisation algorithm grouped the pulsed calls of seal-hunting groups into 8 categories. Two pairs were subsequently lumped into subtypes of a common call type (NASh03i and ii, and NASh04i and ii) as they differed only in certain parts of the calls (Fig. 3). Pulsed calls of herring-eating groups were divided into 7 categories without obvious subdivision into subtypes. Two additional categories contained only a single example and were thus eliminated from the categorisation. We did not find any call types shared by seal-hunting and herring-eating groups.

DISCUSSION

Although killer whales regularly use the waters surrounding Shetland, the complex geography of the islands and often challenging weather conditions limited the number of encounters and the time we could spend with the animals. In spite of these limitations, the data presented here provide valuable information about the vocal behaviour and dietary specialisation of killer whales in Shetland waters.

The vocal behaviour of seal-hunting killer whales around Shetland differs markedly from killer whale populations known to specialise on fish, but shows parallels to that of other populations known to specialise on hunting marine mammals. Fish-eating killer whales in the northeastern Pacific are known to feed predominantly on salmon *Oncorhynchus* spp. (Ford et al. 1998), a prey with insensitive hearing in the frequency bands used by killer whales (Hawkins & Johnstone 1978), and frequently emit pulsed calls and echolocation clicks in all behavioural states (Ford 1989, Barrett-Lennard et al. 1996). Only during resting behaviour are rates of these vocalisations somewhat reduced. Whistles in these animals are known to occur in all contexts but increase significantly (to values around 1 whistle ind.$^{-1}$ min^{-1}) during socialising (Ford 1989, Thomsen et al. 2002). Similar patterns have been doc-

Fig. 2. *Orcinus orca*. Rates of vocal behaviour (vocalisations ind.$^{-1}$ min^{-1}) for seal-hunting groups of killer whales around Shetland, UK, during different behavioural states from 8 focal follows. Rates of pulsed calls, echolocation click trains and whistles are plotted separately. Boxes indicate median and quartile ranges; whiskers delineate full ranges. The number of encounters and total recording time analysed are given for each behavioural state

a Seal-eating killer whales
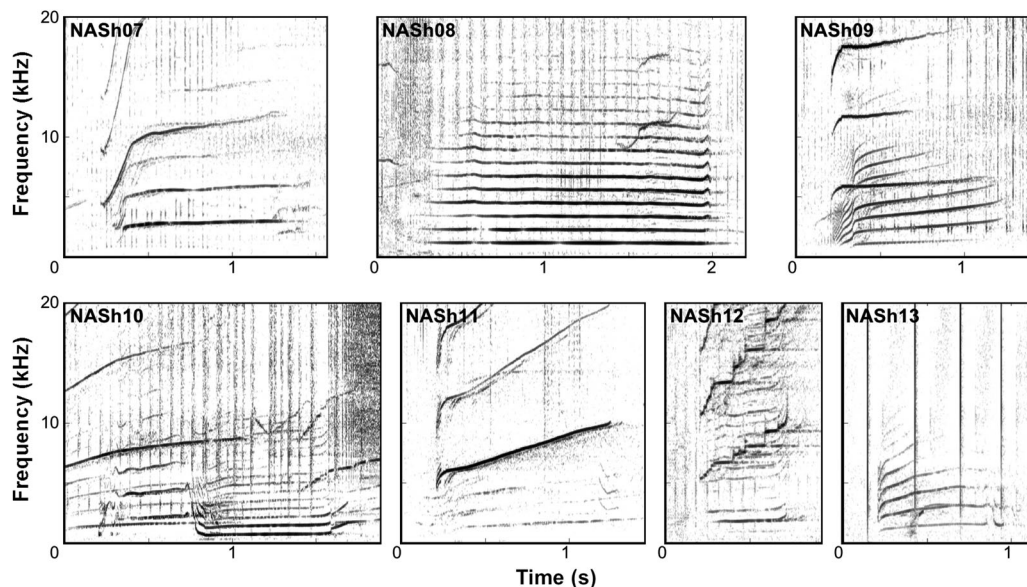

b Herring-eating killer whales

Fig. 3. *Orcinus orca*. Representative spectrograms of different call types produced by (a) seal-hunting and (b) herring-eating killer whales around Shetland, UK. Recordings were made with a sampling rate of 96 kHz. Spectrograms were generated using a Fast Fourier Transform size of 4096 samples, frame length of 1024 samples and 87.5% overlap between frames resulting in a frequency resolution of 23.4 Hz and time resolution of 1.3 ms. A Hann window was used for normalisation

umented for fish-eating killer whales in the northwestern Pacific (Tarasyan et al. 2005).

By contrast, mammal-eating killer whales typically restrict all forms of vocal behaviour to a few, narrowly defined contexts. In the southern Indian Ocean, killer whales tend to be silent when hunting southern elephant seals *Mirounga leonina* around the Crozet Islands, but produce pulsed calls after a successful attack (Guinet 1992). In the northeastern Pacific, tran-

sient killer whales are known to feed almost exclusively on marine mammals (Ford et al. 1998). Compared to sympatric fish-eating populations, these animals restrict the use of echolocation (Barrett-Lennard et al. 1996), whistles (Riesch & Deecke 2011) and pulsed calls (Deecke et al. 2005). Pacific transients produce communicative vocalisations (whistles and pulsed calls) almost exclusively after a successful attack or when engaged in surface-active behaviour

(Deecke et al. 2005, Riesch & Deecke 2011). During behaviours associated with active search for prey, these animals are typically silent. Harbour seals and presumably other marine mammals respond very strongly to pulsed calls of mammal-eating killer whales (Deecke et al. 2002), and mammal-eating killer whales appear to restrict vocal behaviour to avoid alerting their acoustically sensitive prey (Barrett-Lennard et al. 1996, Deecke et al. 2002, 2005).

When compared to killer whales that specialise on marine mammal prey elsewhere, groups hunting seals around Shetland show strikingly similar patterns of vocal behaviour (Fig. 2). The animals often travel in silence for hours and only show significant amounts of vocal behaviour after prey capture or during bouts of surface-active behaviour. The silent hunting strategy suggests that these killer whales actively search for marine mammal prey and do not simply capture marine mammals opportunistically when they come across them. All North Atlantic killer whales examined so far are phylogenetically much closer to fish-eating resident populations in the North Pacific than they are to transients (Morin et al. 2010, Foote et al. 2011), which suggests parallel evolution of a silent hunting strategy in the North Pacific and North Atlantic.

The context of vocal behaviour of herring-eating groups around Shetland is less clear — during one encounter dominated by active feeding, the animals frequently produced echolocation clicks, whistles and pulsed calls. During the other encounter, the animals were primarily travelling (a brief bout of foraging was documented prior to the onset of acoustic monitoring) and emitted only 2 whistles in almost 2 h. Herring hear well in the lower part of the frequency band used by killer whales (Enger 1967) and respond to killer whale vocalisations (Wilson & Dill 2002, Doksæter et al. 2009), although their anti-predator strategies to avoid killer whale predation may not be as effective as those of marine mammals (Domenici 2001). Whereas silent travel is rare in killer whales specialising on salmonids (Ford 1989), Icelandic and Norwegian herring-eating killer whales often remain silent when travelling, and this reduction of vocal behaviour may be a result of the better hearing of their targeted prey (Simon et al. 2007). A similar reduction in vocalisations can be found in bottlenose dolphins when searching for prey (Jones & Sayigh 2002, Quick & Janik 2008).

The 1 July 2009 recording shows that the herring-eating killer whales off Shetland performed underwater tail slaps when feeding (Table 1). Tail slaps have been reported from Norwegian and Icelandic killer whales when feeding on herring and generate a characteristic loud percussive noise as one animal strikes a fish school with the tail flukes (Domenici et al. 2000, Simon et al. 2005, van Opzeeland et al. 2005). Ultra-

sonic whistles are another indication that herring-eating killer whales off Shetland have close affinity with other North Atlantic herring-eating populations. Samarra et al. (2010) reported such whistles with fundamental frequencies exceeding 17 kHz from herring-eating killer whales off Norway, Iceland, as well as the animals recorded on 1 July 2009 off Shetland, but not from mammal-eating or fish-eating populations in the North Pacific. In addition, the Shetland animals produced 5 renditions of call type NASh08, whose structure matches call type I36 of Simon et al. (2006) described from herring-eating killer whales off Iceland but not so far from Norway. In both Shetland and Iceland, this call type is typically followed by a tail slap (Fig. 4) and is hypothesised to elicit tighter schooling in the fish and thus increase the number of fish killed or stunned by the strike (Simon et al. 2006). A comparison of the Shetland call repertoires with published spectrograms from North Atlantic killer whales suggests a possible additional match between Shetland herring-eaters and killer whales from eastern Iceland (call type NASh10 and call type I5 of Moore et al. 1988), although the quality of the published spectrograms is too poor to establish this unequivocally. These findings suggest that the herring-eating killer whales we recorded off Shetland are either part of, or recently diverged from, the Icelandic herring-eating sub-population and may also visit Icelandic waters on occasion. We did not find any obvious matches between call types of any Shetland groups recorded and published call types from Norway (Moore et al. 1988, van Parijs et al. 2004). Systematic comparisons of our call types and identification photographs with catalogues from other North Atlantic populations will be valuable to further delineate the range of Shetland killer whales.

Photo-identification studies of killer whales from wintering and spawning grounds of the Icelandic summer-spawning and Norwegian spring-spawning stocks of Atlantic herring have documented the same individuals in wintering and spawning grounds of each herring stock, but no movement between stocks (Sigurjónsson et al. 1988, Similä et al. 1996, Simon et al. 2007). Results of genetic analyses were also consistent with maternal lineages following each herring stock and little movement between stocks, but herring-eating individuals from Norway, Iceland and Shetland were identified as a single population due to male-mediated gene flow (Foote et al. 2011). Our findings may suggest a recent and rare shift from the Icelandic summer-spawning stock to the North Sea stock of Atlantic herring. The fact that ultrasonic whistles are produced by herring-eating killer whales from Iceland, Norway and the herring-eating group off Shetland, but that sharing of stereotyped pulsed calls has so far only been found between Shetland and Iceland, could sug-
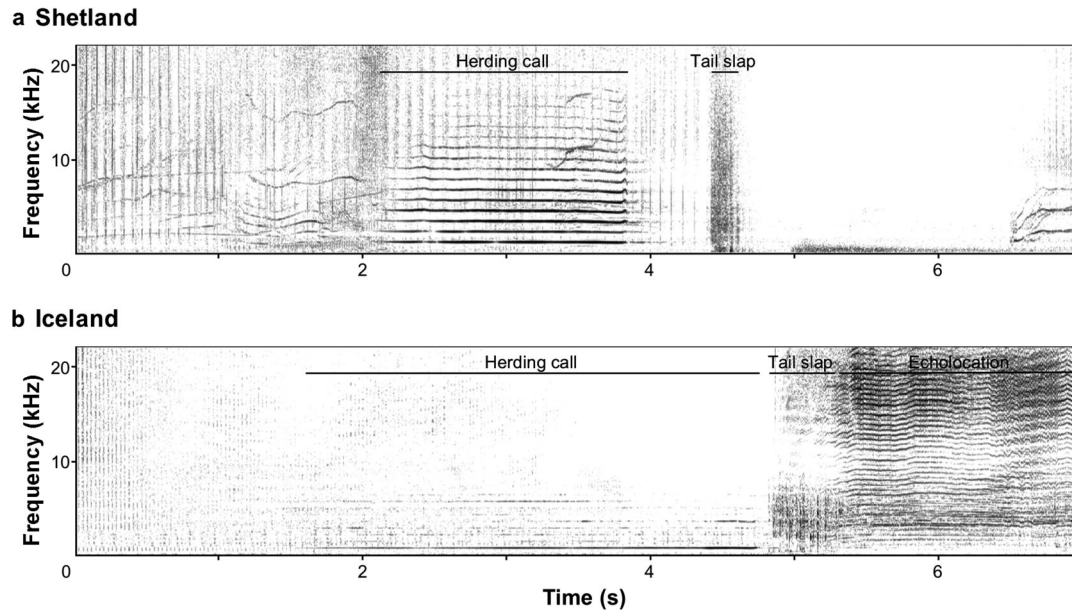
a Shetland

b Iceland

Fig. 4. *Orcinus orca*. Spectrogram of (a) a herding call (NASh08) followed by a tail slap recorded off Unst, Shetland, UK, and (b) a herding call (call type I36 of Simon et al. 2006) followed by a tail slap and a rapid echolocation click train recorded in the Vestmannaeyjar archipelago off Iceland (courtesy of F. Samarra). Spectrograms were generated using a Fast Fourier Transform size of 4096 samples, frame length of 1024 samples and 75% overlap between frames resulting in a frequency resolution of 23.4 Hz and time resolution of 2.6 ms. A Hann window was used for normalisation

gest that whistles and pulsed calls follow different patterns of transmission (as has been described for fish-eating North Pacific killer whales; Riesch et al. 2006). A systematic comparison of call and whistle repertoires of North Atlantic killer whales seems called for to address this question.

We did not record ultrasonic whistles from groups observed hunting seals in nearshore waters around Shetland or find any obvious matches between their call types and published vocal repertoires of other North Atlantic killer whales (Moore et al. 1988, van Parijs et al. 2004). Most of the pulsed calls recorded from Shetland seal hunters came from a single recording session. However, one call type (NASh05) was also recorded on a separate occasion (4 July 2008) from a different set of individuals, which suggests that the seal-hunting individuals listed in Table 1 may form part of the same vocal tradition. The fact that we did not find any call types shared between killer whales observed hunting seals and those foraging on herring around Shetland could suggest that they are not close social affiliates. However, the data come from a limited number of encounters, and in some killer whale populations, groups with entirely different repertoires are known to associate frequently and interbreed (Ford 1991, Barrett-Lennard 2000). Further genetic studies are ultimately required to determine the amount of gene flow between seal-hunting and herring-eating groups off Shetland. Whistles may provide better evi-

dence for social segregation among Shetland killer whales. In situations where discrete repertoires of pulsed calls occur within the same population, stereotyped whistles can be shared across dialect boundaries determined by pulsed call repertoires (Riesch et al. 2006). However, our preliminary data suggest that the usage of whistles differs substantially among Shetland killer whale groups, as ultrasonic whistles produced by herring-eating groups have so far not been recorded from seal-hunting groups. The difference in usage of high-frequency whistles could represent context-specific variation if these signals are part of a herring-feeding strategy, or could constitute a group-specific variation between herring-eating and seal-hunting groups.

In summary, the vocal behaviour of Shetland killer whales suggests a certain degree of specialisation, either within the same population, or in the form of 2 reproductively isolated populations. Based on high variation of stable isotope values within the maternal lineage associated with each of the Norwegian and Icelandic herring stocks, Foote et al. (2009) suggested that there are differences in the proportion of different components of the diet consumed, while presence of tooth wear in all individuals within these lineages suggests that there is a shared dietary component. We have documented effective acoustic strategies in killer whales around Shetland used to exploit different prey types: silent hunting for sea mammals in seal-hunting

groups and herding calls thought to concentrate herring in fish-eating groups. The degree of behavioural flexibility of individual animals, and whether the individuals recorded here switch between both types of strategies, remains to be shown. However, the fact that killer whales around Shetland appear to differ in their dietary preferences must be taken into account when estimating the impact of killer whale predation on pinnipeds and when making management decisions affecting killer whales and their prey around the Northern Isles.

LITERATURE CITED

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