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The role of acoustic signals in interactions within and between species of cetaceans

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Dissertation submitted in partial fulfillment of a
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Abstract

Sound is an important mode for communication and mediates a variety of interactions within and between species. Sociality is thought to promote complexity in communication systems. Cetaceans are highly vocal and social and thus provide excellent models to study acoustic communication. This thesis aimed to investigate the role of acoustic signals in mediating interactions within and between species by examining the acoustic communication of Icelandic killer whales (*Orcinus orca*), their interactions with long-finned pilot whales (*Globicephala melas*) and the role of acoustics within the interactions. A detailed description of the acoustic repertoire of killer whales showed that it is largely shared across locations around Iceland, but that some locations also have unique call types that are not recorded elsewhere. Specific combinations of calls occurred more often than expected by chance and were recorded from several locations and different social clusters. Interactions between long-finned pilot whales and killer whales were common whenever both species co-occurred. While varying in intensity, these interactions appeared to be antagonistic and mediated acoustically. Killer whales showed clear avoidance responses to playbacks of long-finned pilot whale sounds, marked by fast and directed movement away from the sound source, initial increases in calling rate followed by a strong decrease, and increased cohesion and alignment of group members. These results show that Icelandic killer whales have a complex acoustic communication system, and that acoustics also plays an important role in mediating interactions with long-finned pilot whales, therefore demonstrating the importance of sound to these highly social marine top predators.

Útdráttur

Hljóð eru mikilvæg í tjáskiptum margra dýra og eru nýtt jafnt í samskiptum innan tegundar og á milli tegunda. Félagskerfi dýra eru talin stuðla að margbreytilegum samskiptum. Hvalir eru mjög háværar eða söngglaðar félagsverur og eru því fyrirtaks viðfangsefni fyrir rannsóknir á tjáskiptum með hljóðum (oft nefnd köll). Markmið doktorsverkefnisins var að meta hlutverk kalla (hljóðtákna eða bendingar) í mótun samskipta bæði innan tegundar og á milli tegunda, með því að kanna hljóðsamskipti meðal háhyrninga (*Orcinus orca*), samskipti þeirra við grindhvali (*Globicephala melas*) og hlutverk hljóðeðlisfræði í samskiptunum. Ítarleg lýsing á s.k. hljóðefnisskrá háhyrninganna leiddi í ljós að hún var að mestu leyti eins á mismunandi hafsvæðum við Ísland, en á sumum svæðanna reyndust þeir nota einstök köll, sem ekki heyrðust frá háhyrningum á öðrum svæðum. Ákveðnar samsetningar á köllum komu oftar fyrir en búast mætti við vegna tilviljunar, og fundust þessar samsetningar á ýmsum svæðum og frá mismunandi samfélagshópum háhyrninga. Tjáskipti milli grindhvala og háhyrninga voru tíð þegar báðar hvalategundirnar voru á sama svæði. Breytileiki var í fjölda og ákafa tjáskipta og virtust þau vera fjandsamleg og þeim miðlað með hljóðum. Þegar upptökur af hljóðum grindhvala voru spilaðar forðuðu háhyrningar sér yfirleitt hratt og beint frá uppsprettu hljóðsins. Fyrst fylgdu þessu tíðari köll háhyrninganna, en síðan fækkaði þeim og hópurinn þéttist (uppröðun einstaklinga innan hans breyttist). Niðurstöðurnar sýna að Íslenskir háhyrningar hafa flókið tjáskiptakerfi sem byggir á hljóðum og að hljóðin þjóni einnig mikilvægu hlutverki í samskiptum þeirra við grindhvali, og sýna þannig mikilvægi hljóða fyrir þessi mjög svo félagslyndu sjávarrándýr.

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Paper II:

Selbmann A, Miller PJO, Wensveen PJ, Svavarsson J, Samarra FIP (2023) Call combination patterns in Icelandic killer whales (*Orcinus orca*). Scientific Reports 13:21771. doi: 10.1038/s41598-023-48349-1

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Bellon G, Selbmann A, Wensveen P, Rasmussen M, Laute A, Mouy X, Samarra FIP (2024) Killer whale (*Orcinus orca*) occurrence in Icelandic waters revealed by passive acoustic monitoring. Marine Mammal Science e13211. doi: 10.1111/mms.13211

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Samarra FIP, Selbmann A, Aoki K, Miller PJO (2022) Observations of cetaceans in the waters of the Surtsey Nature Reserve between 2008 and 2021. Surtsey Research 15:89–96. doi: 10.33112/surtsey.15.7

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1 Introduction

Being an island, Iceland and its inhabitants are strongly connected to the ocean. Viking explorers arrived by ship around 874, although settlement of the Vestmannaeyjar archipelago might have occurred earlier (Stefánsson 2003). From the beginning, fishing was important for survival and people went out in small open rowing boats to fish in coastal waters. The presence of whales indicated good fishing grounds and the sagas often describe whales as providing protection or aiding navigation (Murray-Bergquist 2017). In the 17th and 18th century, naturalists and scholars Jón (lærði) Guðmundsson (1574-1658) and Jón Ólafsson úr Grunnavík (1705-1779) describe various species of whales, including several species of what we consider today to be killer whales (*Orcinus orca*) and long-finned pilot whales (*Globicephala melas*), as well as some species that might be mythical creatures (*Figure 1*, Hermannsson 1924; Ólafsson et al. 2007). Some are described as harmless to ships and men, while others are portrayed as evil and malicious in nature. Recommended remedies included throwing cow dung or grinding a saw against the hull of the boat, as the whales would avoid the sound of rattling iron (Ólafsson et al. 2007). Although the formal study of acoustics in whales only started much later, these descriptions suggest that people were aware of the importance of sound to whales, and one could even argue that the grinding of saws against hulls were an early form of playback experiments.

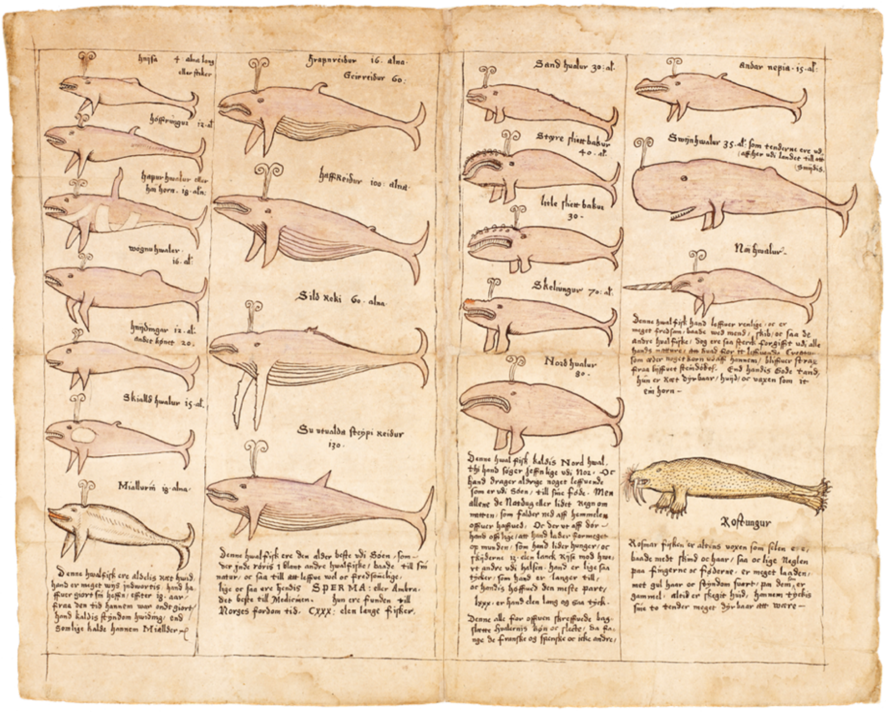


Figure 1: Illustrations of different whale species by Jón Guðmundsson. The third drawing from the top in the left column is of a killer whale and the one below of a pilot whale. Reproduced with permission from the Icelandic Museum of Natural History and the Royal Danish Library, Copenhagen.

1.1 Acoustic signals and communication in cetaceans

Sound is the most important mode of communication in many species. This can be attributed to a few crucial properties: it travels long distances, it does so fast, and it can contain a lot of information (Kershenbaum 2025). Animals will monitor their environment for acoustic cues related to conditions of interest but may also intentionally produce acoustic signals to provide information to receivers. The transmission of a signal from one individual to another that on average benefits both, is what is generally defined as communication (Slater 1983). This process rarely occurs in isolation between two parties and often several individuals are involved, leading to a communication network (Mcgregor and Peake 2000). Within such a network, a signal is produced with the intention of transferring information to one or several receivers, however, unintended receivers may also pick up on cues that were produced unintentionally or aimed at a different receiver (Bradbury and Vehrenkamp 2011).

Acoustic signals are highly diverse, from the chirping of cicadas to the howling of wolves to the songs of birds. This diversity has arisen due to several factors. Different evolutionary histories impact the preadaptation of each species to produce certain signals, and their physiology will constrain the range of signals that can be produced and perceived (Bradbury and Vehrenkamp 2011). In addition, signals are produced within environments, that may be filled with eavesdroppers, sounds of the same and other species. Therefore, trying to get a message across may require specific signal adaptations (Chhaya et al. 2021; Bernal and Page 2023).

Sound travels far and fast underwater and consequently it is very important to marine animals. They use it to communicate, to navigate, to detect prey or avoid threats. Cetaceans exemplify the use of sound underwater and several studies have shown their remarkable capabilities in this domain. For example, sperm whale (*Physeter macrocephalus*) clicks might be the loudest sounds produced by any animal (Møhl et al. 2003), the sounds of blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) are produced at very low frequency and thus travel long distances (Širović et al. 2007), while odontocetes use very high frequencies that, in some cases, may help avoid detection by predators (Morisaka and Connor 2007).

1.1.1 The role of acoustic signals in intraspecific interactions

Successful communication relies on shared signal structures and perceptual mechanisms; therefore, most acoustic signals are directed at individuals of the same species. Acoustic communication within species has been studied widely and revealed important functions in reproduction (e.g. to attract mates or display fitness), territoriality (e.g. to establish and defend territories), social organisation (e.g. to coordinate group behaviour, maintain group structure, establish hierarchies or resolve conflict), parental care (e.g. begging calls in birds), individual recognition, and alarm signalling (Bradbury and Vehrenkamp 2011). Bird song for example, plays an important role in territorial defence, mate attraction, courtship, reproductive isolation, and pair communication (Kroodsma and Byers 1991; Nowicki and Searcy 2004; Brambilla et al. 2008; Rose et al. 2019).

In cetaceans, differences in social structure between baleen whales (mysticetes) and toothed whales (odontocetes) are reflected in their acoustic signals. Baleen whales are generally solitary but may aggregate for mating or at feeding patches. To stay in contact, their vocalisations need to cover great distances, which is thought to have facilitated the evolution of low frequency sounds suited for long-range transmission (Payne and Webb 1971; Stafford et al. 1998; Tsuchiya et al. 2004). Some baleen whale species produce complex songs that consist of repetitive and highly predictable patterns of low-frequency, non-directional acoustic elements that are suitable for transmission over long distances (Payne and McVay 1971; Stafford et al. 2008). These songs are thought to be reproductive advertisement displays, potentially used by males to attract females, but may also mediate male-male interactions, serve as population markers or provide a way to localise and track conspecifics over long distances (Herman 2017; Mercado 2022; McDonald et al. 2023). Toothed whales, on the other hand, often live in large and complex social groups. While all animals must solve complex problems in their environments, social animals have to solve additional (and potentially more complex) problems in their social interactions, requiring a higher diversity of signals. Therefore, the ‘social complexity’ hypothesis suggests that social complexity promotes communicative complexity (Freeberg et al. 2012). Indeed, toothed whales produce a range of sounds, many of which are presumed to have social functions. Beluga whales (*Delphinapterus leucas*) for example, are referred to as the ‘canaries of the sea’ due to the large variety of sounds they produce (O’Corry-Crowe 2009). Like other toothed whales, they produce echolocation clicks, whistles and burst-pulse calls, including combined calls (also referred to as mixed or biphonic calls), that consist of two sounds produced at the same time (Karlsen et al. 2002; Brewer et al. 2023). Belugas live in large groups with complex social organisation and diverse interactions between individuals, which is thought to have led to the evolution of their rich and complex repertoires (O’Corry-Crowe et al. 2020; Brewer et al. 2023). ‘Contact calls’ for example are thought to be used to maintain group cohesion and potentially play a role in individual recognition (Panova et al. 2012; Vergara and Mikus 2019; Panova and Agafonov 2023). Recognition of individuals has been demonstrated in other toothed whales, such as bottlenose dolphins (*Tursiops truncatus*), that produce so-called signature whistles. These are unique, individually distinctive vocalisations that aid individual recognition and are important in the maintenance of group cohesion (Janik et al. 2006; Janik 2009).

1.1.2 The role of acoustic signals in interspecific interactions

While signalling to other individuals of the same species is a fundamental and well-documented function of acoustic communication, acoustic signals can also be used in communication between species. This can occur intentionally, for example when prey species emit alarm calls to signal to a predator that it has been detected (Zuberbühler 1999), or unintentionally, e.g. a competitor might detect a food resource from the vocalisations of another species (Page and Bernal 2020).

In cetaceans, sound plays an important role in competitive and predator-prey interactions. In predator-prey interactions, prey is often detected through sound, either through active sound production (echolocation) or passive listening (eavesdropping). All toothed whale species are capable of echolocation. They emit clicks and from the returning click echo they gather information about their surroundings, including the presence of potential prey (Au 1993). Once detected, they will often emit a series of rapid clicks called a buzz to home in on their prey and such buzzes can be used as indicators of feeding activity (DeRuiter et al. 2009; Holt et al. 2019; Haas et al. 2025). However, toothed whales may also use passive listening to detect their prey, as has been suggested for killer whales hunting marine mammals and shown for bottlenose dolphins listening for fish sounds (Barrett-Lennard et al. 1996; Deecke et al. 2005; Gannon et al. 2005). Potential fish and mammal prey, on the other hand, will also listen for and respond to cues from predators. Several species of cetaceans show strong avoidance responses to the sounds of killer whales (Cummings and Thompson 1971; Fish and Vania 1971; Tyack et al. 2011; Allen et al. 2014; Curé et al. 2015; Sivle et al. 2015; Benti et al. 2021). In many terrestrial mammal and bird species, in addition to predator avoidance, animals respond to the detection of potential predators by emitting alarm calls. These calls can serve several functions, including alerting conspecifics and heterospecifics, recruiting them to join potential mobbing behaviours, or deterring the predator (Bradbury and Vehrenkamp 2011). Alarm calls have not been reported in cetaceans, although killer whales are known to produce 'excitement calls' with many frequency modulations, which are related to high arousal states (Rehn et al. 2011) and similar calls have been reported in response to exposures to naval sonar sounds (Samarra et al. in review). Competitive interactions between cetacean species also rely on acoustic communication. For example, humpback whales (*Megaptera novaeangliae*) feeding on herring (*Clupea harengus*) approach playbacks of killer whales feeding on the same food source and thus seem to use eavesdropping on killer whale sounds to locate prey patches (Jourdain and Vongraven 2017; Benti et al. 2021). Sounds of potentially aggressive competitors can also lead to avoidance responses, as has been shown for sympatric dolphin species, which may lead to fine-scale spatial segregation (Pierry et al. 2023). However, apart from these isolated examples, little is known of how interspecific interactions between cetaceans are mediated by acoustic signalling.

1.2 The killer whale (*Orcinus orca*)

Killer whales are the ocean's apex predators. They exploit virtually all available prey species and this flexibility and their capacity to innovate have been suggested to be major factors in their success as a species (de Bruyn et al. 2013). They occupy all the world's oceans, but are more abundant in cold and temperate regions, as well as in coastal waters (*Figure 2*, Ford 2018). While they are generalists as a species, local populations are often highly specialised on certain prey types or species and several ecotypes have been recognised worldwide, some of which have been proposed to be different species (Morin et al. 2024).

The earliest studies on killer whales were conducted in the Northeast Pacific, where three ecotypes were described: a resident, fish-eating ecotype; a transient, mammal-eating ecotype (also called Bigg's killer whales); and an offshore ecotype thought to mainly feed on sharks (Bigg et al. 1990; Ford and Ellis 1999, 2006; Herman et al. 2005; Dahlheim et al. 2008). Even though they share the same habitat, killer whales from these different ecotypes do no associate and are genetically distinct (Hoelzel et al. 2007; Morin et al. 2010; Foote et al. 2019). As these were the first populations studied in detail, they became a template for killer whale ecology and behaviour. Since then several studies around the world have shown ecotype differentiations between fish-eating and mammal-eating killer whales in other locations (e.g. Antarctica: Pitman and Ensor 2003; Pitman et al. 2011; Kamchatka: Filatova et al. 2015c, 2019, 2023), but these categories do not exist everywhere (de Bruyn et al. 2013). In the North Atlantic for example, killer whales may be fish-specialists but may also switch diet and hunt both fish and marine mammals (Samarra and Foote 2015; Jourdain et al. 2017; Remili et al. 2023).

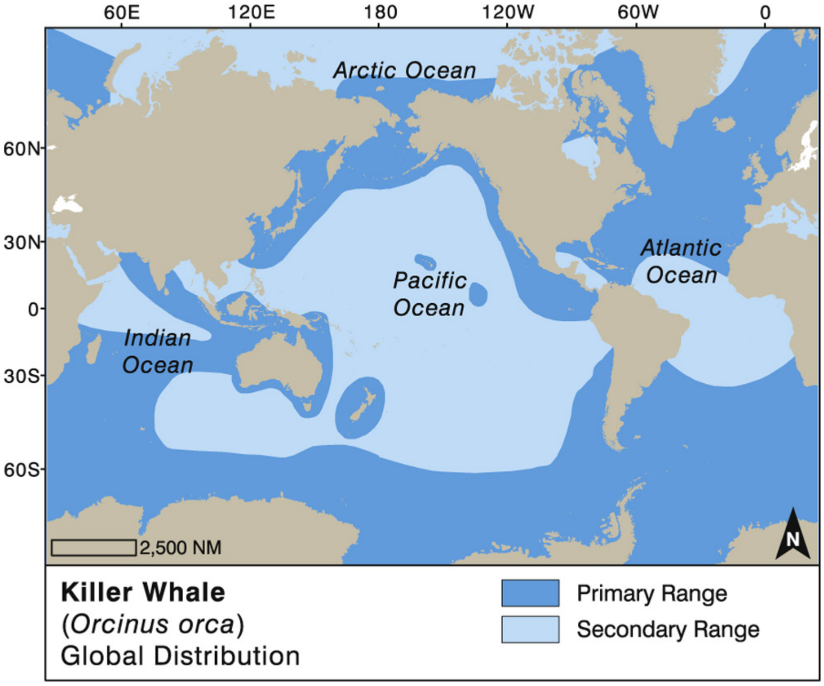


Figure 2: Worldwide distribution of killer whales. Used with permission of Elsevier Science & Technology Journals, from Encyclopedia of Marine Mammals, Würsig, Thewissen and Kovacs, 2018; permission conveyed through Copyright Clearance Center, Inc.

Killer whales live in matrilineal groups and often all male and female offspring remain with their mother throughout their life (Hoelzel et al. 2007; Ellis et al. 2021). Hierarchical social structures are common, where several groups may temporarily join and more closely related groups associate more often (Bigg et al. 1990). In the fish-eating killer whales of the Northeast Pacific for example, a clear nested hierarchical social structure has been described. The smallest unit is the matriline, which contains an adult female with all her offspring. Several matrilines may travel together in larger pods and groups of pods are referred to as clans, which still share a common but older maternal ancestry. Pods and clans that regularly associate are known as communities (Bigg et al. 1990). However, social structures may vary between ecotypes or depending on local conditions (Beck et al. 2012). For instance, some dispersal from the matrilineal group is observed in mammal-eating killer whales in the Northeast Pacific and multilevel societies with looser bonds are reported from the Northeast Atlantic (Bigg et al. 1990; Baird and Whitehead 2000; Tavares et al. 2017).

Most interactions of killer whales with other cetaceans are of a predatory nature (Jefferson et al. 1991). However, neutral or potentially affiliative behaviours have also been observed and while many species avoid killer whales, some are also attracted to them (Jefferson et al. 1991). Humpback whales for example approach killer whales feeding on herring, forming mixed-species aggregations and likely taking advantage of feeding opportunities (Jourdain and Vongraven 2017; Benti et al. 2021). In some interactions, the underlying drivers also remain unclear. Fish-eating killer whales in the Northeast Pacific for example, have been reported harassing and killing porpoises (*Phocoena phocoena* and *Phocoenoides dalli*) without consuming them (Giles et al. 2023).

Killer whales are highly vocal, but their acoustic behaviour may vary between ecotypes. Mammal-eating killer whales for example are mostly silent when they hunt but vocalise after a successful kill or when socialising (Deecke et al. 2005). Fish-eating killer whales on the other hand are vocally active in most behaviours, including during foraging (Ford 1989). These differences in acoustic behaviour may relate to the hearing capabilities of their prey (Deecke et al. 2005). Killer whale vocalisations are generally described as clicks, whistles and burst-pulse calls (*Figure 3*). However, these categories exist along a continuum from individual broadband pulses (clicks) to burst-pulse sounds (calls) and narrow-band sinusoidal signals (whistles), and cannot always be clearly differentiated (Murray et al. 1998).

Clicks are used in echolocation. These short pulses of sound are typically emitted in series and cover a wide frequency bandwidth (Schevill and Watkins 1966; Ford 1989). Frequency peaks and rates of echolocation may vary between different ecotypes, which likely reflects differences in the prey targeted (Barrett-Lennard et al. 1996; Simon et al. 2007a; Leu et al. 2022). Whistles are tonal sounds but are produced through tissue vibrations and not aerodynamically, meaning that the term is functionally inaccurate (Madsen et al. 2012). They are thought to aid close-range communication and are mostly used during socialising behaviours (Thomsen et al. 2002; Riesch et al. 2008; Riesch and Deecke 2011). Whistles generally range in frequency from 2.4-18.5 kHz but may reach ultrasonic frequencies up to 75 kHz (Thomsen et al. 2001; Riesch et al. 2006; Samarra et al. 2010). While a large proportion of whistles is variable, some are stereotyped and appear to be stable in structure over long time periods (Riesch et al. 2006; Souhaut and Shields 2021).

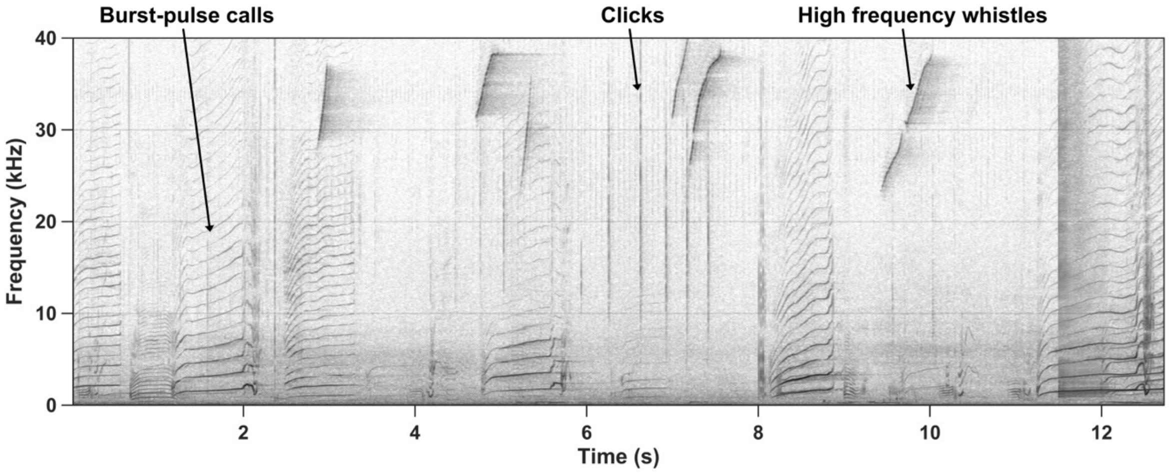


Figure 3: Spectrogram of killer whale sounds recorded in Iceland.

The most common social sounds produced by killer whales are burst-pulse calls (hereafter calls). They have been studied in most detail because of their apparent importance in group coordination, cohesion and organisation of behaviour. Calls are burst-pulse sounds consisting of rapidly repeated pulses. The interval between pulses is so short that they appear tonal with several sidebands (Schevill and Watkins 1966). They cover a wide frequency range, which may vary with ecotype, but most of their energy is generally between 500 Hz and 25 kHz (Miller 2006; Foote and Nystuen 2008; Filatova et al. 2015b). They can be complex in structure and can contain two separately modulated frequency contours. The low frequency component appears to be omnidirectional and can contain several parts separated by abrupt shifts in frequency, while the high (or upper) frequency component is highly directional and generally a single unit (Miller 2002; Yurk 2005).

The majority of calls produced is stereotyped, making them very suitable for classification into call types and subtypes. Highly modified versions of call types can occur, which are called ‘aberrant’ calls and the remainder of calls that cannot be clearly classified and do not appear to be repetitive are referred to as ‘variable’ (Ford 1989). The repertoires of stereotyped calls have been described in several locations and these studies show that repertoires vary between populations, ecotypes and social groups (Moore et al. 1988; Ford 1989; Strager 1995; Deecke et al. 1999, 2005; Saulitis et al. 2005; Filatova et al. 2007; Richlen and Thomas 2008; Filatova et al. 2015b; Wellard et al. 2015; Schall and van Opzeeland 2017; Danishevskaya et al. 2020; Wellard et al. 2020; Madrigal et al. 2021; Sportelli et al. 2022).

Calls are socially learned, rather than genetically encoded and since killer whales live in matrilineal groups repertoires can be a measure of maternal relatedness, with more closely related groups sharing larger parts of their repertoire (Ford 1991; Yurk et al. 2002; Foote et al. 2006; Deecke et al. 2010). Differences in repertoires may accumulate over time when groups split apart but generally, call repertoires tend to be stable over long time periods (Ford 1991; Miller and Bain 2000; Foote and Nystuen 2008). Different call types do not seem to be behaviour specific but the frequency of use of call types may vary between behaviours (Ford 1989; Weiß et al. 2006, 2007; Filatova et al. 2009, 2013). The structure and properties of calls enable their recognition over long distances, against background noise and provide potential for accurate localisation (Ford 1991; Miller and Bain 2000; Yurk et al. 2023). Therefore, calls are thought to function as contact signals, helping to maintain group cohesion and coordinate the group’s behaviour and spatial organisation (Ford 1989; Filatova et al. 2015a).

1.2.1 Killer whales in Icelandic waters

In Iceland, killer whales have long been known to associate with herring. Early studies focused on herring overwintering grounds and killer whales were thus presumed to be herring-specialists (Sigurjonsson et al. 1988). More recent research showed however, that only about half of the known individuals seem to follow the herring year-round (Samarra et al. 2017b; Marchon et al. 2024). These individuals are regularly seen in the current herring summer spawning grounds around the Vestmannaeyjar archipelago in the south of Iceland and in the current overwintering grounds in Breiðafjörður in the west of Iceland (Samarra et al. 2017b; Marchon et al. 2024). The other half has only ever been seen in either the herring spawning or overwintering locations. While it is unclear where most of these individuals go during the rest of the year, some are known to seasonally migrate to Scotland, where they hunt marine mammals (Samarra and Foote 2015; Samarra et al. 2017a). Dietary markers and stable isotope analyses also support the existence of herring specialists and whales with a mixed-diet of fish and marine mammals in this population (Samarra et al. 2017a; Remili et al. 2021). Marine mammal predation has also been reported from locations in the north and northeast of Iceland and killer whales photographed there have not been seen in other parts of the country, indicating that they may be part of an offshore population that occasionally visits the area (Samarra et al. 2018; Marchon et al. 2024). With this mix of dietary patterns, Icelandic killer whales do not seem to follow the template of strictly fish- or mammal-eating ecotypes described elsewhere.

Differences to other populations are also apparent in their social structure. Icelandic killer whales live in a multilevel society with no clear nested hierarchical structure as has been reported from other populations. While strong social bonds exist, the number of these associations is small (Tavares et al. 2017). This fission-fusion social structure appears highly flexible and may be related to their prey. When feeding on herring, Icelandic killer whales use a ‘carousel feeding’ technique: they cooperatively herd schools of fish together, encircle them and then use their tails to slap into the herring mass, which stuns the fish and allows them to be picked up by the killer whales (Similä and Ugarte 1993; Samarra and Miller 2015). While larger groups may be advantageous in this highly coordinated feeding technique, the dynamic nature of herring schools may require constant adjustment, which may favour flexible social associations (Tavares et al. 2017).

Studies on the acoustic behaviour of Icelandic killer whales revealed similarities with other killer whale populations but also unique signals and traits. Icelandic killer whales are highly vocal when they feed on herring and are mostly silent when they travel (Simon et al. 2007b). During feeding on herring, they use a specific call, the ‘herding’ call (I36). This call is relatively low in frequency, long in duration and shows almost no frequency modulation (Simon et al. 2006; Samarra 2015). It is only given immediately before a tail slap and is thought to be directed at the herring prey, likely increasing feeding efficiency (Simon et al. 2006; Samarra 2015). Other unique sounds have been described in Icelandic killer whales, including high frequency whistles and low frequency sounds (Samarra et al. 2010, 2016). While first discovered in the Icelandic population, high frequency whistles have since been described in several locations, but they do not seem to be universal in killer whales (Samarra et al. 2010, 2015; Filatova et al. 2012; Simonis et al. 2012; Trickey et al. 2014; Andriolo et al. 2015; Reyes Reyes et al. 2017). They are thought to play a role in short-range communication (Samarra et al. 2010). Low frequency signals (<330 Hz) on the other hand, have only been reported from the Icelandic killer whale population (Samarra et al. 2016). These sounds may be linked to feeding but their function remains unclear. The call type repertoire of Icelandic killer whales is distinct from the neighbouring population in Norway (Moore et al. 1988; Selbmann et al. 2021). However, three call types were matched to recordings from Scotland, reflecting what is known about the movement patterns of these whales (Deecke et al. 2011; Selbmann et al. 2021). Some movement is confirmed by photographic matches between Iceland and Scotland, but no regular movements are reported between Iceland and Norway (Foote et al. 2010; Samarra and Foote 2015). Apart from these comparisons to other locations in the North Atlantic, little is known on how the Icelandic killer whale call repertoire is structured and how that might vary between locations, social groups or over time.

1.3 Icelandic killer whales as a study system for the role of acoustic signals in intraspecific interactions

Their stereotyped structure, diversity, common use and apparent importance in communication makes killer whale calls an interesting system to study acoustic signalling within a species. As was noted above, Icelandic killer whales differ from populations described elsewhere in their feeding ecology and social structure. Thus, the template of clear social and reproductive separation between fish-eating and mammal-eating ecotypes does not seem to apply to Iceland. While fish specialists exist in the population, mixed-diet whales are also known but both types associate and do not appear to be genetically isolated (Tavares et al. 2017; Baumgartner et al. 2025). Their social structure seems to be fluid, with fission-fusion dynamics and less hierarchically structured than reported from other populations (Beck et al. 2012; Tavares et al. 2017). For example, the nested hierarchical social structure of the fish-eating resident killer whales in the Northeast Pacific is reflected in their acoustic repertoires. Clans, i.e. pods that associate regularly, share part of their repertoire but each pod also has unique calls and shared calls may be rendered differently by different pods or groups of pods (Ford 1991). Icelandic killer whales appear to live in a fission-fusion society, where such clear hierarchical structures are not apparent (Tavares et al. 2017). However, it remains unknown whether and how this is reflected in their acoustic repertoire. The social complexity hypothesis suggests that social complexity should lead to higher communicative complexity, which is often described in terms of repertoire size but can also include other layers, such as repertoire structure or combinations of signals (Freeberg et al. 2012; Kershenbaum et al. 2016).

Killer whales in Iceland are often encountered in large feeding aggregations and recording isolated groups of known individuals is difficult. Therefore, studies on whether group-specific repertoires exist in Iceland are yet to be conducted. However, recordings from different locations in Iceland are available and it is known that not all killer whales visit all of these locations (Samarra et al. 2017b; Marchon et al. 2024). A catalogue of killer whale calls has been compiled (Selbmann et al. 2019), but detailed descriptions of the repertoire, how it varies between locations and over time are lacking. Such descriptions could provide a first step in our understanding on how the communication system of Icelandic killer whales might relate to their social structure and how that might differ from other populations studied to date.

Furthermore, little is known about how killer whales may combine calls into sequences. Early studies on their acoustic behaviour noted that certain calls are highly repetitive, but while some reported no clear structured sequences or patterns (Ford and Fisher 1982), others described calls being organised into themes, occurring in a specific order, comparable to humpback whale song (Bain 1986). Since then, research has confirmed that killer whales tend to repeat calls and a few studies also noted combinations of specific call types (Ford 1989, 1991; Deecke 2003; Miller et al. 2004; Saulitis et al. 2005). However, considering the complexity of killer whale sociality and how closely it is linked to acoustic communication, surprisingly little attention has been given to call combination patterns in the species. Icelandic killer whales appear to produce relatively stereotyped sequences of calls (Samarra FIP, personal communication) and investigating these in detail could provide further information on the acoustic communication system of the species, and potential similarities or differences between Icelandic killer whales and other populations.

1.4 The long-finned pilot whale (*Globicephala melas*)

Pilot whales are widely distributed in tropical, temperate and subarctic waters. Two species are known: the short-finned pilot whale (*Globicephala macrorhynchus*) and the long-finned pilot whale (*G. melas*). The short-finned pilot whale is found in tropical and subtropical regions, while the long-finned pilot whale occupies cold temperate to sub-polar waters

(*Figure 4*, Olson 2018). As long-finned pilot whale populations in the North Atlantic and the Southern hemisphere are widely separated, they are recognised as two different subspecies *G. m. melas* and *G. m. edwardii* (Olson 2018).

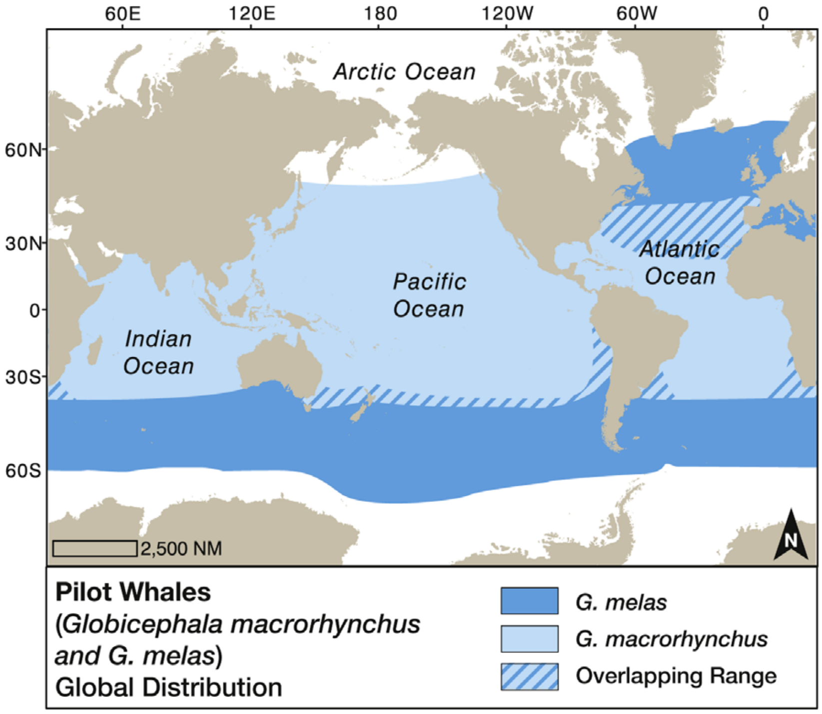


*Figure 4: Worldwide distribution of long-finned pilot whales (*Globicephala melas*) and short-finned pilot whales (*G. macrorhynchus*). Used with permission of Elsevier Science & Technology Journals, from Encyclopedia of Marine Mammals, Würsig, Thewissen and Kovacs, 2018; permission conveyed through Copyright Clearance Center, Inc.*

In the North Atlantic, long-finned pilot whales are known to mainly feed on squid (Desportes and Mouritsen 1993; Gannon et al. 1997; Santos et al. 2014). However, differences in stable isotopes between the eastern and the western North Atlantic indicate some variation in the diet, with western North Atlantic long-finned pilot whales also relying on herring and mackerel (*Scomber scombrus*, Abend and Smith 1995, 1997).

Like killer whales, long-finned pilot whales are highly social and live in matrilineal groups. These groups are likely stable and part of a hierarchical structure, and often several groups will join into large aggregations (Ottensmeyer and Whitehead 2003; de Stephanis et al. 2008b). Squid are found at depth and thus long-finned pilot whales typically conduct deep dives to forage, which they coordinate with other group members, potentially to increase efficiency in exploiting this patchily distributed prey (Visser et al. 2014).

Long- and short-finned pilot whales commonly interact with other cetacean species. Several reports indicate affiliative or neutral interactions, mostly with other delphinids (Norris and Prescott 1961; Scott and Chivers 1990; Baraff and Asmutis-Silvia 1998; Migura and Meadows 2002). However, harassment towards larger cetaceans, including sperm whales, humpback whales as well as killer whales has also been documented and the reasons for these interactions often remain unclear (Weller et al. 1996; Ciano and Jørgensen 2000; Stenersen and Similä 2004; de Stephanis et al. 2014).

Only a few studies have been conducted on acoustic communication in long-finned pilot whales, likely because the graded structure of their vocalisations makes them challenging to study. Like other toothed whale species, long-finned pilot whales produce echolocation clicks, whistles and calls (Weilgart and Whitehead 1990; Nemiroff and Whitehead 2009; Courts et al. 2020). Both whistles and calls are presumed to play a role in the coordination of group behaviour. Calls can be relatively simple or complex in structure and can contain several elements, as well as two separately modulated frequency contours (Nemiroff and Whitehead 2009). Some stereotypy in calls has been observed and classification by observers into broad classes may be possible but automated methods thus far failed at defining and categorising discrete call types (Nemiroff and Whitehead 2009; Vester et al. 2017; Zwamborn and Whitehead 2017; Courts et al. 2020). While some studies report highest call production rates during feeding behaviours (Visser et al. 2017), others show high production rates of calls and whistles during travelling and when many subgroups are present (Weilgart and Whitehead 1990; Nemiroff and Whitehead 2009), but these differences could be due to geographical variation.

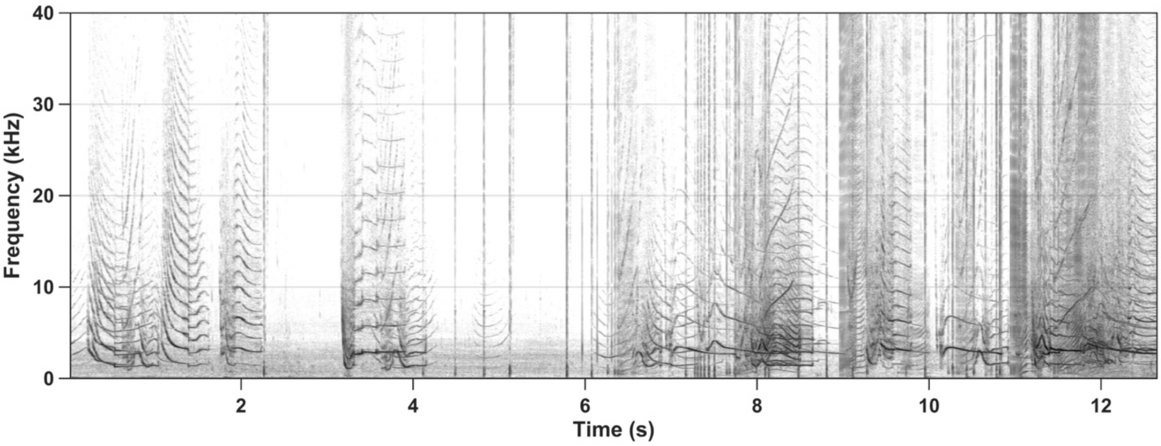


Figure 5: Spectrogram of long-finned whale sounds recorded in Iceland.

1.4.1 Long-finned pilot whales in Icelandic waters

Limited information is available on the occurrence, ecology and behaviour of long-finned pilot whales in Icelandic waters. They reach the northern edge of their distributional range in this region (*Figure 4*), which is reflected in reports from line-transect surveys that indicate high occurrence in Icelandic offshore waters in the southwest and along the continental shelf edge in the south, but no sightings in the north and northeast (Buckland et al. 1993; Pike et al. 2019). In coastal waters, long-finned pilot whales occur sporadically and mass strandings have been reported (Sæmundsson 1932; Sigurjónsson et al. 1993). These occurrences appear to be linked to years of high squid abundance, but little is known about the diet of long-finned pilot whales in the area. Stomach contents of four stranded individuals contained only beaks of the European flying squid (*Todarodes sagittatus*), which is also a major food source for the species in the neighbouring Faroe Islands (Desportes and Mouritsen 1993;

Sigurjónsson et al. 1993). Stable isotope analyses indicate a narrow isotopic niche for long-finned pilot whales stranded on the Icelandic coastline, possibly indicating a specialised diet but did not identify potential prey species (Samarra et al. 2024). Reports of long-finned pilot whales in coastal waters and strandings appear to have increased since 2011 (Jónsson 2019) but little is known about their distribution and occurrence in Icelandic coastal waters.

1.5 Interactions between long-finned pilot whales and killer whales

Long-finned pilot whales and killer whales overlap in their distribution in the North Atlantic, including around Iceland. In other locations in the North Atlantic, namely the Strait of Gibraltar (Spain) and northern Norway, interactions between the two species have been observed (Stenersen and Similä 2004; de Stephanis et al. 2014). In all observations of these interactions, long-finned pilot whales approached killer whales, and killer whales avoided long-finned pilot whales by moving away, sometimes at high speed (Stenersen and Similä 2004; de Stephanis et al. 2014). Competition and anti-predator mobbing are the main hypotheses for the causes of these interactions (Curé et al. 2012, 2019; de Stephanis et al. 2014).

Predation of long-finned pilot whales on killer whales has never been reported and the opposite is rare (Jefferson et al. 1991). Competition between the two species could occur for food or habitat. In the Strait of Gibraltar, stable isotope analyses suggested a clear segregation of isotopic niches, with killer whales feeding at a higher trophic level than the long-finned pilot whales (de Stephanis et al. 2014). Killer whales in this area primarily fed on blue fin tuna (*Thunnus thynnus*), while the long-finned pilot whales likely targeted squid and fish (de Stephanis et al. 2008a; Esteban et al. 2014). Therefore, direct competition for prey seems an unlikely driver for the interactions. However, competition for habitat and feeding areas remains an untested possibility (Curé et al. 2012, 2019; de Stephanis et al. 2014).

Acoustic signals seem to play an important role in the interactions. Playback experiments in Norway showed that long-finned pilot whales approach both fish- and mammal-eating killer whale sounds and indicated that long-finned pilot whales can discriminate between the two stimuli (Curé et al. 2012, 2019). In response to the mammal-eating killer whales, long-finned pilot whales stopped foraging, tightened their groups and spent less time near the surface, therefore showing a fairly cryptic approach, potentially to inspect and evaluate the level of threat (Curé et al. 2019). In response to the fish-eating killer whales, they increased their group size by several groups joining together and increased their calling activity while moving towards the sound source (Curé et al. 2012, 2019). This behaviour is consistent with mobbing behaviours observed in other species, leading to the suggestion that long-finned pilot whales may approach fish-eating killer whales in a mobbing-like behaviour exhibited towards a low threat predator or potential competitor (de Stephanis et al. 2014; Curé et al. 2019).

Interactions between long-finned pilot whales and killer whales have been observed in Iceland (Samarra FIP, personal communication) but have not been studied in detail. As in the other locations where interactions have been reported, the drivers are unclear. Killer whales around Iceland mostly feed on herring (Sigurjonsson et al. 1988; Samarra et al.

2017a), and long-finned pilot whales likely specialise on squid (Sigurjónsson et al. 1993), indicating little potential for food competition. Predation by killer whales on long-finned pilot whales also seems an unlikely driver. Icelandic killer whales occasionally hunt marine mammals but only one potential predation event on long-finned pilot whales is reported from the south of Iceland in 1987, where a group of killer whales attacked long-finned pilot whales and blood was seen in the water (Donovan and Gunnlaugsson 1989; Samarra et al. 2018). The limited knowledge on long-finned pilot whales in Icelandic coastal waters has prevented further studies on the interactions with killer whales in this region.

1.6 Interactions between long-finned pilot whales and killer whales as a study system for the role of acoustic signals in interspecific interactions

Harassing approaches to drive other species away are commonly observed in competitive or predator-prey interactions. These ‘mobbing-like’ behaviours have been described in a variety of taxa, including in birds and mammals (Curio 1978; Driscoll et al. 2022). They often involve an increase in calling activity, which may serve to alert and recruit conspecifics or heterospecifics for a social defence response, or to deter competitors or predators through intimidation (Bradbury and Vehrenkamp 2011). Therefore, mobbing-like behaviours can have several benefits for the mobbing species (Curio 1978; Carlson and Griesser 2022). However, the behavioural responses of the mobbed species and associated biological costs they incur remain largely unexplored (Caro 2005). This gap prevents a full understanding of the mechanisms driving interspecific interactions from the perspectives of both the mobbed and the mobbing species.

The interactions between long-finned pilot whales and killer whales provide a suitable study system to investigate the role of acoustic signals in mediating interspecific interactions. While the mobbing-like behaviour of long-finned pilot whales can be triggered by the detection of killer whale sounds (Curé et al. 2012, 2019), it remains unclear whether killer whales also respond to long-finned pilot whale sounds. Long-finned pilot whales increase their calling activity during approaches to killer whales (Stenersen and Similä 2004; Curé et al. 2019) and it is likely that killer whales perceive these sounds from a distance (Branstetter et al. 2017). Detecting long-finned pilot whale sounds may help killer whales to anticipate a flight and balance associated costs (e.g. energy expenditure, loss of feeding opportunities) by determining the most appropriate response ahead of time. Therefore, investigating the response of killer whales to long-finned pilot whale sounds could provide important insights into the interaction between the two species, as well as the role of acoustic signals in interspecific interactions more generally.

2 Aims of the thesis

The aim of this thesis was to investigate the role of acoustic signals in mediating interactions within and between species of highly social and vocal marine top predators by examining the acoustic communication of Icelandic killer whales, their interactions with long-finned pilot whales and the role of acoustics within the interactions. Specific research objectives were:

1) Investigate the communicative complexity in Icelandic killer whales in terms of their repertoire use in different locations and over time, as well as the combination of calls (**Papers I and II**).
2) Describe the occurrence of long-finned pilot whales and killer whales in Icelandic coastal waters and their interspecific interactions (**Paper III**).
3) Test the role of acoustic signals in the interactions between long-finned pilot whales and killer whales (**Paper IV**).

To compare differences in acoustic communication within species, comprehensive descriptions of repertoires and communication structures were needed. The aim of **paper I** was to provide a detailed description of the Icelandic killer whale call repertoire, to compare it across locations and over time in order to provide a basis for investigating communicative structure in the population. A next step in understanding the communicative complexity within a species was to understand if and how individual vocalisations are stringed together. **Paper II** provides a description of call combinations in Icelandic killer whales and whether these might be specific to certain social groups or behavioural contexts.

To investigate the role of acoustic signals in mediating interspecific interactions, both sides of an interaction should be considered. The interactions between long-finned pilot whales and killer whales provide a relevant case study but information on the occurrence of the two species and detailed descriptions of the interaction were lacking in Iceland. The aim of **paper III** was therefore to investigate the occurrence of both species in different coastal regions around Iceland and assess the spatial and temporal overlap between the two species. Detailed descriptions of the interactions between the two species allowed for the evaluation of the types of behavioural responses observed and their frequency, potential causes and consequences. Finally, **paper IV** explored the role of sound in interactions between long-finned pilot whales and killer whales using playback experiments to investigate whether interspecific interactions can be shaped and driven acoustically from both species' sides of the interaction.

3 Methods

3.1 Study locations

The four studies of this PhD project were carried out across several locations around Iceland (*Figure 6*). Vestmannaeyjar and Breiðafjörður are current herring spawning and overwintering grounds. Killer whales are regularly encountered in both locations, where research has been carried out for several years. Therefore, most data were collected in these locations. **Papers I** and **III** aimed to answer questions on geographical patterns and therefore additional locations with more opportunistic data collection were included in the analyses. To describe the call repertoire of Icelandic killer whales (**paper I**), the aim was to sample as many locations and over as long a timespan as possible, which led to acoustic recordings being used from five locations, collected in 1985-2016. To describe call combinations (**paper II**), only recordings from the animal-attached multisensor archival tags were used, which were available from Vestmannaeyjar and Breiðafjörður. To describe the occurrence and interactions of long-finned pilot whales and killer whales around Iceland (**paper III**), sightings data from research projects and whale watching tour operators around the country were used. Playback experiments to test the role of acoustic cues in the interactions (**paper IV**) were conducted in Vestmannaeyjar, the location where most interactions were observed.

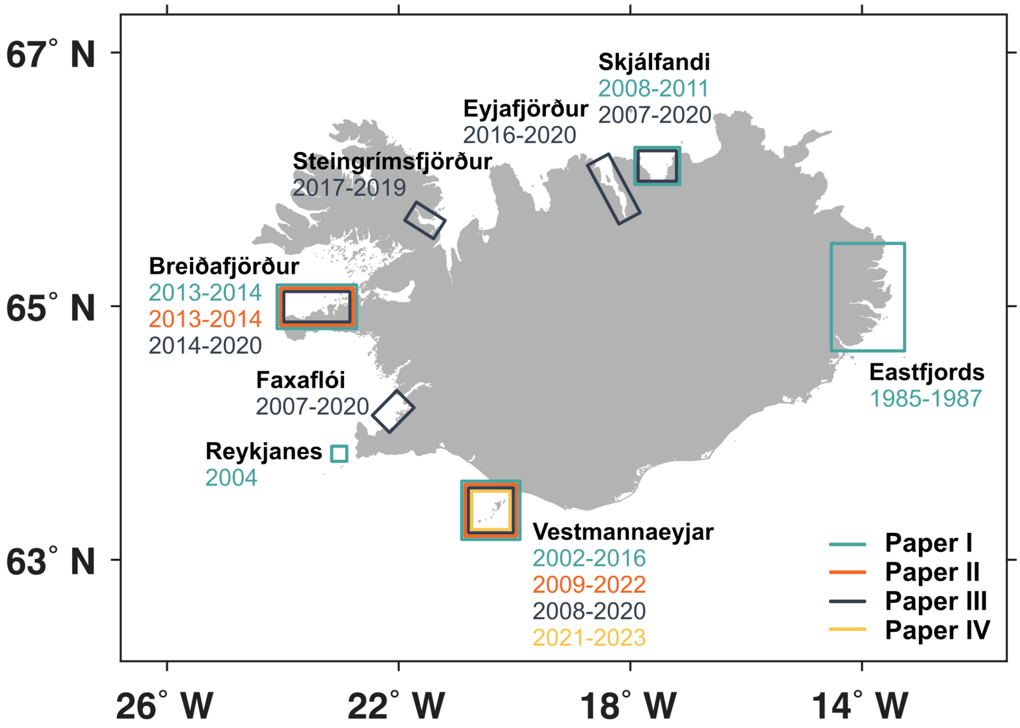


Figure 6: Map of Iceland indicating the study areas and years of data collection per paper.

3.2 Acoustic data collection: papers I, II and IV

Acoustic recordings were collected using a variety of methods, including boat-deployed hydrophones (single hydrophone, or vertical or towed arrays of hydrophones), bottom-moored single hydrophone recorders and multisensor archival tags (with one or two hydrophones each). Exact methods used varied across years and depended upon the research priorities of the field work, but generally, killer whales were searched for from boat or land. Once located, groups of whales were approached and acoustic recordings or tagging attempts were started. In the herring grounds in Vestmannaeyjar and Breiðafjörður, killer whales were often feeding and gathered in large aggregations, which provides many opportunities to record or tag whales but makes it difficult to locate isolated groups and establish group affiliations (Sigurjónsson et al. 1988; Tavares et al. 2017). Concurrent photo-identification was collected during many but not all acoustic recordings.

3.3 Multisensor tags: papers I, II and IV

Data from multisensor archival tags were used in **papers I, II** and **IV**. These tags were attached to killer whales with suction cups, using a 5-m long carbon fibre pole or pneumatic tag launcher (ARTS, Kleivane et al. 2022). Acoustic recordings from one Customized Animal Tracking Solutions (CATS; www.cats.is) Diary tag were used in **paper II** but the remainder of tags used were Dtags (*Figure 7*, Johnson and Tyack 2003). Dtags were equipped with a pressure sensor, temperature sensor, 3D magnetometer, 3D accelerometer, VHF transmitter, two hydrophones and in more recent years, snapshot GPS and a video logger. The tag is typically programmed to stay on the whale for several hours, after which it releases, starts floating and can be collected. Approximate locations of the floating tag are received from the GPS via ARGOS and the VHF beacon, which can be used to pinpoint the location more precisely. For **paper IV**, the pressure data from the tag were converted to depth and the body orientation of the whale was described in terms of pitch, roll and heading,

Figure 7: Dtag in the lab and attached to a killer whale (photo: Tatiana Marchon).

which were based on the acceleration data and magnetic field strength data (Johnson and Tyack 2003). This information was then used in combination with locations from visual sightings and GPS to estimate the horizontal movement track of the whale (Wensveen et al. 2015).

3.4 Acoustic data analysis: papers I, II and IV

All acoustic recordings were inspected using spectrograms, either in the software Audacity versions 2.1.2 and 2.3.1 (www.audacityteam.org) or Adobe Audition 2.0 (Adobe Systems Inc., San Jose CA). Spectrograms had a Hann window, with FFT = 8,192 for 96, 192, and 240 kHz sampling rates and FFT = 4,096 for 44.1, 48, and 64 kHz sampling rates; or a Blackmann-Harris window, with FFT = 2,048 or 4,096, for 96 and 192 kHz sampling rates, respectively. Killer whale calls were marked manually and given a quality rating of high (3), medium (2), or low (1) based on the perceived signal to noise ratio. Only high-quality calls were extracted and classified to call type. The total recording time was ~3600 hours and close to 25.000 high-quality calls were labelled.

Killer whales produce underwater tail slaps when feeding on herring. These tail slaps are clearly audible in acoustic recordings and can be used as indicators of feeding events (Similä and Ugarte 1993; Simon et al. 2005). Killer whales also tend to speed up right before a tail slap, which leads to more flow noise audible in the recording. This flow noise, as well as the signal to noise ratio of the tail slap were used to identify high-, medium- and low-quality tail slaps. No analysis was conducted on the sounds themselves, but high-quality tail slaps were used as indicators of feeding behaviour in **papers II** and **IV**.

3.4.1 Call classification

The recordings from the Eastfjords and some of the recordings collected in Vestmannaeyjar and Breiðafjörður (2008-2016) were previously used to establish call catalogues for Icelandic killer whales (Moore et al. 1988; Selbmann et al. 2019). All additional calls were classified to the call types and subtypes in these catalogues based on visual and aural examination of spectrograms with specific attention to the shape of the call contour, the number of elements and segments, and to a lesser extent, call duration (Ford 1987; Strager 1995). Subtypes were assigned if an element or segment was added/subtracted from a call, if a second frequency component was present/absent, or if a major change in a part of the call occurred (Strager 1995). The term ‘call category’ is used to include both call types and subtypes. For some call types ‘aberrant’ versions existed, where the call could be identified as belonging to a specific category, but showed alterations in frequency or duration (Ford 1989). Calls that could not be clearly assigned to a call category were considered ‘variable’ (Ford 1989). All call classifications were cross-validated by a second observer and a subset of calls from the Selbmann et al. (2019) catalogue were used to validate the classification.

3.4.2 Validation of call classification

The reliability of the manual call classification was tested in **paper I**. This was done using an interobserver agreement test with 11 cetacean acoustics experts, as well as using a classification and regression tree (CART) and random forest analysis. While the experts mostly agreed on call types, some disagreement showed in the distinction of subtypes and resulted in a moderate agreement score between observers (Krippendorff's alpha = 0.57). These differences are likely due to observers being either 'splitters' or 'lumpers', which is a well-known problem in cetacean sound classification and can lead to different classifications even among experienced observers (Oswald et al. 2022). However, the CART and random forest analyses showed high agreement to the manual classification. For each call, 13 metrics were measured and used as predictor variables: start and end frequency, sideband interval at the start, end, and the middle of the call, call duration, time to maximum frequency, time to maximum frequency proportion, frequency trend ratio, frequency range ratio, the number of elements and segments, and the presence/absence of a high-frequency component. The CART correctly classified 85% of calls to the same category as the manual classification and the random forest model had a mean OOB error of 12% ± 0.2% across five trials. These results are on par with or better than results from other cetacean species (Rekdahl et al. 2013, 2017; Garland et al. 2015; Fournet et al. 2018; Sharpe et al. 2019; Epp et al. 2022) and thus provided strong support for the manual classification method.

3.5 Species occurrence data and observations of interactions: paper III

Data on the occurrence of long-finned pilot whales and killer whales used in **paper III** were collected during dedicated research (in Vestmannaeyjar) or opportunistically by researchers and naturalists onboard whale watching tours (other locations). Therefore, survey effort varied between locations and seasons, with the summer months and whale watching tourism centres being covered more extensively. In all locations boat-based observations were recorded, with at least one observer actively searching for cetaceans and taking notes on the species sighted. In Vestmannaeyjar, additional visual surveys were undertaken from a vantage point on land (2017-2020) using 7x50 and 15x70 binoculars, as well as a calibrated digital theodolite to record positions of sightings and track groups of killer whales and/or long-finned pilot whales. From the effort and sightings data, occurrence of long-finned pilot whales and killer whales was calculated as the percentage of days with effort that included sightings of either species.

Observations of interactions between long-finned pilot whales and killer whales were collected ad libitum (Mann 1999). An interaction was defined as either of the two species approaching the other and the approach possibly resulting in a change in behaviour of the second species.

3.6 Playback experiments: paper IV

In **paper IV** playback experiments were conducted to killer whales and their behavioural responses were monitored using Dtags and surface observation. Each experiment consisted of three phases, each 15 minutes in duration: a pre-exposure phase without sound playback, the during-phase with exposure to playback, and the post-phase without sound playback. Usually, two experiments with two different sound stimuli were performed, separated by an additional 15 minutes between the end of the post-exposure of the first stimulus and the start of the pre-exposure of the second stimulus.

Three different types of acoustic stimuli were used in the playbacks: long-finned pilot whale sounds, a broadband noise control, and a 1-2 kHz upsweep signal. The pilot whale stimuli were created from natural sound sequences recorded from long-finned pilot whales in the study area. Field observations suggested that long-finned pilot whales have higher call rates and produce more overlapped sounds when approaching killer whales than in other contexts. Therefore, only recordings collected during clear approaches to killer whales were used in the stimuli. The noise control stimuli were created from the same recordings, using periods without pilot whale sounds that were amplified to have the same average broadband sound level as the pilot whale stimuli. The upsweep stimulus was composed of a 19 s, 1-2 kHz synthetic sound repeated without pause. This stimulus was intended as a control but was removed from the playback procedure after the first year to maximise data collection for the other two stimuli. A total of three different versions for each stimulus type (pilot whale and broadband noise control), were used to reduce pseudoreplication and they were used alternatingly to control for a potential order effect (McGregor 1992).

Observations of the surface behaviour of the tagged whale and its group were collected from a separate boat. The variables included group size, individual spacing, number of individuals in the focal area (200 m), milling index, and line swimming (Visser et al. 2014).

3.7 Statistical analyses

A variety of statistical analyses were applied to test for differences in call repertoire and species occurrence between locations and over time, to test for the ordering of calls, and to test for behavioural responses to the playback experiments.

Variation in call category occurrence within and between locations was investigated in **paper I**, using the similarity index (SI) and the Whittaker similarity index (WSI). Both indices provide a proportion of call categories shared but the similarity index only considers presence/absence, while the Whittaker similarity index also considers the frequency of usage (Ford 1991; Yurk et al. 2002; Crance et al. 2014). Nonparametric Spearman rank correlations were calculated to test for a linear relationship in occurrence of call categories between two locations and between the two years with the longest time between them.

Ordering of call categories was analysed using a first-order Markov model in **paper II**. To test the null hypothesis that transitions between call categories are random, expected and observed transition matrices were compared using a Pearson's chi-squared test. To identify call transitions that occurred more often than expected from the null hypothesis, a post-hoc test for pairwise comparisons with Bonferroni correction for multiple testing was applied.

In **paper III** changes in species occurrence over time were investigated using yearly total percentages of occurrence for each location, Pearson's correlation tests, or Spearman's rank tests.

Behavioural responses of killer whales to long-finned pilot whale sound playbacks were investigated in **paper IV** using hidden Markov models (HMMs) and general estimating equations (GEEs). A 3-state HMM was created using five variables derived from different data streams of the Dtags: horizontal step length, horizontal turning angle, mean depth, acoustic presence/absence of calls, and acoustic presence/absence of tail slaps. Potential changes in behaviour state transition probability and state-specific step length (equivalent to speed) and calling activity were tested for by including a factor covariate with three levels: off (no playback), noise (broadband noise control), PW (long-finned pilot whale sounds). Changes in horizontal movement toward or away from the playback source were investigated using a horizontal movement reaction score. This score compared the observed horizontal track during playback to a projected track of the whale based on its speed and direction of movement prior to the start of the playback (Curé et al. 2012). A negative score indicates an avoidance response (the animal ended farther from the playback compared to its projected position) and a positive score indicates an attraction response. GEEs were used to test for differences in the reaction scores between stimuli and test for changes in acoustic and group behaviour.

4 Summary of results

4.1 Call type repertoire of killer whales (*Orcinus orca*) in Iceland and its variation across regions – Paper I

The paper describes the call repertoire of Icelandic killer whales and how it varies between locations and over time using a 32-year dataset (1985-2016). A total of 91 different call categories (call types and subtypes) were classified. The manual classification was confirmed using a classification and regression tree (CART) and random forest analysis, both of which showed high agreement with the manual classification. Five call categories (I45, I44, I11.4, I36) made up a large proportion (38%) of calls recorded, while all other call categories were below 5%. Most call categories (56%) were found at two or more locations but only one call category was recorded in all five locations (I11.4). The highest proportion of call categories was shared between the herring grounds in Vestmannaeyjar and Breiðafjörður. Both locations, as well as the Eastfjords, also had a proportion of calls that was unique and not recorded elsewhere. The samples from Reykjanes and Skjálfandi were relatively small and did not include unique call categories. In Vestmannaeyjar, data were available covering a 14-year timespan (2002-2016) and indicated long-term stability of the repertoire interspersed by shorter term changes. Most of the call categories recorded in 2002 also occurred in 2016. However, some categories present in the early recordings were absent in 2008-2013 but occurred again from 2014 onwards. These results show that the call repertoire of Icelandic killer whales reflects the movement patterns of these whales and indicate some differences between locations, which could be related to differences in individuals or groups present.

4.2 Call combination patterns in Icelandic killer whales (*Orcinus orca*) – Paper II

Using acoustic data from 22 multisensor tag deployments on killer whales in five years between 2009 and 2022, this paper shows that Icelandic killer whales do not produce calls in a random order. A first-order Markov chain analysis indicated that transitions between call categories were significantly different from random, with repetitions and mixed call combinations occurring more often than expected by chance. Mixed call combinations contained two or three call categories and belonged to three different call combination clusters. Most notable was cluster A, consisting of six call categories (I38.1, I38.2, I39, I11.4, I69, I77) that occurred in different combinations. Cluster B mostly contained two call categories (I63 and I72.3) and cluster C contained three call categories that were all closely linked to call type I45. Call combinations were recorded over several years and across tag deployments on different individuals from different social clusters and age-sex classes. The majority of call combinations (68%) were produced outside of feeding contexts, in particular those of clusters A and B. While the function of call combinations remains unclear, the study provides insights into the communicative complexity in killer whales.

4.3 Occurrence of long-finned pilot whales (*Globicephala melas*) and killer whales (*Orcinus orca*) in Icelandic coastal waters and their interspecific interactions – Paper III

This paper describes the occurrence and interactions of long-finned pilot whales and killer whales in Icelandic coastal waters. It used sightings data from field observations of natural behaviour collected between 2007 and 2020 across six locations around Iceland. Both species were seen in all locations, but sightings (killer whales: n = 647 days, long-finned pilot whales: n = 183 days) varied strongly across time and space. Long-finned pilot whales were only seen in June to September. They were sighted most regularly in Vestmannaeyjar, Breiðafjörður, and Steingrímsfjörður and were only encountered infrequently in the other locations. Their occurrence significantly increased over time in Vestmannaeyjar and Faxaflói. Killer whales occurred year-round but were most commonly seen in Vestmannaeyjar during the summer and in Breiðafjörður during winter and spring. In these two locations, pilot whale occurrence was also high, and these were also the only two areas where interactions between the two species were observed. Interactions between pilot whales and killer whales were observed on 70.6% of the days that both species were observed simultaneously, with most observations in Vestmannaeyjar. In all interactions, pilot whales moved towards the killer whales, but killer whales showed different types of responses. In most interactions (68%) killer whales avoided pilot whales by moving away, in 28% this avoidance was at high speed with both species porpoising, and in 4% a response was not observed. Pilot whale group sizes were larger for high-speed avoidance compared to regular avoidance or when no interaction was observed. The observations indicated that the interactions are complex, with pilot whales sometimes approaching several times over the course of an encounter and killer whales showing different types of responses.

4.4 A top predator on the run: behavioural responses of killer whales to sounds of long-finned pilot whales – Paper IV

Paper IV tests the role of acoustic cues in the interactions between long-finned pilot whales and killer whales using playback experiments. A total of 15 playback experiments were conducted to killer whales equipped with multisensor tags: eight of long-finned pilot whale sounds, five of noise control, and two of a 1-2 kHz upsweep signal. A hidden Markov model (HMM) with three states (travel, feeding, other) indicated that killer whales were more likely to switch to a travelling state in response to playbacks of pilot whale and noise control sounds. Within the travelling state, step length (and thus speed) of killer whales was significantly higher during pilot whale playback compared to noise control or no playback. A horizontal movement reaction score showed that killer whales moved away from pilot whale sounds and showed little change in movement during noise control playbacks. Killer whales initially increased their calling rate during pilot whale sound playbacks but then typically went quiet and remained quiet after the end of the playback. At the group behaviour level, spacing between individuals decreased significantly, killer whales showed a lined-up geometry more often and milling was observed less frequently during pilot whale playback compared to the noise control, but no significant changes in group size were observed. Together, these behavioural changes indicate that long-finned pilot whale sounds lead to a clear avoidance response in killer whales, showing the importance of acoustic signals in interactions between cetacean species.

5 General discussion and conclusions

The aim of this thesis was to investigate the role of acoustic signals in mediating interactions within and between species of two highly social and vocal marine top predators, the killer whale and the long-finned pilot whale. This was achieved by investigating the call repertoire and call combinations in Icelandic killer whales as an example for within species communication and by testing the role of acoustic signals in interactions with long-finned pilot whales.

5.1 Acoustic signals in Icelandic killer whales

The results from the studies on the call repertoire and call combinations (**papers I** and **II**) show that the acoustic communication system of Icelandic killer whales is complex, with variations across space and time and clearly structured sequences of calls.

The investigation of geographical differences in call repertoire around Iceland showed some difference in call categories across locations. These results largely mirror what is known about the movement patterns of killer whales around Iceland from photoidentification studies. About half of the identified individuals regularly move between the herring spawning and overwintering grounds in Vestmannaeyjar and Breiðafjörður (Samarra et al. 2017b; Marchon et al. 2024), which also showed a large degree of call repertoire sharing. Connections to other locations around Iceland exist but are weaker, in particular few whales were identified and matched from the north and east of Iceland to the herring grounds in the south and west (Marchon et al. 2024). Similarly, only a few call categories from the east of Iceland were found in the south and west. Thus, the results from this study show that movement patterns of Icelandic killer whales are reflected in the degree of call repertoire sharing between locations.

A large part of the call repertoire was shared across several regions. The social structure of Icelandic killer whales is more fluid than what has been reported for other locations (Tavares et al. 2017). Therefore, more sharing of calls between groups may be needed in this population to facilitate communication and to allow for the flexibility required in fission-fusion dynamics. This is also supported in the structure of the calls. The two most commonly recorded call types were highly variable, and the graded nature of the variation made it impossible to differentiate subtypes. Despite the original catalogue being generated from a large sample size, intermediate versions of a few call types were observed when classifying new calls recorded in 2021-2023, further emphasising the graded nature of at least some of the Icelandic killer whale call types. The vocal repertories of humpback whales, as well as several primate and anuran species, include both discrete and graded signals (Hammerschmidt and Fischer 1998; Keenan et al. 2013; Toledo et al. 2015; Cusano et al. 2021). Graded vocalisations can convey subtle information such as the caller's internal state, motivation or intent and have the potential to encode greater amounts of information than discrete signals (Hauser 1996; Bradbury and Vehrenkamp 2011). Therefore, a widely shared repertoire including potentially more graded calls may help Icelandic killer whales navigate the variety of social interactions they experience (Freeberg et al. 2012).

Not only calls but also specific combinations of calls were shared across locations and produced by several social clusters. They included the three most commonly recorded call types, one of which was call type I11.4, the only call type recorded at all locations studied and one of three call types matched to Scotland (Deecke et al. 2011; Selbmann et al. 2021). The reported call combinations were recently included in a review comparing the efficiency of acoustic combinations across several cetacean species and humans, which indicated that call combinations of killer whales have the potential to efficiently encode information (Youngblood 2025). As killer whale calls do not seem to be behaviour specific, it had previously been suggested that it is the combination of calls rather than the individual sounds that are of importance (Filatova et al. 2009). In some recordings, call combinations composed a large part of the call production, indicating that they may be important during specific behaviours. Icelandic killer whales are most vocal during feeding, followed by socialising and almost silent when travelling (Simon et al. 2007b). Most call combinations were produced outside of feeding contexts. The social complexity hypothesis suggests that social interactions may place additional demands on the communication system, which could promote the production of combinations of calls (Freeberg et al. 2012). Therefore, their frequent occurrence, their capacity to efficiently encode information and the fact that they were mostly produced outside of feeding contexts, suggests that these call combinations may be produced during socialising behaviours.

Call combinations also have good properties for long-range transmission, indicating that they might be important in long-distance communication with other group members (Saulitis et al. 2005). High frequency components of killer whale calls and buzzes with energy peaks in higher frequencies may be detectable over long distances and in high ambient noise levels (Yurk et al. 2023). All call combinations described contained calls with buzz components, which would transmit well. In addition, while individual calls might not be recognisable across distance or with increasing noise, the structure of a sequence of calls could be retained and thus aid long-distance recognition. Call combinations were observed during one pilot whale sound playback (oo21_184a). The tagged killer whale had been very quiet before the start of the playback but increased calling activity during the playback, before going quiet at the end of the playback. Calls produced were almost exclusively from call combination cluster A. The focal group size reduced during the playback, indicating that some group members may have become separated, which would further support that call combinations may be used to establish contact with distant individuals. In the fluid social structure of Icelandic killer whales, such fission and fusion events are likely to occur often and may explain the frequent occurrence of call combinations.

Overall, the results on acoustic signals in Icelandic killer whales support the social complexity hypothesis (Freeberg et al. 2012). They have a large call repertoire, and calls are often combined into sequences, which may increase information content. Call combinations and large parts of the repertoire appear to be shared across locations and potentially social clusters, and call combinations may be produced during social behaviours and/or aid contact with distant group members. Icelandic killer whales have flexible social associations, with some strong bonds but group sizes may vary, and fission-fusion events can be frequent. Therefore, they would benefit from the described acoustic features, which create a communication system adapted to a fluid social structure.

5.2 Interactions between long-finned pilot whales and killer whales and the role of acoustic signals

The studies on behavioural interactions between long-finned pilot whales and killer whales and the role of acoustic signals in these interactions (**papers III** and **IV**) showed that the interactions are common when the two species overlap in their distribution and that sound seems to play an important role in them.

The study on the occurrence of both species provides important basic information that had been lacking for Icelandic coastal waters, in particular for long-finned pilot whales. While no changes in killer whale occurrence were observed over time, long-finned pilot whale occurrence increased, especially in the south of Iceland. This increase could be due to changes in prey distribution. Squid are thought to be a major food source of long-finned pilot whales in the area and their occurrence is strongly affected by environmental parameters, leading to large fluctuations and so-called ‘squid-years’, where large aggregations of squid appear around Iceland, the Faroe Islands, and off Norway (Sigurjónsson et al. 1993; Jákupsstovu 2002; Hátún et al. 2009). Therefore, the increase in long-finned pilot whale occurrence could be due to fluctuations in their squid prey. However, long-finned pilot whale sightings remained high in Vestmannaeyjar in the years after the study (2021-2024, Icelandic Orca Project, unpublished data), indicating that the increase is not just a temporary shift. Long-finned pilot whales could also feed on mackerel, which is an important prey for the species in the western North Atlantic (Overholtz and Waring 1991; Abend and Smith 1997; Gannon et al. 1997). Mackerel has increased considerably between 2007 and 2014 and is still caught in Icelandic waters (Astthorsson et al. 2012; MFRI 2023). In the 2023 fieldwork season long-finned pilot whales were observed in Vestmannaeyjar with mackerel, potentially feeding and one observation in Breiðafjörður also included a bird feeding on mackerel close to the pilot whales. However, the limited knowledge on the diet and ecology of long-finned pilot whales in the region prevents clear conclusions. Alternatively, long-finned pilot whales might be shifting their distributional range in response to warming waters and moving north, as has been shown for the species in the western North Atlantic (Thorne and Nye 2021). Their increased occurrence in Icelandic coastal waters could potentially indicate a shift in the ecosystem, which is likely to have multiple effects, including changes in species composition and interactions between species (Walther 2010).

Occurrence of long-finned pilot whales and killer whales was highest in the south (Vestmannaeyjar) and west (Breiðafjörður) of Iceland. Whenever both species were seen at the same time in the same area, interactions were common. These interactions are more complex than previously described, with killer whales sometimes tolerating the presence of long-finned pilot whales but mostly avoiding the pilot whales and sometimes avoiding them at high speed. The complexity of these interactions was further underscored when in 2021 and 2022 single newborn long-finned pilot whale calves were observed with groups of killer whales in Icelandic coastal waters on three separate occasions (Mrusczok et al. 2023, Baumgartner et al. accepted). Drivers and functions of these observations remain unclear, but they highlight the potential influence of previously unconsidered factors. In this study, killer whales showed clear avoidance responses to playbacks of long-finned pilot whale sounds, including movement away from the sound source, increases in speed and calling, as well as adjustment of the group spacing and alignment. As described above little is known about long-finned pilot whale diet and ecology in Icelandic waters, preventing a clear identification of the potential causes of the interactions. Thus, a mobbing-like behaviour against a potential predator or competitor (de Stephanis et al. 2014; Curé et al. 2019) remains the most likely explanation.

Most studies on mobbing-like behaviours have focused on the mobbing species, while behavioural responses and biological costs to the species being mobbed remain largely unexplored (Pettifor 1990; Caro 2005; Clark 2005). Similarly, several studies have shown acoustic responses of prey species to the detection of a predator and that they will lead to appropriate responses in conspecifics or other potential prey species (Owings and Virginia 1978; Seyfarth et al. 1980b, a; Johnson et al. 2003; Leavesley and Magrath 2005; Palleroni et al. 2005; Wheeler 2008; Dutour et al. 2017), but few studies have explored whether and how the predators respond to such signals (Zuberbühler 1999; Adams and Kitchen 2018). In this study, killer whales rapidly responded to the acoustic signals from long-finned pilot whales in playback experiments. In combination with playbacks of killer whale sounds to long-finned pilot whales (Curé et al. 2012, 2019), these results show that acoustic signals can mediate interspecific interactions both ways. While the mobbing-like behaviour of pilot whales can be triggered by the detection of killer whale sounds, killer whales also seem to detect long-finned pilot whales, which likely enables them to anticipate and balance the cost of avoidance by determining the most appropriate response ahead of time.

The risk-disturbance hypothesis suggests that animals respond to a threat by balancing a trade-off between the perceived threat-level and the loss of any fitness-enhancing activities, such as feeding or resting (Frid and Dill 2002). Even though killer whales are the ocean's apex predator they regularly opt to avoid long-finned pilot whales, indicating that they either perceive them as a high-level threat or that the cost of avoidance is low. While responses to playbacks never seemed to last very long after the end of the playback, real interactions can last several hours, with the long-finned pilot whales approaching several times. The frequent occurrence of interactions, coupled with the loss of feeding opportunities and potentially high energy expenditure during avoidance mean that the interactions could have considerable cumulative impacts on killer whales. These could manifest for example in changes in habitat use or behaviour of killer whales, which could have population-level consequences.

In summary, the results of the studies on the occurrence of long-finned pilot whales and killer whales and their interactions showed that long-finned pilot whale occurrence increased in Icelandic coastal waters, and spatial-temporal overlap with killer whales leads to antagonistic interactions. These interactions are mediated acoustically with both species responding to the acoustic signals of the other. The most likely driver of the interactions is a mobbing-like behaviour of the long-finned pilot whales towards the killer whales.

5.3 Future directions

This PhD project contributes to our knowledge on the role of acoustic signals in interactions within and between cetacean species, as well as on the occurrence of killer whales and long-finned pilot whales in Icelandic waters and their interactions. However, some questions remain unanswered and several newly emerged from this research.

Marine ecosystems are variable and top predators such as whales or seabirds can provide good indicators of shifts in these systems (Hansen et al. 2021). However, several fundamental pieces of information on the population status, feeding ecology, and behaviour of killer whales and long-finned pilot whales in Icelandic waters are missing. This study confirmed that killer whale occurrence in Icelandic waters is tightly tied to the herring grounds, underscoring the importance of this prey. Nevertheless, a large part of the population does not follow the herring year-round and monitoring outside of herring grounds and whale watching locations would be important to fully understand the movements and ecology of the species. Passive acoustic monitoring can be useful here, as it allows to monitor areas and seasons that are difficult to survey visually. The description of the killer whale call repertoire and the geographical differences found in this study provide important baseline information that will aid such studies and allow for future comparisons across regions. Passive acoustic monitoring could also inform on the presence of long-finned pilot whales but acoustic studies on the repertoire of the species in Icelandic waters are needed.

Information on the feeding ecology and distribution of prey species of long-finned pilot whales and killer whales would be useful to understand the observed increase of pilot whales in Icelandic coastal waters and to tease apart the drivers of the interactions with the killer whales. For example, little is known about the diet and distribution of potential prey of long-finned pilot whales in Icelandic waters. As described above, squid and mackerel might be important. If the distribution of squid would overlap with herring, competition for feeding habitats could be a driver of the interactions. Mackerel often overlaps spatially with herring (Óskarsson et al. 2016). Although no predation events have been observed, it is unknown whether Icelandic killer whales have taken advantage of the incoming mackerel. Therefore, long-finned pilot whales and killer whales may compete directly for prey sources or may be co-occurring due to overlap in the distribution of their prey. These questions could be answered with studies on the diet, ecology, site fidelity and habitat use of both species as well as studies on the distribution and abundance of potential prey species.

Acoustic signals clearly play an important role in the interactions but only stimuli recorded during observed interactions were used, when long-finned pilot whales are highly vocal. Therefore, it remains unclear whether killer whales respond to any pilot whale sounds or just those produced in this specific context and whether they only respond to sounds produced from familiar populations. Future playback experiments testing pilot whale sound stimuli recorded in different behavioural contexts and from different locations could help answer these questions and provide information on the potential impacts of the presence of long-finned pilot whales to killer whales. Furthermore, detailed investigations into the acoustic responses of both species to the detection of the other could provide insights into what kind of information may be transmitted and further our understanding of the role of acoustic signals in interspecific interactions.

Acoustic signals are important in the communication system of killer whales and data collection in the little sampled regions outside the herring grounds as well as offshore would be valuable to better understand geographical patterns of variation in call type repertoire around Iceland. Acoustic studies of isolated groups will be crucial to determine whether group-specific repertoires exist in the population and investigating the behavioural context of calling and the production of call combinations should shed light on the functions of calls and call combinations. Furthermore, investigating the structure of calls, including the degree of stereotypy vs. gradation could provide insights into the amounts and types of information encoded in these signals and how that relates to the social structure of killer whales. Such studies on repertoires, complexity of signal structure and combinations of sounds would benefit from cross-population comparisons to further our understanding of acoustic communication in this highly social species.

References

Abend AG, Smith TD (1995) Differences in ratios of stable isotopes of nitrogen in long-finned pilot whales (*Globicephala melas*) in the western and eastern North Atlantic. *ICES Journal of Marine Science* 52:837–841. doi: 10.1006/jmsc.1995.0080

Abend AG, Smith TD (1997) Differences in stable isotope ratios of carbon and nitrogen between long-finned pilot whales (*Globicephala melas*) and their primary prey in the western north Atlantic. *ICES Journal of Marine Science* 54:500–503. doi: 10.1006/jmsc.1996.0192

Adams DB, Kitchen DM (2018) Experimental evidence that titi and saki monkey alarm calls deter an ambush predator. *Animal Behaviour* 145:141–147. doi: 10.1016/j.anbehav.2018.09.010

Allen AN, Schanze JJ, Solow AR, Tyack PL (2014) Analysis of a Blainville's beaked whale's movement response to playback of killer whale vocalizations. *Marine Mammal Science* 30:154–168. doi: 10.1111/mms.12028

Andriolo A, Reis SS, Amorim TOS, Sucunza F, de Castro FR, Maia YG, Zerbini AN, Bortolotto GA, Dalla Rosa L (2015) Killer whale (*Orcinus orca*) whistles from the western South Atlantic Ocean include high frequency signals. *Journal of the Acoustical Society of America* 138:1696–1701. doi: 10.1121/1.4928308

Astthorsson OS, Valdimarsson H, Gudmundsdottir A, Óskarsson GJ (2012) Climate-related variations in the occurrence and distribution of mackerel (*Scomber scombrus*) in Icelandic waters. *ICES Journal of Marine Science* 69:1289–1297. doi: 10.1093/icesjms/fss084

Au WWL (1993) The sonar of dolphins. Springer, New York

Bain DE (1986) Acoustic behavior of *Orcinus*: Sequences, periodicity, behavioral correlates and an automated technique for call classification. In: Kirkevold BC, Lockard JS (eds) Behavioral biology of killer whales. Alan R. Liss, New York, pp 335–371

Baird RW, Whitehead H (2000) Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Canadian Journal of Zoology* 78:2096–2105. doi: 10.1139/cjz-78-12-2096

Baraff LS, Asmutis-Silvia RA (1998) Long-term association of an individual long-finned pilot whale and Atlantic white-sided dolphins. *Marine Mammal Science* 14:155–161. doi: 10.1111/j.1748-7692.1998.tb00700.x

Barrett-Lennard LG, Ford JKB, Heise KA (1996) The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour* 51:553–565. doi: 10.1006/anbe.1996.0059

Baumgartner C, Selbmann A, Middel H, Schulze J, Bellon G, Samarra FIP (accepted) Interactions between killer whales (*Orcinus orca*) and neonate long-finned pilot whales (*Globicephala melas*) off south Iceland. *Ecology and Evolution*.

Baumgartner CD, Jourdain E, Bonhoeffer S, Borgå K, Heide-Jørgensen MP, Karoliussen R, Laine JT, Rosing-Asvid A, Ruus A, Tavares SB, Ugarte F, Samarra FIP, Foote AD (2025) Kinship clustering within an ecologically diverse killer whale metapopulation. *Heredity* 134:109–119. doi: 10.1038/s41437-024-00740-y

Beck S, Kuningas S, Esteban R, Foote AD (2012) The influence of ecology on sociality in the killer whale (*Orcinus orca*). *Behavioral Ecology* 23:246–253. doi: 10.1093/beheco/arr151

Benti B, Miller P, Biuw M, Curé C (2021) Indication that the behavioural responses of humpback whales to killer whale sounds are influenced by trophic relationships. *Marine Ecology Progress Series* 660:217–232. doi: 10.3354/meps13592

Bernal XE, Page RA (2023) Tactics of evasion: strategies used by signallers to deter eavesdropping enemies from exploiting communication systems. *Biological Reviews* 98:222–242. doi: 10.1111/brv.1290

Bigg MA, Olesiuk PF, Ellis GM, Ford JKB, Balcomb KC (1990) Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Reports of the International Whaling Commission* 12:383–405.

Bradbury JW, Vehrenkamp SL (2011) Principles of animal communication. Sinauer Associates, Inc., Sunderland

Brambilla M, Janni O, Guidali F, Sorace A (2008) Song perception among incipient species as a mechanism for reproductive isolation. *Journal of Evolutionary Biology* 21:651–657. doi: 10.1111/j.1420-9101.2008.01523.x

Branstetter BK, St. Leger J, Acton D, Stewart J, Houser D, Finneran JJ, Jenkins K (2017) Killer whale (*Orcinus orca*) behavioral audiograms. *Journal of the Acoustical Society of America* 141:2387–2398. doi: 10.1121/1.4979116

Brewer AM, Castellote M, Van Cise AM, Gage T, Berdahl AM (2023) Communication in Cook Inlet beluga whales: Describing the vocal repertoire and masking of calls by commercial ship noise. *Journal of the Acoustical Society of America* 154:3487–3505. doi: 10.1121/10.0022516

Buckland ST, Bloch D, Cattanach KL, Gunnlaugsson T, Hoydal K, Lens S, Sigurjónsson J (1993) Distribution and abundance of long-finned pilot whales in the North Atlantic, estimated from NASS-87 and NASS-89 data. *Report of the International Whaling Commission Special Issue* 14:33–49.

Carlson NV, Griesser M (2022) Mobbing in animals: a thorough review and proposed future directions. In: Advances in the Study of Behavior. Academic Press, pp 1–41

Caro T (2005) Antipredator defenses in birds and mammals. University of Chicago Press

Chhaya V, Lahiri S, Jagan MA, Mohan R, Pathaw NA, Krishnan A (2021) Community Bioacoustics: Studying Acoustic Community Structure for Ecological and Conservation Insights. *Frontiers in Ecology and Evolution* 9:706445. doi: 10.3389/fevo.2021.706445

Ciano JN, Jørgensen R (2000) Observations on an interaction between a humpback whale (*Megaptera novaeangliae*) and pilot whales (*Globicephala melas*). *Marine Mammal Science* 16:245–248. doi: 10.1111/j.1748-7692.2000.tb00916.x

Clark RW (2005) Pursuit-deterrent communication between prey animals and timber rattlesnakes (*Crotalus horridus*): the response of snakes to harassment displays. *Behavioral Ecology and Sociobiology* 59:258–261. doi: 10.1007/s00265-005-0032-9

Courts R, Erbe C, Wellard R, Boisseau O, Jenner KC, Jenner MN (2020) Australian long-finned pilot whales (*Globicephala melas*) emit stereotypical, variable, biphonic, multi-component, and sequenced vocalisations, similar to those recorded in the northern hemisphere. *Scientific Reports* 10:1–14. doi: 10.1038/s41598-020-74111-y

Crance JL, Bowles AE, Garver A (2014) Evidence for vocal learning in juvenile male killer whales, *Orcinus orca*, from an adventitious cross-socializing experiment. *Journal of Experimental Biology* 217:1229–1237. doi: 10.1242/jeb.094300

Cummings WC, Thompson PO (1971) Gray whales, *Eschrichtius robustus*, avoid the underwater sounds of killer whales, *Orcinus orca*. *Fishery Bulletin* 69:525–530.

Curé C, Antunes R, Samarra F, Alves AC, Visser F, Kvadsheim PH, Miller PJO (2012) Pilot whales attracted to killer whale sounds: Acoustically-mediated interspecific interactions in cetaceans. *Plos One* 7:e52201. doi: 10.1371/journal.pone.0052201

Curé C, Sivle LD, Visser F, Wensveen PJ, Isojunno S, Harris CM, Kvadsheim PH, Lam FPA, Miller PJO (2015) Predator sound playbacks reveal strong avoidance responses in a fight strategist baleen whale. *Marine Ecology Progress Series* 526:267–282. doi: 10.3354/meps11231

Curé C, Isojunno S, Vester H, Visser F, Oudejans MG, Biassoni N, Massenet M, Wensveen PJ, Sivle LD, Tyack PL, Miller PJOM (2019) Discrimination between feeding sounds of fish and mammal eating killer whale ecotypes by long-finned pilot whales. *Animal Cognition* 22:863–882. doi: 10.1007/s10071-019-01282-1

Curio E (1978) The Adaptive Significance of Avian Mobbing I. Teleonomic Hypotheses and Predictions. *Zeitschrift für Tierpsychologie* 48:175–183. doi: 10.1111/j.1439-0310.1978.tb00254.x

Cusano DA, Paton D, Noad MJ, Dunlop RA (2021) Socially Complex Breeding Interactions in Humpback Whales Are Mediated Using a Complex Acoustic Repertoire. *Frontiers in Marine Science* 8:665186. doi: 10.3389/fmars.2021.665186

Dahlheim ME, Schulman-Janiger A, Black N, Ternullo R, Ellifrit D, Balcomb Iii KC (2008) Eastern temperate North Pacific offshore killer whales (*Orcinus orca*): Occurrence, movements, and insights into feeding ecology. *Marine Mammal Science* 24:719–729. doi: 10.1111/j.1748-7692.2008.00206.x

Danishevskaya AYu, Filatova OA, Samarra FIP, Miller PJO, Ford JKB, Yurk H, Matkin CO, Hoyt E (2020) Crowd intelligence can discern between repertoires of killer whale ecotypes. *Bioacoustics* 29:15–27. doi: 10.1080/09524622.2018.1538902

de Bruyn PJN, Tosh CA, Terauds A (2013) Killer whale ecotypes: is there a global model? *Biological Reviews* 88:62–80. doi: 10.1111/j.1469-185X.2012.00239.x

de Stephanis R, García-Tiscar S, Verborgh P, Esteban-Pavo R, Pérez S, Mivielle-Sebastia L, Guinet C (2008a) Diet of the social groups of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar. *Marine Biology* 154:603–612. doi: 10.1007/s00227-008-0953-8

de Stephanis R, Verborgh P, Pérez S, Esteban R, Minvielle-Sebastia L, Guinet C (2008b) Long-term social structure of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar. *Acta Ethologica* 11:81–94. doi: 10.1007/s10211-008-0045-2

de Stephanis R, Cornulier T, Verborgh P, Sierra JS, Gimeno NP, Guinet C (2008) Summer spatial distribution of cetaceans in the Strait of Gibraltar in relation to the oceanographic context. *Marine Ecology Progress Series* 353:275–288. doi: 10.3354/meps07164

de Stephanis R, Giménez J, Esteban R, Gauffier P, García-Tiscar S, Sinding MHS, Verborgh P (2014) Mobbing-like behavior by pilot whales towards killer whales: a response to resource competition or perceived predation risk? *Acta Ethologica* 18:69–78. doi: 10.1007/s10211-014-0189-1

Deecke VB (2003) The vocal behaviour of transient killer whales (*Orcinus orca*): Communicating with costly calls. PhD Thesis, University of St. Andrews

Deecke VB, Ford JKB, Spong P (1999) Quantifying complex patterns of bioacoustic variation: Use of a neural network to compare killer whale (*Orcinus orca*) dialects. *Journal of the Acoustical Society of America* 105:2499–2507. doi: 10.1121/1.426853

Deecke VB, Ford JKB, Slater PJB (2005) The vocal behaviour of mammal-eating killer whales: Communicating with costly calls. *Animal Behaviour* 69:395–405. doi: 10.1016/j.anbehav.2004.04.014

Deecke VB, Barrett-Lennard LG, Spong P, Ford JKB (2010) The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (*Orcinus orca*). *Naturwissenschaften* 97:513–518. doi: 10.1007/s00114-010-0657-z

Deecke VB, Nykänen M, Foote AD, Janik VM (2011) Vocal behaviour and feeding ecology of killer whales *Orcinus orca* around Shetland, UK. *Aquatic Biology* 13:79–88. doi: 10.3354/ab00353

DeRuiter SL, Bahr A, Blanchet M-A, Hansen SF, Kristensen JH, Madsen PT, Tyack PL, Wahlberg M (2009) Acoustic behaviour of echolocating porpoises during prey capture. *Journal of Experimental Biology* 212:3100–3107. doi: 10.1242/jeb.030825

Desportes G, Mouritsen R (1993) Preliminary results on the diet of long-finned pilot whales off the Faroe Islands. *Report of the International Whaling Commission Special Issue* 14:305–324.

Donovan GP, Gunnlaugsson T (1989) North Atlantic sightings survey 1987: report of the aerial survey off Iceland. *Report to the International Whaling Commission* 39:437-441

Driscoll I, Manser M, Thornton A (2022) Function of meerkats' mobbing-like response to secondary predator cues: recruitment not teaching. *Animal Behaviour* 194:111–126. doi: 10.1016/j.anbehav.2022.09.019

Dutour M, Léna JP, Lengagne T (2017) Mobbing calls: a signal transcending species boundaries. *Animal Behaviour* 131:3–11. doi: 10.1016/j.anbehav.2017.07.004

Ellis S, Franks DW, Weiss MN, Cant MA, Domenici P, Balcomb KC, Ellifrit DK, Croft DP (2021) Mixture models as a method for comparative sociality: social networks and demographic change in resident killer whales. *Behavioral Ecology and Sociobiology* 75:75. doi: 10.1007/s00265-021-03006-3

Epp MV, Fournet MEH, Davoren GK (2022) Humpback whale call repertoire on a northeastern Newfoundland foraging ground. *Marine Mammal Science* 38:256–273. doi: 10.1111/mms.12859

Esteban R, Verborgh P, Gauffier P, Giménez J, Afán I, Cañadas A, García P, Murcia JL, Magalhães S, Andreu E, de Stephanis R (2014) Identifying key habitat and seasonal patterns of a critically endangered population of killer whales. *Journal of the Marine Biological Association of the United Kingdom* 94:1317–1325. doi: 10.1017/S002531541300091X

Filatova OA, Fedutin ID, Burdin AM, Hoyt E (2007) The structure of the discrete call repertoire of killer whales *Orcinus orca* from southeast Kamchatka. *Bioacoustics* 16:261–280. doi: 10.1080/09524622.2007.9753581

Filatova OA, Fedutin ID, Nagaylik MM, Burdin AM, Hoyt E (2009) Usage of monophonic and biphonic calls by free-ranging resident killer whales (*Orcinus orca*) in Kamchatka, Russian Far East. *Acta Ethologica* 12:37–44. doi: 10.1007/s10211-009-0056-7

Filatova OA, Ford JK, Matkin CO, Barrett-Lennard LG, Burdin AM, Hoyt E (2012) Ultrasonic whistles of killer whales (*Orcinus orca*) recorded in the North Pacific (L). *Journal of the Acoustical Society of America* 132:3618–3621. doi: 10.1121/1.4764874

Filatova OA, Guzeev MA, Fedutin ID, Burdin AM, Hoyt E (2013) Dependence of killer whale (*Orcinus orca*) acoustic signals on the type of activity and social context. *Biology Bulletin* 40:790–796. doi: 10.1134/S1062359013090045

Filatova OA, Samarra FIP, Deecke VB, Ford JKB, Miller PJO, Yurk H (2015a) Cultural evolution of killer whale calls: background, mechanisms and consequences. *Behaviour* 152:2001–2038. doi: 10.1163/1568539X-00003317

Filatova OA, Miller PJO, Yurk H, Samarra FIP, Hoyt E, Ford JKB, Matkin CO, Barrett-Lennard LG (2015b) Killer whale call frequency is similar across the oceans, but varies across sympatric ecotypes. *Journal of the Acoustical Society of America* 138:251–257. doi: 10.1121/1.4922704

Filatova OA, Borisova EA, Shpak OV, Meschersky IG, Tiunov AV, Goncharov AA, Fedutin ID, Burdin AM (2015c) Reproductively isolated ecotypes of killer whales *Orcinus orca* in the seas of the Russian Far East. *Biology Bulletin* 42:674–681. doi: 10.1134/S1062359015070043

Filatova OA, Shpak OV, Ivkovich TV, Volkova EV, Fedutin ID, Ovsyanikova EN, Burdin AM, Hoyt E (2019) Large-scale habitat segregation of fish-eating and mammal-eating killer whales (*Orcinus orca*) in the western North Pacific. *Polar Biology* 42:931–941. doi: 10.1007/s00300-019-02484-6

Filatova OA, Fedutin ID, Belonovich OA, Borisova EA, Volkova EV, Ivkovich TV, Ismail ME, Meschersky IG, Titova OV, Fomin SV, Shpak OV (2023) Differences in the Diet of Reproductively Isolated Ecotypes of Killer Whales (*Orcinus orca* Linnaeus, 1758) in the Seas of the Russian Far East. *Russian Journal of Marine Biology* 49:477–487. doi: 10.1134/S1063074023060032

Fish JF, Vania JS (1971) Killer whale, *Orcinus orca*, sounds repel white whale, *Delphinapterus leucas*. *Fishery Bulletin* 69:531–535.

Foote AD, Nystuen JA (2008) Variation in call pitch among killer whale ecotypes. *Journal of the Acoustical Society of America* 123:1747–1752. doi: 10.1121/1.2836752

Foote AD, Griffin RM, Howitt D, Larsson L, Miller PJO, Hoelzel AR (2006) Killer whales are capable of vocal learning. *Biology letters* 2:509–512. doi: 10.1098/rsbl.2006.0525

Foote AD, Similä T, Vikingsson GA, Stevick PT (2010) Movement, site fidelity and connectivity in a top marine predator, the killer whale. *Evolutionary Ecology* 24:803–814. doi: 10.1007/s10682-009-9337-x

Foote AD, Martin MD, Louis M, Pacheco G, Robertson KM, Sinding MHS, Amaral AR, Baird RW, Baker CS, Ballance L, Barlow J, Brownlow A, Collins T, Constantine R, Dabin W, Dalla Rosa L, Davison NJ, Durban JW, Esteban R, Ferguson SH, Gerrodette T, Guinet C, Hanson MB, Hoggard W, Matthews CJD, Samarra FIP, de Stephanis R, Tavares SB, Tixier P, Totterdell JA, Wade P, Excoffier L, Gilbert MTP, Wolf JBW, Morin PA (2019) Killer whale genomes reveal a complex history of recurrent admixture and vicariance. *Molecular Ecology* 28:3427–3444. doi: 10.1111/mec.15099

Ford JKB (1987) A catalogue of underwater calls produced by killer whales (*Orcinus orca*) in British columbia.

Ford JKB (1989) Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Canadian Journal of Zoology* 67:727–745. doi: 10.1139/z89-105

Ford JKB (1991) Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology* 69:1454–1483. doi: 10.1139/z91-206

Ford JKB (2018) Killer Whale. In: Würsig B, Thewissen JGM, Kovacs KM (eds) Encyclopedia of Marine Mammals. Academic Press, pp 531–537

Ford JKB, Ellis GM (1999) Transients: Mammal-Hunting Killer Whales of B.C., Washington State, and Southeast Alaska. UBC Press, Vancouver

Ford JKB, Ellis GM (2006) Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. *Marine Ecology Progress Series* 316:185–199. doi: 10.3354/meps316185

Ford JKB, Fisher DH (1982) Killer whale (*Orcinus orca*) dialects as an indicator of stocks in British Columbia. *Report to the International Whaling Commission* 32:671–679.

Fournet MEH, Gabriele CM, Culp DC, Sharpe F, Mellinger DK, Klinck H (2018) Some things never change: multi-decadal stability in humpback whale calling repertoire on Southeast Alaskan foraging grounds. *Scientific Reports* 8:13186. doi: 10.1038/s41598-018-31527-x

Freeberg TM, Dunbar RIM, Ord TJ (2012) Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:1785–1801. doi: 10.1098/rstb.2011.0213

Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6:11. doi: 10.5751/ES-00404-060111

Gannon DP, Read AJ, Craddock E, Fristrupl KM, Nicolas JR (1997) Feeding ecology of long-finned pilot whales *Globicephala melas* in the western North Atlantic. *Marine Ecology Progress Series* 148:1–10. doi: 10.3354/meps148001

Gannon DP, Barros NB, Nowacek DP, Read AJ, Waples DM, Wells RS (2005) Prey detection by bottlenose dolphins, *Tursiops truncatus*: An experimental test of the passive listening hypothesis. *Animal Behaviour* 69:709–720. doi: 10.1016/j.anbehav.2004.06.020

Garland EC, Castellote M, Berchok CL (2015) Beluga whale (*Delphinapterus leucas*) vocalizations and call classification from the eastern Beaufort Sea population. *Journal of the Acoustical Society of America* 137:3054–3067. doi: 10.1121/1.4919338

Giles DA, Teman SJ, Ellis S, Ford JKB, Shields MW, Hanson MB, Emmons CK, Cottrell PE, Baird RW, Osborne RW, Weiss M, Ellifrit DK, Olson JK, Towers JR, Ellis G, Matkin D, Smith CE, Raverty SA, Norman SA, Gaydos JK (2023) Harassment and killing of porpoises ("phocoenacide") by fish-eating Southern Resident killer whales (*Orcinus orca*). *Marine Mammal Science* 40:e13073. doi: 10.1111/mms.13073

Haas CE, Wensveen PJ, Hooker SK, Miller PJO (2025) Acoustic characteristics and context of buzzes and rasps produced by northern bottlenose whales (*Hyperoodon ampullatus*). *Bioacoustics* 34:93–119. doi: 10.1080/09524622.2025.2451955

Hammerschmidt K, Fischer J (1998) The Vocal Repertoire of Barbary Macaques: A Quantitative Analysis of a Graded Signal System. *Ethology* 104:203–216. doi: 10.1111/j.1439-0310.1998.tb00063.x

Hansen ES, Sandvik H, Erikstad KE, Yoccoz NG, Anker-Nilssen T, Bader J, Descamps S, Hodges K, Mesquita M d. S, Reiertsen TK, Varpe Ø (2021) Centennial relationships between ocean temperature and Atlantic puffin production reveal shifting decennial trends. *Global Change Biology* 27:3753–3764. doi: 10.1111/gcb.15665

Hátún H, Payne MR, Beaugrand G, Reid PC, Sandø AB, Drange H, Hansen B, Jacobsen JA, Bloch D (2009) Large bio-geographical shifts in the north-eastern Atlantic Ocean: From the subpolar gyre, via plankton, to blue whiting and pilot whales. *Progress in Oceanography* 80:149–162. doi: 10.1016/j.pocean.2009.03.001

Hauser MD (1996) The Evolution of Communication. MIT Press, Cambridge

Herman D, Burrows D, Wade P, Durban J, Matkin C, LeDuc R, Barrett-Lennard L, Krahn M (2005) Feeding ecology of eastern North Pacific killer whales *Orcinus orca* from fatty acid, stable isotope, and organochlorine analyses of blubber biopsies. *Marine Ecology Progress Series* 302:275–291. doi: 10.3354/meps302275

Herman LM (2017) The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: review, evaluation, and synthesis. *Biological Reviews* 92:1795–1818. doi: 10.1111/brv.12309

Hermannsson H (1924) Jón Guðmundsson and his Natural History of Iceland. Cornell University Library, Ithaca, NY

Hoelzel AR, Hey J, Dahlheim ME, Nicholson C, Burkanov V, Black N (2007) Evolution of Population Structure in a Highly Social Top Predator, the Killer Whale. *Molecular Biology and Evolution* 24:1407–1415. doi: 10.1093/molbev/msm063

Holt MM, Hanson MB, Emmons CK, Haas DK, Giles DA, Hogan JT (2019) Sounds associated with foraging and prey capture in individual fish-eating killer whales, *Orcinus orca*. *Journal of the Acoustical Society of America* 146:3475–3486. doi: 10.1121/1.5133388

Jákupsstovu SH (2002) The pelagic fish stocks, pilot whales and squid in Faroese waters - migration pattern, availability to fisheries and possible links to oceanographic events. 2002 ICES Annual Science Conference, Copenhagen, Denmark. CM 2002/N:07. doi: 10.17895/ices.pub.25443178

Janik VM (2009) Acoustic communication in Delphinids. In: Vocal Communication in Birds and Mammals. Academic Press

Janik VM, Sayigh LS, Wells RS (2006) Signature whistle shape conveys identity information to bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America* 103:8293–8297. doi: 10.1073/pnas.0509918103

Jefferson T, Stacey P, Baird R (1991) A review of Killer whale interactions with other marine mammals. *Mammal Review* 21:151–180. doi: 10.1111/j.1365-2907.1991.tb00291.x

Johnson FR, McNaughton EJ, Shelley CD, Blumstein DT (2003) Mechanisms of heterospecific recognition in avian mobbing calls. *Australian Journal of Zoology* 51:577–585. doi: 10.1071/ZO03031

Johnson MP, Tyack PL (2003) A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering* 28:3–12. doi: 10.1109/JOE.2002.808212

Jónsson ÁI (2019) Mikill fjöldi grindhvala en fá svínhveli. Morgunblaðið 23. October 2019

Jourdain E, Vongraven D (2017) Humpback whale (*Megaptera novaeangliae*) and killer whale (*Orcinus orca*) feeding aggregations for foraging on herring (*Clupea harengus*) in Northern Norway. *Mammalian Biology* 86:27–32. doi: 10.1016/j.mambio.2017.03.006

Jourdain E, Vongraven D, Bisther A, Karoliussen R (2017) First longitudinal study of seal-feeding killer whales (*Orcinus orca*) in Norwegian coastal waters. *Plos One* 12:e0180099. doi: 10.1371/journal.pone.0180099

Karlsen J, Bisther A, Lydersen C, Haug T, Kovacs K (2002) Summer vocalisations of adult male white whales (*Delphinapterus leucas*) in Svalbard, Norway. *Polar Biology* 25:808–817. doi: 10.1007/s00300-002-0415-6

Keenan S, Lemasson A, Zuberbühler K (2013) Graded or discrete? A quantitative analysis of Campbell’s monkey alarm calls. *Animal Behaviour* 85:109–118. doi: 10.1016/j.anbehav.2012.10.014

Kershenbaum A (2025) Why animals talk: The New Science of Animal Communication. Penguin

Kershenbaum A, Blumstein DT, Roch MA, Akçay Ç, Backus G, Bee MA, Bohn K, Cao Y, Carter G, Cäsar C, Coen M, DeRuiter SL, Doyle L, Edelman S, Ferrer-i-Cancho R, Freeberg TM, Garland EC, Gustison M, Harley HE, Huetz C, Hughes M, Hyland Bruno J, Ilany A, Jin DZ, Johnson M, Ju C, Karnowski J, Lohr B, Manser MB, Mccowan B, Mercado E, Narins PM, Piel A, Rice M, Salmi R, Sasahara K, Sayigh L, Shiu Y, Taylor C, Vallejo EE, Waller S, Zamora-Gutierrez V (2016) Acoustic sequences in non-human animals: A tutorial review and prospectus. *Biological Reviews* 91:13–52. doi: 10.1111/brv.12160

Kleivane L, Kvadsheim PH, Bocconcelli A, Øien N, Miller PJO (2022) Equipment to tag, track and collect biopsies from whales and dolphins: the ARTS, DFHorten and LKDart systems. *Animal Biotelemetry* 10:32. doi: 10.1186/s40317-022-00303-0

Kroodsma DE, Byers BE (1991) The Function (s) of Bird Song. *American Zoologist* 328:318–328. doi: 10.1093/icb/31.2.318

Leavesley AJ, Magrath RD (2005) Communicating about danger: Urgency alarm calling in a bird. *Animal Behaviour* 70:365–373. doi: 10.1016/j.anbehav.2004.10.017

Leu AA, Hildebrand JA, Rice A, Baumann-Pickering S, Frasier KE (2022) Echolocation click discrimination for three killer whale ecotypes in the Northeastern Pacific. *Journal of the Acoustical Society of America* 151:3197–3206. doi: 10.1121/10.0010450

Madrigal BC, Crance JL, Berchok CL, Stimpert AK (2021) Call repertoire and inferred ecotype presence of killer whales (*Orcinus orca*) recorded in the southeastern Chukchi Sea. *Journal of the Acoustical Society of America* 150:145–158. doi: 10.1121/10.0005405

Madsen PT, Jensen FH, Carder D, Ridgway S (2012) Dolphin whistles: a functional misnomer revealed by heliox breathing. *Biology Letters* 8:211–213. doi: 10.1098/rsbl.2011.0701

Mann J (1999) Behavioral sampling methods for cetaceans: A review and critique. *Marine Mammal Science* 15:102–122. doi: 10.1111/j.1748-7692.1999.tb00784.x

Marchon TMJ, Rasmussen MH, Basran CJ, Whittaker M, Bertulli CG, Harlow C, Lott R, Boisseau O, Gendron F, Guo L, Hudson T, Jónsson H, Kershaw A, Kinni J, Lionnet LAMG, Louis M, Messina M, Michel H, Neubarth BK, Ovide BG, Podt AE, Rempel JN, Ryan C, Savage E, Scott J, Smit R, Verdaat H, Vignisson SR, Samarra FIP (2024) Geographical movements, site fidelity and connectivity of killer whales within and outside herring grounds in Icelandic coastal waters. *Marine Biology* 171:30. doi: 10.1007/s00227-023-04345-7

McDonald MA, Mesnick SL, Hildebrand JA (2023) Biogeographic characterisation of blue whale song worldwide: using song to identify populations. *Journal of Cetacean Research and Management* 8:55–65. doi: 10.47536/jcrm.v8i1.702

McGregor PK (1992) Playback and studies of animal communication. Plenum Press, New York

Mcgregor PK, Peake TM (2000) Communication networks: Social environments for receiving and signalling behaviour. *Acta Ethologica* 2:71–81. doi: 10.1007/s102110000015

Mercado E (2022) Intra-individual variation in the songs of humpback whales suggests they are sonically searching for conspecifics. *Learning & Behavior* 50:456–481. doi: 10.3758/s13420-021-00495-0

MFRI (2023) MFRI Assessment Reports 2023, Mackerel. Marine and Freshwater Research Institute, Iceland

Migura KA, Meadows DW (2002) Short-finned pilot whales (*Globicephala macrorhynchus*) interact with melon-headed whales (*Peponocephala electra*) in Hawaii. *Aquatic Mammals* 28:294–297. doi: 10.1515/mamm.2004.020

Miller PJO (2002) Mixed-directionality of killer whale stereotyped calls: A direction of movement cue? *Behavioral Ecology and Sociobiology* 52:262–270. doi: 10.1007/s00265-002-0508-9

Miller PJO (2006) Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *Journal of Comparative Physiology* 192:449–459. doi: 10.1007/s00359-005-0085-2

Miller PJO, Bain DE (2000) Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*. *Animal Behaviour* 60:617–628. doi: 10.1006/anbe.2000.1503

Miller PJO, Shapiro AD, Tyack PL, Solow AR (2004) Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*. *Animal Behaviour* 67:1099–1107. doi: 10.1016/j.anbehav.2003.06.017

Møhl B, Wahlberg M, Madsen PT, Heerfordt A, Lund A (2003) The monopulsed nature of sperm whale clicks. *Journal of the Acoustical Society of America* 114:1143–1154. doi: 10.1121/1.1586258

Moore SE, Francince JK, Bowles AE, Ford JKB (1988) Analysis of calls of killer whales, *Orcinus orca*, from Iceland and Norway. *Rit Fiskideildar* 11:226–250.

Morin PA, Archer FI, Foote AD, Vilstrup J, Allen EE, Wade P, Durban J, Parsons K, Pitman R, Li L, Bouffard P, Nielsen SCA, Rasmussen M, Willerslev E, Gilbert MTP, Harkins T (2010) Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species. *Genome Research* 20:908–916. doi: 10.1101/gr.102954.109.908

Morin PA, McCarthy ML, Fung CW, Durban JW, Parsons KM, Perrin WF, Taylor BL, Jefferson TA, Archer FI (2024) Revised taxonomy of eastern North Pacific killer whales (*Orcinus orca*): Bigg's and resident ecotypes deserve species status. *Royal Society Open Science* 11:231368. doi: 10.1098/rsos.231368

Morisaka T, Connor RC (2007) Predation by killer whales (*Orcinus orca*) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes. *Journal of Evolutionary Biology* 20:1439–1458. doi: 10.1111/j.1420-9101.2007.01336.x

Mrusczok M-T, Zwamborn E, von Schmalensee M, Ramallo SR, Stefansson RA (2023) First account of apparent alloparental care of a long-finned pilot whale calf (*Globicephala melas*) by a female killer whale (*Orcinus orca*). *Canadian Journal of Zoology* 101:288–293. doi: 10.1139/cjz-2022-0161

Murray SO, Mercado E, Roitblat HL (1998) Characterizing the graded structure of false killer whale (*Pseudorca crassidens*) vocalizations. *Journal of the Acoustical Society of America* 104:1679–1688. doi: 10.1121/1.424380

Murray-Bergquist K (2017) “To Talk of Many Things”: Whales, Walrus, and Seals in Medieval Icelandic Literature. MA thesis, Háskoli Íslands

Nemiroff L, Whitehead HAL (2009) Structural characteristics of pulsed calls of long-finned pilot whales *Globicephala melas*. *Bioacoustics* 19:67–92. doi: 10.1080/09524622.2009.9753615

Norris KS, Prescott JH (1961) Observations on Pacific Cetaceans of Californian and Mexican Waters. *University of California Publications in Zoology* 63:291–402.

Nowicki S, Searcy WA (2004) Song Function and the Evolution of Female Preferences: Why Birds Sing, Why Brains Matter. *Annals of the New York Academy of Sciences* 1016:704–723. doi: 10.1196/annals.1298.012

O’Corry-Crowe G, Suydam R, Quakenbush L, Smith TG, Lydersen C, Kovacs KM, Orr J, Harwood L, Litovka D, Ferrer T (2020) Group structure and kinship in beluga whale societies. *Scientific Reports* 10:11462. doi: 10.1038/s41598-020-67314-w

O’Corry-Crowe GM (2009) Beluga Whale: *Delphinapterus leucas*. In: Würsig B, Thewissen JGM, Kovacs KM (eds) Encyclopedia of Marine Mammals. Academic Press, pp 93–96

Ólafsson J, Kvaran G, Hjartadóttir ÞB (2007) Náttúrufræði: fiskafræði, steinafræði. Góðvinir Grunnavíkur-Jóns, Reykjavík

Olson PA (2018) Pilot whales. In: Würsig B, Thewissen JGM, Kovacs KM (eds) Encyclopedia of Marine Mammals. Academic Press, pp 707–705

Óskarsson GJ, Gudmundsdottir A, Sveinbjörnsson S, Sigurðsson Þ (2016) Feeding ecology of mackerel and dietary overlap with herring in Icelandic waters. *Marine Biology Research* 12:16–29. doi: 10.1080/17451000.2015.1073327

Oswald JN, Erbe C, Gannon WL, Madhusudhana S, Thomas JA (2022) Detection and Classification Methods for Animal Sounds. In: Exploring Animal Behavior Through Sound: Volume 1. Springer International Publishing, pp 269–317

Ottensmeyer CA, Whitehead H (2003) Behavioural evidence for social units in long- finned pilot whales. *Canadian Journal of Zoology* 81:1327–1338. doi: 10.1139/Z03-127

Overholtz WJ, Waring GT (1991) Diet composition of pilot whales *Globicephala* sp. and common dolphins *Delphinus delphis* in the Mid-Atlantic Bight during spring 1989. *Fishery Bulletin* 89:723–728.

Owings DH, Virginia RA (1978) Alarm Calls of California Ground Squirrels (*Spermophilus beecheyi*). *Zeitschrift für Tierpsychologie* 46:58–70. doi: 10.1111/j.1439-0310.1978.tb01438.x

Page RA, Bernal XE (2020) The challenge of detecting prey: Private and social information use in predatory bats. *Functional Ecology* 34:344–363. doi: 10.1111/1365-2435.13439

Palleroni A, Hauser M, Marler P (2005) Do responses of galliform birds vary adaptively with predator size? *Animal Cognition* 8:200–210. doi: 10.1007/s10071-004-0250-y

Panova E, Agafonov A (2023) Possible occurrence of contact calls in all-male groups of free-ranging beluga whales. *Journal of Zoology* 320:29–41. doi: 10.1111/jzo.13054

Panova EM, Belikov RA, Agafonov AV, Bel'kovich VM (2012) The relationship between the behavioral activity and the underwater vocalization of the beluga whale (*Delphinapterus leucas*). *Oceanology* 52:79–87. doi: 10.1134/S000143701201016X

Payne R, Webb D (1971) Orientation By Means of Long Range Acoustic Signaling in Baleen Whales. *Annals of the New York Academy of Sciences* 188:110–141. doi: 10.1111/j.1749-6632.1971.tb13093.x

Payne RS, McVay S (1971) Songs of humpback whales. *Science* 173:585–597. doi: 10.1126/science.173.3997.585

Pettifor RA (1990) The effects of avian mobbing on a potential predator, the European kestrel, *Falco tinnunculus*. *Animal Behaviour* 39:821–827. doi: 10.1016/S0003-3472(05)80945-5

Pierry JC, Wedekin LL, Flores PAC, Rossi-Santos MR, Daura-Jorge FG (2023) Escape response of Guiana dolphins to bottlenose dolphin playback. *Journal of Experimental Marine Biology and Ecology* 566:151925. doi: 10.1016/j.jembe.2023.151925

Pike DG, Gunnlaugsson T, Desportes G, Mikkelsen B, Víkingsson GA, Bloch D (2019) Estimates of the relative abundance of long-finned pilot whales (*Globicephala melas*) in the Northeast Atlantic from 1987 to 2015 indicate no long-term trends. *NAMMCO Scientific Publications* 11. doi: doi.org/10.7557/3.4643

Pitman RL, Ensor P (2003) Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *Journal of Cetacean Research and Management* 5:131–139. doi: doi.org/10.47536/jcrm.v5i2.813

Pitman RL, Durban JW, Greenfelder M, Guinet C, Jorgensen M, Olson PA, Plana J, Tixier P, Towers JR (2011) Observations of a distinctive morphotype of killer whale (*Orcinus orca*), type D, from subantarctic waters. *Polar Biology* 34:303–306. doi: 10.1007/s00300-010-0871-3

Rehn N, Filatova OA, Durban JW, Foote AD (2011) Cross-cultural and cross-ecotype production of a killer whale “excitement” call suggests universality. *Naturwissenschaften* 98:1–6. doi: 10.1007/s00114-010-0732-5

Rekdahl M, Tisch C, Cerchio S, Rosenbaum H (2017) Common nonsong social calls of humpback whales (*Megaptera novaeangliae*) recorded off northern Angola, southern Africa. *Marine Mammal Science* 33:365–375. doi: 10.1111/mms.12355

Rekdahl ML, Dunlop RA, Noad MJ, Goldizen AW (2013) Temporal stability and change in the social call repertoire of migrating humpback whales. *Journal of the Acoustical Society of America* 133:1785–1795. doi: 10.1121/1.4789941

Remili A, Letcher RJ, Samarra FIP, Dietz R, Sonne C, Desforges JP, Víkingsson G, Blair D, McKinney MA (2021) Individual Prey Specialization Drives PCBs in Icelandic Killer Whales. *Environmental Science and Technology* 55:4923–4931. doi: 10.1021/acs.est.0c08563

Remili A, Dietz R, Sonne C, Samarra FIP, Rikardsen AH, Kettemer LE, Ferguson SH, Watt CA, Matthews CJD, Kiszka JJ, Jourdain E, Borgå K, Ruus A, Granquist SM, Rosing-Asvid A, McKinney MA (2023) Quantitative fatty acid signature analysis reveals a high level of dietary specialization in killer whales across the North Atlantic. *Journal of Animal Ecology* 92:1216–1229. doi: 10.1111/1365-2656.13920

Reyes Reyes MV, Baumann-Pickering S, Simonis A, Melcón ML, Trickey J, Hildebrand J, Iñíguez M (2017) High-frequency modulated signals recorded off the Antarctic Peninsula area: Are killer whales emitting them? *Acoustics Australia* 45:253–260. doi: 10.1007/s40857-017-0103-x

Richlen MF, Thomas JA (2008) Acoustic behavior of antarctic killer whales (*Orcinus orca*) recorded near the ice edge of McMurdo sound, Antarctica. *Aquatic Mammals* 34:448–457. doi: 10.1578/AM.34.4.2008.448

Riesch R, Deecke VB (2011) Whistle communication in mammal-eating killer whales (*Orcinus orca*): Further evidence for acoustic divergence between ecotypes. *Behavioral Ecology and Sociobiology* 65:1377–1387. doi: 10.1007/s00265-011-1148-8

Riesch R, Ford JKB, Thomsen F (2006) Stability and group specificity of stereotyped whistles in resident killer whales, *Orcinus orca*, off British Columbia. *Animal Behaviour* 71:79–91. doi: 10.1016/j.anbehav.2005.03.026

Riesch R, Ford JKB, Thomsen F (2008) Whistle sequences in wild killer whales (*Orcinus orca*). *Journal of the Acoustical Society of America* 124:1822–1829. doi: 10.1121/1.2956467

Rose EM, Coss DA, Haines CD, Danquah SA, Studds CE, Omland KE (2019) Why do females sing?—pair communication and other song functions in eastern bluebirds. *Behavioral Ecology* 30:1653–1661. doi: 10.1093/beheco/arz130

Sæmundsson B (1932) Spendýrin (Mammalia Islandiæ). Bókaverslun Sigfúsar Eymundssonar, Reykjavík

Samarra F, Vighi M, Aguilar A, Víkingsson G (2017a) Intra-population variation in isotopic niche in herring-eating killer whales off Iceland. *Marine Ecology Progress Series* 564:199–210. doi: 10.3354/meps11998

Samarra F, Borrell A, Selbmann A, Chosson V, Chicco C, Haas C, Basran C, Smith A, Ovide B, Einarsson G, Halldórson S, O'Brien E, Eleman A, Sigurðsson G, Aguilar A (2024) Trophic ecology, based on stable isotope values, of long-finned pilot whales *Globicephala melas* stranded on the Icelandic coast. *Marine Ecology Progress Series* 748:163–174. doi: 10.3354/meps14708

Samarra FIP (2015) Variations in killer whale food-associated calls produced during different prey behavioural contexts. *Behavioural Processes* 116:33–42. doi: 10.1016/j.beproc.2015.04.013

Samarra FIP, Foote A (2015) Seasonal movements of killer whales between Iceland and Scotland. *Aquatic Biology* 24:75–79. doi: 10.3354/ab00637

Samarra FIP, Miller PJO (2015) Prey-induced behavioural plasticity of herring-eating killer whales. *Marine Biology* 162:809–821. doi: 10.1007/s00227-015-2626-8

Samarra FIP, Deecke VB, Vinding K, Rasmussen MH, Swift RJ, Miller PJO (2010) Killer whales (*Orcinus orca*) produce ultrasonic whistles. *Journal of the Acoustical Society of America* 128:205–210. doi: 10.1121/1.3462235

Samarra FIP, Deecke VB, Simonis AE, Miller PJO (2015) Geographic variation in the time-frequency characteristics of high-frequency whistles produced by killer whales (*Orcinus orca*). *Marine Mammal Science* 31:688–706. doi: 10.1111/mms.12195

Samarra FIP, Deecke VB, Miller PJO (2016) Low-frequency signals produced by Northeast Atlantic killer whales (*Orcinus orca*). *Journal of the Acoustical Society of America* 139:1149–1157. doi: 10.1121/1.4943555

Samarra FIP, Tavares SB, Béesau J, Deecke VB, Fennell A, Miller PJO, Pétursson H, Sigurjónsson J, Víkingsson GA (2017b) Movements and site fidelity of killer whales (*Orcinus orca*) relative to seasonal and long-term shifts in herring (*Clupea harengus*) distribution. *Marine Biology* 164:159. doi: 10.1007/s00227-017-3187-9

Samarra FIP, Bassoi M, Béesau J, Elíasdóttir MÓ, Gunnarsson K, Mrusczok M-T, Rasmussen M, Rempel JN, Thorvaldsson B, Víkingsson GA (2018) Prey of killer whales (*Orcinus orca*) in Iceland. *Plos One* 13:e0207287. doi: 10.1371/journal.pone.0207287

Samarra FIP, Wensveen PJ, Selbmann A, Kvadsheim PH, Lam F-PA, Tyack PL, von Benda-Beckmann AM, Miller PJO (submitted) Killer Whale (*Orcinus orca*) Acoustic Responses to Naval Sonar. *Aquatic Mammals*

Santos MB, Monteiro SS, Vingada JV, Ferreira M, López A, Martínez Cedeira JA, Reid RJ, Brownlow A, Pierce GJ (2014) Patterns and trends in the diet of long-finned pilot whales (*Globicephala melas*) in the northeast Atlantic. *Marine Mammal Science* 30:1–19. doi: 10.1111/mms.12015

Saulitis EL, Matkin CO, Fay FH (2005) Vocal repertoire and acoustic behavior of the isolated AT1 killer whale subpopulation in southern Alaska. *Canadian Journal of Zoology* 83:1015–1029. doi: 10.1139/z05-089

Schall E, van Opzeeland I (2017) Calls produced by ecotype C killer whales (*Orcinus orca*) off the Eckström Iceshelf, Antarctica. *Aquatic Mammals* 43:117–126. doi: 10.1578/AM.43.2.2017.117

Schevill WE, Watkins WA (1966) Sound structure and directionality in *Orcinus* (killer whale). *Zoologica* 51:71–76. doi: 10.5962/p.203283

Scott MD, Chivers SJ (1990) Distribution and Herd Structure of Bottlenose Dolphins in the Eastern Tropical Pacific Ocean. In: Leatherwood S, Reeves RR (eds) The Bottlenose Dolphin. Academic Press, pp 386–402

Selbmann A, Deecke VB, Fedutin ID, Filatova OA, Miller PJO, Samarra FIP (2019) A catalogue of pulsed calls produced by killer whales (*Orcinus orca*) in Iceland 2008-2016. Report of the Marine and Freshwater Research Institute HV 2019-23.

Selbmann A, Deecke VB, Fedutin ID, Filatova OA, Miller PJO, Svavarsson J, Samarra FIP (2021) A comparison of Northeast Atlantic killer whale (*Orcinus orca*) stereotyped call repertoires. *Marine Mammal Science* 37:268–289. doi: 10.1111/mms.12750

Seyfarth RM, Cheney DL, Marler P (1980a) Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science* 210:801–803. doi: 10.1126/science.7433999

Seyfarth RM, Cheney DL, Marler P (1980b) Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour* 28:1070–1094. doi: 10.1016/S0003-3472(80)80097-2

Sharpe DL, Castellote M, Wade PR, Cornick LA (2019) Call types of Bigg's killer whales (*Orcinus orca*) in western Alaska: using vocal dialects to assess population structure. *Bioacoustics* 28:74–99. doi: 10.1080/09524622.2017.1396562

Sigurjonsson J, Lyrholm T, Leatherwood S, Jonsson E, Vikingsson G (1988) Photoidentification of killer whales, *Orcinus orca*, off Iceland, 1981 through 1986. *Rit Fiskideildar* 11:99–114.

Sigurjónsson J, Lyrholm T, Leatherwood S, Jónsson E, Víkingsson G (1988) Photoidentification of killer whales, *Orcinus orca*, off Iceland, 1981 through 1986. *Rit Fiskideildar* 11:99–114.

Sigurjónsson J, Víkingsson G, Lockyer C (1993) Two mass strandings of pilot whales (*Globicephala melas*) on the coast of Iceland. *Report to the International Whaling Commission Special Issue* 14:407–423.

Similä T, Ugarte F (1993) Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology* 71:1494–1499. doi: 10.1139/z93-210

Simon M, Wahlberg M, Ugarte F, Miller LA (2005) Acoustic characteristics of underwater tail slaps used by Norwegian and Icelandic killer whales (*Orcinus orca*) to debilitate herring (*Clupea harengus*). *Journal of Experimental Biology* 208:2459–2466. doi: 10.1242/jeb.01619

Simon M, Ugarte F, Wahlberg M, Miller LEEA (2006) Icelandic killer whales *Orcinus orca* use a pulsed call suitable for manipulating the schooling behaviour of herring *Clupea harengus*. *Bioacoustics* 16:57–74. doi: 10.1080/09524622.2006.9753564

Simon M, Wahlberg M, Miller LA (2007a) Echolocation clicks from killer whales (*Orcinus orca*) feeding on herring (*Clupea harengus*) (L). *Journal of the Acoustical Society of America* 121:749–752. doi: 10.1121/1.2404922

Simon M, McGregor PK, Ugarte F (2007b) The relationship between the acoustic behaviour and surface activity of killer whales (*Orcinus orca*) that feed on herring (*Clupea harengus*). *Acta Ethologica* 10:47–53. doi: 10.1007/s10211-007-0029-7

Simonis AE, Baumann-Pickering S, Oleson E, Melcón ML, Gassmann M, Wiggins SM, Hildebrand J a (2012) High-frequency modulated signals of killer whales (*Orcinus orca*) in the North Pacific. *Journal of the Acoustical Society of America* 131:EL295-301. doi: 10.1121/1.3690963

Širović A, Hildebrand JA, Wiggins SM (2007) Blue and fin whale call source levels and propagation range in the Southern Ocean. *Journal of the Acoustical Society of America* 122:1208–1215. doi: 10.1121/1.2749452

Sivle LD, Kvadsheim PH, Curé C, Isojunno S, Wensveen PJ, Lam FPA, Visser F, Kleivane L, Tyack PL, Harris CM, Miller PJO (2015) Severity of expert-identified behavioural responses of humpback whale, minke whale, and northern bottlenose whale to naval sonar. *Aquatic Mammals* 41:469–502. doi: 10.1578/AM.41.4.2015.469

Slater PJB (1983) The study of communication. In: Halliday TR, Slater PJB (eds) Animal behaviour: Communication. Blackwell Scientific Publications, Oxford, pp 9–42

Souhaut M, Shields MW (2021) Stereotyped whistles in southern resident killer whales. *PeerJ* 9:e12085. doi: 10.7717/peerj.12085

Sportelli JJ, Jones JM, Frasier KE, Westdal KH, Higdon JW, Hildebrand JA (2022) Killer Whale (*Orcinus orca*) Pulsed Calls in the Eastern Canadian Arctic. *Arctic*. doi: 10.14430/arctic75350

Stafford KM, Fox CG, Clark DS (1998) Long-range acoustic detection and localization of blue whale calls in the northeast Pacific Ocean. *Journal of the Acoustical Society of America* 104:3616–3625. doi: 10.1121/1.423944

Stafford KM, Moore SE, Laidre KL, Heide-Jørgensen MP (2008) Bowhead whale springtime song off West Greenland. *Journal of the Acoustical Society of America* 124:3315–3323. doi: 10.1121/1.2980443

Stefánsson M (2003) The Norse island communities of the Western Ocean. In: Helle K (ed) The Cambridge History of Scandinavia. Cambridge University Press, pp 202–220

Stenersen J, Similä T (2004) Norwegian killer whales. Tringa Forlag, Henningsvær

Strager H (1995) Pod-specific call repertoires and compound calls of killer whales, *Orcinus orca* Linnaeus, 1758, in the waters of northern Norway. *Canadian Journal of Zoology* 73:1037–1047. doi: 10.1139/z95-124

Tavares SB, Samarra FIP, Miller PJO (2017) A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. *Behavioral Ecology* 28:500–514. doi: 10.1093/beheco/arw179

Thomsen F, Franck D, Ford JKB (2001) Characteristics of whistles from the acoustic repertoire of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Journal of the Acoustical Society of America* 109:1240–1246. doi: 10.1121/1.1349537

Thomsen F, Franck D, Ford JK (2002) On the communicative significance of whistles in wild killer whales (*Orcinus orca*). *Naturwissenschaften* 89:404–407. doi: 10.1007/s00114-002-0351-x

Thorne LH, Nye JA (2021) Trait-mediated shifts and climate velocity decouple an endothermic marine predator and its ectothermic prey. *Scientific Reports* 11:18507. doi: 10.1038/s41598-021-97318-z

Toledo LF, Martins IA, Bruschi DP, Passos MA, Alexandre C, Haddad CFB (2015) The anuran calling repertoire in the light of social context. *Acta Ethologica* 18:87–99. doi: 10.1007/s10211-014-0194-4

Trickey JS, Reyes MV, Baumann-Pickering S, Melcón ML, Hildebrand JA, Iñíguez MA (2014) Acoustic encounters of killer and beaked whales during the 2014 SORP cruise. International Whaling Commission Scientific Committee Meeting Papers SC-65b-SM12rev

Tsuchiya T, Naoi J, Futa K, Kikuchi T (2004) Difference in Simulated Low-Frequency Sound Propagation in the Various Species of Baleen Whale. *Japanese Journal of Applied Physics* 43:3193. doi: 10.1143/JJAP.43.3193

Tyack PL, Zimmer WMX, Moretti D, Southall BL, Claridge DE, Durban JW, Clark CW, D'Amico A, DiMarzio N, Jarvis S, McCarthy E, Morrissey R, Ward J, Boyd IL (2011) Beaked whales respond to simulated and actual navy sonar. *Plos One*. doi: 10.1371/journal.pone.0017009

Vergara V, Mikus M (2019) Contact call diversity in natural beluga entrapments in an Arctic estuary: Preliminary evidence of vocal signatures in wild belugas. *Marine Mammal Science* 35:434–465. doi: 10.1111/mms.12538

Vester H, Hallerberg S, Timme M, Hammerschmidt K (2017) Vocal repertoire of long-finned pilot whales (*Globicephala melas*) in northern Norway. *Journal of the Acoustical Society of America* 141:4289–4299. doi: 10.1121/1.4983685

Visser F, Miller PJO, Antunes RN, Oudejans MG, Mackenzie ML, Aoki K, Lam FPA, Kvadsheim PH, Huisman J, Tyack PL (2014) The social context of individual foraging behaviour in long-finned pilot whales (*Globicephala melas*). *Behaviour* 151:1453–1477. doi: 10.1163/1568539X-00003195

Visser F, Kok ACM, Oudejans MG, Scott-Hayward LAS, DeRuiter SL, Alves AC, Antunes RN, Isojunno S, Pierce GJ, Slabbekoorn H, Huisman J, Miller PJO (2017) Vocal foragers and silent crowds: context-dependent vocal variation in Northeast Atlantic long-finned pilot whales. *Behavioral Ecology and Sociobiology* 71:170. doi: 10.1007/s00265-017-2397-y

Walther GR (2010) Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2019–2024. doi: 10.1098/rstb.2010.0021

Weilgart LS, Whitehead H (1990) Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. *Behavioral Ecology and Sociobiology* 26:399–402. doi: 10.1007/BF00170896

Weiß BM, Ladich F, Spong P, Symonds H (2006) Vocal behavior of resident killer whale matrilines with newborn calves: The role of family signatures. Journal of the Acoustical Society of America 119:627–635. doi: 10.1121/1.2130934

Weiß BM, Symonds H, Spong P, Ladich F (2007) Intra- and intergroup vocal behavior in resident killer whales, *Orcinus orca*. Journal of the Acoustical Society of America 122:3710–3716. doi: 10.1121/1.2799907

Wellard R, Erbe C, Fouda L, Blewitt M (2015) Vocalisations of killer whales (*Orcinus orca*) in the Bremer Canyon, Western Australia. *Plos One* 10:e0136535. doi: 10.1371/journal.pone.0136535

Wellard R, Pitman RL, Durban J, Erbe C (2020) Cold call: the acoustic repertoire of Ross Sea killer whales (*Orcinus orca*, Type C) in McMurdo Sound, Antarctica. *Royal Society Open Science* 7:191228. doi: 10.1098/rsos.191228

Weller DW, Würsig B, Whitehead H, Norris JC, Lynn SK, Davis RW, Clauss N, Brown P (1996) Observations of an Interaction Between Sperm Whales and Short-Finned Pilot Whales in the Gulf of Mexico. *Marine Mammal Science* 12:588–594. doi: 10.1111/j.1748-7692.1996.tb00071.x

Wensveen PJ, Thomas L, Miller PJO (2015) A path reconstruction method integrating dead-reckoning and position fixes applied to humpback whales. *Movement Ecology* 3:31. doi: 10.1186/s40462-015-0061-6

Wheeler BC (2008) Selfish or altruistic? An analysis of alarm call function in wild capuchin monkeys, *Cebus apella nigritus*. *Animal Behaviour* 76:1465–1475. doi: 10.1016/j.anbehav.2008.06.023

Youngblood M (2025) Language-like efficiency in whale communication. *Science Advances* 11:eads6014.

Yurk H (2005) Vocal culture and social stability in resident killer whales (*Orcinus orca*). PhD Thesis, University of British Columbia

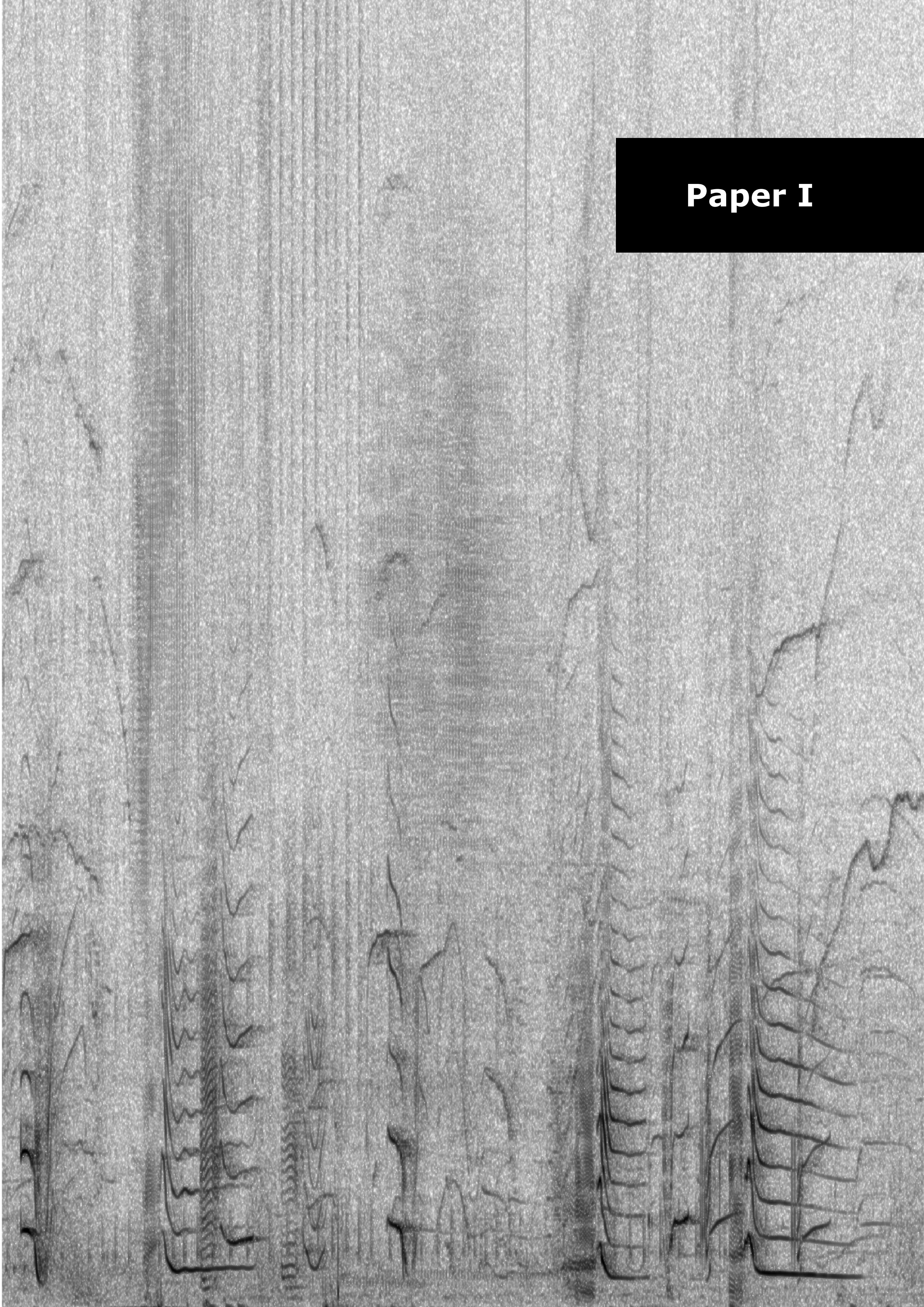
Yurk H, Barrett-Lennard L, Ford JKB, Matkin CO (2002) Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. *Animal Behaviour* 63:1103–1119. doi: 10.1006/anbe.2002.3012

Yurk H, O’Neill C, Quayle LS, Vagle S, Mouy X, Austin M, Wladichuk J, Morrison C, LeBlond WT (2023) Adaptive Call Design to Escape Masking While Preserving Complex Social Functions of Calls in Killer Whales. In: Popper AN, Sisneros J, Hawkins AD, Thomsen F (eds) The Effects of Noise on Aquatic Life. Springer International Publishing

Zuberbühler K (1999) The Predator Deterrence Function of Primate Alarm Calls. *Ethology* 105:447–490. doi: 10.1046/j.1439-0310.1999.00396.x

Zwamborn EMJ, Whitehead H (2017) The baroque potheads: modification and embellishment in repeated call sequences of long-finned pilot whales. *Behavioral Ecology and Sociobiology* 154:963–979. doi: 10.1163/1568539X-00003451

Paper I



Call type repertoire of killer whales (*Orcinus orca*) in Iceland and its variation across regions

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ARTICLE

Marine Mammal Science

Call type repertoire of killer whales (*Orcinus orca*) in Iceland and its variation across regions

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Abstract

Killer whales (*Orcinus orca*) have group-specific call repertoires that can be used to track groups and populations using passive acoustic monitoring. To provide a detailed description of the Icelandic killer whale repertoire and its variation, we analyzed acoustic data collected in five locations between 1985 and 2016. Calls were classified manually, and CART and random forest analyses were employed to validate the manual classification. A total of 91 call categories (including call types and subtypes) were defined. Most call categories were recorded in more than one

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location, with the highest proportion shared between herring grounds in Vestmannaeyjar (South) and Breiðafjörður (West). However, both locations included call categories that were not recorded elsewhere in Iceland. Recordings from past herring wintering grounds in eastern Iceland included few call categories that matched other locations. Sample sizes from Reykjanes (Southwest) and Skjálfandi (North) were small and did not include unique call categories. The relative occurrence of call categories in Vestmannaeyjar changed little over a 14-year period (2002–2016), although shorter-term changes between years were observed that appeared to correlate to changes in individuals identified. This comparison of acoustic repertoires provides valuable information on the social structure and movement patterns of herring-eating killer whales around Iceland.

KEYWORDS
acoustic behavior, call repertoire, geographic variation, Northeast Atlantic, passive acoustic monitoring

1 | INTRODUCTION

Communication is a central aspect of animal behavior and understanding animal vocalizations can provide important insights into behavior, social structure, ecology, and evolution (Bradbury & Vehrencamp, 2011). For many marine mammal species, acoustic communication is particularly important as sound propagates farther and faster in water compared to air, and visibility is generally limited (Au & Hastings, 2008). Recent advances in technology have increased possibilities for underwater acoustic data collection, e.g., through passive acoustic monitoring (PAM). PAM provides many advantages: it is noninvasive, relatively inexpensive, and it can be applied in poor visibility (e.g., during night, high sea states). Thus, it enables long-term and year-round data collection in locations that are remote or difficult to survey, such as high latitude regions (Erbe, 2013; van Opzeeland et al., 2013; van Parijs et al., 2009). However, the first critical step in understanding vocal communication and using methods such as PAM, is to document the vocal repertoire, i.e., the sum of acoustic signals used by a species, as well as the variability within signal categories (Mellinger et al., 2007).

Killer whales (*Orcinus orca*) are highly vocal and most commonly produce pulsed calls (Ford, 1989). Pulsed calls (hereafter calls) are thought to play a key role in killer whale behavior, serving as contact signals, aiding group recognition, cohesion, and coordination of the spatial organization of the group (Ford, 1989; Miller, 2002). Killer whale calls are burst-pulse sounds consisting of rapidly repeated pulses, where the interpulse interval is so short that they appear tonal, as frequency-modulated sounds with several sidebands (Schevill & Watkins, 1966). They often have several components with abrupt changes in pitch and can contain two separately modulated frequency contours (Ford, 1987; Miller & Bain, 2000; Strager, 1995). The majority of killer whale calls are discrete, meaning that they have a distinctive structure, are repetitive and can be classified into call types and subtypes (Ford, 1989; Sharpe et al., 2019; Strager, 1995; van Opzeeland et al., 2005; Wellard et al., 2020; Yurk et al., 2002). The acoustic characteristics of killer whale calls appear as readily discernible features in spectrograms (Sharpe et al., 2019; Wellard et al., 2020; Yurk et al. 2002) and human observers have been shown to classify odontocete signals into biologically meaningful categories (Danishevskaya et al., 2020; Deecke et al., 1999; Deecke & Janik, 2006; Janik, 1999).

Variation in the call repertoires of killer whales is observed between ecotypes, populations, social groups, or in different behavioral contexts. For example, in the Northeast Pacific, different ecotypes have been described, which have unique call repertoires (Ford et al., 1996). The fish-eating "resident" and mammal-eating "transient" (or "Bigg's") ecotypes use distinct call types that differ in structure (Deecke et al., 2005; Saulitis et al., 2005), and tonal frequency (Filatova et al., 2015; Foote & Nystuen, 2008). In the residents, call repertoires are linked to maternal relatedness, with closely related groups sharing more of their call repertoire than more distantly related groups (Deecke et al., 2010; Ford, 1991, Yurk et al., 2002). Transient killer whales, on the other hand, have a relatively small call repertoire that is shared more widely across social groups. Variation is only observed at the community level (Deecke, 2003; Sharpe et al., 2019).

The main purpose of diversity in group repertoires of killer whales is thought to be the transmission of group identity (Filatova et al., 2011; Ford, 1991; Miller & Bain, 2000). Group identity is important for killer whales in mate choice and survival. Genetic evidence indicates that mates are chosen from distantly related groups, with choice potentially based on dissimilar dialects to avoid inbreeding (Barrett-Lennard, 2000), contributing to evolutionary pressure to diversify the repertoire. Individual survival, on the other hand, is directly associated with group membership (Foster et al., 2012), creating the need to conform to the group and standardize the repertoire. These opposing selection pressures (diversifying and standardizing) are thought to lead to "the maximum diversity within the permitted range" (Filatova et al., 2012).

While most killer whale calls do not appear to be behavior-specific, the frequency of usage can be related to different behavioral or social contexts (Filatova et al., 2009, 2013; Ford, 1989; Weiß et al., 2006, 2007). However, relative call type occurrence appears to vary little between years and killer whale call repertoires have been shown to be stable over decades (Foote et al., 2008; Ford, 1991; Wellard et al., 2020). The stereotypy of killer whale calls, their long-term stability, and variations between ecotypes, populations, and social groups make these sounds very suitable for PAM methods, e.g., to study the spatial and temporal occurrence of different killer whale social groups (e.g., Yurk et al., 2010) and ecotypes (e.g., Myers et al., 2021; Rice et al., 2017; Riera et al., 2019). However, descriptions of the repertoires are lacking in several regions, including the Northeast Atlantic.

Acoustic studies across the region show that the call repertoire of killer whales from Iceland is distinct from Norway but has some overlap to Shetland, UK (Deecke et al., 2011; Moore et al., 1988; Selbmann et al., 2021), which supports the current understanding of the connectivity between these regions (Foote et al., 2010; Samarra & Foote, 2015; Sigurjónsson et al., 1988). However, finer-scale differences of the repertoire around Iceland remain unexplored. Icelandic killer whales exhibit variation in their movement patterns but understanding of the distributional range of the population and its substructure is still limited. Early studies consistently observed killer whales in herring (*Clupea harengus*) grounds (Sigurjónsson et al., 1988) and thus it was presumed that they were herring specialists, following the Icelandic summer-spawning herring stock (hereafter Icelandic herring). However, recent photo-identification studies have indicated that not all whales follow the herring year-round (Samarra et al., 2017). About half of the individuals identified were seen in both the herring wintering grounds in the west of Iceland and the spawning grounds in the south, but the other half were only sighted in either of the two locations. A few individuals seen only in the herring wintering grounds have been sighted repeatedly in Scotland during summer, where they appear to hunt seals (Foote et al., 2010; Samarra & Foote, 2015; Samarra et al., 2017). Movement and foraging patterns for the rest of the population remain unclear. In the 1980s and 1990s, the Icelandic herring wintering grounds were located to the east of Iceland, where killer whales were regularly sighted with herring (Foote et al., 2010; Sigurjónsson et al., 1988). Only a small proportion of whales identified there could be matched to sightings in the recent wintering grounds off western Iceland (Samarra et al., 2017). Occasional sightings of killer whales in north and southwest Iceland, outside herring grounds, are also reported, especially during winter and spring (Selbmann et al., 2022). The sporadic nature of these sightings makes photo-identification data from these areas scarce. To date, knowledge of the connectivity between different regions of Iceland is limited.

With an increasing number of deployments of PAM devices in the North Atlantic (e.g., Conservation of Arctic Flora and Fauna, 2020), a comprehensive description of the repertoires of killer whales in Icelandic waters and how they vary among locations could aid our understanding of the range and movement patterns of these whales. Here, we first use acoustic data collected over 32 years (1985–2016) in various locations around Iceland to provide a detailed description of the Icelandic killer whale call repertoire. We then investigate whether and how call repertoires differ between locations in Iceland and examine variation in the repertoire over a period of 14 years at one study site.

2 | METHODS

2.1 | Data collection

Data were collected in five locations around Iceland using a variety of recording methods (Table 1, Figure 1). Recordings were collected from boats that searched for whales and used boat-deployed hydrophones to record groups whenever possible, or using multisensor archival tags (Dtags, Johnson & Tyack, 2003) attached to whales, or moored hydrophones recording continuously or on a duty cycle (Table 1). The oldest set of recordings were collected in 1985–1987 in several small fjords in the east of Iceland (hereafter Eastfjords), then a wintering ground of Icelandic herring. The majority of calls analyzed from these recordings stem from one encounter with a large group of 60–80 individuals. In Vestmannaeyjar, a spawning ground of Icelandic herring in the south of Iceland, acoustic recordings were collected during eight summer field seasons (2002, 2008–2010, and 2013–2016). In Breiðafjörður, a current wintering ground of Icelandic herring in the west of Iceland, acoustic recordings were collected during two winter field seasons (2013–2014). Killer whales often gather in large aggregations of 50–100 whales in the herring grounds, which means that isolating groups and establishing group affiliations can be difficult (Sigurjónsson et al., 1988; Tavares et al., 2017). In all three locations, recordings were generally collected when whales were feeding on herring, as indicated from surface observations and photographs of herring floating at the surface or being taken by seabirds. Concurrent photo-identifications were available, except for recordings from Vestmannaeyjar in 2002 and 2016 and part of the moored hydrophone recordings from 2014 in Breiðafjörður. Individual identification data from Samarra et al. (2017) were used to estimate the number of whales present during recording days.

Two small samples of recordings were available from the southwest and the north of Iceland. A small sample of recordings was collected in 2004 southwest of the Reykjanes Peninsula in Southwest Iceland (hereafter Reykjanes) around two small groups of 1–10 killer whales. In northern Iceland, recordings from bottom-moored acoustic recorders (EARs; Lammers et al., 2008) were collected in Skjálfandi Bay (Magnúsdóttir et al., 2014, 2015). The EARs recorded for 1 min every 15 min (2008–2010) or 10 min every 15 min (2011). Identification photographs were not available for these two sets of recordings.

2.2 | Data processing and call categorization

Some recordings used here have been analyzed in previous studies for varying purposes. Most of the recordings from the Eastfjords (about 5 hr) had previously been analyzed and are the basis of a call catalog describing Icelandic call types I1–I35 (Moore et al., 1988). The recordings from Vestmannaeyjar collected in 2002 were previously analyzed for tail slaps and calling rates and led to the description of call type I36, the "herding call," which has been associated with feeding on herring (Simon et al., 2005, 2006, 2007). The 2008–2016 recordings from Vestmannaeyjar and the 2013–2014 recordings from Breiðafjörður were used to establish a call catalog (Selbmann et al., 2019). This data set was also used in a study comparing the repertoires of killer whales in Iceland, Norway, and Scotland (Selbmann et al., 2021). During the initial classification of the call types from Vestmannaeyjar and Breiðafjörður (Selbmann et al., 2019), comparisons to the catalog of Moore et al. (1988) were made whenever possible but comparability was limited as spectrograms of Moore et al. (1988) were only available in print without sound files. For the present study, parts of the original recordings were made available, making it possible to find examples from the

TABLE 1 Summary of acoustic recordings from Iceland that were inspected for killer whale calls. For details on recording methods in Vestmannaeyjar and Breiðafjörður see Selbmann et al. (2021). No. days refers to the number of different recording events (days) when the data were collected. No. calls refers to the number of high-quality (i.e., high perceived signal-to-noise ratio, little/no overlap with other sounds, clearly audible) calls extracted from the recordings. No. individuals ID indicates the mean number of whales identified per day from photographs collected alongside acoustic recordings.

Region	Year	Months	Sampling rate (kHz)	Duration (hh:mm)	Recording method	No. days	No. calls	No. individuals ID ± *SD* (min–max)
Eastfjords	1985	Oct	44.1	02:38	Single hydrophone (custom), Marantz PMD 360 recorder, frequency response: 0.05–15 kHz ±3 dB	3	46	11 ± 4 (7–14)
“	1986	Oct–Nov	44.1, 48	03:02	Single hydrophone (InterOcean T-902), Sony WM-D6C recorder, frequency response: 0.05–15 kHz ±3 dB	7	84	13 ± 12 (3–32)
“	1987	Oct	48	00:35	“	1	12	NA
Vestmannaeyjar	2002	Jun–Jul	48	15:29	Single hydrophone (Woods Hole Oceanographic Institute, frequency response flat within ±4 dB up to 20 kHz), Sony TCD-D8 digital audio tape recorder (flat frequency response 0.1–22 kHz)	13	234	NA
“	2008	Jun–Jul	96	15:52	4-element vertical array	7	5	10 ± 6 (4–20)
“	2009	Jul	96, 192	58:49	2- and 16-element towed arrays, 4-element vertical array, Dtags	15	2,912	21 ± 14 (4–45)
“	2010	Jul	48, 96	07:17	Single hydrophone, 2-element towed array	5	163	30 ± 22 (5–64)
“	2013	Jul	96	04:37	4-element vertical array	9	12	20 ± 16 (4–35)
“	2014	Jul	48, 96, 192	23:51	Single hydrophone, 2-element towed array	12	1,021	44 ± 25 (14–85)
“	2015	Jul	96, 192	54:46	Single hydrophone, 2-element towed array	18	899	24 ± 18 (4–72)
“	2016	Jul	96, 192	35:21	2-element towed array	12	994	NA
Reykjanes	2004	Jul	96	00:43	2-element towed array with Benthos AQ-4 hydrophones (Teledyne Benthos, Falmouth, MA) and preamplifiers (flat frequency response 0.01–15 kHz) connected to a National Instruments PCI-6013 data acquisition board and recorded directly to hard-disk	2	30	NA

TABLE 1 (Continued)

Region	Year	Months	Sampling rate (kHz)	Duration (hh:mm)	Recording method	No. days	No. calls	No. individuals ID ± *SD* (min–max)
Skjálfandi	2008–2009	Sep–Feb	64	258:43	Ecological Acoustic Recorder (EAR, Lammers et al. 2008), frequency response: 1–28 kHz, ±1.5 dB	163	0	NA
“	2009	Apr–Nov	64	508:18	“	160	0	NA
“	2009–2010	Nov–May	64	292:18	“	184	13	NA
“	2010	May–Sep	64	223:35	“	141	0	NA
“	2011	Jan–Mar, Jul–Aug	16	1422:50	“	93	0	NA
Breiðafjörður	2013–2014	Feb–Mar	96, 240	23:33	Single hydrophone, 4-element vertical array, Dtags	24	1,515	42 ± 32 (1–159)
“	2014	Feb–Mar	64, 96, 192	442:44	Single hydrophone, 4-element vertical array, Dtags, Ecological Acoustic Recorder (EAR)	41	1,472	17 ± 15 (1–62)[a]

[a] Photo-identification not available for all days of EAR deployment.

catalog in the recordings, create clearer spectrograms as well as sound clips, and compare those to calls from other recordings. Not all call categories described by Moore et al. (1988) were found in the available recordings from the Eastfjords. This is likely due to the strict call quality criteria applied in this study and because not all recordings used by Moore et al. (1988) were available. A comparison of previously established catalogs showed only one match: call type I67 (Selbmann et al., 2019) was a match to I13.1 (Moore et al., 1988).

Recordings were analyzed aurally and visually from spectrograms using Audacity versions 2.1.2 and 2.3.1 (https://audacityteam.org/) with a Hann window, FFT = 8,192 for 96, 192, and 240 kHz sampling rates and FFT = 4,096 for 44.1, 48, and 64 kHz sampling rates. Due to the many hours of recording time, the recordings from Skjálfandi were first scanned for possible killer whale calls using a frequency contour algorithm detecting tonal signals in the frequency range 2,000–8,000 Hz (FFT 512 and 2,048 for 64 and 16 kHz sampling rates, respectively, 75% overlap, Hamming window) in the software package Ishmael 1.0 (Mellinger, 2001; Mellinger et al., 2011). Subsequently, each file with a detection from the software was analyzed. Each call was marked and assigned a quality from 1 (poor) to 3 (high) based on the perceived signal-to-noise ratio, overlap with other sounds, and the clarity of the call. Only high-quality calls were extracted and used for further analysis.

Calls were classified based on visual and aural examination of spectrograms with specific attention to the shape of the call contour, the number of elements and segments, and to a lesser extent, call duration (Ford, 1987; Strager, 1995). Elements were defined as parts of a call separated by an abrupt shift in pulse repetition rate of the low-frequency component (Figure 2; Sharpe et al., 2019; Yurk et al., 2002). Segments separated parts of a call by a very short (<0.2 s) silent interval (Sharpe et al., 2019; Yurk et al., 2002). Subtypes were assigned if an element or segment was added/subtracted from a call, if a second frequency component was present/absent, or if a major change in an element occurred (Strager, 1995; see Figure 3 for examples). Variation occurs in all call types and some are more variable than others (Ford, 1989). A subtype was only created if the variation was discrete rather than graded. At least three occurrences of a call were required to define a new type or subtype (Sharpe et al., 2019; Wellard et al. 2020). The classification was performed by AS and cross-validated by FIPS.

2.3 | Validation of classification

The reliability of the classification was tested using two methods. First, observers with experience in cetacean acoustics were presented with a random subset of 60 pairs of calls. In an online questionnaire they were provided with the above definition of call type and subtype and presented the acoustic files and corresponding spectrograms. They were then asked to score each pair of calls as (1) different call types, (2) same call type but different subtypes, or (3) same call type and same subtype. Krippendorff's alpha was computed to test for observer agreement. The coefficient consists of a value between 0 and 1, with 1 indicating perfect agreement between observers and 0 absence of agreement (Hayes & Krippendorff, 2007). Second, classification and regression tree (CART) and random forest analyses were applied using the rpart and randomForest packages (Liaw & Wiener, 2002; Therneau & Atkinson, 2019) in R version 4.1.2 (R Core Team, 2021). CARTs and random forests are widely used in cetacean sound classification (Epp et al., 2022; Fournet et al., 2018; Garland et al., 2015; Rekdahl et al., 2013, 2017; Risch et al., 2013) and random forests have been successfully applied to killer whale calls (Sharpe et al., 2019). These analyses are robust to outliers, nonnormality, and nonindependent data and can handle correlated variables and small sample sizes (Breiman, 2001; Breiman et al., 1984). Following Sharpe et al. (2019), 13 metrics were measured for each call and used as predictor variables in the CART and random forest analyses: start and end frequency, sideband interval at the start, end, and the middle of the call, call duration, time to maximum frequency, time to maximum frequency proportion, frequency trend ratio, frequency range ratio, the number of elements and segments, and the presence/absence of a high-frequency component (Figure 2, Table S1). Sharpe et al. (2019) had measured 12 variables and recommended adding the middle sideband interval to improve the accuracy of the random forest. Measurements were taken from spectrograms (Hann window; FFT = 4,096, 2,048, or 1,024 for 240 and 192 kHz, 96 and 64 kHz, or 48 kHz sampling rates,

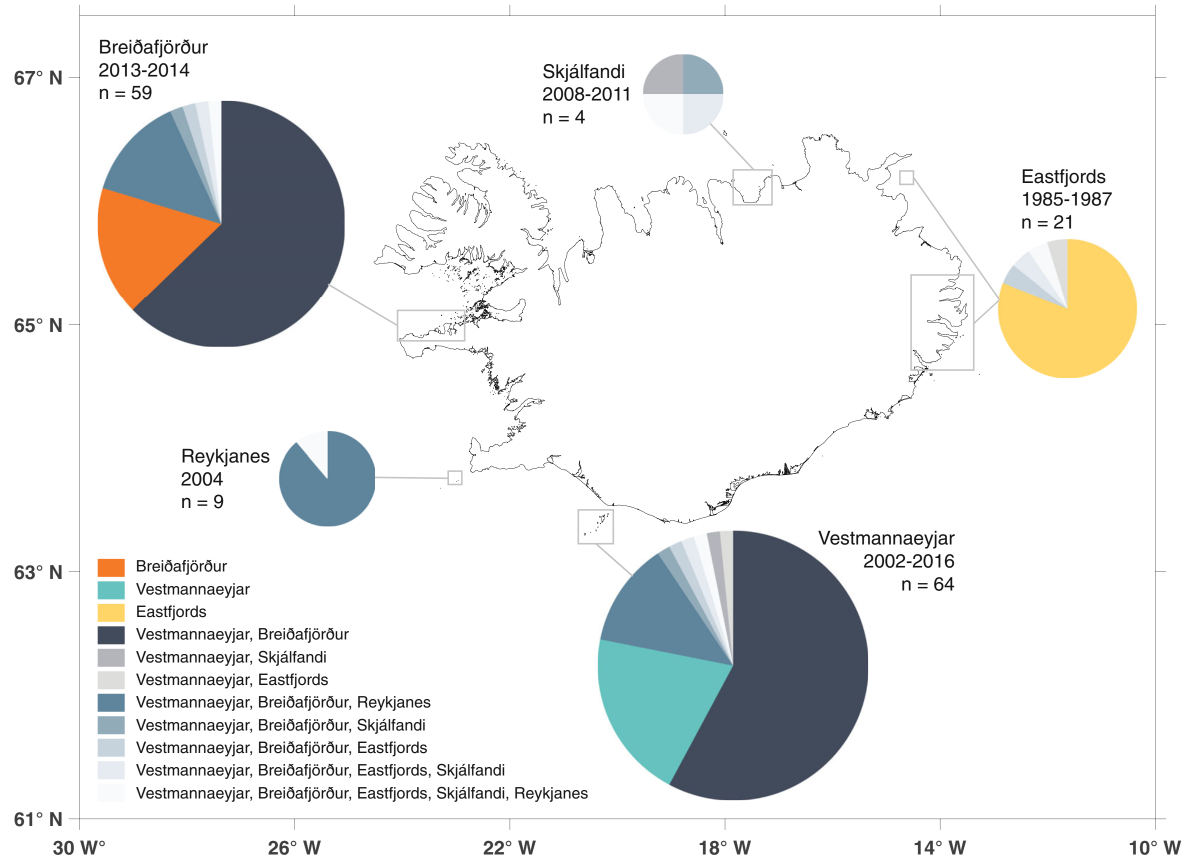

FIGURE 1 Map of Iceland showing the locations where acoustic recordings of killer whales were collected, including recording years. Pie charts show the patterns of call category matching between areas (n = number of call categories per location). Call categories occurring in only one location are indicated in yellow (Eastfjords), orange (Breiðafjörður), and turquoise (Vestmannaeyjar), while call categories occurring in multiple areas are indicated by varying shades of blue and gray. Pie chart size represents relative sample size (number of classified calls per location, log transformed due to very different sample sizes).

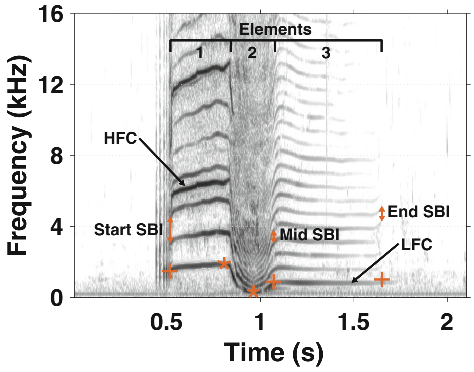

FIGURE 2 Spectrogram of an Icelandic killer whale call showing different metrics considered in the classification and measurements taken to obtain these metrics. Measurements taken on the low frequency component (LFC) were the start, mid, and end frequency (crosses) and maximum and minimum frequency (asterisks). Presence/absence of a high frequency component (HFC) was noted. Measurements of the sideband interval (SBI) were taken at the start, middle, and end of the call (double-ended arrows). Brackets indicate abrupt shifts in pulse repetition rate used to distinguish elements. Spectrogram parameters: Hann window; FFT size: 4,096; 87.5% overlap; frequency resolution: 46.88 Hz; time resolution: 2.67 ms.

respectively; 87.5% overlap) using a custom routine in MATLAB R2017a (https://www.mathworks.com). Due to the large number of samples in some call categories, a maximum of 100 calls were measured for each category, resulting in a total of 1,999 calls measured. The CART used the Gini index to determine the “goodness of split” at each node (Breiman et al., 1984) and the terminal nodes were set to have a minimum sample of five, as most call categories had a sample larger than this. Cross-validation was applied before pruning to the tree with the smallest cross-validation error (Epp et al., 2022; Garland et al., 2015, Rekdahl et al., 2013, 2017). For the random forest, the number of preselected variables available for the split at each node was set to three, the number of trees grown was 1,000, and the decrease in the Gini index was used to assess the importance of each variable (Epp et al., 2022; Fournet et al., 2018; Garland et al., 2015; Sharpe et al., 2019). The random forest model was run five times and the final out-of-bag (OOB) error was obtained by averaging errors across all runs.

2.4 | Analysis of variation in call repertoire over time and between locations

Recordings at Vestmannaeyjar covered a time span of 14 years (2002–2016), providing the opportunity to investigate variation in call types recorded over time in this location and compare it to differences in repertoires between locations (Vestmannaeyjar and Breiðafjörður). Therefore, to examine variation in call type occurrence within and between locations over time, we investigated the relative call type production in the two locations (Vestmannaeyjar and Breiðafjörður) and across years within Vestmannaeyjar. We used two indices that have previously been applied in studies on killer whale call repertoires: (1) The similarity index (SI), which is an adaptation of Dice's coefficient of association (Ford, 1991; Yurk et al., 2002) and was calculated as:

$$\mathrm{SI} = \frac{2N_c}{R_1 + R_2}$$

where N_c is the total number of call categories shared between locations or years and R_1 and R_2 are the numbers of call categories at the two locations or in the two years. The index gives the proportion of call types shared, based on presence/absence. (2) The Whittaker Similarity index (WSI) furthermore considers the frequency of usage of different call categories (Crance et al., 2014) and was calculated as:

$$\mathrm{WSI} = \sum_{i=1}^{N} \min\left(p_{i,a},\; p_{i,b}\right)$$

where N is the total number of call categories, i is the individual call category, a and b are the locations or years being compared, and p is the proportion of the repertoire composed of a particular call, which is calculated as:

$$p_{i,a} = \frac{\text{calls of category } a \text{ produced in location/year } a}{\text{total calls in location/year } a}$$

Both indices produce values ranging from 0 to 1, with 1 indicating identical repertoires and 0 indicating fully distinct repertoires. A nonparametric Spearman rank correlation was applied to test for a linear relationship between locations (Vestmannaeyjar and Breiðafjörður) and between the two years with the longest time between them (2002 and 2016), due to the nonnormality of the distributions (Shapiro–Wilk normality tests: $p < .01$). All statistical analyses were performed using R version 4.1.2 (R Core Team, 2021). Call occurrence is expected to vary with the identity of groups being recorded or behavioral context (e.g., Filatova et al., 2009, 2013; Ford 1989, 1991); however, we did not have such data to investigate potential explanations for differences in call occurrence over time or between locations. Therefore, we provide only a general overview of the frequency with which different call categories were recorded at different locations or across time.

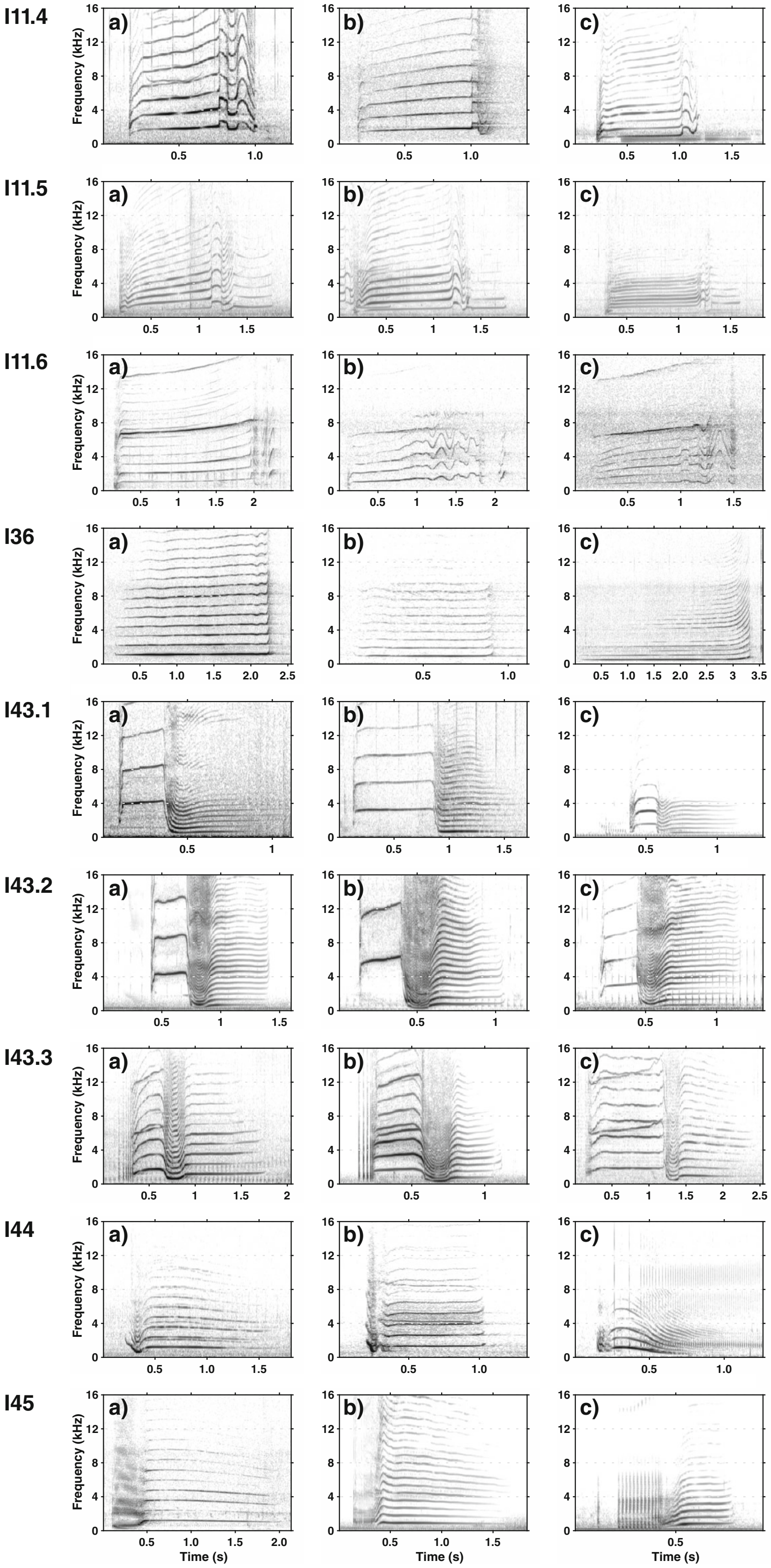

FIGURE 3 Legend on next page.

3 | RESULTS

3.1 | Repertoire description and variation across regions

A total of 3,395 hr of recordings were used, and 9,412 high-quality calls were extracted (Table 1). The majority of recording time (92.4%) was from long-term EAR deployments in Breiðafjörður and Skjálfandi. In Skjálfandi, these recordings included very few killer whale calls.

Approximately 88% ($n = 8{,}321$) of all extracted calls were considered discrete and were manually classified. They were classified into 52 call types, 18 of which consisted of several subtypes (57 subtypes in total; Table S2). We use the term "call category" to include both call types and subtypes, where each call type and subtype is counted as one entity. In the case of call types that were composed of call subtypes we did not count the call type itself but only the number of subtypes. For example, call type I38, which has no subtypes, counts as one unique call category. On the other hand, call type I42, which is composed of subtypes I42.1, I42.2, and I42.3 counts as only three unique call categories. This approach allowed us to compare the number of shared categories across locations (rather than compare just the number of shared call types or just the number of subtypes). Therefore, a total of 91 call categories were classified from all the available recordings (see Table S2 for a complete list).

The classification success of the CART and random forest models was high. The CART correctly classified 84.8% (root node error: $n = 1899/1999$) of calls to the same category as the manual classification (Table S3) and the random forest model had a mean OOB error of 12.0% ± 0.2% across five trials (Table S4). These results improved only slightly when call subtypes were combined under their call type, i.e., call subtypes I11.4, I11.5, and I11.6, for example, were all combined under call type I11 (CART correctly classified 87.3%, random forest OOB error 9.4% ±0.1%). The most important variables in the random forest model, as indicated by the decrease in Gini index, were the sideband interval at the start, the frequency range, the sideband interval in the middle, and the duration of the call. Highest misclassification rates occurred for call categories with small sample sizes and few misclassification errors derived from the similarities between subtypes (Tables S3 and S4).

Agreement between the 11 observers and our classification was moderate (Krippendorff's alpha $= 0.57$). This result was driven primarily by distinguishing subtypes; when the data were subsampled to account only for comparisons of calls of different types or calls from the same type and subtype, interobserver agreement was very high (Krippendorff's alpha $= 0.84$). Due to time constraints, the interobserver test only included comparisons of two call samples. Finer distinctions (i.e., subtypes) often require a larger sample that provides more information, such as whether variation is graded or discrete and whether there are intermediates. This information was not present in the test and likely explains the moderate agreement on subtypes. As the CART and random forest analyses provided strong support for the initial classification and showed only minor improvements when call subtypes were combined under their call type, subsequent analyses were conducted including all call types and subtypes. Nevertheless, to ensure call classification at the subtype level was not driving the results, analyses were repeated with call subtypes combined under their call type (referred to as analysis at the call type level).

FIGURE 3 Three sample spectrograms of commonly recorded killer whale call categories in Iceland. Samples were selected to show the variation within each call category. Call categories I11.4, I36, I44, and I45 made up 38% of calls recorded. Subtypes I11.5 and I11.6 show examples where a subtype was created due to the addition of an element and the addition of a high frequency component. Call types I43.1 and I43.2 show a major change within an element that led to the creation of a subtype and I43.3 shows another example of the addition of a high frequency component. Recordings were sampled at 64 kHz (I11.4b, I11.6a-c, I36a-c, I45a, I53.1c), 96 kHz (I44b), and 192 kHz (I11.4b-c, I11.5a-c, I43.1a-c, I43.2a-c, I43.3a-c, I44a,c, I45b-c). Spectrogram parameters: Hann window, 87.5% overlap. For 64 kHz recordings: FFT size: 2,048, frequency resolution: 31.25 Hz, time resolution: 4.0 ms; for 96 kHz recordings: FFT size: 4,096, frequency resolution: 23.44 Hz, time resolution: 5.33 ms; for 192 kHz recordings: FFT size: 4,096, frequency resolution: 46.88 Hz, time resolution: 2.67 ms.

The relative rate of occurrence varied considerably across call categories (Figure 4). The most common call categories were I45, I44, I11.4, and I36, comprising 13.5%, 8.5%, 8.0%, and 7.5% of recorded calls respectively. All other call categories represented <5% of recorded calls. All four commonly recorded call categories had a relatively simple call structure and/or included elements that made them easily recognizable (Figure 3). The two most common call types (I44 and I45) were highly variable but the graded nature of the variation within the categories precluded further division into subtypes. These call types included calls that may seem very different if viewed on their own but other examples fall between these extremes, which made it impossible to draw a line for division into subtypes. For example, call type I45 had a very simple structure, consisting of a short segment of clicks, followed by a downsweep contour, and showed considerable variation, e.g., in duration. This call type includes calls that have a duration of ~1.5 s, while other examples last for <0.5 s (Figure 3, I45a and c). However, examination of all calls of this type showed no clear distinction of shorter or longer calls but a continuum of durations. Call type I44 is characterized by a distinctive start segment and was thus easy to recognize and classify. This call type also shows variation, with some calls having little frequency modulation and other calls having a distinct downsweep in fundamental frequency. Since it was not possible to distinguish clearly between these two variants, they were kept together but further sampling may lead to the definition of subtypes in the future. Call type I11.4 had a distinct ending with several frequency modulations. It was recorded in all locations. Call type I36, the herding call, was low in frequency, long in duration, and showed very little frequency modulation. It was noticeably more common in Breiðafjörður, despite the overall larger sample of calls from Vestmannaeyjar. Recordings from Vestmannaeyjar were only collected during daytime, while the sample from Breiðafjörður included many hours of recordings collected at night with the EAR when herding calls occurred more frequently (Richard et al., 2017).

Single-component call categories (containing only a low-frequency component, LFC, i.e., monophonic or single-voiced) were more common (68.1%, $n = 62$) than two-component call categories (containing both a LFC and a high-frequency component, HFC, i.e., biphonic or two-voiced, 31.9%, $n = 29$), but call types shared across locations showed no clear tendency to be predominantly single-component or two-component calls (Figure S1).

Most call categories (56%) were found at two or more locations but only one call category was recorded in all five locations (Figure 1, see Table S2 for a detailed list of call types and subtypes). The remaining 44% of call categories were unique to one of three locations: 19% were recorded only in the Eastfjords, 14% only in Vestmannaeyjar, and 11% only in Breiðafjörður. Both Skjálfandi and Reykjanes had very few call categories (four and nine, respectively) that were all found in at least one other location. These results remained similar at the call type level: 65% of call types were shared between two or more locations, while unique call types were found in the Eastfjords (17%), Breiðafjörður (10%), and Vestmannaeyjar (8%).

In Vestmannaeyjar and Breiðafjörður, the locations with most data, the majority of call categories were recorded in both locations, making up 77% and 83%, respectively, of the call categories recorded in each location. A total of 21 call categories were found in the Eastfjords, the majority of which (81.0%) were recorded only in the Eastfjords and in none of the other locations. Four call categories (19.0%) from the Eastfjords were also found in other locations: one in Vestmannaeyjar (I13.1/I67), one in Vestmannaeyjar and Breiðafjörður (I11.6), one in Vestmannaeyjar, Breiðafjörður, and Skjálfandi (I59.1), and one in all other locations (I11.4).

Photo-identification data were available for the locations and seasons where most of the acoustic data came from (Vestmannaeyjar 2008–2015, Breiðafjörður, except for recordings from the EAR, and the Eastfjords 1985–1986) and were used to investigate the possibility that the individuals recorded in different regions might be the same. A total of 431 individual whales were identified in days when acoustic data were collected, with a mean and standard deviation of 26 ± 24 (range 1–159) whales identified per recording day. Most whales were identified either only in Vestmannaeyjar, only in Breiðafjörður, or in both regions (see below). In the Eastfjords, 71 identified individuals were present during recordings but only one of those was also present in one recording day in Breiðafjörður in 2013.

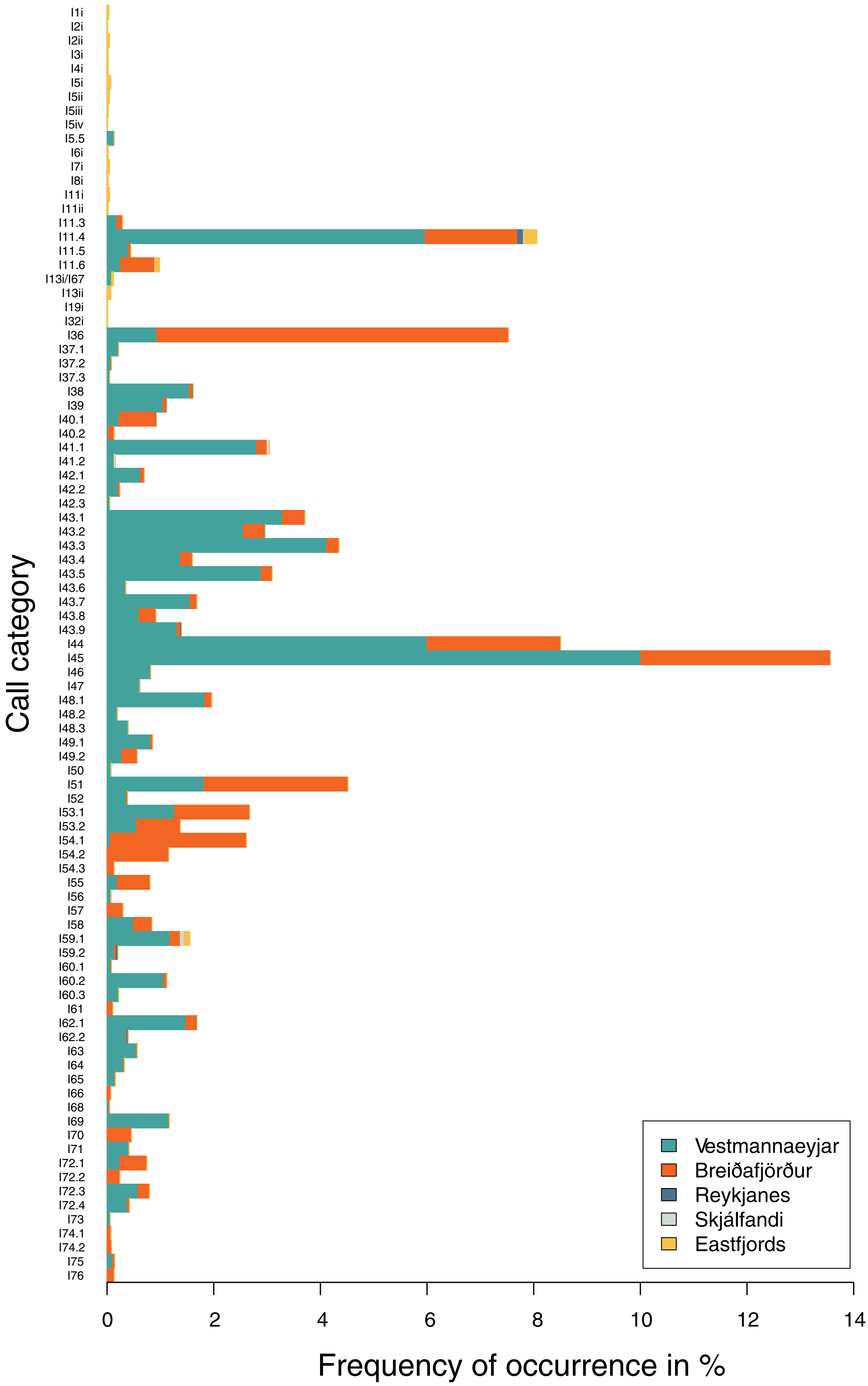

FIGURE 4 Relative rate of occurrence of different killer whale call categories in five locations around Iceland.

3.2 | Comparison of call repertoires recorded in Vestmannaeyjar and Breiðafjörður

Vestmannaeyjar and Breiðafjörður had large sample sizes, allowing a more detailed analysis of variation between locations. Recordings in Vestmannaeyjar were collected on 91 days for a total of 216 hr and 2 min. The mean number of individual whales photo-identified per recording day (2008–2015) was 26 ± 21 (range 4–85). In Breiðafjörður, recordings were collected on 65 days and resulted in 466 hr and 17 min of recordings. A little over 430 hr came from an EAR deployment and thus included many hours without killer whale calls. Photo-identification data were available for 44 of the 65 recording days and a mean of 31 ± 29 (range 1–159) whales were identified per recording day. In total, 361 whales were identified; of these 141 (39.1%) were present during recording days in both locations, 129 (35.7%) were present only in Breiðafjörður and 91 (25.2%) only in Vestmannaeyjar.

From the acoustic recordings from Vestmannaeyjar, 5,588 calls were classified into 64 call categories. Of these, 15 call categories were only recorded in Vestmannaeyjar and not in Breiðafjörður. In Breiðafjörður, 2,612 calls were classified into 59 call categories, 10 of which were only recorded in Breiðafjörður and not in Vestmannaeyjar. In some cases, the unique call categories were one or more subtypes of a call type and other subtypes occurred in both locations. For example, I48.1 was recorded in both locations but the two other subtypes (I48.2 and I48.3) were only recorded in Vestmannaeyjar. Similarly, I54.1 was recorded in both locations but other subtypes (I54.2 and I54.3) were only recorded in Breiðafjörður (see Table S2 for details). Nevertheless, results remained similar at the call type level, with 37 call types in Vestmannaeyjar (7 of them unique to this location) and 36 call types in Breiðafjörður (6 of them unique to the location).

The SI for Vestmannaeyjar and Breiðafjörður was 0.80 (0.82 at call type level), indicating high similarity of the call categories present. However, the WSI was 0.46 (0.49 at call type level), showing that when the frequency of occurrence is considered, the two locations were less similar. These different patterns of relative production rate of call categories in the two locations can also be seen in Figure 4. In Breiðafjörður, a few call types dominated the repertoire, while the rest were recorded only rarely. In Vestmannaeyjar, the rate of occurrence of different call types was more evenly distributed. Thus, although a large proportion of call categories were recorded in both locations, they were not recorded at the same rates. Despite these differences, there was strong evidence that the relative occurrence of different call categories at both sites was positively correlated, although the correlation was weak (Spearman's correlation: $r_s = 0.30$, $p = .008$, $n_{\mathrm{Vestmannaeyjar}} = 5{,}588$ calls, 216 hr, $n_{\mathrm{Breiðafjörður}} = 2{,}612$ calls, 466 hr; Figure 5a).

3.3 | Comparison of call repertoires recorded in Vestmannaeyjar over time

A discovery curve (Figure 6; Figure S2 for analysis at call type level) indicated that the detection of new call categories in Vestmannaeyjar levelled off in 2016, suggesting good coverage of the repertoire at this location. However, it also showed a distinct increase in call categories recorded in 2014 ($n = 16$, 10 of which were new subtypes and 6 new call types). This corresponded with an increase in new individuals identified photographically ($n = 84$; Table S5). Individuals that were regularly sighted before 2014 continued to be detected but additional individuals not previously photographed were sighted from 2014 onwards (Figure S3 and Table S5), indicating that the increase in individuals and call categories does not represent a shift from one group to another. Similarly, call categories that were commonly recorded between 2008 and 2013 remained common in 2014–2016, and a different set of call categories was added in 2014–2016 (Figure S4).

Analysis of the long-term data set showed general stability in the repertoire with some variation between years (Table 2; Table S6 for analysis at call type level). The SI and WSI show a similar pattern of differences between years, but the WSI is overall more uniform. This shows that while there may be differences in the presence/absence of call categories, these are less pronounced when the frequency of occurrence is considered. The years 2008 and 2013 stand out as most different, which is likely due to the small sample sizes from these years (5 and 42 calls,

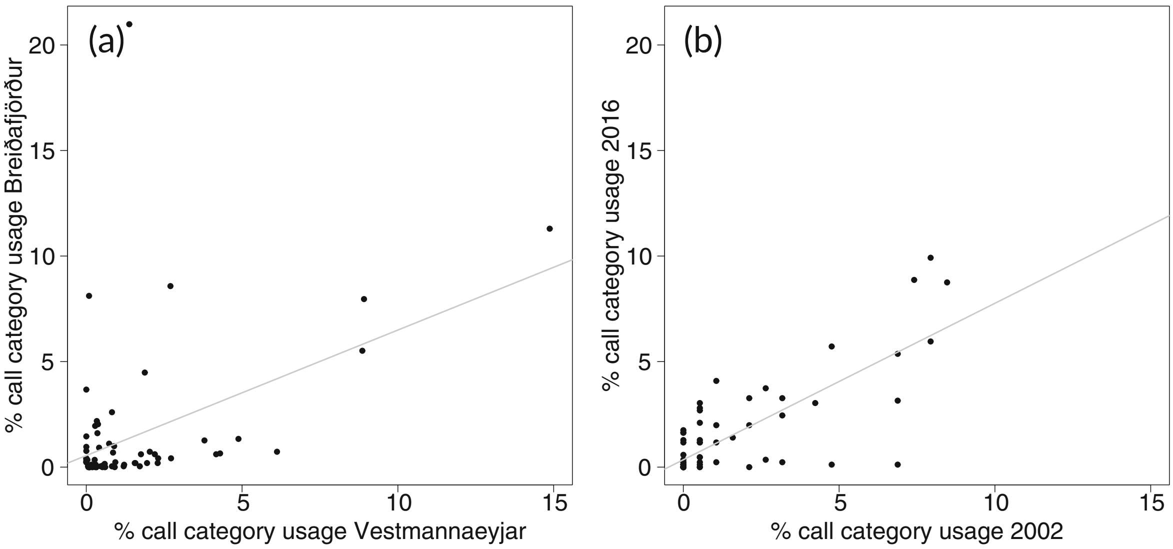

FIGURE 5 Relative production of call categories in a) Vestmannaeyjar compared to Breiðafjörður, b) Vestmannaeyjar in the year 2016 in comparison to 2002. Both were significantly positively correlated but the correlation was weaker between locations (Spearman's correlation: $r_s = 0.30$, $p = .008$) than between years (Spearman's correlation: $r_s = 0.71$, $p < .0001$). Each dot represents a call category (type or subtype).

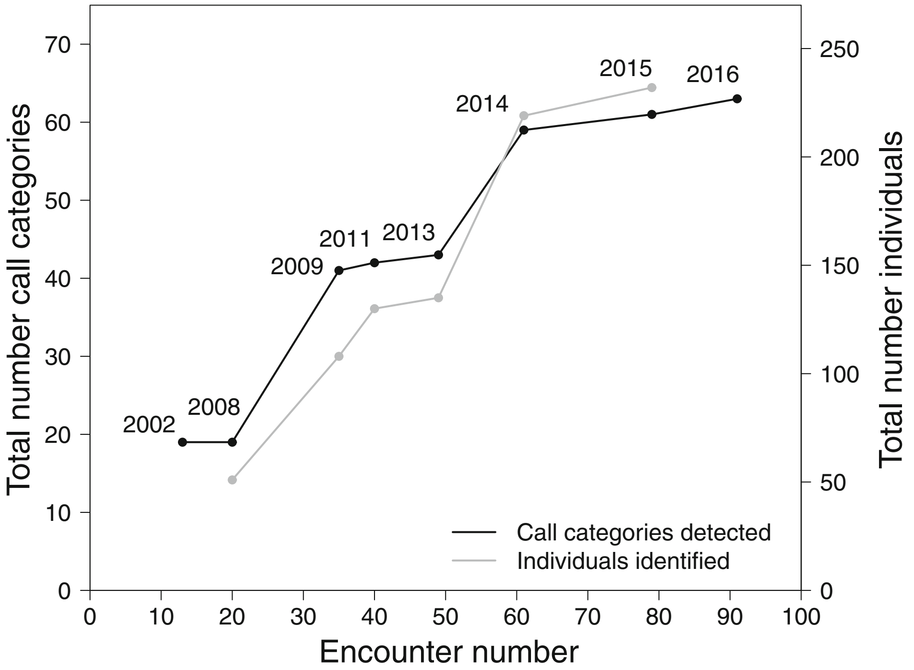

FIGURE 6 Discovery curve indicating the cumulative number of call categories recorded (black) and individual killer whales photo-identified during recordings (gray) in Vestmannaeyjar between 2002 and 2016.

respectively). The years with the highest similarity are 2014–2016, which are also similar to 2002. Indeed, there was strong evidence that the frequency of occurrence of different call categories in Vestmannaeyjar was positively correlated between 2002 and 2016 (Spearman's correlation: $r_s = 0.71$, $p < .001$, $n_{2002} = 189$ calls, 15 hr, $n_{2016} = 857$ calls, 35 hr, Figure 5b), suggesting similarity in the occurrence of call categories recorded in this region over time. A total of 49 call categories were recorded in 2002 and 2016 combined, of which 33 (67.3%) occurred in both years.

TABLE 2 Comparison of the call repertoire of killer whales in Vestmannaeyjar between 2002 and 2016 based on the Similarity Index (SI) and Whittaker Similarity Index (WSI). Boxes are color-coded based on repertoire similarity in increments of 0.25 with darker shades showing the highest values of similarity.

Index	Year	2002	2008	2009	2010	2013	2014	2015	2016
SI	2002	1							
	2008	0.20	1						
	2009	0.56	0.15	1					
	2010	0.55	0.35	0.47	1				
	2013	0.14	0	0.24	0.24	1			
	2014	0.79	0.16	0.52	0.50	0.20	1		
	2015	0.75	0.17	0.58	0.51	0.24	0.81	1	
	2016	0.80	0.16	0.54	0.58	0.15	0.84	0.80	1
WSI	2002	1							
	2008	0.24	1						
	2009	0.42	0.28	1					
	2010	0.47	0.32	0.38	1				
	2013	0.08	0	0.07	0.20	1			
	2014	0.67	0.30	0.53	0.41	0.05	1		
	2015	0.55	0.30	0.41	0.51	0.24	0.51	1	
	2016	0.69	0.28	0.44	0.52	0.08	0.65	0.61	1

Figure 7 shows the relative production of each call category, further supporting that relative call category production was similar between these periods.

4 | DISCUSSION

4.1 | Variation in call repertoire across regions

Comparing killer whale call types and subtypes recorded in different locations around Iceland and spanning 32 years (1985–2016), we found a complex pattern of repertoire variation between regions. The majority of call categories recorded were shared between Vestmannaeyjar and Breiðafjörður, known Icelandic herring spawning and overwintering grounds that killer whales frequent seasonally to feed on herring. However, both locations also had a proportion of call categories that were not recorded elsewhere. Recordings from the Eastfjords, where Icelandic herring previously overwintered, included few call categories that matched other locations. The samples from Reykjanes and Skjálfandi were small, and it is unlikely that the full repertoire was captured at these locations, thus limiting conclusions that could be drawn. It is noteworthy that the sample from Skjálfandi in the north of Iceland matched call categories recorded around the country and that Reykjanes only included matches to Vestmannaeyjar and Breiðafjörður, except I11.4 which was recorded in all five locations.

These findings generally agree with what is currently known about the movement patterns of killer whales around Iceland. Photo-identification studies indicate that a minimum of 45% ($n = 146$) of the Icelandic killer whale population regularly moves between the herring spawning and wintering grounds in Vestmannaeyjar and Breiðafjörður, while 20% ($n = 64$) of individuals have only been sighted in Vestmannaeyjar, and 35% ($n = 117$) only in Breiðafjörður (Samarra et al., 2017). Similarly, in this study, we found that of all the call categories recorded, 54%

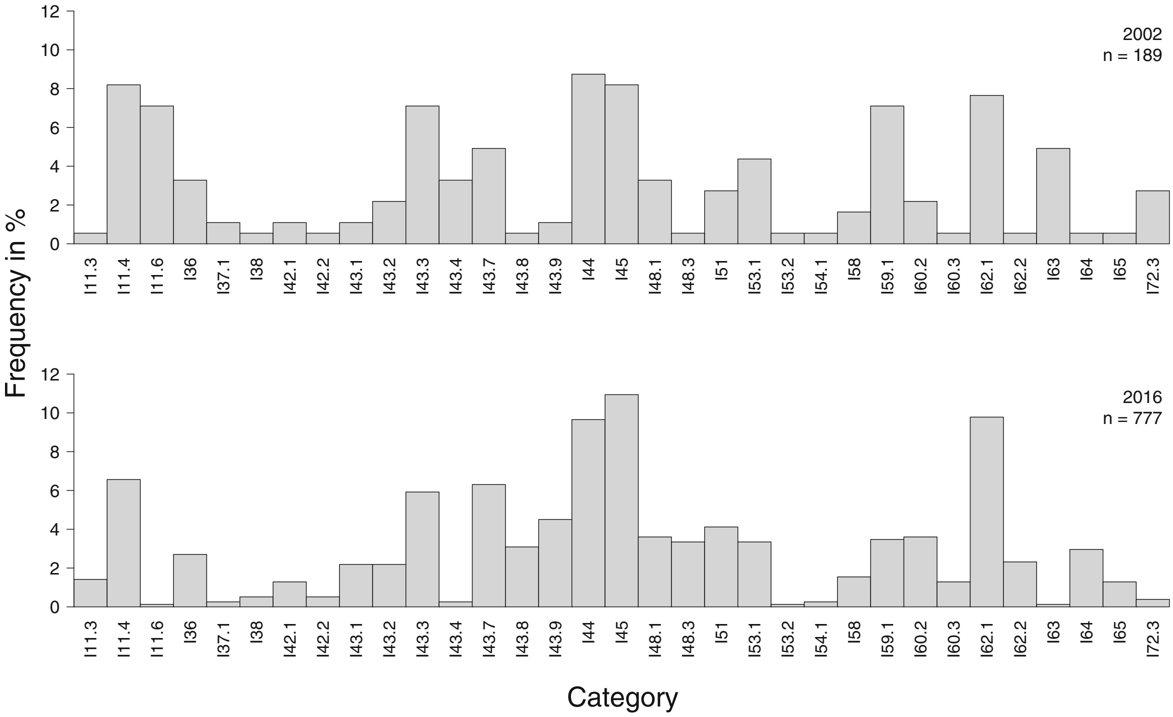

FIGURE 7 Relative frequency of occurrence (%) of call categories in Vestmannaeyjar in both 2002 (top) and 2016 (bottom). Note that only call categories occurring in both years ($n = 33$), and not the full repertoire recorded in each year, are displayed. The total number of call categories recorded was 36 in 2002 and 46 in 2016.

were found in both locations, 16% were only recorded in Vestmannaeyjar, and 11% only in Breiðafjörður. The SI for Vestmannaeyjar and Breiðafjörður was high, indicating similarity in the presence/absence of call categories but the WSI was lower, showing differences in the frequency of occurrence of these call categories. Likewise, the frequencies of occurrence of different call categories at the two locations were positively correlated (Figure 5). However, the correlation was weak, indicating some differences in the frequency of occurrence of shared call types and subtypes. The observed differences in call categories recorded in both locations and frequency of occurrence of different call categories support photo-identification studies showing differences in the individuals occurring in both areas (T. M. J. Marchon, personal communication, March 28, 2023). It could therefore be hypothesized that individuals or groups have different acoustic repertoires or that they use their repertoires differently in different social or environmental contexts. Future studies on group-specific repertoires would help elucidate these patterns.

Only 16 individuals (5%) from previous herring wintering grounds in eastern Iceland were photographically re-identified in current wintering grounds in Breiðafjörður (Samarra et al., 2017). Similarly, only four call categories (19%) recorded in the previous herring wintering grounds in the east of Iceland could be matched to other locations. Samarra et al. (2017) mention that the lack of photographic matches between past and current herring wintering grounds could have been due to a true difference in the individuals visiting both areas or due to missed detections resulting from the difficulty in matching individuals re-sighted over a time interval of up to 30 years. Assuming that individual killer whales in Iceland maintain their call type repertoire in the long-term, as observed in other areas (Foote et al., 2008; Ford, 1991), the lack of acoustic matches in this study suggests that both areas may indeed have been used by different individuals. An important caveat to this comparison is the limited sample size for the Eastfjords compared to Breiðafjörður which also could have resulted in the low number of acoustic matches.

Previous acoustic comparisons matched three call categories (I5.5, I11.4, and I36) between Iceland and Shetland (Deecke et al., 2011; Selbmann et al., 2021), and a part of the Icelandic killer whale population is known to regularly move between Breiðafjörður in Iceland and Scotland (Samarra & Foote, 2015; Samarra et al., 2017). Of the call types occurring in Iceland and Shetland, call type I11.4 was commonly recorded in this study and was found in all locations. Call type I36, the herding call, was only recorded in Vestmannaeyjar and Breiðafjörður, although a likely match was also found in lower quality calls from the Eastfjords that were not included in this study. Call type I5.5 was only recorded in Vestmannaeyjar and not in any of the other locations, which is interesting because movement between Vestmannaeyjar and Scotland has not been documented to date. However, only a few examples ($n = 11$) were recorded in Vestmannaeyjar, and it is possible that larger samples from other locations would include this call type. Other subtypes of this call type were also recorded in the Eastfjords. Individuals matched between Iceland and Scotland have only been sighted in the North, East/Southeast, or West of Iceland. Future photo-identification and acoustic recording comparisons using data collected from various regions in Iceland would be useful to further investigate the distribution range of whales traveling between both locations.

4.2 | Variation in call repertoire recorded over time

At the Vestmannaeyjar study site, long-term stability (2002–2016) and shorter-term changes (2008–2013 versus 2014–2016) in call repertoire were observed. Most of the call categories recorded in 2002 also occurred in 2016 and relative call occurrence changed little between 2002 and 2016 (Figures 5b and 7). However, some of the call categories that were recorded in 2002 were not present in 2008–2013 and occurred again in 2014–2016. This was accompanied by an increase of newly identified call categories in 2014 (Figure 6). The pattern of call occurrence indicates that call categories that were commonly recorded before 2014 remained common and that the new categories increased the total number of call categories recorded rather than replacing the existing repertoire.

This could be due to differences in sampling or differences in individuals present. While the time periods 2008–2013 and 2014–2016 have a similar sample size of calls included in the analysis (2,831 and 2,568 calls respectively), the sample from 2002 only included 189 classified calls. Most of the calls recorded in 2008–2013 were recorded from Dtags in 2009 ($n = 2{,}590$, see Table S7 and Figure S5). All calls from 2002 and 2014–2016 were recorded using single hydrophones, towed, and vertical hydrophone arrays. Dtag recordings are biased towards the tagged individual and its group (Johnson et al., 2009). Nevertheless, the Dtags were placed on four individuals each from a different social cluster (Tavares et al., 2017) and recordings included a total of 34 call categories, thus likely capturing a variety of individuals and groups. Furthermore, photo-identification data showed a distinct influx of new individuals. Individuals present varied between years but individuals that were regularly sighted before 2014 remained regular visitors to Vestmannaeyjar in 2014–2015. These results suggest that new individuals, that did not occur in this area in 2008–2013, arrived in 2014 and returned to the area in subsequent years. These variations in individuals present appear to be reflected in changes in call categories recorded.

Killer whale call repertoires have been shown to be stable over decades and relative call type occurrence also appears to vary little between years in other killer whale populations (Foote et al., 2008; Ford, 1991; Wellard et al., 2020). In our study, photo-identification data to determine whether the same individuals were sighted in 2002 and 2016 were not available. Nevertheless, Samarra et al. (2017) found high site fidelity to Vestmannaeyjar: the same individuals returned to the area in the summer months between 2008 and 2015. In addition, 27 individuals first identified in 1997–2007 in Vestmannaeyjar were resighted between 2008 and 2015, suggesting long-term site fidelity of at least some individuals to this area (Samarra et al., 2017). Assuming the stability in call type repertoire and usage in killer whales in Iceland follows the patterns described elsewhere, our results therefore suggest that individuals/groups return to this area in the long term. The movement patterns of this population are known to be varied; however, there is little knowledge about how movement patterns may change over time (Samarra et al., 2017). The results presented here highlight the value of long-term studies to fully capture the acoustic repertoire of this population, which can help understand long-term variation in site fidelity and movements even under conditions that limit on-water surveys.

4.3 | Validation of the call classification

The CART and random forest analyses both showed high agreement with the initial manual classification, achieving results comparable to other cetacean studies. The CART correctly classified 84.8% of calls, which is similar to classification success in beluga (*Delphinapterus leucas*) and humpback whale (*Megaptera novaeangliae*) sounds (83%, Garland et al., 2015, and 70%–95%, Epp et al., 2022; Fournet et al., 2018; Rekdahl et al., 2013, 2017). The random forest model had an OOB error of 12%, which is higher than what has been previously reported in killer whales (4.4%, Sharpe et al., 2019), but this could be due to substantive differences in sample size between both studies ($n = 232$ in Sharpe et al., 2019 and $n = 1{,}999$ in this study). Compared to other cetaceans, the OOB error reported here was lower (17% for belugas and 15%–30% for humpback whales, Epp et al., 2022; Garland et al., 2015; Fournet et al., 2018; Rekdahl et al., 2013, 2017). The high agreement between the quantitative methods and the manual classification suggests the classification is reliable. To date, automated methods generally do not perform better than human observers in classifying odontocete sounds into biologically meaningful categories (Deecke et al., 1999; Deecke & Janik, 2006; Janik, 1999) but future work could benefit from clearer standards for killer whale call classification and standardized validation methods.

The interobserver reliability test indicated overall moderate agreement between observers when both call types and subtypes were considered. However, agreement was higher when differentiating at the call type level (i.e., distinguishing different call types or identifying calls of the same type and subtype) but lower on finer variations (i.e., when to differentiate between subtypes). These differences likely arose because some people are "splitters" and others "lumpers" and thus even experienced observers classify sounds differently (Oswald et al., 2022). A shortcoming of the interobserver reliability test was that observers were asked to directly compare between only two call samples, thus lacking information for finer distinctions (i.e., subtypes), such as whether variation is graded or discrete and whether there are intermediates. This was done to keep the task less time-intensive. However, interobserver tests that ask observers to classify a subset into as many categories as they think are appropriate have shown higher agreement rates compared to two-choice tests (e.g., Janik, 1999; Riesch & Deecke, 2011).

4.4 | Frequency of call occurrence

Four call types were more frequently recorded than the others, making up a total of 38% of calls recorded. The two most common call types (I44 and I45) were only recorded in Vestmannaeyjar and Breiðafjörður. A possible match to I45 was found in the recordings from the Eastfjords (I8i in the catalog by Moore et al., 1988) but could not be confirmed unequivocally. The other two commonly recorded call types (I11.4 and I36) were both previously found in Shetland as well (Deecke et al., 2011; Selbmann et al., 2021). Call type I11.4 was recorded in all locations and I36 was recorded in Vestmannaeyjar and Breiðafjörður.

All four call types are comparatively simple in structure. The herding call (I36) is known to be associated with feeding and may function in modifying prey behavior rather than strictly communication (Samarra, 2015; Simon et al., 2006). Since most of the recordings were collected in a feeding context, this likely explains why this call type was recorded frequently. However, the prevalence of I36 was mainly driven by its frequent occurrence in Breiðafjörður. Richard et al. (2017) found that the herding call was recorded more often at night. A large proportion of the recordings from Breiðafjörður was collected in the winter months using an EAR and thus included many hours of night-time recording, while recordings from Vestmannaeyjar were only collected during daytime and in summer. Therefore, the difference in the occurrence of I36 could be due to the timing of recordings.

Apart from Icelandic call type I36, killer whale call types are generally not restricted to specific behavioral contexts (Ford, 1991). However, the frequency of occurrence of specific call types may vary with behavior and social context (Filatova et al., 2009, 2013; Ford, 1989; van Opzeeland et al., 2005; Weiß et al., 2006). Northeast

Pacific resident killer whales, for example, appear to increase their matriline-specific calls after the birth of a calf (Weiß et al., 2006) or in the presence of more distantly related or unrelated groups (Weiß et al., 2007). Differences may also occur in the use of single-component and two-component calls. For example, Kamchatkan resident killer whales increase the use of two-component calls when several pods are present compared to single-pod encounters, when single-component calls dominate, indicating that two-component calls may be important family or pod markers (Filatova et al., 2009, 2013). Future work using recordings where behavioral context can be related to the sounds of an isolated group will be useful to better understand the nuances of call type usage in the Icelandic population.

4.5 | Call repertoire sharing and social structure

Varying levels of call repertoire sharing have been shown in other killer whale populations and differences in social organization could explain the different degrees of sharing in vocal patterns (Ford & Ellis, 1999). In the North Pacific, resident killer whales live in closed social groups with no immigration or emigration and closely related groups share more of their call repertoire than more distantly related groups (Bigg et al., 1990; Ford, 1991), while transients have a more widely shared repertoire and show dispersal of males and females from matrilines (Baird & Whitehead, 2000; Deecke, 2003).

Icelandic killer whales appear to live in a society without a clearly nested hierarchical structure (Tavares et al., 2017), although more data are necessary to clearly understand the population's social structure. Associations between individuals are nonrandom but a few strong social bonds exist, and associations are not assorted by the different movement patterns of individuals (Tavares et al., 2017). An early study based on the recordings from the Eastfjords suggested group-specific repertoires in Icelandic killer whales (Moore et al., 1988). This suggestion was likely based on the pattern observed in the Pacific Northwest, the only point of comparison available at the time, and the available data set was small. Even using the longer-term photographic identifications and acoustic recordings available to us now, we have not found the evidence needed to characterize group-specific repertoires or dialects in the Icelandic population. However, our study does suggest some repertoire differences between regions known to be visited by different whales. Thus, even though we do not know which individuals were recorded, this study supports the existence of a certain degree of differentiation of call repertoires among groups in Iceland. Further work using recordings from known individuals and combined with a better understanding of the population's social structure will be necessary to understand the relationship between social organization and acoustic repertoires in Icelandic killer whales.

4.6 | Conclusions

This study contributes to our knowledge of killer whale call repertoires around Iceland and will be useful in PAM applications. Despite sample sizes from different regions varying greatly, the results highlight regional variation in killer whale call repertoires, which can help us understand movement patterns and distribution ranges of these whales. Some limitations of this study could be addressed in the future. Continued acoustic monitoring effort is needed, in particular in less-studied areas, as well as offshore, to better understand regional variation in call repertoires in Icelandic waters. Furthermore, it remains unclear whether group-specific repertoires exist in Icelandic killer whales. This is mainly due to their apparent nonhierarchical social structure and the fact that the whales are often encountered in large feeding aggregations, which makes it difficult to assign social units and to obtain recordings from isolated groups. Further research into group-specificity of Icelandic killer whale calls, call usage and how these might differ from populations with different social association patterns would aid our understanding of drivers of variation in killer whale call repertoires.

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AUTHOR CONTRIBUTIONS

Anna Selbmann: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; validation; visualization; writing - original draft; writing - review & editing. **Volker B. Deecke:** Funding acquisition; investigation; methodology; resources; writing – review and editing. **Olga Filatova:** Funding acquisition; investigation; resources; writing – review and editing. **Ivan D. Fedutin:** Investigation; resources; writing – review and editing. **Patrick Miller:** Funding acquisition; investigation; resources; writing – review and editing. **Malene Simon:** Funding acquisition; investigation; resources; writing – review and editing. **Ann E Bowles:** Investigation; resources; writing – review and editing. **Thomas Lyrholm:** Investigation; resources; writing – review and editing. **Claire Lacey:** Funding acquisition; investigation; resources; writing – review and editing. **Edda Elísabet Magnúsdóttir:** Data curation; funding acquisition; investigation; resources; writing – review and editing. **William Maunder:** Data curation; investigation; writing – review and editing. **Paul Wensveen:** Funding acquisition; supervision; writing – review and editing. **Jörundur Svavarsson:** Funding acquisition; supervision; writing – review and editing. **Filipa Samarra:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – original draft; writing – review and editing.

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REFERENCES

Au, W. W. L., & Hastings, M. C. (2008) *Principles of marine bioacoustics*. Springer.

Baird, R. W., & Whitehead, H. (2000). Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Canadian Journal of Zoology*, *78*(12), 2096–2105. https://doi.org/10.1139/cjz-78-12-2096

Barrett-Lennard, L. G. (2000). *Population structure and mating patterns of killer whales*, Orcinus orca, *as revealed by DNA analysis* [Doctoral dissertation]. University of British Columbia.

Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B., & Balcomb, K. C. (1990). Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Reports of the International Whaling Commission*, *12*(12), 383–405.

Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication*. Sinauer Associates.

Breiman, L. (2001). Random forests. *Machine Learning*, *45*(1), 5–32. https://doi.org/https://doi.org/10.1023/A:1010933404324

Breiman, L., Friedman, J. H., Olshen, R. A., & Stone, C. J. (1984). *Classification and regression trees*. Chapman and Hall.

Conservation of Arctic Flora and Fauna. (2020). *Pan-arctic passive acoustic monitoring network*. https://caff.is/marine/underwater-noise

Crance, J. L., Bowles, A. E., & Garver, A. (2014). Evidence for vocal learning in juvenile male killer whales, *Orcinus orca*, from an adventitious cross-socializing experiment. *Journal of Experimental Biology*, *217*(8), 1229–1237. https://doi.org/10.1242/jeb.094300

Danishevskaya, A. Y., Filatova, O. A., Samarra, F. I. P., Miller, P. J. O., Ford, J. K. B., Yurk, H., Matkin, C. O., & Hoyt, E. (2020). Crowd intelligence can discern between repertoires of killer whale ecotypes. *Bioacoustics*, *29*(1), 15–27. https://doi.org/10.1080/09524622.2018.1538902

Deecke, V. B. (2003). The vocal behaviour of transient killer whales (*Orcinus orca*): Communicating with costly calls [Doctoral dissertation]. University of St Andrews.

Deecke, V. B., Barrett-Lennard, L. G., Spong, P., & Ford, J. K. B. (2010). The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (*Orcinus orca*). *Naturwissenschaften*, *97*(5), 513–518. https://doi.org/10.1007/s00114-010-0657-z

Deecke, V. B., Ford, J. K. B., & Slater, P. J. B. (2005). The vocal behaviour of mammal-eating killer whales: Communicating with costly calls. *Animal Behaviour*, *69*(2), 395–405. https://doi.org/10.1016/j.anbehav.2004.04.014

Deecke, V. B., Ford, J. K. B., & Spong, P. (1999). Quantifying complex patterns of bioacoustic variation: Use of a neural network to compare killer whale (*Orcinus orca*) dialects. *Journal of the Acoustical Society of America*, *105*(4), 2499–2507. https://doi.org/10.1121/1.426853

Deecke, V. B., & Janik, V. M. (2006). Automated categorization of bioacoustic signals: Avoiding perceptual pitfalls. *Journal of the Acoustical Society of America*, *119*(1), 645–653. https://doi.org/10.1121/1.2139067

Deecke, V. B., Nykänen, M., Foote, A. D., & Janik, V. M. (2011). Vocal behaviour and feeding ecology of killer whales *Orcinus orca* around Shetland, UK. *Aquatic Biology*, *13*(1), 79–88. https://doi.org/10.3354/ab00353

Erbe, C. (2013). Underwater passive acoustic monitoring & noise impacts on marine fauna—a workshop report. *Australian Acoustical Society*, *41*(1), 113–119.

Epp, M. V., Fournet, M. E. H., & Davoren, G. K. (2022). Humpback whale call repertoire on a northeastern Newfoundland foraging ground. *Marine Mammal Science*, *38*(1), 256–273. https://doi.org/10.1111/mms.12859

Filatova, O. A., Deecke, V. B., Ford, J. K. B., Matkin, C. O., Barrett-Lennard, L. G., Guzeev, M. A., Burdin, A. M., & Hoyt, E. (2012) Call diversity in the North Pacific killer whale populations: Implications for dialect evolution and population history. *Animal Behaviour*, *83*(3), 595–603. https://doi.org/10.1016/j.anbehav.2011.12.013

Filatova, O. A., Fedutin, I. D., Burdin, A. M., & Hoyt, E. (2011) Responses of Kamchatkan fish-eating killer whales to playbacks of conspecific calls. *Marine Mammal Science*, *27*(2), 1–17. https://doi.org/10.1111/j.1748-7692.2010.00433.x

Filatova, O. A., Fedutin, I. D., Nagaylik, M. M., Burdin, A. M., & Hoyt, E. (2009). Usage of monophonic and biphonic calls by free-ranging resident killer whales (*Orcinus orca*) in Kamchatka, Russian Far East. *Acta Ethologica*, *12*(1), 37–44. https://doi.org/10.1007/s10211-009-0056-7

Filatova, O. A., Guzeev, M. A., Fedutin, I. D., Burdin, A. M., & Hoyt, E. (2013). Dependence of killer whale (*Orcinus orca*) acoustic signals on the type of activity and social context. *Biology Bulletin*, *40*(9), 790–796. https://doi.org/10.1134/S1062359013090045

Filatova, O. A., Miller, P. J. O., Yurk, H., Samarra, F. I. P., Hoyt, E., Ford, J. K. B., Matkin, C. O., & Barrett-Lennard, L. G. (2015). Killer whale call frequency is similar across the oceans, but varies across sympatric ecotypes. *Journal of the Acoustical Society of America*, *138*(1), 251–257. https://doi.org/10.1121/1.4922704

Foote, A. D., & Nystuen, J. A. (2008). Variation in call pitch among killer whale ecotypes. *Journal of the Acoustical Society of America*, *123*(3), 1747–1752. https://doi.org/10.1121/1.2836752

Foote, A. D., Osborne, R. W., & Hoelzel, A. R. (2008). Temporal and contextual patterns of killer whale (*Orcinus orca*) call type production. *Ethology*, *114*(6), 599–606. https://doi.org/10.1111/j.1439-0310.2008.01496.x

Foote, A. D., Similä, T., Vikingsson, G. A., & Stevick, P. T. (2010). Movement, site fidelity and connectivity in a top marine predator, the killer whale. *Evolutionary Ecology*, *24*(4), 803–814. https://doi.org/10.1007/s10682-009-9337-x

Ford, J. K. B. (1987). A catalogue of underwater calls produced by killer whales (*Orcinus orca*) in British Columbia. *Canadian Data Report of Fisheries and Aquatic Sciences No. 633*.

Ford, J. K. B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Canadian Journal of Zoology*, *67*(3), 727–745. https://doi.org/https://doi.org/10.1139/z89-105

Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology*, *69*(6), 1454–1483. https://doi.org/10.1139/z91-206

Ford, J. K. B., & Ellis, G. M. (1999). *Transients: Mammal-hunting killer whales of B.C., Washington State, and Southeast Alaska*. UBC Press.

Ford, J. K. B., Ellis, G. M., & Balcomb, K. C. (1996). *Killer whales: The natural history and genealogy of* Orcinus orca *in British Columbia and Washington*. UBC Press.

Foster, E. A., Franks, D. W., Mazzi, S., Darden, S. K., Balcomb, K. C., Ford, J. K. B., & Croft, D. P. (2012) Adaptive prolonged postreproductive life span in killer whales. *Science*, *337*(6100), 1313. https://doi.org/10.1126/science.1224198

Fournet, M. E. H., Gabriele, C. M., Culp, D. C., Sharpe, F., Mellinger, D. K., & Klinck, H. (2018). Some things never change: multi-decadal stability in humpback whale calling repertoire on Southeast Alaskan foraging grounds. *Scientific Reports*, *8*(1), Article 13186. https://doi.org/10.1038/s41598-018-31527-x

Garland, E. C., Castellote, M., & Berchok, C. L. (2015). Beluga whale (*Delphinapterus leucas*) vocalizations and call classification from the eastern Beaufort Sea population. *Journal of the Acoustical Society of America*, *137*(6), 3054–3067. https://doi.org/10.1121/1.4919338

Hayes, A. F., & Krippendorff, K. (2007). Answering the call for a standard reliability measure for coding data. *Communication Methods and Measures*, *1*(1), 77–89. https://doi.org/10.1080/19312450709336664

Janik, V. M. (1999). Pitfalls in the categorization of behaviour: a comparison of dolphin whistle classification methods. *Animal Behaviour*, *57*(1), 133–143. https://psycnet.apa.org/doi/10.1006/anbe.1998.0923

Johnson, M., de Soto, N. A., & Madsen, P. T. (2009). Studying the behaviour and sensory ecology of marine mammals using acoustic recording tags: A review. *Marine Ecology Progress Series*, *395*, 55–73. https://doi.org/10.3354/meps08255

Johnson, M. P., & Tyack, P. L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering*, *28*(1), 3–12. https://doi.org/10.1109/joe.2002.808212

Lammers, M. O., Brainard, R. E., Au, W. W. L., Mooney, T. A., & Wong, K. B. (2008). An ecological acoustic recorder (EAR) for long-term monitoring of biological and anthropogenic sounds on coral reefs and other marine habitats. *Journal of the Acoustical Society of America*, *123*(3), 1720–1728. https://doi.org/10.1121/1.2836780

Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R News*, *2*(3), 18–22.

Magnúsdóttir, E. E., Miller, P. J. O., Lim, R., Rasmussen, M. H., Lammers, M. O., & Svavarsson, J. (2015). Humpback whale (*Megaptera novaeangliae*) song unit and phrase repertoire progression on a subarctic feeding ground. *Journal of the Acoustical Society of America*, *138*(5), 3362–3374. https://doi.org/10.1121/1.4935517

Magnúsdóttir, E. E., Rasmussen, M. H., Lammers, M. O., & Svavarsson, J. (2014). Humpback whale songs during winter in subarctic waters. *Polar Biology*, *37*(3), 427–433. https://doi.org/10.1007/s00300-014-1448-3

Mellinger, D. K. (2001). *Ishmael 1.0 user's guide* (NOAA Technical Memorandum OAR PMEL-120). Pacific Marine Environmental Laboratory. https://repository.library.noaa.gov/view/noaa/11056

Mellinger, D. K., Martin, S. W., Morrissey, R. P., Thomas, L., & Yosco, J. J. (2011). A method for detecting whistles, moans, and other frequency contour sounds. *Journal of the Acoustical Society of America*, *129*(6), 4055–4061. https://doi.org/10.1121/1.3531926

Mellinger, D. K., Stafford, K. M., Moore, S. E., Dziak, R. P., & Matsumoto, H. (2007). An overview of fixed passive acoustic observation methods for cetaceans. *Oceanography*, *20*(4), 36–45. https://doi.org/10.5670/oceanog.2007.03

Miller, P. J. O. (2002). Mixed-directionality of killer whale stereotyped calls: A direction of movement cue? *Behavioral Ecology and Sociobiology*, *52*(3), 262–270. https://doi.org/10.1007/s00265-002-0508-9

Miller, P. J. O. & Bain, D. E. (2000). Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*. *Animal Behaviour*, *60*(5), 617–628. https://doi.org/10.1006/anbe.2000.1503

Moore, S. E., Francince, J. K., Bowles, A. E., & Ford, J. K. B. (1988). Analysis of calls of killer whales, *Orcinus orca*, from Iceland and Norway. *Rit Fiskideildar*, *11*, 226–250.

Myers, H. J., Olsen, D. W., Matkin, C. O., Horstmann, L. A. & Konar, B. (2021). Passive acoustic monitoring of killer whales (*Orcinus orca*) reveals year-round distribution and residency patterns in the Gulf of Alaska. *Scientific Reports*, *11*(1), Article 20284. https://doi.org/10.1038/s41598-021-99668-0

Oswald, J. N., Erbe, C., Gannon, W. L., Madhusudhana, S., & Thomas, J. A. (2022). Detection and classification methods for animal sounds. In C. Erbe & J. A. Thomas (Eds.), *Exploring animal behavior through sound* (Vol. 1, pp. 269–317). Springer. https://doi.org/10.1007/978-3-030-97540-1_8

R Core Team (2021). *R: A language and environment for statistical computing* [Computer software]. R Foundation for Statistical Computing.

Rekdahl, M. L., Dunlop, R. A., Noad, M. J., & Goldizen, A. W. (2013). Temporal stability and change in the social call repertoire of migrating humpback whales. *Journal of the Acoustical Society of America*, *133*(3), 1785–1795. https://doi.org/10.1121/1.4789941

Rekdahl, M., Tisch, C., Cerchio, S., & Rosenbaum, H. (2017). Common nonsong social calls of humpback whales (*Megaptera novaeangliae*) recorded off northern Angola, southern Africa. *Marine Mammal Science*, *33*(1), 365–375. https://doi.org/10.1111/mms.12355

Rice, A., Deecke, V. B., Ford, J. K. B., Pilkington, J. F., Oleson, E. M., Hildebrand, J. A., & Širovíc, A. (2017). Spatial and temporal occurrence of killer whale ecotypes off the outer coast of Washington State, USA. *Marine Ecology Progress Series*, *572*, 255–268. https://doi.org/10.3354/meps12158

Richard, G., Filatova, O. A., Samarra, F. I. P., Fedutin, I. D., Lammers, M., & Miller, P. J. (2017). Icelandic herring-eating killer whales feed at night. *Marine Biology*, *164*(2), Article 32. https://doi.org/10.1007/s00227-016-3059-8

Riera, A., Pilkington, J. F., Ford, J. K. B., Stredulinsky, E. H., & Chapman, N. R. (2019). Passive acoustic monitoring off Vancouver Island reveals extensive use by at-risk Resident killer whale (*Orcinus orca*) populations. *Endangered Species Research*, *39*, 221–234. https://doi.org/10.3354/esr00966

Riesch, R., & Deecke, V. B. (2011). Whistle communication in mammal-eating killer whales (*Orcinus orca*): Further evidence for acoustic divergence between ecotypes. *Behavioral Ecology and Sociobiology*, *65*(7), 1377–1387. https://doi.org/10.1007/s00265-011-1148-8

Risch, D., Clark, C. W., Dugan, P. J., Popescu, M., Siebert, U., & Van Parijs, S. M. (2013). Minke whale acoustic behavior and multi-year seasonal and diel vocalization patterns in Massachusetts Bay, USA. *Marine Ecology Progress Series*, *489*, 279–295. https://doi.org/10.3354/meps10426

Samarra, F. I. P. (2015). Variations in killer whale food-associated calls produced during different prey behavioural contexts. *Behavioural Processes*, *116*, 33–42. https://doi.org/10.1016/j.beproc.2015.04.013

Samarra, F. I. P., & Foote, A. (2015). Seasonal movements of killer whales between Iceland and Scotland. *Aquatic Biology*, *24*(1), 75–79. https://doi.org/10.3354/ab00637

Samarra, F. I. P., Tavares, S. B., Béesau, J., Deecke, V. B., Fennell, A., Miller, P. J. O., Pétursson, H., Sigurjónsson, J., & Víkingsson, G. A. (2017). Movements and site fidelity of killer whales (*Orcinus orca*) relative to seasonal and long-term shifts in herring (*Clupea harengus*) distribution. *Marine Biology*, *164*, Article 159. https://doi.org/10.1007/s00227-017-3187-9

Saulitis, E. L., Matkin, C. O., & Fay, F. H. (2005). Vocal repertoire and acoustic behavior of the isolated AT1 killer whale subpopulation in southern Alaska. *Canadian Journal of Zoology*, *83*(8), 1015–1029. https://doi.org/10.1139/z05-089

Schevill, W. E., & Watkins, W. A. (1966). Sound structure and directionality in *Orcinus* (killer whale). *Zoologica*, *51*(6), 71–76.

Selbmann, A., Basran, C. J., Bertulli, C. G., Hudson, T., Mrusczok, M.-T., Rasmussen, M. H., Rempel, J. N., Scott, J., Svavarsson, J., Wensveen, P. J., Whittaker, M., & Samarra, F. I. P. (2022). Occurrence of long-finned pilot whales (*Globicephala melas*) and killer whales (*Orcinus orca*) in Icelandic coastal waters and their interspecific interactions. *Acta Ethologica*, *25*, 141–154. https://doi.org/10.1007/s10211-022-00394-1

Selbmann, A., Deecke, V. B., Fedutin, I. D., Filatova, O. A., Miller, P. J. O., & Samarra, F. I. P. (2019). *A catalogue of pulsed calls produced by killer whales* (Orcinus orca) *in Iceland 2008–2016* (Report HV 2019–23). Marine and Freshwater Research Institute.

Selbmann, A., Deecke, V. B., Fedutin, I. D., Filatova, O. A., Miller, P. J. O., Svavarsson, J., & Samarra, F. I. P. (2021). A comparison of Northeast Atlantic killer whale (*Orcinus orca*) stereotyped call repertoires. *Marine Mammal Science*, *37*(1), 268–289. https://doi.org/10.1111/mms.12750

Sharpe, D. L., Castellote, M., Wade, P. R., & Cornick, L. A. (2019). Call types of Bigg's killer whales (*Orcinus orca*) in western Alaska: using vocal dialects to assess population structure. *Bioacoustics*, *28*(1), 74–99. https://doi.org/10.1080/09524622.2017.1396562

Sigurjónsson, J., Lyrholm, T., Leatherwood, S., Jonsson, E., & Vikingsson, G. (1988). Photoidentification of killer whales, *Orcinus orca*, off Iceland, 1981 through 1986. *Rit Fiskideildar*, *11*, 99–114.

Simon, M., McGregor, P. K., & Ugarte, F. (2007). The relationship between the acoustic behaviour and surface activity of killer whales (*Orcinus orca*) that feed on herring (*Clupea harengus*). *Acta Ethologica*, *10*(2), 47–53. https://doi.org/10.1007/s10211-007-0029-7

Simon, M., Ugarte, F., Wahlberg, M., & Miller, L. E. E. A. (2006). Icelandic killer whales *Orcinus orca* use a pulsed call suitable for manipulating the schooling behaviour of herring *Clupea harengus*. *Bioacoustics*, *16*(1), 57–74. https://doi.org/10.1080/09524622.2006.9753564

Simon, M., Wahlberg, M., Ugarte, F., & Miller, L. A. (2005). Acoustic characteristics of underwater tail slaps used by Norwegian and Icelandic killer whales (*Orcinus orca*) to debilitate herring (*Clupea harengus*). *Journal of Experimental Biology*, *208*(12), 2459–2466. https://doi.org/10.1242/jeb.01619

Strager, H. (1995). Pod-specific call repertoires and compound calls of killer whales, *Orcinus orca* Linnaeus, 1758, in the waters of northern Norway. *Canadian Journal of Zoology*, *73*(6), 1037–1047. https://doi.org/10.1139/z95-124

Tavares, S. B., Samarra, F. I. P., & Miller, P. J. O. (2017). A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. *Behavioral Ecology*, *28*(2), 500–514. https://doi.org/10.1093/beheco/arw179

Therneau, T., & Atkinson, B. (2019). *rpart: Recursive partitioning and regression trees* (R package version 4.1-15) [Computer software]. https://cran.r-project.org/package=rpart

van Opzeeland, I., Corkeron, P. J., Leyssen, T., Simila, T. & van Parijs, S. M. (2005). Acoustic behaviour of Norwegian killer whales, *Orcinus orca*, during carousel and seiner foraging on spring-spawning herring. *Aquatic Mammals*, *31*(1), 110–119. https://doi.org/10.1578/AM.31.1.2005.110

van Opzeeland, I., van Parijs, S., Kindermann, L., Burkhardt, E., & Boebel, O. (2013). Calling in the cold: Pervasive acoustic presence of humpback whales (*Megaptera novaeangliae*) in Antarctic coastal waters. *PloS ONE*, *8*(9), Article e73007. https://doi.org/10.1371/journal.pone.0073007

van Parijs, S. M., Clark, C. W., Sousa-Lima, R. S., Parks, S. E., Rankin, S., Risch, D., & van Opzeeland, I. C. (2009). Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales. *Marine Ecology Progress Series*, *395*, 21–36. https://doi.org/10.3354/meps08123

Weiß, B. M., Ladich, F., Spong, P. & Symonds, H. (2006). Vocal behavior of resident killer whale matrilines with newborn calves: The role of family signatures. *Journal of the Acoustical Society of America*, *119*(1), 627–635. https://doi.org/10.1121/1.2130934

Weiß, B. M., Symonds, H., Spong, P., & Ladich, F. (2007). Intra- and intergroup vocal behavior in resident killer whales, *Orcinus orca*. *Journal of the Acoustical Society of America*, *122*(6), 3710–3716. https://doi.org/10.1121/1.2799907

Wellard, R., Pitman, R. L., Durban, J., & Erbe, C. (2020). Cold call: the acoustic repertoire of Ross Sea killer whales (*Orcinus orca*, Type C) in McMurdo Sound, Antarctica. *Royal Society Open Science*, *7*(2), 191228. https://doi.org/10.1098/rsos.191228

Yurk, H., Barrett-Lennard, L. G., Ford, J. K. B., & Matkin, C. O. (2002). Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, *63*(6), 1103–1119. https://doi.org/10.1006/anbe.2002.3012

Yurk, H., Filatova, O., Matkin, C. O., Barrett-Lennard, L. G., & Brittain, M. (2010). Sequential habitat use by two resident killer whale (*Orcinus orca*) clans in Resurrection Bay, Alaska, as determined by remote acoustic monitoring. *Aquatic Mammals*, *36*(1), 67–78. https://doi.org/10.1578/AM.36.1.2010.67

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Supplementary material

Table S1: Description of metrics measured used as predictor variables in the CART and random forest models. Measurements taken of the fundamental contour of the low frequency component.

Measured metric	Description
Duration (s)	Time from start to end of call
Time of maximum frequency (s)	Time until frequency maximum
Time to max proportion (ratio)	Time until frequency maximum/duration
Start frequency (Hz)	Starting frequency
End frequency (Hz)	Ending frequency
Frequency trend ratio (ratio)	Ratio start/final frequency
Frequency range ratio (ratio)	Ratio of maximum/minimum frequency
Start SBI (Hz)	Sideband interval at start of call
End SBI (Hz)	Sideband interval at end of call
Mid SBI (Hz)	Sideband interval in middle of call
Elements (n)	Distinguished by abrupt shifts in SBI
Segments (n)	Elements separated by silence
HFC presence (yes/no)	Presence or absence of a high frequency component

Table S2: Summary of call types and subtypes recorded in different locations around Iceland. For details on call types see full call catalogue (Selbmann et al., 2019). *call types defined by Moore et al. (1988), **call type defined by Simon et al. (2006). With the extended sample size and the recordings available from the Eastfjords, call type I67 described by Selbmann et al. (2019) was found to be a match to I13.1 by Moore et al. (1988).

Call (sub-)type	**Vestmannaeyjar**	**Breiðafjörður**	**Reykjanes**	**Skjálfandi**	**Eastfjords**
I1*					X
I2.1*					X
I2.2*					X
I3*					X
I4*					X
I5.1*					X
I5.2*					X
I5.3*					X
I5.4*					X
I5.5	X				
I6*					X
I7*					X
I8*					X
I11.1*					X
I11.2*					X
I11.3	X	X			
I11.4	X	X	X	X	X
I11.5	X	X			
I11.6	X	X			X
I13.1*/I67	X				X
I13.2*					X
I19*					X
I32*					X
I36**	X	X			
I37.1	X				
I37.2	X	X			
I37.3	X				
I38	X	X	X		
I39	X	X	X		
I40.1	X	X	X		
I40.2	X	X			
I41.1	X	X		X	
I41.2	X			X	
I42.1	X	X			
I42.2	X	X			
I42.3	X				
I43.1	X	X			
I43.2	X	X	X		
I43.3	X	X			
I43.4	X	X			
I43.5	X	X			
I43.6	X				
I43.7	X	X			

I43.8	X	X			
I43.9	X	X	X		
I44	X	X			
I45	X	X			
I46	X	X			
I47	X				
I48.1	X	X			
I48.2	X				
I48.3	X				
I49.1	X	X			
I49.2	X	X			
I50	X				
I51	X	X			
I52	X	X			
I53.1	X	X			
I53.2	X	X			
I54.1	X	X			
I54.2		X			
I54.3		X			
I55	X	X			
I56	X				
I57		X			
I58	X	X			
I59.1	X	X		X	X
I59.2	X	X	X		
I60.1	X	X			
I60.2	X	X			
I60.3	X				
I61		X			
I62.1	X	X	X		
I62.2	X	X	X		
I63	X	X			
I64	X	X			
I65	X	X			
I66		X			
I68	X	X			
I69	X	X			
I70		X			
I71	X				
I72.1	X	X			
I72.2		X			
I72.3	X	X			
I72.4	X	X			
I73	X				
I74.1		X			
I74.2		X			
I75	X	X			
I76		X			

Table S3: CART confusion matrix for killer whale call categories in Iceland. The overall classification success was 84.8%. The manual call classification is given in column 1, subsequent columns list the number of calls assigned to each category by the CART analysis. The percent agreement per call category is given in the final column.

	I5.5	I11.3	I11.4	I11.5	I11.6	I36	I37.1	I37.2	I37.3	I38	I39	I40.1	I40.2	I41.1	I41.2	I42.1	I42.2	I43.1	I43.2	I43.3	I43.4	I43.5	I43.6	I43.7	I43.8	I43.9	I44	I45	I46	I47	I48.1	I48.2	I48.3	I49.1	I49.2	I51	I52	I53.1	I53.2	I54.1	I54.2	I54.3	I55	I56	I57	I58	I59.1	I59.2	I60.1	I60.2	I60.3	I61
I5.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I11.3	-	6	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I11.4	-	-	99	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I11.5	-	-	-	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I11.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
I36	-	1	-	-	-	95	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I37.1	-	-	-	-	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I37.2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I37.3	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I38	-	-	-	-	-	-	-	-	-	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I39	-	-	1	-	-	-	-	-	-	2	46	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	1	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I40.1	-	1	-	-	-	-	-	-	-	-	-	46	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I40.2	-	-	2	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I41.1	-	-	-	-	-	4	3	-	-	-	-	-	-	87	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I41.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I42.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
I42.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	98	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	96	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	98	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.5	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	90	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	35	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	2	28	2	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.9	-	-	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I44	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	3	-	1	-	-	-	1	-	-	88	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I45	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	86	-	-	-	-	-	1	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I46	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	5	30	-	1	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I47	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	47	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I48.1	-	-	-	-	-	-	-	-	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	76	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I48.2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I48.3	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I49.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I49.2	-	-	-	-	-	2	1	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I51	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	95	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I52	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I53.1	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	56	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I53.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-	-	-	-	-	-	-	-	-
I54.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	18	-	-	-	-	-	-	-	-	-	-	-	-
I54.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	13	-	-	-	-	-	-	-	-	-	-	-
I54.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-
I55	-	5	-	-	-	2	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I56	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I57	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I58	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I59.1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	32	-	-	-	-	-
I59.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
I60.1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I60.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-	-
I60.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-
I61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I62.1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I62.2	-	-	5	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I63	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I64	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I65	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I66	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
I70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I71	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I72.1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I72.2	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I72.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
I72.4	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
I73	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I74.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I74.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	I62.1	I62.2	I63	I64	I65	I66	I67	I70	I71	I72.1	I72.2	I72.3	I72.4	I73	I74.1	I74.2	I75	n	Agreement (%)
I5.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	0
I11.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	75
I11.4	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	100	99
I11.5	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	4	100
I11.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	9	0
I36	3	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	100	0
I37.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	100
I37.2	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	3	0
I37.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	100
I38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18	83
I39	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	57	81
I40.1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	48	96
I40.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	0
I41.1	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	1	100	87
I41.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	100
I42.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24	96
I42.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	71
I43.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	98
I43.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	99	97
I43.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	98
I43.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	100
I43.5	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	100	90
I43.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	0
I43.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	36	97
I43.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	35	80
I43.9	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	26	62
I44	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	100	88
I45	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	89
I46	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	43	70
I47	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	47	100
I48.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	82	93
I48.2	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	8	0
I48.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	0
I49.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	86
I49.2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	0
I51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	95
I52	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21	81
I53.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	59	96
I53.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	100
I54.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24	75
I54.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17	76
I54.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	0
I55	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	12	0
I56	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	0
I57	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	0
I58	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	6	0
I59.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	36	89
I59.2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	3	0
I60.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0
I60.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	15	80
I60.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	100
I61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	0
I62.1	55	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	59	93
I62.2	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	10	0
I63	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24	83
I64	1	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	9	78
I65	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0
I66	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	0
I67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	3	0
I70	-	-	-	-	-	-	-	7	-	2	-	-	1	-	-	-	-	11	64
I71	2	-	-	-	-	-	-	-	19	-	-	-	-	-	-	-	-	21	90
I72.1	-	-	-	-	-	-	-	-	-	8	-	1	-	-	-	-	-	16	50
I72.2	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	7	0
I72.3	-	-	-	-	-	-	-	-	-	1	-	4	-	-	-	-	-	9	44
I72.4	-	-	-	-	-	-	-	-	-	1	-		4	-	-	-	-	7	57
I73	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	0
I74.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0
I74.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	5	100
I75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	9	33

Table S4: Example confusion matrix from random forest model for killer whale call categories in Iceland. The overall OOB error was 12.0% ±0.2% across five trials. The manual call classification is given in column 1, subsequent columns list the number of calls assigned to each category by the random forest analysis. The class error is given in the final column.

	I5.5	I11.3	I11.4	I11.5	I11.6	I36	I37.1	I37.2	I37.3	I38	I39	I40.1	I40.2	I41.1	I41.2	I42.1	I42.2	I43.1	I43.2	I43.3	I43.4	I43.5	I43.6	I43.7	I43.8	I43.9	I44	I45	I46	I47	I48.1	I48.2	I48.3	I49.1	I49.2	I51	I52	I53.1	I53.2	I54.1	I54.2	I54.3	I55	I56	I57	I58	I59.1	I59.2	I60.1	I60.2	I60.3	I61
I5.5	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I11.3	-	4	1	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
I11.4	-	-	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I11.5	-	-	-	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I11.6	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
I36	-	-	-	-	-	95	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I37.1	-	-	-	-	-	-	6	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I37.2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I37.3	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I38	-	-	-	-	-	-	-	-	-	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I39	-	-	-	-	-	-	-	-	-	-	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	1	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I40.1	-	-	-	-	-	-	-	-	-	-	-	46	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I40.2	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I41.1	-	-	-	-	-	1	-	-	-	-	-	-	-	92	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I41.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I42.1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-
I42.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
I43.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	99	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	97	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	97	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	33	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	30	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I43.9	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2	-	-	4	-	-	-	15	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	2	-	-	91	1	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
I45	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	89	-	-	2	-	-	-	-	-	2	2	-	-	-	-	-	2	-	-	-	-	-	-	-	-
I46	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	35	-	3	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I47	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	46	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I48.1	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	4	4	1	-	70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I48.2	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	4	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I48.3	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I49.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I49.2	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I51	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	97	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I52	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	1	-	-	-	-	-	16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I53.1	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	55	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I53.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-	-	-	-	-	-	-	-	-
I54.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	19	2	-	-	-	-	-	-	-	-	-	-	-
I54.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	15	-	-	-	-	-	-	-	-	-	-	-
I54.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	3	-	-	-	-	-	-	-	-	-	-
I55	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	9	-	-	-	-	-	-	-	-	-
I56	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I57	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-
I58	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-
I59.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	32	1	-	-	-	-
I59.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-
I60.1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I60.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-	-
I60.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-
I61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I62.1	-	-	-	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I62.2	-	-	3	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I63	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I64	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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I66	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	1
I70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I71	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I72.1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I72.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	4	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I72.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I72.4	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I73	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I74.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I74.2	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	I62.1	I62.2	I63	I64	I65	I66	I67	I70	I71	I72.1	I72.2	I72.3	I72.4	I73	I74.1	I74.2	I75	n	Class error
I5.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-
I11.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	0.50
I11.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	-
I11.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-
I11.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	9	0.56
I36	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	0.05
I37.1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	8	0.25
I37.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1.00
I37.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	0.33
I38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18	-
I39	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	57	0.12
I40.1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	48	0.04
I40.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	1.00
I41.1	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	100	0.08
I41.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-
I42.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24	0.17
I42.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	0.29
I43.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	0.01
I43.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	99	0.02
I43.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	-
I43.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	0.04
I43.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	0.03
I43.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	0.33
I43.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	36	0.08
I43.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	35	0.14
I43.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	26	0.42
I44	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	100	0.09
I45	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	0.11
I46	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	43	0.19
I47	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	47	0.02
I48.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	82	0.15
I48.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	0.50
I48.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1.00
I49.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	0.14
I49.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	0.25
I51	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	0.03
I52	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21	0.24
I53.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	59	0.07
I53.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	-
I54.1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	24	0.21
I54.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17	0.12
I54.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	0.57
I55	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	0.25
I56	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	1.00
I57	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	0.50
I58	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	0.50
I59.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	36	0.11
I59.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1.00
I60.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1.00
I60.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	0.20
I60.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-
I61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1.00
I62.1	52	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	59	0.12
I62.2	2	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	10	0.90
I63	-	-	22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24	0.08
I64	1	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	9	0.22
I65	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1.00
I66	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	2	-
I67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1.00
I70	-	-	-	-	-	-	-	8	-	-	-	-	1	-	-	-	-	11	0.27
I71	-	-	-	-	-	-	-	-	18	-	-	-	-	-	-	-	-	21	0.14
I72.1	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	16	0.63
I72.2	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	7	0.86
I72.3	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	9	0.78
I72.4	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	7	0.14
I73	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	3	0.67
I74.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1.00
I74.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	5	0.20
I75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	9	0.33

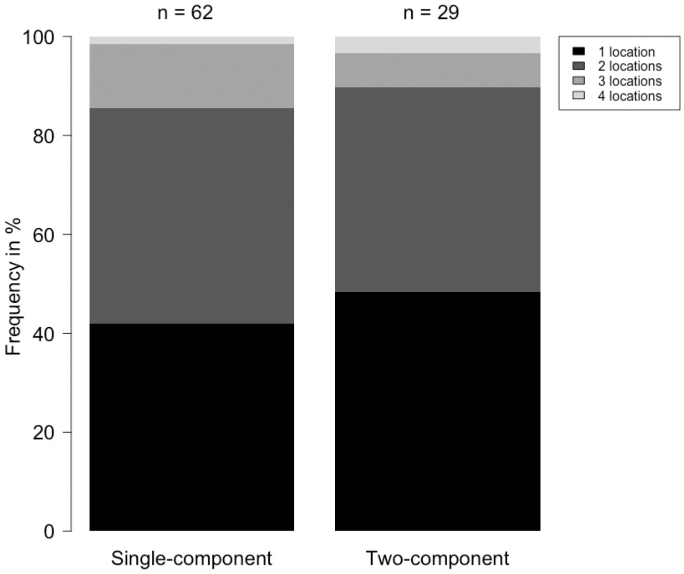


Figure S1: Frequency of occurrence of single-component and two-component call categories by number of locations.

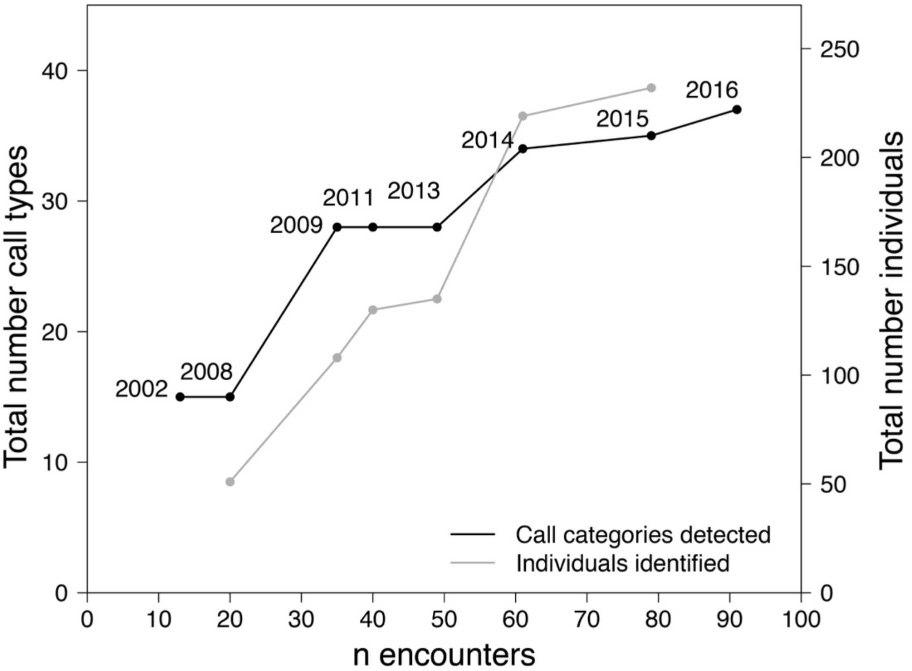


Figure S2: Discovery curve indicating the cumulative number of call types recorded (black) and individual killer whales photo-identified during recordings (gray) in Vestmannaeyjar between 2002 and 2016.

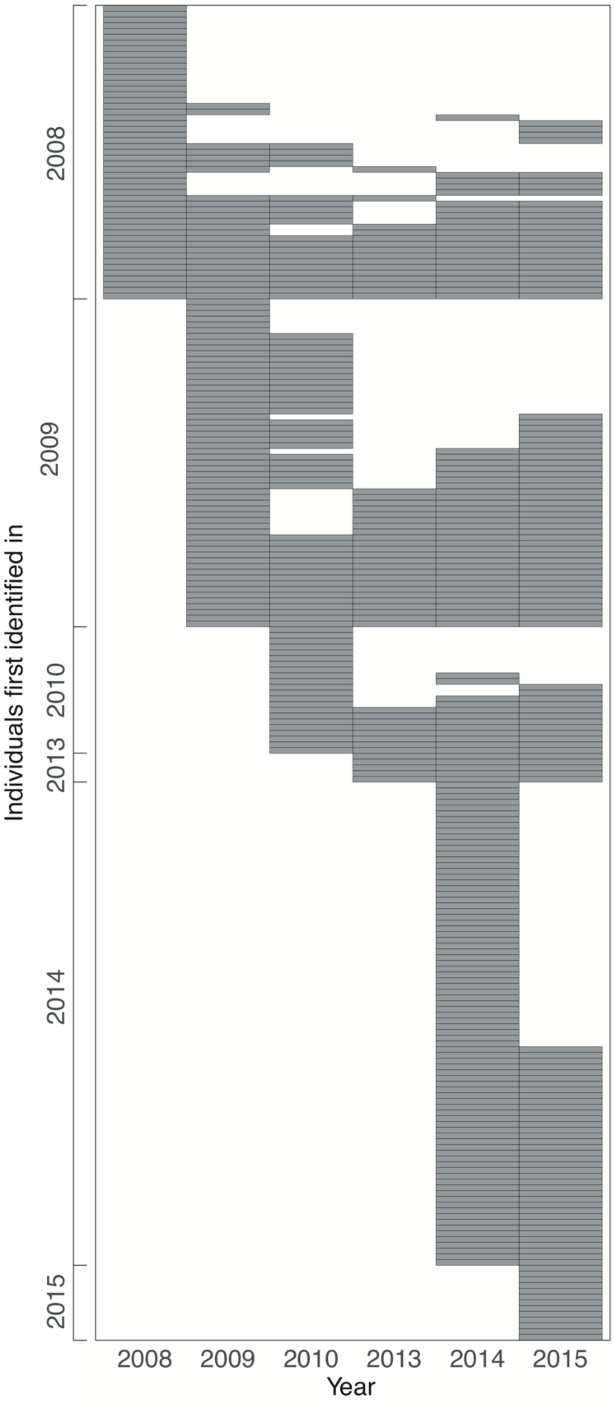


Figure S3: Sighting records of individual killer whales in Vestmannaeyjar 2008-2015. Each row represents an identified individual and each column a sampling year. Presence of individuals is indicated by a gray box, so that individuals sighted every year are shown by a complete gray row. Note that individuals identified in the early years tend to be sighted in subsequent years, but in 2014-2015 there is a large influx of new individuals that had not been sighted previously.

Table S5: Summary of photo-identification records of killer whales present during recordings in Vestmannaeyjar, with the number of individuals sighted based on which year they were first sighted in. The year of the first sighting of an individual is in the vertical and consecutive years of sightings in the horizontal axis. Total indicates the total number of whales identified each year and cumulative shows how many different individuals were identified overall.

Sighted → **First identified ↓**	**2008**	**2009**	**2010**	**2013**	**2014**	**2015**
2008	51	25	21	14	22	26
2009		57	41	24	32	39
2010			22	8	12	13
2013				5	5	5
2014					84	38
2015						13
Total	51	82	84	51	155	134

Table S6: Comparison of the call repertoire of killer whales in Vestmannaeyjar between 2002 and 2016 based on the Similarity Index (SI) and Whittaker Similarity Index (WSI) on the call type level. Boxes are color-coded based on repertoire similarity in increments of 0.25 with darker shades showing the highest values of similarity.

Index	Year	2002	2008	2009	2010	2013	2014	2015	2016
SI	2002	1							
	2008	0.32	1						
	2009	0.55	0.30	1					
	2010	0.69	0.44	0.54	1				
	2013	0.30	0.20	0.34	0.40	1			
	2014	0.76	0.29	0.51	0.68	0.33	1		
	2015	0.72	0.27	0.65	0.70	0.38	0.80	1	
	2016	0.82	0.25	0.63	0.67	0.29	0.81	0.85	1
WSI	2002	1							
	2008	0.40	1						
	2009	0.56	0.48	1					
	2010	0.60	0.42	0.47	1				
	2013	0.30	0.20	0.32	0.37	1			
	2014	0.72	0.50	0.65	0.55	0.31	1		
	2015	0.67	0.45	0.52	0.70	0.49	0.60	1	
	2016	0.79	0.45	0.58	0.64	0.33	0.70	0.68	1

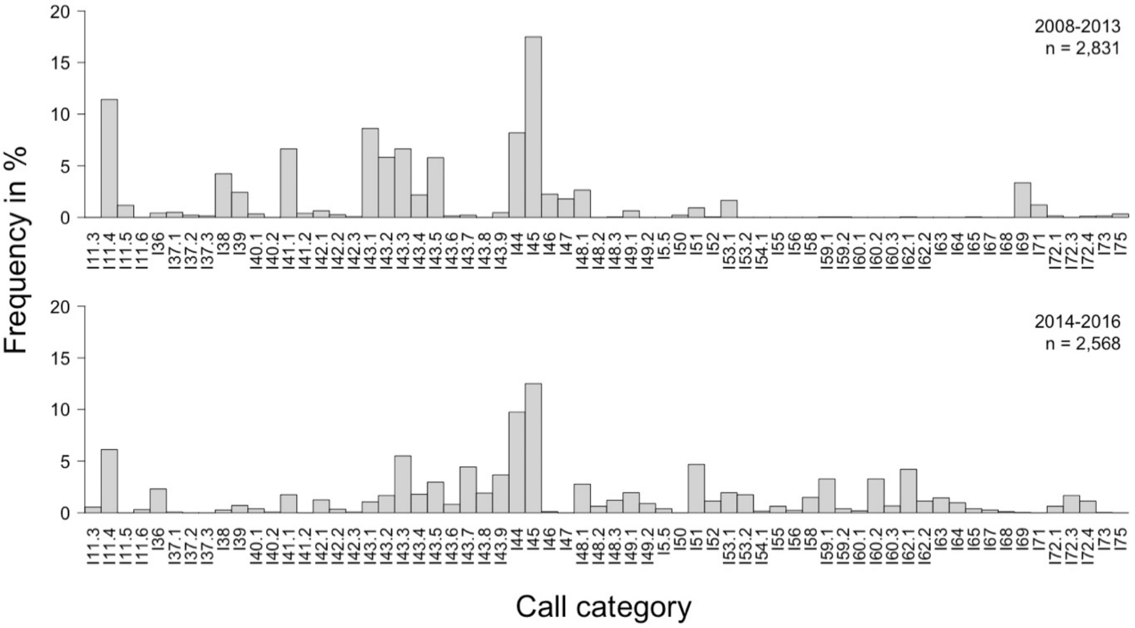


Figure S4: Relative frequency (%) of call categories recorded in Vestmannaeyjar. In total 64 call categories were recorded in Vestmannaeyjar, 55% (*n* = 35) were recorded in both time periods, 33% (*n* = 21) did not occur before 2014 and 13% (*n* = 8) not after 2014. There was no significant correlation in relative call category occurrence between the two time periods (Spearman's correlation: $r_s = 0.20$, $p = 0.12$).

Table S7: Summary of recordings obtained from Dtags in 2009, indicating the social cluster the tagged individual belonged to (based on Tavares et al., 2017), the number of high-quality calls classified from each tag, with the percentage that it represents in parentheses and how many call categories that included. All tags combined included 34 different call categories.

Tag	Cluster	n calls classified	n categories
194a	L	659 (25%)	14
200a	P	1566 (59%)	19
201a	Q	349 (13%)	14
209a	D	16 (1%)	2

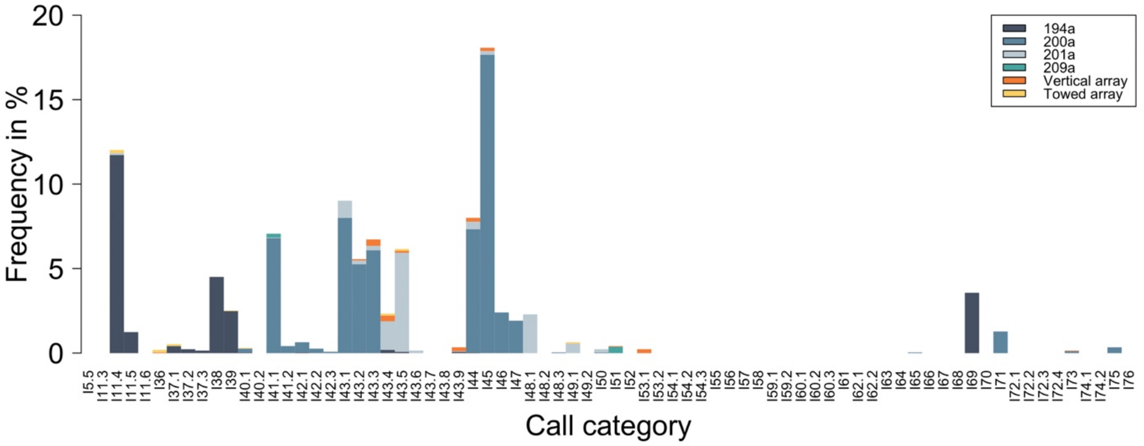


Figure S5: Relative frequency of occurrence (%) of killer whale call categories recorded in Vestmannaeyjar in 2009 from four different Dtags (194a, 200a, 201a, 209a) and other recording methods (vertical and towed array).

REFERENCES

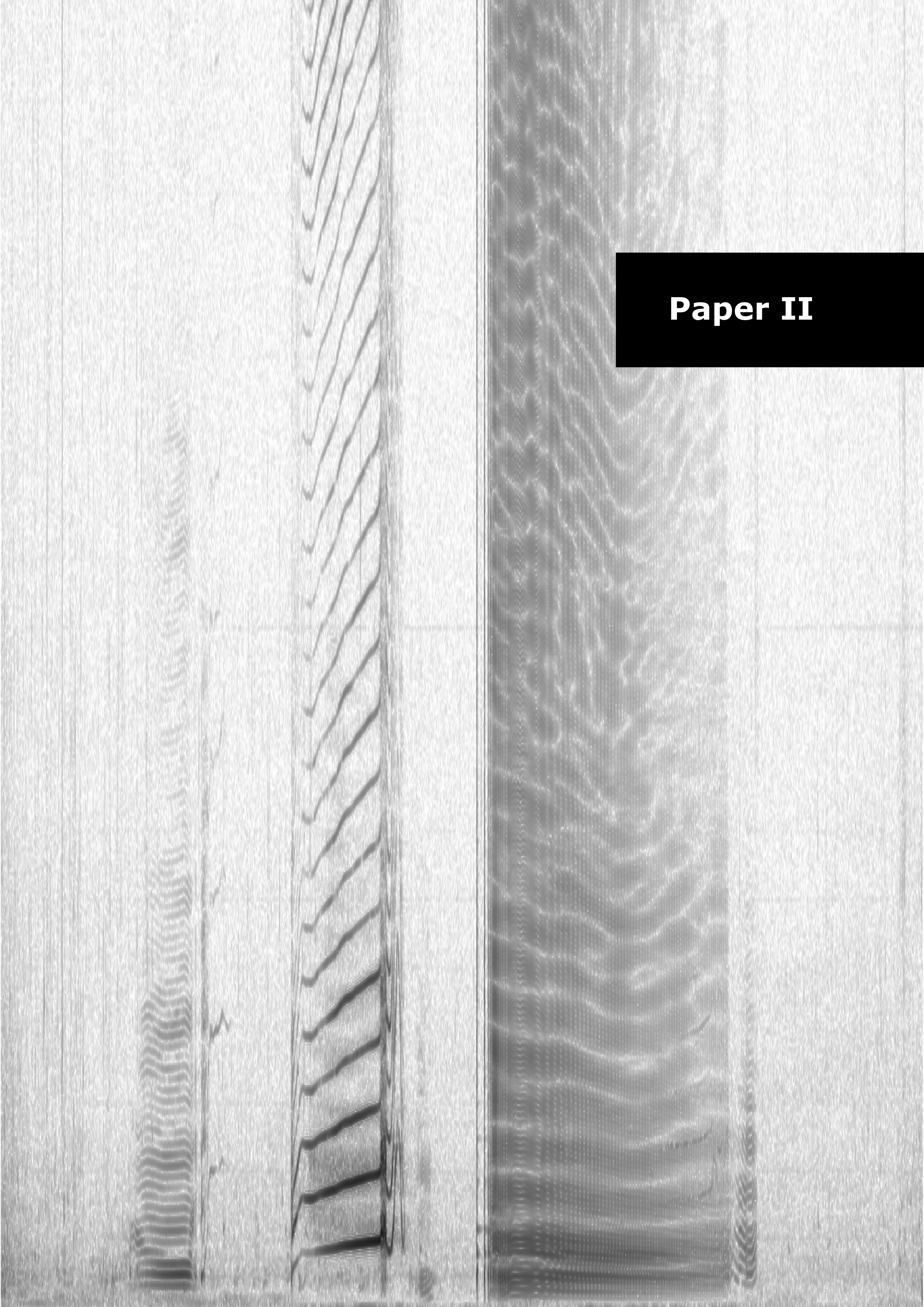
Moore, S. E., Francince, J. K., Bowles, A. E., & Ford, J. K. B. (1988). Analysis of calls of killer whales, *Orcinus orca*, from Iceland and Norway. Rit Fiskideildar, 11, 226–250.

Selbmann, A., Deecke, V. B., Fedutin, I. D., Filatova, O. A., Miller, P. J. O., Svavarsson, J., & Samarra, F. I. P. (2020). A comparison of Northeast Atlantic killer whale (*Orcinus orca*) stereotyped call repertoires. Marine Mammal Science, 37, 268-289. doi: 10.1111/mms.12750. doi:10.1111/mms.12750

Simon, M., Ugarte, F., Wahlberg, M., & Miller, L. E. E. A. (2006). Icelandic killer whales *Orcinus orca* use a pulsed call suitable for manipulating the schooling behaviour of herring *Clupea harengus*. Bioacoustics, 16, 57–74.

Tavares, S. B., Samarra, F. I. P., & Miller, P. J. O. (2017). A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. Behavioral Ecology, 28, 500–514. doi:10.1093/beheco/arw179

Paper II



Call combination patterns in Icelandic killer whales (*Orcinus orca*)

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Call combination patterns in Icelandic killer whales (*Orcinus orca*)

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Acoustic sequences have been described in a range of species and in varying complexity. Cetaceans are known to produce complex song displays but these are generally limited to mysticetes; little is known about call combinations in odontocetes. Here we investigate call combinations produced by killer whales (*Orcinus orca*), a highly social and vocal species. Using acoustic recordings from 22 multisensor tags, we use a first order Markov model to show that transitions between call types or subtypes were significantly different from random, with repetitions and specific call combinations occurring more often than expected by chance. The mixed call combinations were composed of two or three calls and were part of three call combination clusters. Call combinations were recorded over several years, from different individuals, and several social clusters. The most common call combination cluster consisted of six call (sub-)types. Although different combinations were generated, there were clear rules regarding which were the first and last call types produced, and combinations were highly stereotyped. Two of the three call combination clusters were produced outside of feeding contexts, but their function remains unclear and further research is required to determine possible functions and whether these combinations could be behaviour- or group-specific.

Communication is generally thought to consist of a signal produced by a sender that is received and interpreted by one or several receivers[1]. To encode a variety of messages, an animal can increase its repertoire by creating new signals, and repertoire size is thought to be one indicator of communicative complexity[2,3]. In acoustic communication, this mechanism is limited by the abilities of the sender to produce novel sounds and of the receiver to perceive and differentiate them. This limitation can be overcome by combining sounds from a smaller vocal repertoire into a sequence, which is likely to be more efficient and less prone to errors[4]. Thus, it is not surprising that vocal sequences have been reported for a variety of species from different taxa[5].

The simplest form of a vocal sequence is the repetition of the same signal, where either the number of repetitions or the length of the pause between signals can be of importance. For example, the number of repetitions encodes different contexts in pied babblers (*Turdoides bicolor*)[6] and alarm calling rates increase with urgency in several mammal species[7–9]. More complex vocal sequences can be made up of two or more different signals, with the number of different sounds, their order, or timing providing information[5]. Such mixed call combinations can range from simple combinations of two sounds to complex displays such as bird or whale song with multiple distinct units. Putty-nosed monkeys (*Cercopithecus nictitans*), for example, combine two alarm calls into sequences that elicit different responses from conspecifics depending on the order in which the calls are given[10,11]. In many bird species, on the other hand, it seems that the overall diversity of sounds rather than their specific order is of importance[12].

Cetaceans are known to produce complex song displays, but these appear to be generally limited to mysticete species, such as humpback (*Megaptera novaeangliae*) or bowhead whales (*Balaena mysticetus*)[13,14]. In the odontocetes, several species are known to produce repeated vocalisations[15–20]. The 'social complexity hypothesis' suggests that sociality requires high communicative complexity[2], which should promote call combinations. While socially complex lifestyles are common in this group[21], knowledge on mixed call combinations remains limited[22]. Bottlenose dolphins (*Tursiops truncatus*) produce non-random sequences of whistles[23,24] and so-called bray sequences, which are related to feeding[25–28]. Stereotyped vocal sequences have also been reported for northern right whale dolphins (*Lissodelphis borealis*)[29], striped dolphins (*Stenella coeruleoalba*)[30], long-finned pilot whales (*Globicephala melas*)[15], narwhals (*Monodon monoceros*)[31], and killer whales (*Orcinus orca*)[32–35].

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Killer whales produce stereotyped calls that are thought to be important group and population markers[32,36]. In some populations, dialects have been described, with more closely related individuals sharing larger parts of their repertoire, while in other populations calls seem to be shared more widely across social groups[32,37–40]. Calls are learned, rather than innate[41,42] and vocal repertoires are stable over long periods of time in many populations[32,43–45]. Most calls do not seem to be behaviour specific but the frequency with which they are used may vary with behavioural or social context[33,46–48].

Early studies on killer whale acoustic signals noted that certain calls are highly repetitive, but while some reported no clear structured sequences or patterns[49], others described calls being organised into themes, occurring in a specific order, comparable to humpback whale song[50]. In the following years, more extensive studies confirmed that killer whale calls tend to be given in repetition and that these repetitions can be given by the same individual or in exchange between individuals[18,33,34]. A few studies from the North Pacific also noted combinations of specific call types[32–34,37], such as call types N7 and N8 in the resident killer whales. N8 never occurred without being preceded by N7, but N7 was not always followed by N8[32,33]. In Norway, so-called compound calls were described, which consist of more than one discrete call type[51,52]. It has been suggested that calls in this population are assembled from smaller subunits[53], leading to the idea that combining calls might be a mechanism in the evolution of new signals[41]. However, considering its social complexity and how strongly social association patterns are reflected in their call repertoires, surprisingly little attention has been given to the way different call types may be combined in this species.

Here, we use data from animal-borne recording devices to investigate call combinations produced by Icelandic killer whales. We identified these sequences using strict criteria on call quality and timing, as well as a first order Markov model to quantify call transitions. Furthermore, we investigated which individuals or groups may emit call combinations and whether they are related to feeding contexts.

Results

A total of 22 multisensor tags were deployed (21 Dtags and one CATS tag) in five years between 2009 and 2022, resulting in 112 h and 48 min of acoustic recordings (Table 1). From these recordings 8,045 high-quality calls were extracted, of which 7058 calls (87.7%) were classified into 70 distinct call categories (call types or subtypes). The remainder of calls were considered variable and not included in the analysis. Using 5624 transitions, a bout criterion interval (BCI) of 1.72 s was estimated based on maximum likelihood estimation. Only transitions between calls that fell within 1.72 s of each other were considered in further analyses ($n = 2614$). They included 62 call categories, leading to 3,844 possible transitions between call categories but only 289 of these transitions were observed.

First-order Markov chain analysis indicated that transitions between call categories were significantly different from random ($\chi^2 = 38{,}331$, $p < 0.005$). Post-hoc analysis revealed 111 out of the 289 observed transitions that occurred significantly more often than expected. However, many of them ($n = 78$) occurred only a few times and to avoid influence of these small sample sizes, we illustrate only those that occurred more than 10 times ($n = 33$, Table 2). Many of these transitions were repetitions of the same call category but specific combinations of transitions across call categories were also observed. Transitions between call categories are illustrated in Fig. 1, showing that specific combinations of call categories were very common. Three distinct clusters of call combinations emerged from the post-hoc analysis, containing transitions that occurred more often than expected by chance. In total, 50.3% of transitions ($n = 1314/2614$) were part of these call combination clusters and 30.3% of transitions ($n = 791/2614$) were repetitions of the same call type or same subtype. Most notable was call combination cluster A ($n = 753$ transitions), consisting of six call categories (I38.1, I38.2, I39, I11.4, I69, I77) that occurred in different combinations of two or three call categories (Figs. 2 and 3, Supplementary Audio A1–A6). The two-call combinations started with I38.1 or I38.2 and mostly transitioned to I11.4 or I39 and I77, respectively. When extended to a three-call combination, the final call was always I69. These combinations were often repeated. The second cluster of calls, cluster B ($n = 298$ transitions), mostly contained two call categories (I63 and I72.3). Typically, I63 was followed by I72.3 and this combination was often repeated (Figs. 2 and 4, Supplementary Audio A7). The third cluster, cluster C ($n = 263$ transitions), contained three call categories that were closely linked to I45 (Figs. 2 and 5, Supplementary Audio A8–A10). The consistency in amplitude and the lack of overlap suggested that each call combination was produced by one individual.

These call combinations were recorded over several years, across tags on different individuals from different social clusters and from all age-sex classes (Table 1). No call combinations were recorded in 2013 and 2014, which is likely due to small sample sizes in these years (Table 1). Call combinations from clusters A and C were recorded in 2009, 2021 and 2022 and those from cluster B in 2021. Cluster A was recorded on ten tags that were deployed on two individuals without ID and eight different individuals from four social clusters. The combination of I63 and I72.3 (cluster B) was recorded on two tags, on different individuals, one of them from a known social cluster. Combinations of cluster C were recorded on six tags, on four identified individuals, and at least four social clusters.

The majority of call combinations (68.3%, $n = 2197/2614$ transitions) were produced outside of feeding contexts, i.e. > 5 min from a tail slap. However, this varied greatly between different call combination clusters. Call combinations of cluster C were commonly produced close to tail slaps (78.3%, $n = 206/263$), while combinations of cluster A (21.7%, $n = 163/753$) and cluster B (16.1%, $n = 48/298$) were less commonly produced close in time to tail slaps.

Year	Tag ID	Individual ID	Social cluster	Age-sex class	Sampling rate (kHz)	Recording duration (hh:mm)	No. of calls	No. of transitions	No. of tail slaps	Call combinations (n)
2009	oo09_194a	IS074	L	F	192	04:16	655	250	–	A (198)
	oo09_200a	–	–	–	192	06:28	1751	565	34	C (217)
	oo09_201a	IS071	Q	M	96	04:13	344	93	6	C (2)
	oo09_209a	IS049	D	F	192	01:33	17	6	–	–
2013	oo13_068a	–	–	–	240	00:39	64	7	–	–
	oo13_071a	IS165	B	M	240	01:57	14	–	1	–
	oo13_072a	IS405	L	O	240	02:05	166	26	7	–
2014	oo14_048a	IS011	–	M	192	05:14	28	6	–	–
2021	oo21_175a	IS042	–	M	240	16:06	220	49	1	A (41)
	oo21_182a	IS401	I	M	240	03:18	134	13	1	C (1)
	oo21_183a	IS389	C	J	240	09:46	1267	439	27	A (3) B (263) C (16)
	oo21_184a	IS064	G	F	240	03:17	683	198	–	A (99)
	oo21_186a	IS382	G	O	240	05:57	592	176	30	A (81) C (2)
	oo21_188a	-	–	J	240	00:11	24	8	–	–
	oo21_189a	IS406	L	F	240	01:47	93	22	1	–
	oo21_199a	IS118	L	M	240	01:39	182	40	34	A (7)
	oo21_202b	IS273	–	M	240	02:07	211	66	6	B (35)
2022	oo22_166a	–	–	–	240	04:38	336	92	7	A (69)
	oo22_170a	–	–	J	240	17:10	402	98	16	A(1) C (25)
	oo22_171a	IS266	N	M	240	06:30	472	228	2	A (187)
	oo22_195a*	IS251	–	M	96	10:56	377	146	18	A (67)
	oo22_228a	–	–	J	240	03:01	13	–	2	–
Total						112:48	8045	2528	193	

Table 1. Summary of recordings of Icelandic killer whales (*Orcinus orca*) analysed. Recordings were made using Dtags and a CATS Diary tag (*). Individual ID was based on photo-identification from an existing catalogue[54], and social cluster information was obtained from a previous study conducted on Icelandic killer whales[55]. Age-sex class is given as female (F), male (M), juvenile (J) or other (O) at the time of tagging. The number of calls and tail slaps only includes sounds that were rated as high quality. The number of transitions is the number of call transitions that were within the bout criterion interval. Call combinations refers to clusters of calls that included non-random transitions between specific call categories with the number of transitions in parentheses.

Discussion

This study shows that Icelandic killer whales rarely produce calls in a random order, instead repetitions and specific call transitions produced within seconds of each other are common. These call combinations were composed of call pairs or triplets and could be assigned to one of three call combination clusters. A total of 50% of the transitions included in the analysis were part of a call combination cluster. They were recorded across a range of tag deployments, over several years, on different individuals from several social clusters and from all age- and sex-classes, indicating that they might play an important role in the communication system of Icelandic killer whales.

A review of acoustic sequences in non-human animals[5], suggested six paradigms for encoding information in sequences: repetition, diversity, combination, ordering, overlapping, and timing. Our study indicates that at least two of these paradigms (repetition and ordering) are of importance in killer whales. Many call categories were most likely to be followed by themselves, adding to the evidence that repetition of calls is common in killer whales[18,33,34]. The mixed call combinations we describe here, appear to follow an ordering paradigm, where a set of units is combined, and their order is of importance (e.g., AB is different from BA). While all call categories that were part of the mixed call combinations were recorded within and outside of combinations, some (e.g., I38.1 and I69) were found only very rarely outside of combinations. Thus, they might operate like an extension or suffix to other call categories.

Similarly, previous studies on killer whale calls have reported strong associations between call types, with some call types never being produced without the other in the fish-eating resident and mammal-eating transient populations of the North Pacific[32,33,37]. However, it remains unclear whether these repeated and combined units encode information that is different from each individual unit. This can ultimately only be tested using playback experiments, for which a better understanding of the function of different killer whale call types would be essential.

	Following call category																							
Preceding call category	I11.4	I37.1	I38.1	I38.2	I39	I40.1	I41.1	I41.2	I42.1	I43.1	I43.2	I43.3	I43.5	I44	I45	I46	I51	I53.1	I59.1	I62.1	I63	I69	I72.3	I77
I11.4			■																			■		
I37.1		░																						
I38.1	■				■																			
I38.2																								■
I39																						■		
I40.1						░																		
I41.1							░	▓																
I41.2							▓																	
I42.1							▓																	
I43.1										░	▓													
I43.2															■									
I43.3												░												
I43.5													░											
I44															■									
I45											■			■	░	■								
I46															■									
I51																	░							
I53.1																		░						
I59.1																			░					
I62.1																				░				
I63																					░		■	
I69			■																					
I72.3									■												■		░	
I77																						■		

Table 2. Transitions between call categories of Icelandic killer whales (*Orcinus orca*) that occurred significantly more often than expected based on a Pearson's chi-square and consequent post-hoc testing ($p = 0.05$) and that were observed more than 10 times. Rows are the preceding call category and columns the subsequent call category. Repetitions of the same category in light grey, repetitions of the same call type but different subtypes in dark grey and other transitions marked black. The term 'call category' includes both, call types and subtypes (see Methods section).

A previous study showed that two lone males of the AT1 transient population in Alaska called in stereotyped patterns, with some three- and four-call sequences given more often than expected[34]. However, unlike in this study, the most common of these sequences were repetitions of the same call types and mixed call combinations made up only a small percentage of the total of calls recorded. In Norway, so-called compound calls were described from killer whales[51,52]. These were defined as multicomponent calls consisting of more than one discrete call. They were differentiated from other call types with multiple components in that all calls composing the compound call had to also be given individually as discrete calls or they had to be used in combinations with different discrete call types[51,52]. Most of these multicomponent calls were near continuous concatenations of sounds. The call combinations from Icelandic killer whales described here consist of individual sounds that were clearly separated by a period of silence shorter than the BCI of 1.72 s.

Most striking were call combinations derived from cluster A, which included six call categories that were given in sequences of two or three. The combinations were highly stereotyped and, although different combinations were generated, there were clear rules regarding which were the first and last call types used. This makes these combinations very conspicuous in acoustic recordings and they are even picked up on by novice listeners. Call combinations from this cluster were found in ten out of 22 tags, which were deployed over a 13-year period and placed on individuals from four social clusters, plus two individuals of unknown social clusters and two unknown individuals. While all these tags were deployed in Vestmannaeyjar (South Iceland), call combinations from cluster A were also noticed in other recordings, including from a moored hydrophone deployed in Breiðafjörður (West Iceland) in March 2014, as well as from single hydrophones and towed arrays in Vestmannaeyjar in July 2015 and 2016. This indicates that these call combinations are widely spread and commonly used.

The function of call combinations in Icelandic killer whales remains unclear. In other species, vocal sequences have been related to a variety of contexts, including predation[56], travelling[10,11,57], social[58] or feeding contexts[26,27,59,60]. Most individual killer whale calls do not seem to be behaviour specific[33,47], leading to the suggestion that it could be the combination of sounds rather than the individual calls that are of importance[46]. While call combinations comprised only part of the killer whale vocal production, they were produced in most tags, on individuals from different social clusters and all age- and sex-classes, as well as in most years sampled. In some tags call combinations composed a large part of the call production (Table 1), indicating that these combinations may be important during specific behaviours. Our results indicate that call combinations of cluster C may be related to feeding, but those of clusters A and B mostly occurred outside of feeding contexts. Icelandic killer whales are most vocal during feeding, followed by socialising, and almost silent when travelling[61]. The

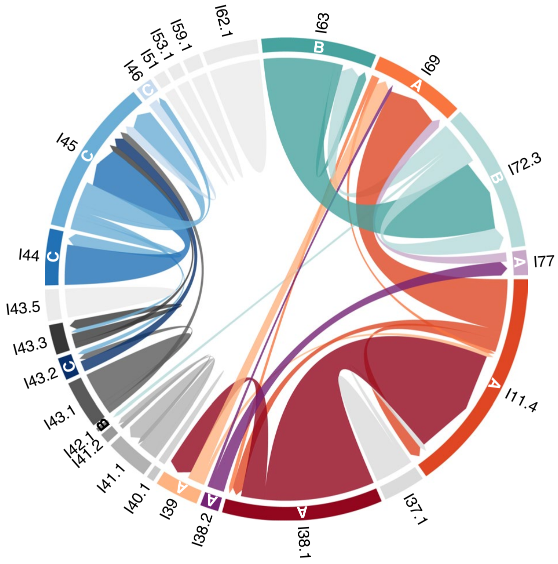

Figure 1. Chord diagram illustrating transitions between call categories of Icelandic killer whales (*Orcinus orca*). The width of each sector in the outer circle represents the sample size. The chords indicate transitions between call categories, with the arrow at the end indicating their direction, and their width reflecting the strength of the relation between call categories (which is proportional to the sample size). Transitions between different categories that occurred significantly more often than expected are highlighted in colours and indicated by letters A, B, and C. Red, orange and purple tones show call combinations of cluster A, turquoise denotes cluster B and blues denote cluster C (see Fig. 2). Other transitions and repetitions of the same call category in greyscale. Transitions that occurred < 10 times were removed for clarity.

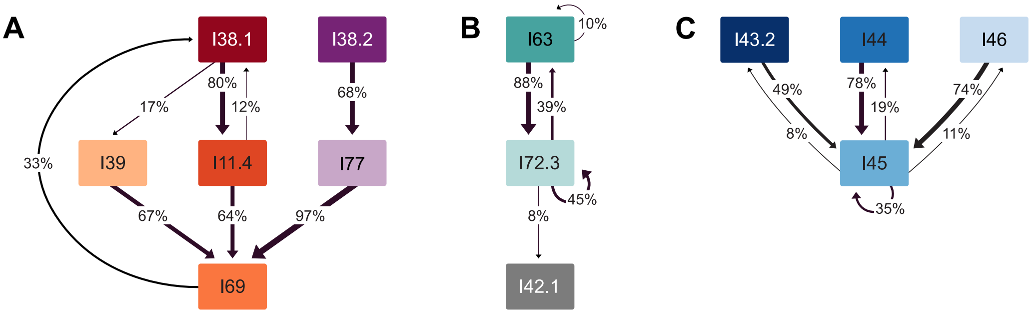

Figure 2. Transitions between different call categories of Icelandic killer whales (*Orcinus orca*). Transitions shown were indicated to be non-random by a Pearson's chi-square and consequent post-hoc test and occurred > 10 times. Each call category is indicated with a coloured rectangle and transitions are shown with arrows. The thickness and directions of arrows shown represent the probability of one call category being immediately followed by a second category. For example, I38.1 was followed by I11.4 and I39 in 80% and 17% of cases, respectively (and followed by other, not displayed call categories in the remaining 3% of cases). Three distinct clusters of calls were apparent: cluster A consisted of a combination of six different call categories that were given in combinations of two or three, cluster B was a combination of mostly two call categories with infrequent transitions to a third category, cluster C consisted of one call category (I45) that was mainly combined with three other categories.

social complexity hypothesis suggests that social contexts may place additional demands on the communication system, favouring the combination of calls[2]. Since call combinations of clusters A and B were common but occurred mostly outside of feeding contexts, they could indicate socialising. However, we only provide a basic and preliminary investigation into behavioural context based on the acoustic record of the tags and only distinguish feeding and non-feeding contexts. Detailed studies using the other tag sensor data (e.g. accelerometer, magnetometer, depth, video), that were outside the scope of this study, could provide more comprehensive information on this topic in the future.

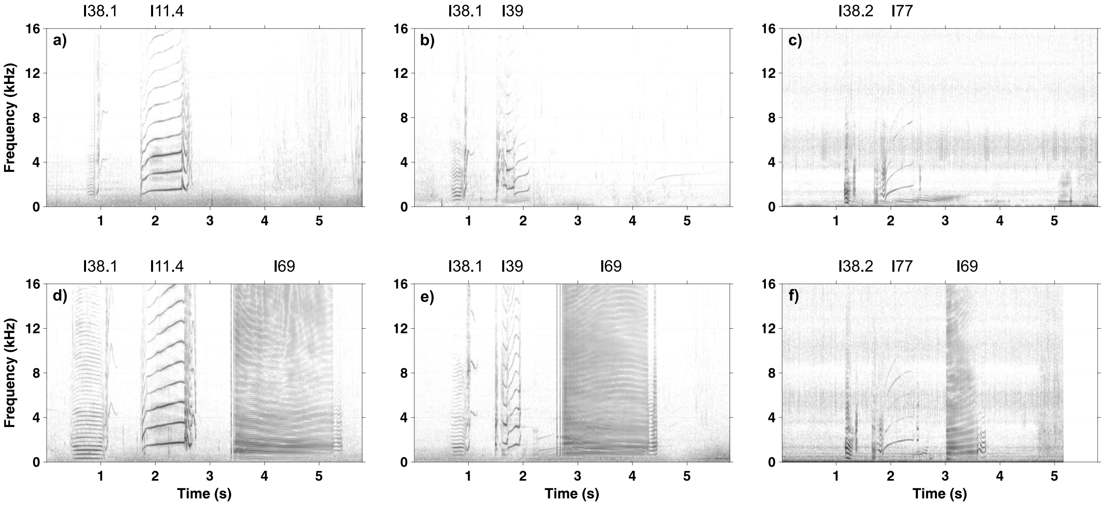

Figure 3. Example spectrograms of call combinations from cluster A recorded from Icelandic killer whales (*Orcinus orca*). Spectrograms (**a**–**c**) show two-call combinations of I38.1 with I11.4, I38.1 with I39, and I38.2 with I77. Spectrograms (**d**–**f**) show three-call combinations with I69 added to each. Recordings sampled at 96 and 192 kHz. Spectrogram parameters: Hann window; 87.5% overlap; FFT size: 4,096; frequency resolution: 23.44 Hz and 46.88 Hz; time resolution: 5.33 ms and 2.67 ms. Corresponding sound files available in Supplementary Audio A1–A6.

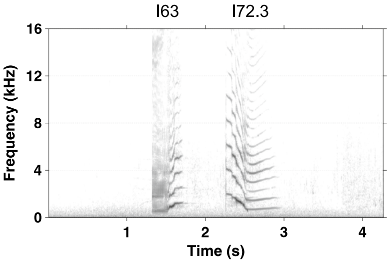

Figure 4. Example spectrogram of the most common call combination from cluster B recorded from Icelandic killer whales (*Orcinus orca*). The combination was of I63 and I72.3 and was often repeated. Recording sampled at 240 kHz. Spectrogram parameters: Hann window; 87.5% overlap; FFT size: 4,096; frequency resolution: 58.62 Hz; time resolution: 2.13 ms. Corresponding sound file available in Supplementary Audio A7.

Previous studies on killer whale and narwhal vocal sequences suggested that they may play a role in long-distance communication with other group members[31,34]. Recent work on killer whale sounds shows that as ambient noise levels increase, high frequency components of killer whale calls and buzzes with energy peaks in higher frequencies may be detectable over longer distances[62]. While none of the call categories in the described combinations contained a second, high frequency component, all combinations contained calls with buzz components. In particular, I69 (call combination cluster A) is a long, buzz-like call. Such a sound should transmit over long distances and contains frequencies that lie within the best hearing range of killer whales[62]. The spectrograms presented in the study[62] also indicate that while individual calls might be rendered unrecognisable with distance or increasing noise, the structure of a sequence of calls could be retained and contribute to detectability over long distances. Therefore, call combinations and in particular those of cluster A could be used in long distance communication but further study, e.g. on source levels, would be required to determine their function.

Another possibility is that call combinations serve as identifiers of different individuals or social groups, as has been suggested for long-finned pilot whales[20]. Icelandic killer whales live in a fission–fusion society, where associations between individuals are non-random and some strong social bonds exist, allowing for a grouping of individuals into social clusters[55]. Due to the strict quality criteria applied in this study, we consider it likely that the calls described herein were either produced by the tagged whale itself or another individual in very close proximity, which would likely belong to the same social cluster. While it is unclear whether Icelandic killer whales have group-specific repertoires, there is variation in the repertoire with location[44] and differences in call combination patterns between social clusters would further support the idea of some differentiation in calling behaviour between groups. While none of the call combination clusters appeared to be exclusive to a

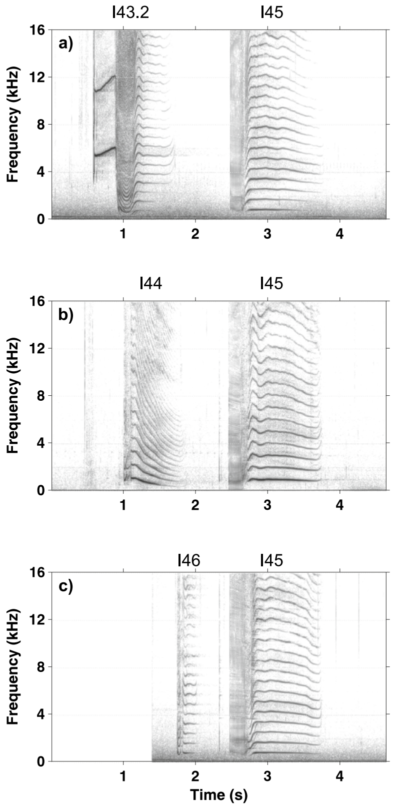

Figure 5. Example spectrograms of the most common call combinations from cluster C recorded from Icelandic killer whales (*Orcinus orca*). In all examples I45 is the second call. It is preceded by (**a**) I43.2, (**b**) I44 and (**c**) I46. Recordings sampled at 192 kHz. Spectrogram parameters: Hann window; 87.5% overlap; FFT size: 4096; frequency resolution: 46.88 Hz; time resolution: 2.67 ms. Corresponding sound files available in Supplementary Audio A8–A10.

single social cluster, several social clusters only produced one of the three call combination clusters. Thus, we have little evidence of whether or not call combinations could be group specific. So far, we only covered nine of the 18 described social clusters[55] and further group-specific recordings are required to clarify whether call combinations could be group markers.

This study provides a first detailed description of call combination patterns, not likely to occur by chance, produced by Icelandic killer whales. Some of these sequence patterns are, at least in part, similar to what has been described from other populations, but lack of consistency in methodology and definitions used hinders further comparisons. A cross-population comparison of call combinations using a unified approach could be highly informative for the study of killer whale acoustic behaviour and call evolution. Furthermore, linking the detected call combinations to specific behaviours could provide information on the function of these combinations which would be beneficial e.g., for the interpretation of long-term passive acoustics data. For the Icelandic population in particular, group-specific recordings and further investigation of their social structure is required to better understand the usage of call combinations.

Methods

Data collection

Data were collected in 2009 and 2021–2022 in Vestmannaeyjar, South Iceland, and in 2013–2014 in Breiðafjörður, West Iceland. These locations are herring spawning and overwintering grounds, respectively, and killer whales are known to gather there in large numbers during summer or winter/spring to feed on herring[63]. Digital acoustic recording tags (Dtags, flat frequency response: 0.6–45 kHz)[64] and a Customized Animal Tracking Solutions (CATS; www.cats.is) Diary tag with an integrated hydrophone (HTI-96-Min; flat frequency response up to 30 kHz) were attached to killer whales using a carbon fibre pole or pneumatic tag launcher (ARTS)[65]. Tags attached to the body of the whale with suction cups. During some tag deployments, animals were subject to playback experiments. Only data prior to the start of sound transmission were used from those deployments.

Acoustic analysis

Acoustic recordings from the tags deployed in 2013–2022 were inspected using spectrograms (Hann window, NFFT = 8,192) in the software Audacity version 2.3.1 (www.audacityteam.org). For the tags deployed in 2009, the software Adobe Audition 2.0 (Adobe Systems Inc., San Jose CA) was used to generate the spectrograms (Blackmann-Harris window, FFT = 2048 or 4096, for 96 and 192 kHz sampling rates, respectively). Calls were given a quality rating of high, medium, or low based on the perceived signal to noise ratio (SNR) and overlap with other sounds. Only high-quality calls were extracted. These calls were clearly visible and audible, showed several sidebands, and had little or no overlap with other sounds. The SNR was measured whenever possible using a custom routine in MATLAB version 9.14.0 (R2023a, www.mathworks.com). The routine compared the sound pressure level of the call to that of a 200 ms segment of ambient noise (without any calls or other transients) within a few seconds before the call. The sound pressure level of the call was based on its 90% sound energy duration. Recordings were filtered using a 3rd-order Butterworth bandpass filter with cut-off frequencies of 450 Hz and 10 kHz to retain the dominant frequency range of Icelandic killer whale calls[66]. Generally, only calls with a SNR higher than 10 dB were used in further analyses. However, in a few cases (n = 235, 3%) flow or boat noise around and below 1 kHz appeared to influence the SNR measurements while contours of the call were clearly visible at higher frequencies. These calls were included despite a SNR below 10 dB. Calls from 2009 to 2014 were previously classified to call type and subtype and included in a call catalogue for Icelandic killer whales[44,67]. This classification was validated using classification and regression tree (CART) and random forest analyses, as well as an interobserver test with 11 observers[44]. Calls from 2021–2022 were classified by AS following the same protocol as used in the call catalogue[44]. We use the term 'call category' to include both, call types and subtypes. New call categories were created whenever appropriate, following the same protocol. Variable calls that did not appear to be stereotyped were marked as 'unknown'.

Sequence analysis

Preliminary inspection of the recordings showed that possible combinations of calls occurred with relatively short silent gaps of around 0.5–1.0 s. Like many other behaviours, calling occurs in bouts and a bout criterion interval (BCI) can be determined to separate behaviours within and between bouts. The BCI can be identified based on the gap between behaviours, where the distributions of gaps are considered to be a combination of two or more Poisson processes that separate behaviours within bouts (fast process) from behaviours between bouts (slow process)[68]. In acoustic behaviours, the behavioural gap is the silent interval between sounds, which was calculated by subtracting the end time of a call from the start time of the following call. The BCI was determined based on maximum likelihood estimation[69,70], using the fitMLEbouts function of the DiveMove package[71] in R version 4.1.2 (www.R-project.org). Based on exploratory analysis, only pauses less than 30 s were included to reduce potential bias introduced by a few very long pauses.

Transitions between call categories that were within the BCI were analysed using a first-order Markov model. Expected and observed transition matrices were compared using a Pearson's chi-squared test to test the null hypothesis that transitions were random. As several of the expected occurrences of transitions were low, a Monte Carlo simulation with 2000 replicates was applied to calculate the p-values (stats package in R). A post-hoc test for pairwise comparisons was run using the 'chisq.posthoc.test' package[72] with a Bonferroni correction for multiple testing. Multiple category sequences were specified to have occurred when all first-order transitions in the sequence were found to be significantly unlikely due to chance, in the post-hoc analysis.

Individual identification and behavioural context

Photographs for identification of individual whales were taken during tagging and/or when the tag was on the whale. Individuals were identified from the shape and size of the dorsal fin, the saddle patch, and nicks and scars present on the body[73], and their photographs were matched to an existing photo-identification catalogue[54]. Age- and sex-class were assigned either based on body size and the shape and size of the dorsal fin, or based on genetic sexing. Males were defined as adult or sub-adult individuals with a distinctly taller dorsal fin, females as mature in size and consistently seen with a calf in echelon position, and juveniles as more than one year of age but not mature-sized. Other mature-sized individuals without clear sex determination were marked as 'other'[63]. Social cluster information was obtained from a previous study on social structure in Icelandic killer whales[55].

Acoustic records of the tags were inspected to investigate whether call combinations were related to feeding contexts. Killer whales feeding on herring employ a carousel feeding strategy, in which they use tail slaps to debilitate herring[74]. The tail slaps are clearly audible in nearby acoustic recordings[75]. The acoustic record of each tag was inspected for tail slaps and each was given a quality rating of high, medium, or low. Only high-quality tail slaps were included in the analysis to ensure that the tail slaps were produced either by the tagged whale or an individual in close proximity. Call combinations occurring within five minutes of a tail slap were considered to be produced in a feeding context, as this time interval captured feeding contexts well in previous studies[76].

Data availability

Data used in this study (comprising a list of calls used in this study, their start/end times, pauses between calls, and signal to noise ratio) is available in the Supplementary Information.

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References

1. Bradbury, J. W. & Vehrenkamp, S. L. *Principles of Animal Communication* (Sinauer Associates Inc, 2011).

2. Freeberg, T. M., Dunbar, R. I. M. & Ord, T. J. Social complexity as a proximate and ultimate factor in communicative complexity. *Philos. Trans. R. Soc. B: Biol. Sci.* **367**, 1785–1801 (2012).
3. Griebel, U. & Oller, D. K. Evolutionary forces favoring communicative flexibility. In *Evolution of Communicative Flexibility: Complexity, Creativity, and Adaptability in Human and Animal Communication* (MIT Press, 2008).
4. Nowak, M. A., Krakauer, D. C. & Dress, A. An error limit for the evolution of language. *Proc. R. Soc. Lond. B* **266**, 2131–2136 (1999).
5. Kershenbaum, A. *et al.* Acoustic sequences in non-human animals: A tutorial review and prospectus. *Biol. Rev.* **91**, 13–52 (2016).
6. Engesser, S., Ridley, A. R. & Townsend, S. W. Element repetition rates encode functionally distinct information in pied babbler 'clucks' and 'purrs'. *Anim. Cogn.* **20**, 953–960 (2017).
7. Blumstein, D. T. & Armitage, K. B. Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. *Anim. Behav.* **53**, 143–171 (1997).
8. Lemasson, A., Ouattara, K., Bouchet, H. & Zuberbühler, K. Speed of call delivery is related to context and caller identity in Campbell's monkey males. *Naturwissenschaften* **97**, 1023–1027 (2010).
9. Manser, M. B. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proc. R. Soc. B: Biol. Sci.* **268**, 2315–2324 (2001).
10. Arnold, K. & Zuberbühler, K. The alarm-calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini*. *Anim. Behav.* **72**, 643–653 (2006).
11. Arnold, K. & Zuberbühler, K. Meaningful call combinations in a non-human primate. *Curr. Biol.* **18**, 202–203 (2008).
12. Catchpole, C. & Slater, P. J. B. *Bird Song: Biological Themes and Variations* (Cambridge University Press, 2008).
13. Payne, R. S. & McVay, S. Songs of humpback whales. *Science* **173**, 585–597 (1971).
14. Stafford, K. M. *et al.* Spitsbergen's endangered bowhead whales sing: Through the polar night. *Endang. Species Res.* **18**, 95–103 (2012).
15. Courts, R. *et al.* Australian long-finned pilot whales (*Globicephala melas*) emit stereotypical, variable, biphonic, multi-component, and sequenced vocalisations, similar to those recorded in the northern hemisphere. *Sci. Rep.* **10**, 1–14 (2020).
16. Herzing, D. Synchronous and rhythmic vocalizations and correlated underwater behavior of free-ranging atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas. *Anim. Behav. Cogn.* **2**, 14–29 (2015).
17. Kaplan, M. B., Aran-Mooney, T., Sayigh, L. S. & Baird, R. W. Repeated call types in Hawaiian melon-headed whales (*Peponocephala electra*). *J. Acoust. Soc. Am.* **136**, 1394–1401 (2014).
18. Miller, P. J. O., Shapiro, A. D., Tyack, P. L. & Solow, A. R. Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*. *Anim. Behav.* **67**, 1099–1107 (2004).
19. Sayigh, L., Quick, N., Hastie, G. & Tyack, P. Repeated call types in short-finned pilot whales, *Globicephala macrorhynchus*. *Mar. Mammal Sci.* **29**, 312–324 (2013).
20. Zwamborn, E. M. J. & Whitehead, H. Repeated call sequences and behavioural context in long-finned pilot whales off Cape Breton, Nova Scotia, Canada. *Bioacoustics* **26**, 69–183 (2017).
21. Gowans, S. Grouping behaviors of dolphins and other toothed whales. In *Ethology and Behavioral Ecology of Odontocetes* (ed. Würsig, B.) 3–24 (Springer International Publishing, 2019).
22. Janik, V. M. Acoustic communication in Delphinids. In *Vocal Communication in Birds and Mammals* (Academic Press, 2009).
23. Ferrer-i-Cancho, R. & McCowan, B. The span of correlations in dolphin whistle sequences. *J. Stat. Mech. Theory Exp.* **2012**, 6002. https://doi.org/10.1088/1742-5468/2012/06/P06002 (2012).
24. McCowan, B., Hanser, S. F. & Doyle, L. R. Quantitative tools for comparing animal communication systems: Information theory applied to bottlenose dolphin whistle repertoires. *Anim. Behav.* **57**, 409–419 (1999).
25. dos Santos, M. E., Ferreira, A. J. & Harzen, S. Rythmic sound sequences emitted by aroused bottlenose dolphins in the Sado estuary, Portugal. In *Sensory Systems of Aquatic Mammals* (eds. Kastelein, R. A. *et al.*) 325–334 (De Spil Publishers, 1995).
26. Janik, V. M. Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). *Proc. R. Soc. B: Biol. Sci.* **267**, 923–927 (2000).
27. Luís, A. R., Alves, I. S., Sobreira, F. V., Couchinho, M. N. & dos Santos, M. E. Brays and bits: Information theory applied to acoustic communication sequences of bottlenose dolphins. *Bioacoustics* **28**, 286–296 (2019).
28. Pace, D. S. *et al.* Bray-call sequences in the Mediterranean common bottlenose dolphin (*Tursiops truncatus*) acoustic repertoire. *Biology* **11**, 367 (2022).
29. Rankin, S., Oswald, J., Barlow, J. & Lammers, M. Patterned burst-pulse vocalizations of the northern right whale dolphin, *Lissodelphis borealis*. *J. Acoust. Soc. Am.* **121**, 1213–1218 (2007).
30. Papale, E. *et al.* The social role of vocal complexity in striped dolphins. *Front. Mar. Sci.* **7**, 103. https://doi.org/10.3389/fmars.2020.584301 (2020).
31. Walmsley, S. F., Rendell, L., Hussey, N. E. & Marcoux, M. Vocal sequences in narwhals (*Monodon monoceros*). *J. Acoust. Soc. Am.* **147**, 1078–1091 (2020).
32. Ford, J. K. B. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Can. J. Zool.* **69**, 1454–1483 (1991).
33. Ford, J. K. B. Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Can. J. Zool.* **67**, 727–745 (1989).
34. Saulitis, E. L., Matkin, C. O. & Fay, F. H. Vocal repertoire and acoustic behavior of the isolated AT1 killer whale subpopulation in southern Alaska. *Can. J. Zool.* **83**, 1015–1029 (2005).
35. Riesch, R., Ford, J. K. B. & Thomsen, F. Whistle sequences in wild killer whales (*Orcinus orca*). *J. Acoust. Soc. Am.* **124**, 1822–1829. https://doi.org/10.1121/1.2956467 (2008).
36. Filatova, O. A. *et al.* Call diversity in the North Pacific killer whale populations: Implications for dialect evolution and population history. *Anim. Behav.* **83**, 595–603 (2012).
37. Deecke, V. B. The vocal behaviour of transient killer whales (*Orcinus orca*): Communicating with costly calls. *PhD Thesis* (University of St. Andrews, 2003).
38. Deecke, V. B., Barrett-Lennard, L. G., Spong, P. & Ford, J. K. B. The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (*Orcinus orca*). *Naturwissenschaften* **97**, 513–518 (2010).
39. Sharpe, D. L., Castellote, M., Wade, P. R. & Cornick, L. A. Call types of Bigg's killer whales (*Orcinus orca*) in western Alaska: Using vocal dialects to assess population structure. *Bioacoustics* **28**, 74–99 (2019).
40. Yurk, H., Barrett-Lennard, L., Ford, J. K. B. & Matkin, C. O. Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska. *Anim. Behav.* **63**, 1103–1119 (2002).
41. Filatova, O. A. *et al.* Cultural evolution of killer whale calls: Background, mechanisms and consequences. *Behaviour* **152**, 2001–2038 (2015).
42. Foote, A. D. *et al.* Killer whales are capable of vocal learning. *Biol. Lett.* **2**, 509–512 (2006).
43. Foote, A. D., Osborne, R. W. & Hoelzel, A. R. Temporal and contextual patterns of killer whale (*Orcinus orca*) call type production. *Ethology* **114**, 599–606 (2008).
44. Selbmann, A. *et al.* Call type repertoire of killer whales (*Orcinus orca*) in Iceland and its variation across regions. *Mar. Mammal Sci.* **39**, 1136–1160 (2023).
45. Wellard, R., Pitman, R. L., Durban, J. & Erbe, C. Cold call: The acoustic repertoire of Ross Sea killer whales (*Orcinus orca*, Type C) in McMurdo Sound Antarctica. *R. Soc. Open Sci.* **7**, 191228 (2020).

46. Filatova, O. A., Fedutin, I. D., Nagaylik, M. M., Burdin, A. M. & Hoyt, E. Usage of monophonic and biphonic calls by free-ranging resident killer whales (*Orcinus orca*) in Kamchatka, Russian Far East. *Acta Ethol.* **12**, 37–44 (2009).
47. Filatova, O. A., Guzeev, M. A., Fedutin, I. D., Burdin, A. M. & Hoyt, E. Dependence of killer whale (*Orcinus orca*) acoustic signals on the type of activity and social context. *Biol. Bull.* **40**, 790–796 (2013).
48. Weiß, B. M., Symonds, H., Spong, P. & Ladich, F. Intra- and intergroup vocal behavior in resident killer whales, *Orcinus orca*. *J. Acoust. Soc. Am.* **122**, 3710–3716 (2007).
49. Ford, J. K. B. & Fisher, D. H. Killer whale (*Orcinus orca*) dialects as an indicator of stocks in British Columbia. *Rep. Int. Whaling Commiss.* **32**, 671–679 (1982).
50. Bain, D. E. Acoustic behavior of Orcinus: Sequences, periodicity, behavioral correlates and an autmoated technique for call classification. In *Behavioural biology of killer whales* (eds. Kirkevold, B. C. & Lockard, J. S.) 335–371 (Alan R. Liss, 1986).
51. Strager, H. Catalogue of underwater calls from killer whales (*Orcinus orca*) in northern Norway. *MSc Thesis* (University of Aarhus, 1993).
52. Strager, H. Pod-specific call repertoires and compound calls of killer whales, *Orcinus orca* Linnaeus, 1758, in the waters of northern Norway. *Can. J. Zool.* **73**, 1037–1047 (1995).
53. Shapiro, A. D., Tyack, P. L. & Seneff, S. Comparing call-based versus subunit-based methods for categorizing Norwegian killer whale, *Orcinus orca*, vocalizations. *Anim. Behav.* **81**, 377–386 (2011).
54. Samarra, F. I. P., Tavares, S. B., Miller, P. J. O. & Víkingsson, G. A. Killer whales of Iceland 2016–2015. In *Report to the Marine and Freshwater Research Institute* 78 (2017).
55. Tavares, S. B., Samarra, F. I. P. & Miller, P. J. O. A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. *Behav. Ecol.* **28**, 500–514 (2017).
56. Zuberbühler, K. Chapter 8 survivor signals. The biology and psychology of animal alarm calling. *Adv. Study Behav.* **40**, 277–322 (2009).
57. Crockford, C. & Boesch, C. Call combinations in wild chimpanzees. *Behaviour* **142**, 397–421 (2005).
58. Collier, K., Townsend, S. W. & Manser, M. B. Call concatenation in wild meerkats. *Anim. Behav.* **134**, 257–269 (2017).
59. Clay, Z. & Zuberbühler, K. Food-associated calling sequences in bonobos. *Anim. Behav.* **77**, 1387–1396 (2009).
60. Clay, Z. & Zuberbühler, K. Bonobos extract meaning from call sequences. *PLoS ONE* **6**, 4. https://doi.org/10.1371/journal.pone.0018786 (2011).
61. Simon, M., McGregor, P. K. & Ugarte, F. The relationship between the acoustic behaviour and surface activity of killer whales (*Orcinus orca*) that feed on herring (*Clupea harengus*). *Acta Ethol.* **10**, 47–53 (2007).
62. Yurk, H. *et al.* Adaptive call design to escape masking while preserving complex social functions of calls in killer whales. In *The Effects of Noise on Aquatic Life* (eds. Popper, A. N. *et al.*) 1–15 (Springer International Publishing, 2023). https://doi.org/10.1007/978-3-031-10417-6_187-1.
63. Samarra, F. I. P. *et al.* Movements and site fidelity of killer whales (*Orcinus orca*) relative to seasonal and long-term shifts in herring (*Clupea harengus*) distribution. *Mar. Biol.* **164**, 159 (2017).
64. Johnson, M. P. & Tyack, P. L. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J. Ocean. Eng.* **28**, 3–12 (2003).
65. Kleivane, L., Kvadsheim, P. H., Bocconcelli, A., Øien, N. & Miller, P. J. O. Equipment to tag, track and collect biopsies from whales and dolphins: The ARTS, DFHorten and LKDart systems. *Anim. Biotelem.* **10**, 32 (2022).
66. Filatova, O. A. *et al.* Killer whale call frequency is similar across the oceans, but varies across sympatric ecotypes. *J. Acoust. Soc. Am.* **138**, 251–257 (2015).
67. Selbmann, A. *et al.* A catalogue of pulsed calls produced by killer whales (*Orcinus orca*) in Iceland 2008-2016. In *Report of the Marine and Freshwater Research Institute HV 2019-23* 93 (2019).
68. Sibly, R. M., Nott, H. M. R. & Fletchert, D. J. Splitting behaviour into bouts. *Anim. Behav.* **39**, 63–69 (1990).
69. Langton, S. D., Collett, D. & Sibly, R. M. Splitting behaviour into Bouts, a maximum likelihood approach. *Behaviour* **132**, 781–799 (1995).
70. Luque, S. P. & Guinet, C. A maximum likelihood approach for identifying Dive Bouts improves accuracy precision and objectivity. *Behaviour* **144**, 1315–1332 (2007).
71. Luque, S. P. Diving behaviour analysis in R. *R News* **7**, 8–14 (2007).
72. Ebbert, D. chisq.posthoc.test: A Post Hoc Analysis for Pearson's Chi-Squared Test for Count Data (2019).
73. Bigg, M. An Assessment of Killer Whale (*Orcinus orca*) Stocks off Vancouver Island, British Columbia. *Rep. Int. Whaling Commiss.* **32**, 655–666 (1982).
74. Similä, T. & Ugarte, F. Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Can. J. Zool.* **71**, 1494–1499 (1993).
75. Simon, M., Wahlberg, M., Ugarte, F. & Miller, L. A. Acoustic characteristics of underwater tail slaps used by Norwegian and Icelandic killer whales (*Orcinus orca*) to debilitate herring (*Clupea harengus*). *J. Exp. Biol.* **208**, 2459–2466 (2005).
76. Samarra, F. I. P. & Miller, P. J. O. Prey-induced behavioural plasticity of herring-eating killer whales. *Mar. Biol.* **162**, 809–821 (2015).

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Author contributions

A.S. conceptualized the study and prepared the manuscript under the supervision of F.I.P.S., P.J.W., and J.S. Data collection was organized, and funding provided by P.J.O.M., F.I.P.S., P.J.W. and J.S. Data were analyzed by A.S. and F.I.P.S. All authors reviewed, edited, and provided feedback on the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to A.S.

Supplementary material

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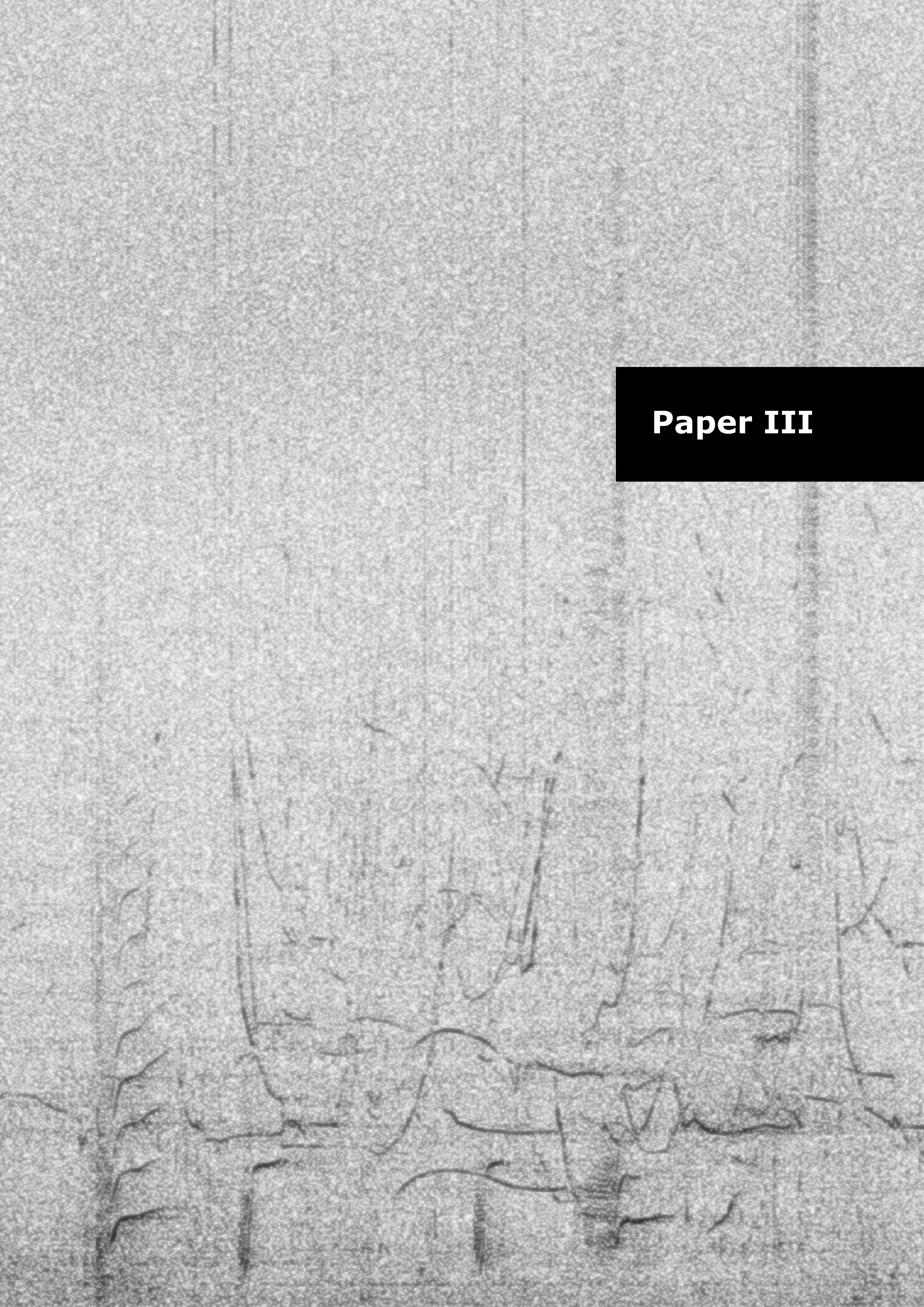
Data used in this study (comprising a list of calls used in this study, their start/end times, pauses between calls, and signal to noise ratio).

Audio examples for each call combination.

Paper III



Occurrence of long-finned pilot whales (*Globicephala melas*) and killer whales (*Orcinus orca*) in Icelandic coastal waters and their interspecific interactions

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ORIGINAL PAPER

Occurrence of long-finned pilot whales (*Globicephala melas*) and killer whales (*Orcinus orca*) in Icelandic coastal waters and their interspecific interactions

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Abstract

Long-finned pilot whales and killer whales are widely distributed across the North Atlantic, but few studies have reported their occurrence in Icelandic coastal waters. Here, we use sightings data from research platforms and whale watching tours in six regions of Iceland from 2007 to 2020 to show that the occurrence of long-finned pilot and killer whales varied with region and season. Killer whales were regularly encountered in the south of Iceland during summer and west of Iceland during winter/spring. Long-finned pilot whales were only seen during the summer and were most often encountered in the south, west, and northwest of Iceland. Long-finned pilot whale occurrence in the south of Iceland appeared to increase during the study period but killer whale occurrence showed no noticeable changes. Long-finned pilot whales were sighted often in the areas that were also frequented by killer whales and interspecific interactions were commonly observed when both species co-occurred. Interactions appeared to be antagonistic, with killer whales often avoiding long-finned pilot whales and sometimes fleeing at high speed, similar to what has been described elsewhere in the North Atlantic. In the majority of interactions observed (68%), killer whales avoided long-finned pilot whales by moving away, but in 28% avoidance was at high speed with both species porpoising. This variability in the type of behavioural responses indicates that interactions may be more complex than previously described. We discuss regional trends in long-finned pilot whale and killer whale sightings and potential drivers of the observed interactions.

Keywords Interspecific interactions · Antagonism · Distribution shifts · Opportunistic data

Introduction

Pilot whales and killer whales are widely distributed in the world's oceans (Ford 2018; Olson 2018), and in the case of pilot whales, two different species are recognised, which have only some areas where occurrence overlaps: the short-finned (*Globicephala macrorhynchus*) and long-finned pilot whale (*Globicephala melas*). The first has a pantropical and pan-temperate distribution, whereas the latter is found in cold temperate to sub-polar waters of the North Atlantic and the Southern hemisphere. The long-finned pilot whale (hereafter, pilot whale) has two recognised extant subspecies separated by a wide tropical belt: *G. m. melas* and *G. m. edwardii* (Olson 2018). Pilot whales overlap with killer whales in their geographical range in the North Atlantic and Southern Ocean (Ford 2018; Olson 2018); however, the two species appear to have different habitat preferences. Killer whales

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more commonly occur in shallow coastal waters, while pilot whales prefer deep-water habitats on the continental shelf break and slopes but often move seasonally between coastal and offshore waters (Ford 2018; Olson 2018).

In the Northeast Atlantic, line-transect surveys conducted in the summer since 1987 indicate a widespread offshore distribution of pilot whales (Buckland et al. 1993; Pike et al. 2019). Around Iceland, high occurrence is reported in the southwest and along the continental shelf edge in the south, but not in the north and northeast (Buckland et al. 1993; Pike et al. 2019). However, the occurrence of the species in coastal waters is irregular and thus its distribution and occurrence patterns are understudied. Pilot whale mass strandings occur in Iceland occasionally (Sigurjónsson et al. 1993), and Sæmundsson (1937, 1939) suggested that these could be linked to changes in the migration of their squid prey into Icelandic coastal waters. However, little is known of the diet of pilot whales occurring in this region and the only information comes from four animals stranded in 1982 that contained only beaks of flying squid (*Todarodes sagittatus*) in their stomachs (Sigurjónsson et al. 1993).

Killer whales are encountered offshore in the Northeast Atlantic but encounter rates tend to be low and irregular (Pike et al. 2020). Thus, the precision of abundance estimates from line-transect surveys is low and population trends remain unclear (Foote et al. 2007; Pike et al. 2020). While sightings occur all around Iceland, highest densities are reported to the east and northeast (Pike et al. 2020). In certain coastal areas around Iceland on the other hand, killer whales are known to occur commonly and regularly, particularly in areas where herring (*Clupea harengus*) gathers to spawn or overwinter (Sigurjónsson et al. 1988; Samarra et al. 2017). A large part of the population appears to feed on herring, following the Icelandic summer-spawning herring migration between their spawning grounds around the Vestmannaeyjar archipelago in the south and their wintering grounds in Breiðafjörður in the west of Iceland (Samarra et al. 2017). However, these are also the regions where most research efforts have focused on, and so, little is known of the occurrence of killer whales in other coastal regions.

In Norway and the Strait of Gibraltar (Spain), where killer whales and pilot whales regularly co-occur in coastal waters, interactions between both species have been observed (Stenersen and Similä 2004; de Stephanis et al. 2014). In all of the interactions reported, the pilot whales moved towards the killer whales which caused the killer whales to move directly away, sometimes at high speed (Stenersen and Similä 2004; de Stephanis et al. 2014). Playback experiments simulating killer whale presence showed that both short- and long-finned pilot whales are strongly attracted to killer whale sounds (Curé et al. 2012, 2019; Bowers et al. 2018), unlike other marine mammal species in similar experiments (e.g. Deecke et al. 2002; Curé et al. 2015). Two main hypotheses for the observed antagonistic interactions between pilot whales and killer whales have been brought forward: the interactions could be driven by food competition or could be a mobbing strategy based on anti-predator behaviour (Stenersen and Similä 2004; Curé et al. 2012; de Stephanis et al. 2014). However, much remains unclear as to why these interactions occur, what their relevance could be, and what the consequences are to both species. Possible impacts of such interactions are likely higher if interactions occur regularly due to spatial and temporal overlap.

Here, we investigated the occurrence of pilot whales and killer whales in different coastal regions of Iceland to assess the spatial and temporal overlap between both species. Then, we provide the first detailed descriptions of observed interactions between the two species in Iceland, discussing their frequency, the types of behavioural responses observed, and their potential causes and consequences.

Methods

Data were collected from 2007 to 2020 in six areas around Iceland (Fig. 1). Effort and sightings data came from dedicated research (Vestmannaeyjar) or opportunistic data collection by researchers and naturalists onboard whale watching tours (all other locations). Whale watching tours were operated on different types of boats (12–34 m length) but generally included lookouts a few metres above sea level. At least one observer was actively searching for whales and taking notes on species sighted. In Faxaflói, Breiðafjörður, and Eyjafjörður boats departed from different harbours but generally search areas varied little and thus were considered as one region. The boat-based research in Vestmannaeyjar was conducted from small boats (6–8 m length) with at least one dedicated observer onboard, who either took notes on paper

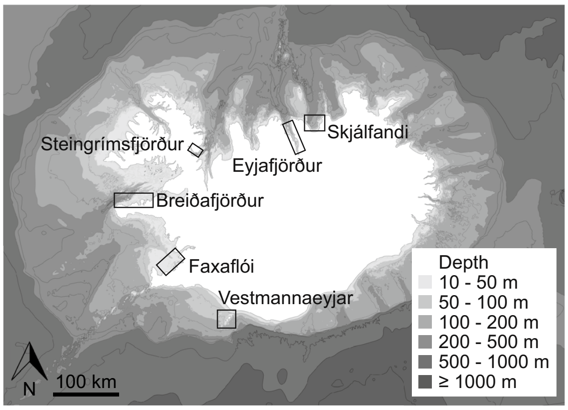

Fig. 1 Map of Iceland indicating study areas and bathymetry. Bathymetric data: Icelandic Coast Guard, Hydrographic Department

or recorded audio notes. Research focus varied between years but notes were generally taken on the species sighted, including estimates of group size and behaviour, with particular attention to feeding behaviours and prey species. In Vestmannaeyjar, visual surveys were also undertaken from a vantage point on land (2017–2020), located at 100 m height at the southern tip of Heimaey, the main island of the Vestmannaeyjar archipelago. Several small islands obstruct the view in some areas but the location generally provides a good overview of the study area. Typically, 2–5 observers conducted regular scan surveys, as well as periods of opportunistic search, throughout the day using 7 × 50 (Steiner Navigator pro) and 15 × 70 (Helios Stellar-II) binoculars. All marine mammal species sighted were recorded, including estimates of group size and behaviour. A calibrated digital theodolite (Sokkia DT-510) was used with the software VADAR (Visual and Acoustic Detection and Ranging, E. Kniest, University of Newcastle) to record positions of sightings and track groups of killer whales and/or pilot whales whenever possible.

Survey effort varied between seasons and locations, with the summer months being covered more extensively due to longer daylight hours and higher tourism activity (up to six whale watching tours per day in some locations, approximately 3 h each). The winter daylight hours often only allowed for one whale watching tour per day. In 2020, effort across all locations was much reduced due to the COVID-19 pandemic. Certain individuals or groups may avoid or approach boats more than others, which can lead to a bias in individuals observed but due to the opportunistic nature of the data collection, it was not possible to control for such potential biases.

Occurrence of pilot and killer whales was calculated as the percentage of days with effort that included sightings of either species. Changes in occurrence over time were investigated using yearly total percentages of occurrence for each location and using Pearson's correlation or Spearman's rank tests if data were not normally distributed based on a Shapiro–Wilk test (significance level 0.05).

Observations of interactions between pilot whales and killer whales were collected ad libitum (Mann 1999). An interaction was defined as either of the two species approaching the other and the approach possibly resulting in a change in behaviour of the second species. The start and end of an interaction were defined as the first and last concurrent sightings of both species. The end could have several reasons: either species could move out of the area or could disappear from view behind an island, or in the case of observations from a boat, the boat could leave the area. Group sizes during interactions were generally recorded by the observers as best estimates but sometimes as ranges or minimum estimates, in which case the mean or minimum values were used in the analysis (e.g. 25 for a recorded 20–30 individuals and 50 for a recorded 50 + individuals). If several groups were seen, group sizes could refer to the size of the group involved in the interaction or the total of individuals in the area. Only in a few cases were such differences clearly noted and thus further analysis was conducted on group sizes of the total individuals seen. In Vestmannaeyjar, the same interaction could sometimes be observed from the boat and land. In these cases, only observations from land were analysed, as observers from land generally had a better overview of the interactions and groups of whales in the area.

Results

Occurrence of pilot and killer whales

In total, 8090 days of effort were recorded from 2007 to 2020 across all locations, including 183 days (2.3%) with pilot whale and 647 days (8.0%) with killer whale sightings. However, effort and occurrence of the two species varied considerably between sites (Table 1).

Pilot whales were only encountered from June to September (Fig. 2). Pilot whale occurrence increased over the study period in four out of six locations (all except Steingrímsfjörður and Skjálfandi), but its correlation with year was

Table 1 Occurrence of pilot whales (PW) and killer whales (KW), their interactions, and the total survey effort in different locations around Iceland, 2007–2020. Occurrence and interactions are given as percentage of effort days, with the total number of days in brackets. 'Co-occurrence' refers to days with sightings of both pilot whales and killer whales, but where both species were not necessarily sighted at the same time

Region	Location	Occurrence PW % (days)	Occurrence KW % (days)	Co-occurrence % (days)	Interactions % (days)	Effort days
Northeast	Skjálfandi	0.1 (2)	1.1 (21)	0	0	1928
Northeast	Eyjafjörður	0.7 (8)	0.7 (8)	0	0	1146
Northwest	Steingrímsfjörður	15.8 (37)	3.4 (8)	0	0	234
West	Breiðafjörður	8.3 (84)	38.1 (387)	0.7 (7)	0.4 (4)	1017
Southwest	Faxaflói	0.4 (14)	1.5 (55)	0	0	3552
South	Vestmannaeyjar	17.8 (38)	80.3 (171)	17.4 (37)	9.4 (20)	213

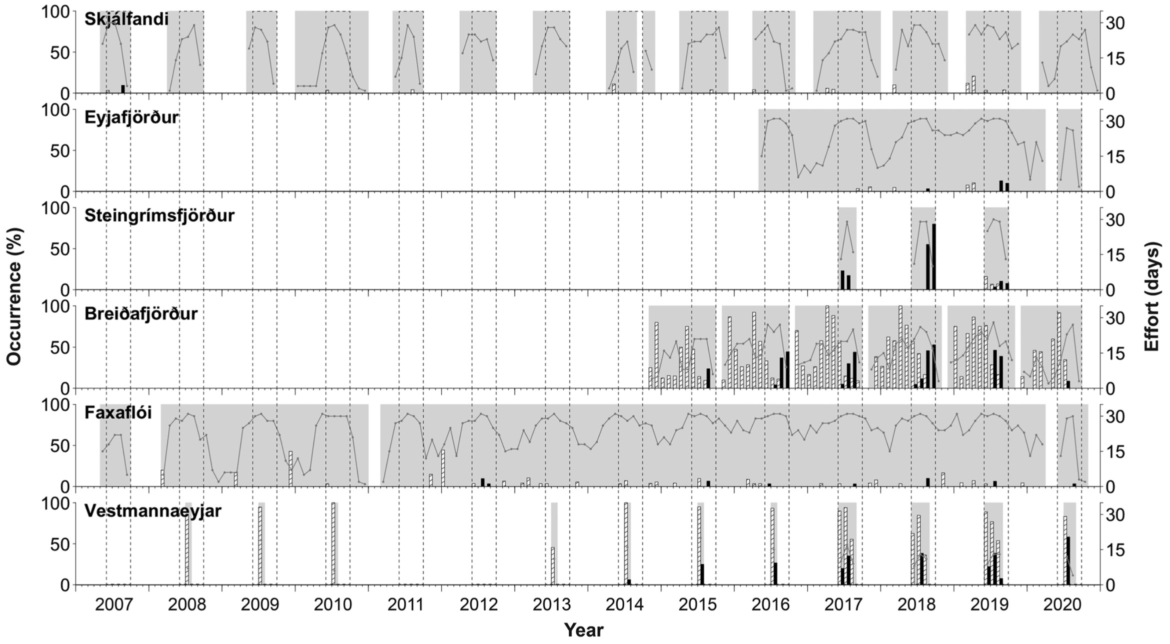

Fig. 2 Monthly occurrence of pilot whales (black bars) and killer whales (hatched bars) at different locations in Icelandic coastal waters. Periods with effort highlighted in grey with number of days of effort per month as a line, and summer periods (June–September) indicated with dashed boxes

statistically significant only in Vestmannaeyjar ($r_{(9)} = 0.85$, $p < 0.01$) and Faxaflói ($r_s = 0.69$, $p < 0.01$). Pilot whales were sighted most regularly in Vestmannaeyjar, Breiðafjörður, and Steingrímsfjörður. In all other locations, sightings were irregular and infrequent (Table 1 and Fig. 2).

Killer whales were encountered year-round but occurrence varied between seasons and locations (Fig. 2). They were sighted regularly in the summer months in Vestmannaeyjar. In Breiðafjörður, occurrence was highest in winter and spring. In all other locations, killer whale encounters were infrequent and there was no clear seasonal pattern in their occurrence. There was no significant positive or negative correlation in occurrence of killer whales with year for any location. In the two areas with the highest occurrence of killer whales, Vestmannaeyjar and Breiðafjörður, occurrence of pilot whales was also high (Table 1 and Fig. 2). These were also the only two locations where both species were sighted on the same days and behavioural interactions between the two species were observed (Table 1).

Interactions between pilot and killer whales

Although both killer whales and pilot whales occurred in the same area on 44 days of effort (Table 1), some of these sightings occurred at different times of the day such that both species were not simultaneously present. In 34 of these 44 days, pilot and killer whales were observed simultaneously, providing the potential for interactions to occur (Table 2). Interactions were observed on 70.6% of these days, or on a total of 24 days, 20 in Vestmannaeyjar and four in Breiðafjörður. The difference between these two locations may be due to a greater temporal overlap of the two species in Vestmannaeyjar, where both were common in summer. In contrast, in Breiðafjörður pilot whales were mostly seen in summer and killer whales were most common in winter and spring (Fig. 2). The mean duration of the observed interactions was 62 ± 71 min (mean ± standard deviation; range 6–286). The mean number of killer whales and pilot whales involved in the interactions was 27 ± 27 individuals (range 4–100) and 52 ± 39 individuals (range 20–150), respectively.

In all interactions, pilot whales moved towards killer whales, causing the killer whales in most cases to move directly away from the pilot whales. Pilot whales typically approached killer whales at high speed, often porpoising, a behaviour used as an indicator of high-speed travel (Weihs 2002). The interactions could be divided into three categories, based on the behavioural response of the killer whales: no response, avoidance, and high-speed avoidance. In very few cases, the pilot whales approached and the killer whales showed no visible response (Table 2). Regular avoidance included instances where killer whales moved away from pilot whales at low to moderate speed, showed minor evasive behaviour, or

Table 2 Summarised simultaneous observations of pilot whales (PW) and killer whales (KW) in Iceland, and interactions between them. Number of individuals refers to the total number of animals observed. If several groups were seen, not all of them always responded in the same manner and details on the number of individuals involved in the interactions are given in the comments

Location	Date	Observation platform	Interaction duration (min)	KW number	PW number	KW response	Comments
Vestmannaeyjar	2014–07–06	Boat	NA	~100	NA	Avoidance	PW approach at high speed, KW move away
	2015–07–11	Boat	58	NA	NA	Avoidance	PW approach twice, KW move away
	2015–07–13	Boat	6	NA	NA	No response, avoidance	Two groups of KW. PW approach fast and one group of KW moves away, the other stays and continues feeding
	2015–07–17	Boat	69	NA	NA	Avoidance	Two groups of KW. PW are seen several times and once clearly approach the KW and the KW move away
	2015–07–18	Boat	168	NA	NA	Avoidance	PW approach KW at high speed. KW are not seen for ~ 30 min but are then sighted again further away. PW approach again and KW move away
	2016–07–20	Boat	130	NA	NA	Avoidance	PW approach KW at high speed twice, KW move away
	2016–07–21	Boat	37	NA	NA	High-speed avoidance	PW approach at high speed, KW move away at high speed (porpoising)
	2016–07–22	Boat	NA	NA	NA	Avoidance	PW approach KW, KW move away. KW described as 'fleeing' but porpoising not confirmed. Possible but unconfirmed high-speed avoidance
	2016–07–27	Boat	NA	NA	NA	NA	PW approach KW at high speed but not known how KW respond
	2017–06–18	Land	6	4–5	NA	High-speed avoidance	PW approach KW at high speed, KW move away at high speed (porpoising)
	2017–06–19	Land	NA	4+	10–30+	Avoidance	PW approach KW, KW move away. KW described as being 'chased' by PW but porpoising not confirmed. Possible but unconfirmed high-speed avoidance
		Boat	NA	12	~50	NA	KW observed but sight of them lost for ~ 20 min. They are resighted after PW passed. Likely the same interaction as observed from land
	2017–07–04	Land	NA	1+	9+	NA	One sighting of a KW with a group of PW right behind but no further information recorded

Table 2 (continued)

Location	Date	Observation platform	Interaction duration (min)	KW number	PW number	KW response	Comments
	2017–07-24	Land	NA	9	10	NA	KW and PW sighted simultaneously but no further information recorded
	2017–07-27	Land	21	19–30	NA	Avoidance	PW approach KW, KW move away. Possible but unconfirmed high-speed avoidance (porpoising not confirmed). A single male KW is encircled by PW for a short time
	2017–07-30	Boat	51	NA	NA	Avoidance	PW approach KW, KW disappear from view. KW resighted and PW approach again at high speed, KW move away. Possible but unconfirmed high-speed avoidance (porpoising not confirmed)
	2018–07–10	Land	27	6–8	20	Avoidance	PW approach KW at high speed, KW move away fast. Possible but unconfirmed high-speed avoidance (porpoising not confirmed)
	2018–07–12	Boat	NA	12	20–28	No interaction	PW and KW sighted in the same area but no interaction observed. Two white-beaked dolphins (*Lagenorhynchus albirostris*) observed close to PW
	2018–07–14	Boat	94	16–37	30	Avoidance	Three groups of KW (16 individuals in total) at the start, after ~ 1 h several KW groups join (37 individuals in total). PW approach KW several times throughout, KW move away
	2018–07–24	Land	NA	NA	10–20	NA	KW and PW sighted simultaneously but KW only once and response unknown
	2019–06–23	Boat	46	20	30–40	Avoidance	PW approach KW at high speed twice, KW move away
	2019–06–30	Land	8	9–11	30–40	No response, avoidance	Two groups of KW. PW approach one KW group (4 individuals) at high speed. This KW group moves away. The other KW group (5–7 individuals) shows no response

Table 2 (continued)

Location	Date	Observation platform	Interaction duration (min)	KW number	PW number	KW response	Comments
	2019–07–17	Land	NA	5–6	30–40	No interaction	PW and KW sighted simultaneously but neither approaching the other. KW stay in the same area. PW are ~ 4 km from KW and move further away
	2019–07–22	Land	NA	8–10	20–50+	No interaction	PW and KW sighted simultaneously but neither approaching the other. KW stay in the same area. PW are ~ 5 km from KW and move further away
	2019–07–23	Land	286	5–8	11, 50+	No response	11 PW approach KW, KW stay in the same area, and PW eventually move away. Later, 50 + PW approach KW, KW stay in the same area, and PW eventually move away (Fig. 5). About 15 min later, the boat observes a high-speed avoidance in the same area but it was not possible to confirm if this involved the same individuals
		Boat	24	26–28	80–100	High-speed avoidance	Five groups of KW are present in the area. PW approach at high speed and one group of KW (6 individuals) moves away at high speed (porpoising, Figs. 3 and 5). The other groups stay behind. This observation is about 15 min after the observations from land end but it is unknown if this was the same group that had previously been approached by PW without responding in the observations from land
	2019–07–26	Boat	NA	5	30	Avoidance	PW approach, KW disappear from view
	2020–07–20	Boat	42	6	10+	No interaction	PW and KW sighted in the same area but no interaction observed
	2020–07–21	Land	139	19	40–45	Avoidance, high-speed avoidance	Four groups of KW and 2–3 groups of PW. One group of PW approach a group of KW (6 individuals), KW move away. The other two groups of PW approach different group of KW (4 individuals) at high speed, KW move away at high speed (porpoising)

Table 2 (continued)

Location	Date	Observation platform	Interaction duration (min)	KW number	PW number	KW response	Comments
		Boat	74	13	20–30	Avoidance	Same interaction as seen from land but high-speed avoidance not observed. Only 1–2 KW groups close enough to estimate group size and only one group of PW seen
	2020–07–24	Land	15	12–14	20–25	Avoidance	Two groups of KW. PW approach one group of KW (6 individuals) at high speed, KW move away
		Boat	24	9	20–30	Avoidance	Same interaction as seen from land but only one group of KW seen. The smaller group size observed from land might be because fewer individuals were clearly seen from that distance
	2020–07–25	Land	NA	6	5	NA	PW and KW sighted simultaneously but sight of KW lost shortly after as they went behind an island
Breiðafjörður	2017–08–02	Boat	18	15	150	High-speed avoidance	PW approach KW at high speed, KW move away at high speed (porpoising)
	2019–07–22	Boat	27	60	80	Avoidance	PW approach KW at high speed, KW move away
	2019–07–25	Boat	NA	40	40	High-speed avoidance	PW approach KW at high speed, KW move away at high speed (porpoising)
	2019–07–26	Boat	14	20	100	High-speed avoidance	PW approach KW at high speed, KW move away at high speed (porpoising)
	2020–07–19	Boat	NA	35	50	No interaction	PW and KW sighted in the same area but no interaction observed. A humpback whale (*Megaptera novaeangliae*) is observed surrounded by PW

Fig. 3 Pilot whales (left, photograph by Katarína Klementisová) and killer whales (right, photograph by Curt Hanson) porpoising during a high-speed avoidance observed in Vestmannaeyjar, Iceland, on 23 July 2019

disappeared from view for a few minutes and were then sighted some distance away. High-speed avoidance was assigned when killer whales were observed porpoising out of the water, with the pilot whales chasing the killer whales at high speed (Fig. 3, Video in Supplementary Material). Obvious aggressive physical contact between the two species was never observed. The interactions either ended with the pilot whales leaving the area or, in the case of high-speed avoidance behaviour, with both species slowing down and becoming less directional in their movements.

The majority of interactions were categorised as regular avoidance (68.0%), but this should be considered a maximum estimate as the absence of porpoising was not always confirmed (Table 2). High-speed avoidance was confirmed in 28% of interactions. Pilot whale group size differed between regular avoidance, high-speed avoidance, and when no interaction was observed (Kruskal–Wallis test, $x^2(2) = 8.06$, $p < 0.05$, Fig. 4). No interaction reflected times when both species were present in the same area simultaneously but there was no interaction between them. Observations of pilot whale approaches where killer whales showed no response (i.e. an interaction with no response) were too few to include in the comparison ($n = 1$). Pilot whale group sizes were highest during high-speed avoidance (85 ± 46, range 40–150, $n = 5$) compared to regular avoidance (34 ± 20, range 20–80, $n = 8$) and no interaction (31 ± 15, range 10–50, $n = 5$) but due to the small sample sizes, no further tests were performed. There was no evidence that the group size of killer whales varied across the three categories (Kruskal–Wallis, $x^2(2) = 1.09$, $p > 0.5$, Fig. 4), although group sizes were largest for regular avoidance. However, usually several groups of killer whales were in the area and it was not always clearly recorded in the field notes whether all or only some groups responded. We could therefore only compare the total number of individuals observed.

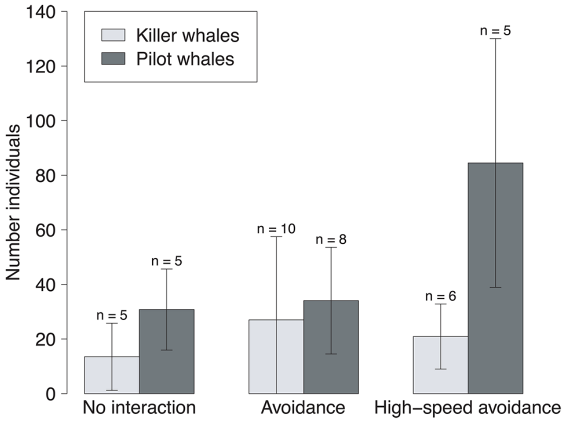

Fig. 4 Group sizes during pilot whale approaches to killer whales, as a function of the behaviour of killer whales, and when no interaction was observed (i.e. both species were present in the same area simultaneously but no interaction was observed). Regular avoidance: the killer whales moved away from the approaching pilot whales at low to regular speed (i.e. an interaction); high-speed avoidance: the killer whales moved away from the approaching pilot whales and were observed 'porpoising' (i.e. an interaction). Interactions where killer whales showed no response were too few to be included. Bars represent the mean and error bars represent ± 1 standard deviation

Examples of interactions between pilot and killer whales

Examples with movement tracks of three subsequent interactions can be seen in Fig. 5 and are briefly described here. These visual observations were collected on 23rd July 2019 in the Vestmannaeyjar archipelago and were made by boat, or from land with binoculars and a theodolite. Throughout the day, several groups of killer and pilot whales were observed. Visual observation of killer whales from land was obscured by islands during the second and third interaction events, but the boat was in proximity of killer whales throughout the entire observation period (10:51–17:03 UTC).

During the first approach, the pilot whales were only observed from the land station and no clear response of the killer whales was observed. At 11:29, 2–3 subgroups of pilot whales with 11 individuals in total were sighted. The groups were noted to merge and split several times while travelling fast towards the killer whales. Between 12:30 and 12:46, five killer whales were seen near one of the islands. At 12:45, the pilot whales made a sharp turn and started heading away from the killer whales. The pilot whales split and changed direction several times and then all started moving southwest at 12:51 and again towards the killer whales at 13:11. The killer whales changed direction frequently but stayed in the same area ('milling'). At 13:35, the pilot whales were very close to the killer whales and changed direction a few times but then stopped travelling. The killer whales were logging at the surface. The pilot whales were not seen again until 14:00 when they were heading away from the killer whales.

The second approach was also observed from land and began at 14:45 when a group of 50+ pilot whales was sighted coming from the area where the previous group of pilot whales was last seen. Five killer whales were seen at 14:46 feeding close to one of the islands. At 14:50, the pilot whales split into two groups, both of which started approaching the killer whales at high speed and tracking of the two groups began at 14:56 and 15:07. At 15:24, one position measurement could be taken of the killer whales before they disappeared from view behind an island. Soon after (at 15:27), one of the two groups of pilot whales appeared to stop for a short time, and then at 15:36, the two subgroups merged. At 15:51, a group of eight killer whales was sighted close to the island but no coordinates could be measured. The pilot whales started to head away from the killer whales and were last

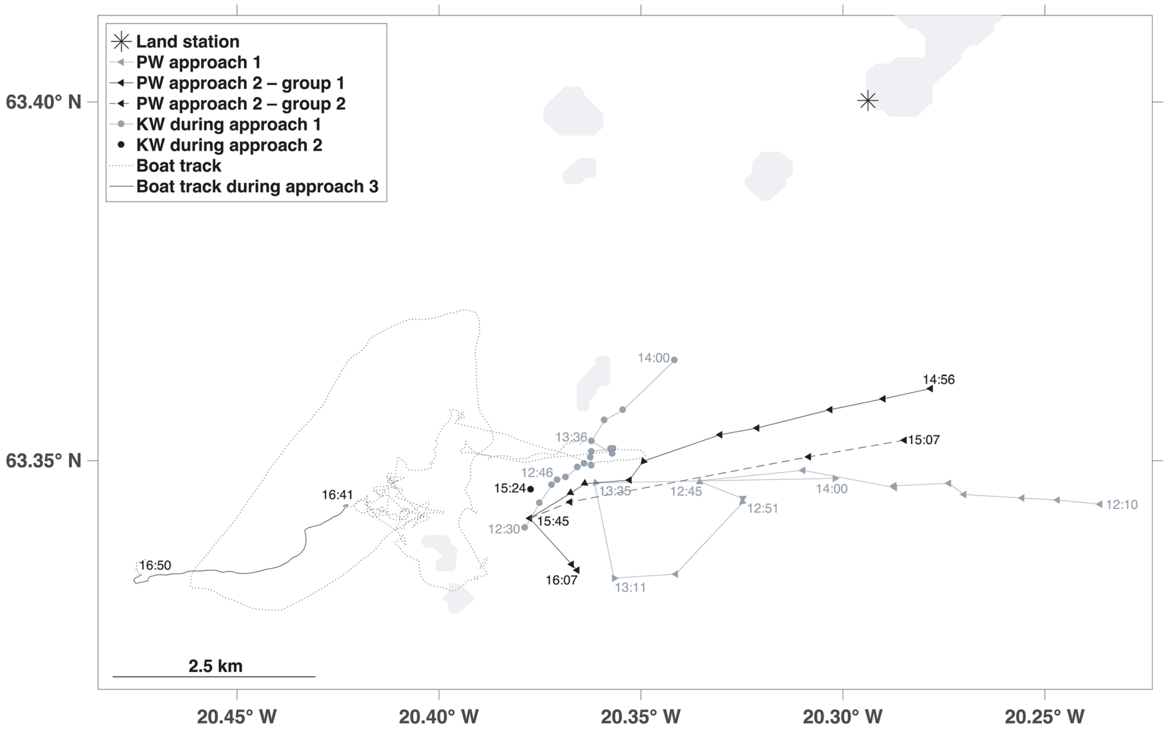

Fig. 5 Example observation of interactions between pilot whales (PW) and killer whales (KW) in Vestmannaeyjar, Iceland, on 23 July 2019. Approaches 1 and 2 were observed from land and tracking data were collected with a theodolite. Approach 3 was observed from the boat. The boat closely followed the killer whales and thus the boat track can be considered the approximate track of the killer whales

seen at 16:15. As the killer whales were located close to an island that obstructed the view during parts of the approach, it is unclear whether they actively avoided the pilot whales.

The last approach by pilot whales was observed from the boat only. Five groups of killer whales with 26–28 individuals in total were observed from the boat between 16:01 and 16:36. At 16:35, 80–100 pilot whales were seen approaching from the east. A group of killer whales initially turned towards the pilot whales but then turned away, and at 16:41, the pilot whales were pursuing this group of six killer whales at high speed, with both species porpoising (Fig. 3, Video in Supplementary Material). The boat closely followed the killer whales for a short period (Fig. 5), allowing us to estimate a minimum swimming speed of at least 8 knots (15 km/h) and a maximum of 13.5 knots (25 km/h). At 16:50, the distance between the two species increased and both were slowing down. At this point, it is noted that several killer whales had stayed behind and had not been part of the group showing high-speed avoidance.

Discussion

This study provides the first evidence of interspecific interactions between pilot whales and killer whales in Iceland, in regions where both species co-occur seasonally. The interactions appeared to be antagonistic, as suggested by previous studies in Spain and Norway, but in our study, interspecific interactions varied in intensity and not all close encounters of the two species led to observable interactions. These interactions are therefore more complex and widespread in the North Atlantic than previously thought. We observed changes in pilot whale occurrence along the Icelandic coast, particularly in the south where sightings appear to have increased over the study period, whereas killer whale occurrence did not change noticeably. The occurrence of both species overlapped spatially, with the south (Vestmannaeyjar) and west (Breiðafjörður) of Iceland recording regular sightings, and to a lesser degree also temporally, with both species regularly occurring in summer, especially in the south. In the west, killer whales were sighed more often in winter to early summer and pilot whales in late summer, so their temporal overlap was lower than in the south of Iceland.

Estimates for pilot whale population size in offshore areas of the Northeast Atlantic between 1987 and 2015 showed no significant population growth or decline (Pike et al. 2019); thus, it appears that changes in population size are unlikely to have led to the apparent increase in pilot whale sightings in coastal waters off south Iceland. The offshore occurrence of pilot whales was consistently highest in the waters southwest of Iceland and along the continental edge in south Iceland (Buckland et al. 1993; Pike et al. 2019), areas that are geographically close to most of the coastal waters that had high pilot whale occurrence in this study. Similarly, strandings were also reported most often in the southwest, west, and northwest of Iceland (Sigurjónsson et al. 1993). Therefore, it is possible that rather than changes in population size, it is changes in distribution that may explain the apparent increase observed in this study, with pilot whales that generally inhabit offshore waters venturing inshore in some years.

A change in a predator's distribution from offshore to inshore waters could be due to changes in prey availability (McComb-Turbitt et al. 2021). Pilot whales in the North Atlantic appear to feed predominantly on squid (Desportes and Mouritsen 1993; Sigurjónsson et al. 1993; Gannon et al. 1997; Santos et al. 2014). Squid undergo extensive migrations for feeding and spawning but their occurrence is highly irregular and likely influenced by environmental conditions (Jákupsstovu 2002; Hátún et al. 2009). In so-called squid years, large aggregations of squid appear around Iceland, the Faroe Islands, and off Norway, and are associated with higher catches of pilot whales around the Faroe Islands (Jákupsstovu 2002; Hátún et al. 2009). Similarly, catch numbers and stranding reports from Iceland suggest periods of higher occurrence of pilot whales could be linked to irregular migration of squid (Sæmundsson 1937, 1939; Sigurjónsson et al. 1993). Pilot whale sightings in Icelandic coastal waters in this study were only reported in June–September, which coincides with high abundance of squid and pilot whales around the Faroe Islands, particularly in years of high squid occurrence (Jákupsstovu 2002). Thus, the observed increase of occurrence of pilot whales around Iceland could be due to a period of high squid abundance in Icelandic coastal waters.

Alternatively, pilot whales could be following mackerel (*Scomber scombrus*), which appears to be an important prey of pilot whales elsewhere in the North Atlantic (Overholtz and Waring 1991; Abend and Smith 1997; Gannon et al. 1997). Mackerel abundance increased dramatically in Icelandic offshore and coastal waters between 2007 and 2014 and is still caught in Icelandic waters to date (Astthorsson et al. 2012; MFRI 2021a). Since pilot whales typically feed at depth, observing feeding behaviour and identifying prey species from surface observations is difficult (Baird et al. 2002; Visser et al. 2014). One of our observations in Breiðafjörður included a gull picking up a mackerel near a group of pilot whales apparently feeding but this was the only time a possible prey species was identified in this study. Finally, pilot whale distribution could also be influenced by climatic changes (van Weelden et al. 2021). Pilot whales in the western North Atlantic are shifting north at rates faster than their prey, likely showing a direct response to warming waters (Thorne and Nye 2021). Icelandic waters have been warming (based on sea surface temperature) over the last 20 years (Óskarsson et al. 2021), which could impact the distribution of highly mobile species, such as pilot whales. Data collection for our study was mostly opportunistic. This could have led to a bias in coverage of areas and time of year, as well as the individuals sampled, that was not possible to control for. In addition, coverage differed highly between locations, years, and seasons (Table 1 and Fig. 2). Thus, it is difficult to make conclusive inferences about changes over time. Systematic, long-term data collection on pilot whale occurrence and diet will be required to fully understand the patterns and the drivers of distribution in Iceland.

Killer whale occurrence did not appear to change throughout the study period but did show regional and seasonal variations. Killer whales were most frequently encountered in Vestmannaeyjar and Breiðafjörður, which are important herring grounds. Herring abundance in Iceland has declined since mackerel became abundant (MFRI 2021a, b) and the distribution of the two species often overlaps (Óskarsson et al. 2016). Opportunistic observations in Vestmannaeyjar and Breiðafjörður indicate the presence of mackerel in summer in some years. It is unknown to what extent killer whales in Iceland have taken advantage of the incoming mackerel, but in neighbouring regions of the North Atlantic, it is known to be an important prey, even for whales suspected to feed on herring as well (Luque et al. 2007; Foote et al. 2012; Nøttestad et al. 2014). Pilot whale stomach contents in Iceland and the Faroe Islands have not included herring or mackerel (Desportes and Mouritsen 1993; Sigurjónsson et al. 1993). Thus, pilot whales may occur most often in locations where killer whales are also frequently seen due to an overlap in the distribution of preferred prey (herring and squid or herring and mackerel). Alternatively, the possibility that both species are feeding on mackerel or herring, and therefore competing for resources, cannot be excluded at present. Given that the extent of temporal overlap of occurrence of pilot and killer whales in the south and west of Iceland is not identical, further research into the diet and habitat use of both species in both locations would be necessary to establish potential dietary overlap.

In the locations that had concurrent sightings of pilot whales and killer whales, interspecific interactions were common, particularly in south Iceland where their seasonal occurrence also overlapped to the greatest extent. These interactions appeared to be antagonistic, with killer whales often avoiding pilot whales and sometimes fleeing at high speed. Similar interactions have been previously reported from northern Norway and the Strait of Gibraltar, Spain (Stenersen and Similä 2004; de Stephanis et al. 2014). In our observations, not all sightings of the two species in the same area resulted in interactions, and high-speed avoidance with porpoising was only observed in 28% of interactions. On several days, pilot whales approached killer whales multiple times and killer whale responses to these approaches could vary from no response to avoidance or high-speed avoidance with observed porpoising. This indicates that these interactions are complex and it remains unclear what exactly triggers the avoidance by killer whales and, in particular, the high-speed response. Our results suggest that responses by killer whales could be related to the group size of pilot whales, with larger pilot whale groups leading to high-speed avoidance. However, as data were collected ad libitum and pilot whale group sizes are difficult to estimate (Pike et al. 2019), we cannot rule out that the increased speed during these events led to more whales being visible at the surface, which could have inflated estimates. Similarly, it was not always clear whether all killer whale groups present responded in the same manner and thus what was the number of individuals in the responding group(s). This emphasises the need to systematically study these interactions, with a standardised data collection protocol, in the future. Previous studies have suggested that acoustic cues could play a role in triggering the behavioural response of killer whales (Stenersen and Similä 2004). Thus, further studies on the role of acoustic behaviour during interactions could help elucidate the triggers for different types of responses by killer whales.

Interactions between pilot whales and killer whales have previously been suggested to be driven by competition or predator deterrence (Stenersen and Similä 2004; Curé et al. 2012, 2019; de Stephanis et al. 2014). Competition could occur, for example, for habitat, foraging areas, or prey. As mentioned above, there is a possibility for spatial overlap in prey species or dietary overlap between pilot whales and killer whales in Icelandic waters. In this study, pilot whales were not often observed displaying behaviour consistent with feeding at depth (i.e. milling at the surface and spreading out; Visser et al. 2014). However, killer whales were often observed feeding when the pilot whales approached in many of the interactions. Overall, feeding was the most common behavioural state that was observed in killer whales in this study and it remains unclear whether pilot whales preferentially approached feeding killer whales.

Stable isotope analyses from the Strait of Gibraltar suggested little dietary overlap and no predation of either species on the other (de Stephanis et al. 2014). Playback experiments further indicate that simulated killer whale presence does not induce foraging behaviour in pilot whales and that pilot whales can distinguish between the sounds of familiar fish-eating and unfamiliar mammal-eating killer whales, perceiving the former as a lower threat than the latter (Curé et al. 2019). Thus, the observed interactions between pilot and killer whales were suggested to be an active intimidation behaviour against a perceived low-threat predator (de Stephanis et al. 2014; Curé et al. 2019). Killer whale predation on short- or long-finned pilot whales has been reported occasionally (Jefferson et al. 1991; Nishiwaki and Handa 1958), including a potential predation event in Iceland (Donovan and Gunnlaugsson 1989), but interactions without aggressive behaviour or mixed aggregations of both species have also been reported (Jefferson et al. 1991). In Iceland, reports of predation by killer whales on cetacean species are infrequent (Samarra et al. 2018). Thus, pilot whales in Iceland may perceive killer whales as a low-threat predator and exhibit a mobbing response, but competition between both species cannot be excluded until further information on their habitat use, behaviour, and feeding ecology is gathered.

Killer whales commonly abandoned feeding events when avoiding pilot whales; thus, the occurrence of these interspecific interactions may carry energetic consequences for killer whales. Reduction in foraging effort can have considerable energetic impacts (Williams et al. 2006), which could increase due to energy expenditure in high-speed avoidance (Allen et al. 2022). Therefore, more detailed research into pilot-killer whale interactions, including their ecological and evolutionary drivers and energetic impacts, would be highly relevant to inform conservation management for both species.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10211-022-00394-1.

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Availability of data and material Data provided as supplementary material.

Declarations

Conflict of interest TH was employed by Whale Watching Akureyri, MTM and JSc were employed by Láki Tours, JNR was employed by Special Tours and MW was employed by Elding Whale Watching. These commercial affiliations do not alter our adherence to Acta ethologica policies on sharing data and materials.

References

Abend AG, Smith TD (1997) Differences in stable isotope ratios of carbon and nitrogen between long-finned pilot whales (*Globicephala melas*) and their primary prey in the western north Atlantic. ICES J Mar Sci 54:500–503. https://doi.org/10.1006/jmsc.1996.0192

Allen AS, Read AJ, Shorter KA, Gabaldon J, Blawas AM, Rocho-Levine J, Fahlman A (2022) Dynamic body acceleration as a proxy to predict the cost of locomotion in bottlenose dolphins. J Exp Biol 225:jeb243121. https://doi.org/10.1242/jeb.243121

Astthorsson OS, Valdimarsson H, Gudmundsdottir A, Óskarsson GJ (2012) Climate-related variations in the occurrence and distribution of mackerel (*Scomber scombrus*) in Icelandic waters. ICES J Mar Sci 69:1289–1297. https://doi.org/10.1093/icesjms/fss084

Baird RW, Borsani JF, Hanson MB, Tyack PL (2002) Diving and night-time behavior of long-finned pilot whales in the Ligurian Sea. Mar Ecol Prog Ser 237:301–305. https://doi.org/10.3354/meps237301

Bowers MT, Friedlaender AS, Janik VM, Nowacek DP, Quick NJ, Southall BL, Read AJ (2018) Selective reactions to different killer whale call categories in two delphinid species. J Exp Biol 221:1–12. https://doi.org/10.1242/jeb.162479

Buckland ST, Bloch D, Cattanach KL, Gunnlaugsson T, Hoydal K, Lens S, Sigurjónsson J (1993) Distribution and abundance of long-finned pilot whales in the North Atlantic, estimated from NASS-87 and NASS-89 data. Report of the International Whaling Commission Special Issue 14:33–49

Curé C, Antunes R, Samarra F, Alves AC, Visser F, Kvadsheim PH, Miller PJO (2012) Pilot whales attracted to killer whale sounds: acoustically-mediated interspecific interactions in cetaceans. PLoS ONE 7:e52201. https://doi.org/10.1371/journal.pone.0052201

Curé C, Sivle LD, Visser F, Wensveen PJ, Isojunno S, Harris CM, Kvadsheim PH, Lam FPA, Miller PJO (2015) Predator sound playbacks reveal strong avoidance responses in a fight strategist baleen whale. Mar Ecol Prog Ser 526:267–282. https://doi.org/10.3354/meps11231

Curé C, Isojunno S, Vester H, Visser F, Oudejans MG, Biassoni N, Massenet M, Wensveen PJ, Sivle LD, Tyack PL, Miller PJO (2019) Discrimination between feeding sounds of fish and mammal eating killer whale ecotypes by long-finned pilot whales. Anim Cogn 22(863–882):0123456789. https://doi.org/10.1007/s10071-019-01282-1

Deecke VB, Slater PJB, Ford JKB, Fish MP (2002) Selective habituation shapes acoustic predator recognition in harbour seals. Nature 729:171–173. https://doi.org/10.1038/nature01030

de Stephanis R, Giménez J, Esteban R, Gauffier P, García-Tiscar S, Sinding MHS, Verborgh P (2014) Mobbing-like behavior by pilot whales towards killer whales: a response to resource competition or perceived predation risk? Acta Ethologica 18:69–78. https://doi.org/10.1007/s10211-014-0189-1

Desportes G, Mouritsen R (1993) Preliminary results on the diet of long-finned pilot whales off the Faroe Islands. Report of the International Whaling Commission Special Issue 14:305–324

Donovan GP, Gunnlaugsson T (1989) North Atlantic sightings survey 1987: report of the aerial survey off Iceland. Report of the International Whaling Commission 39:437–441

Foote AD, Víkingsson GA, Øien N, Bloch D, Davis CG, Dunn TE, Harvey PV, Mandleberg L, Whooley P, Thomson PM (2007) Distribution and abundance of killer whales in the North East Atlantic. Paper SC/59/SM5 presented to the IWC Scientific Committee 1–10

Foote AD, Vester H, Víkingsson GA, Newton J (2012) Dietary variation within and between populations of northeast Atlantic killer whales, *Orcinus orca*, inferred from δ13C and δ15N analyses. Mar Mamm Sci 28:472–485. https://doi.org/10.1111/j.1748-7692.2012.00563.x

Ford JKB (2018) Killer whale: *Orcinus orca*. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of marine mammals. Academic Press, London 650–657. https://doi.org/10.1016/B978-0-12-804327-1.00010-8

Gannon DP, Read AJ, Craddock E, Fristrup KM, Nicolas JR (1997) Feeding ecology of long-finned pilot whales *Globicephala melas* in the western North Atlantic. Mar Ecol Prog Ser 148:1–10. https://doi.org/10.3354/meps148001

Hátún H, Payne MR, Beaugrand G, Reid PC, Sandø AB, Drange H, Hansen B, Jacobsen JA, Bloch D (2009) Large bio-geographical shifts in the north-eastern Atlantic Ocean: from the subpolar gyre, via plankton, to blue whiting and pilot whales. Prog Oceanogr 80:149–162. https://doi.org/10.1016/j.pocean.2009.03.001

Jákupsstovu SH (2002) The pelagic fish stocks, pilot whales and squid in Faroese waters - migration pattern, availability to fisheries and possible links to oceanographic events. ICES CM, 2002/N:07 1–37

Jefferson T, Stacey P, Baird R (1991) A review of Killer whale interactions with other marine mammals. Mammal Rev 21:151–180. https://doi.org/10.1111/j.1365-2907.1991.tb00291.x

Luque PL, Davis CG, Reid DG, Wang J, Pierce GJ (2007) Opportunistic sightings of killer whales from Scottish pelagic trawlers fishing for mackerel and herring off North Scotland (UK) between 2000 and 2006. Aquat Living Resour 19:403–410. https://doi.org/10.1051/alr:2007009

Mann J (1999) Behavioral sampling methods for cetaceans: a review and critique. Marine Mammal Science 15:102–122. https://doi.org/10.1111/j.1748-7692.1999.tb00784.x

McComb-Turbitt S, Costa J, Whitehead H, Auger-Méthé M (2021) Small-scale spatial distributions of long-finned pilot whales change over time, but foraging hot spots are consistent: Significance for marine wildlife tourism management. Mar Mamm Sci 37:1196-1211. https://doi.org/10.1111/mms.12821

MFRI (2021a) MFRI Assessment Reports 2021a, Mackerel. Marine and Freshwater Research Institute, Iceland

MFRI (2021b) MFRI Assessment Reports 2021b, Herring. Marine and Freshwater Research Institute, Iceland

Nishiwaki M, Handa C (1958) Killer whales caught in the coastal waters off Japan for recent 10 years. Scientific Reports of the Whales Research Institute 13:85–96

Nøttestad L, Sivle LD, Krafft BA, Langård L, Anthonypillai V, Bernasconi M, Langøy H, Fernö A (2014) Prey selection of offshore killer whales *Orcinus orca* in the Northeast Atlantic in late summer: spatial associations with mackerel. Mar Ecol Prog Ser 499:275–283. https://doi.org/10.3354/meps10638

Olson PA (2018) Pilot whales: *Globicephala melas* and *G. macrorhynchus*. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of marine mammals. Academic Press, London 847–852. https://doi.org/10.1016/B978-0-12-804327-1.00194-1

Óskarsson GJ, Gudmundsdottir A, Sveinbjörnsson S, Sigurðsson Þ (2016) Feeding ecology of mackerel and dietary overlap with herring in Icelandic waters. Mar Biol Res 12:16–29. https://doi.org/10.1080/17451000.2015.1073327

Óskarsson GJ, Þórðarson G, Guðbergsson G, Jónsdóttir IG, Guðjónsson S, Ólafsdóttir SR (2021) Staða umhverfis og vistkerfa í hafinu við Ísland og horfur næstu áratuga. Haf- og vatnarannsóknir, HV 2021–14

Overholtz WJ, Waring GT (1991) Diet composition of pilot whales *Globicephala* sp. and common dolphins *Delphinus delphis* in the Mid-Atlantic Bight during spring 1989. Fish Bull 89:723–728

Pike DG, Gunnlaugsson T, Desportes G, Mikkelsen B, Víkingsson GA, Bloch D (2019) Estimates of the relative abundance of long-finned pilot whales (*Globicephala melas*) in the Northeast Atlantic from 1987 to 2015 indicate no long-term trends. NAMMCO Scientific Publications. https://doi.org/10.7557/3.4643

Pike DG, Gunnlaugsson T, Mikkelsen B, Víkingsson G, Desportes G (2020) Distribution and abundance of killer whales in the Central North Atlantic, 1987–2015. NAMMCO Scientific Publications. https://doi.org/10.7557/3.5579

Sæmundsson B (1937) Fiskirannsóknir 1935–36. Skyrsla Til Stjórnarrádsins Andvari 62:22–61

Sæmundsson B (1939) Mammalia. Zoology of Iceland IV(76):1–38

Samarra FIP, Tavares SB, Béesau J, Deecke VB, Fennell A, Miller PJO, Pétursson H, Sigurjónsson J, Víkingsson GA (2017) Movements and site fidelity of killer whales (*Orcinus orca*) relative to seasonal and long-term shifts in herring (*Clupea harengus*) distribution. Mar Biol. https://doi.org/10.1007/s00227-017-3187-9

Samarra FIP, Bassoi M, Béesau J, Elíasdóttir MÓ, Gunnarsson K, Mrusczok MT, Rasmussen M, Rempel JN, Thorvaldsson B, Víkingsson GA (2018) Prey of killer whales (*Orcinus orca*) in Iceland. PLoS ONE 13:e0207287. https://doi.org/10.1371/journal.pone.0207287

Santos MB, Monteiro SS, Vingada JV, Ferreira M, López A, Martínez Cedeira JA, Reid RJ, Brownlow A, Pierce GJ (2014) Patterns and trends in the diet of long-finned pilot whales (*Globicephala melas*) in the northeast Atlantic. Mar Mamm Sci 30:1–19. https://doi.org/10.1111/mms.12015

Sigurjónsson J, Lyrholm T, Leatherwood S, Jónsson E, Víkingsson G (1988) Photoidentification of killer whales, *Orcinus orca*, off Iceland, 1981 through 1986. Rit Fiskideildar 11:99–114

Sigurjónsson J, Víkingsson G, Lockyer C (1993) Two mass strandings of pilot whales (*Globicephala melas*) on the coast of Iceland. Report of the International Whaling Commission Special Issue 14:407–423

Stenersen J, Similä T (2004) Norwegian killer whales. Tringa Forlag, Henningsvær

Thorne LH, Nye JA (2021) Trait-mediated shifts and climate velocity decouple an endothermic marine predator and its ectothermic prey. Sci Rep 11:18507. https://doi.org/10.1038/s41598-021-97318-z

van Weelden C, Towers JR, Bosker T (2021) Impacts of climate change on cetacean distribution, habitat and migration. Climate Change Ecology 1:100009. https://doi.org/10.1016/j.ecochg.2021.100009

Visser F, Miller PJO, Antunes RN, Oudejans MG, Mackenzie ML, Aoki K, Lam FPA, Kvadsheim PH, Huisman J, Tyack PL (2014) The social context of individual foraging behaviour in long-finned pilot whales (*Globicephala melas*). Behaviour 151:1453–1477. https://doi.org/10.1163/1568539X-00003195

Weihs D (2002) Dynamics of dolphin porpoising revisited. Integr Comp Biol 42:1071–1078. https://doi.org/10.1093/icb/42.5.1071

Williams R, Lusseau D, Hammond PS (2006) Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). Biol Cons 133:301–311. https://doi.org/10.1016/j.biocon.2006.06.010

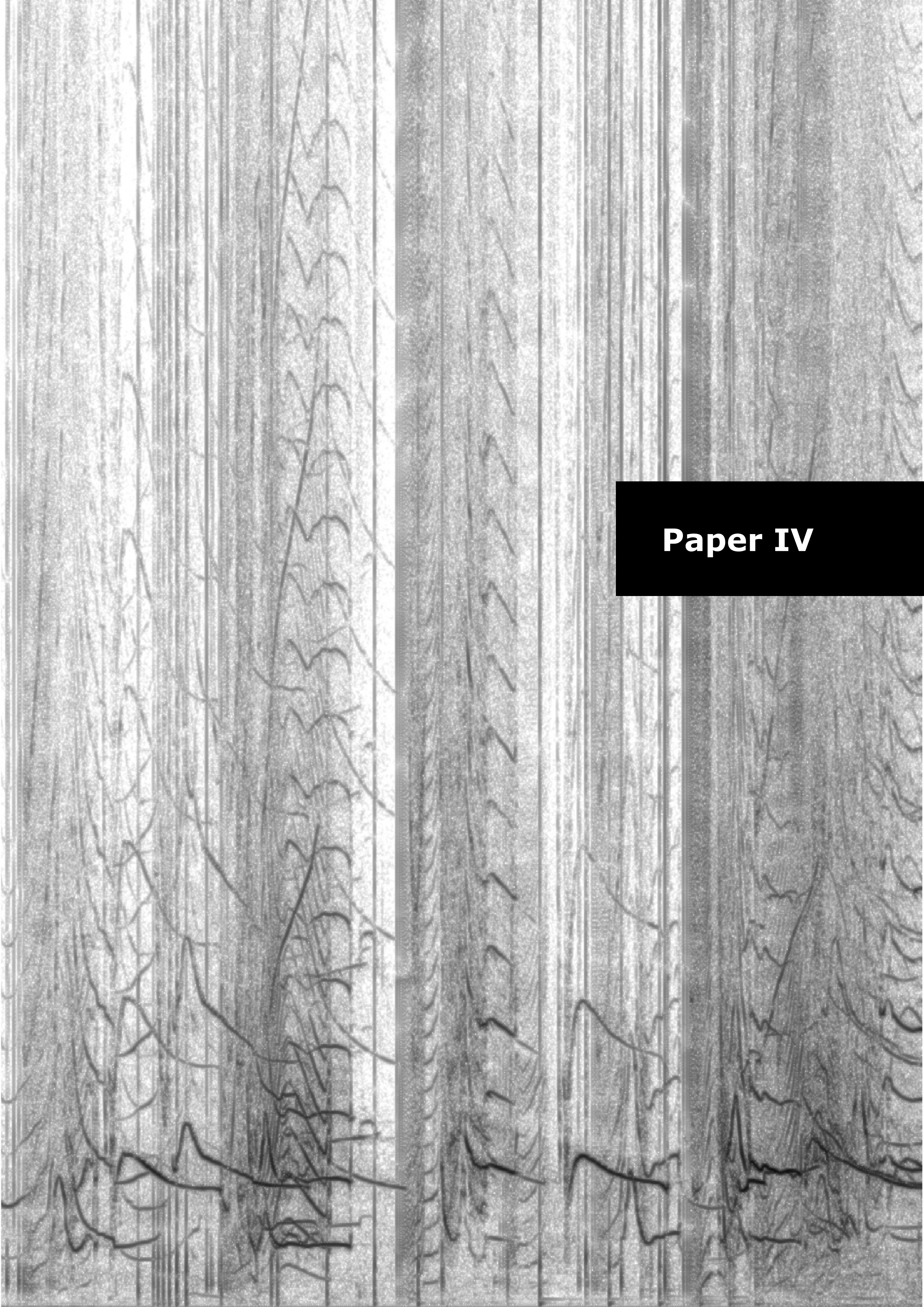
Supplementary material

Supplementary material available at doi: 10.1007/s10211-022-00394-1

Sightings data used in this study (comprising a list of locations, years, months, days of effort, and days with sightings of killer whales and long-finned pilot whales).

Video recording of an interaction observed in Vestmannaeyjar.

Paper IV



A top predator on the run: behavioural responses of killer whales to sounds of long-finned pilot whales

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Manuscript

A top predator on the run: behavioural responses of killer whales to sounds of long-finned pilot whales

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Abstract

Acoustic communication plays an important role in interspecific interactions but is often only studied in one of the species. Long-finned pilot whales (*Globicephala melas*) have been attracted to killer whale (*Orcinus orca*) sounds, leading to antagonistic interactions. To test whether the interaction between these species is acoustically mediated in both directions, playback experiments (n = 15) with pilot whale and control stimuli were conducted with killer whales (n = 8 groups) carrying Dtags. To assess behavioural responses to the playbacks, we fitted hidden Markov models to the tags' movement and acoustic data, as well as univariate regression models with a horizontal movement reaction score, group size and spacing, and calling rate. The tagged whales showed an avoidance response to the pilot whale sounds, marked by fast and directed movement away from the sound source, initial increases in calling rate followed by a strong decrease, and increased cohesion and alignment of the group members. These findings demonstrate that killer whales, the oceans' apex predator, respond to acoustic signals of pilot whales and likely perceive their presence as a disturbance threat. This study provides important insights into the complexity of cetacean behaviour and the mechanisms that structure the dynamics of multi-species communities.

1 Introduction

All species interact with other species, forming a network that links and affects them in multiple ways. These interspecific interactions include a range of fascinating behaviours that are important from an ecological perspective, to explain the stable co-existence of multi-species communities and ultimately to understand the evolution of complex ecosystems. In competition or predator-prey interactions, species may approach or avoid each other. For instance, a competitor might approach an opponent to intimidate and displace it from a prey source patch or habitat. In a predator-prey context, the predator needs to approach its prey to feed, while targeted prey will generally avoid predators but in some cases actually approach the predator as a defensive strategy to deter the threat (Begon and Townsend 2021). Such harassing approaches typically involve multiple individuals that approach, harass or attack a threat, often using increased vocalisation to drive the predator or competitor away. These 'mobbing-like' behaviours play a key role in competitive and predator-prey interactions and have been described in a variety of taxa, including birds and mammals (Curio 1978; de Stephanis et al. 2014; Driscoll et al. 2022). Whereas several hypotheses have been brought forward with regards to the benefits for the mobbing species (Curio 1978; Carlson and Griesser 2022), behavioural responses of the species being mobbed and associated biological costs to them remain largely unexplored (Caro 2005). This gap prevents a full understanding of the mechanisms driving interspecific interactions from both perspectives.

In cetaceans, various interactions between species have been reported, including affiliative behaviours (see Syme et al. 2021 for a review) and agonistic interactions (e.g. Weller et al. 1996; Palacios and Mate 2006; Cotter et al. 2012; Koper and Plön 2016; Pitman et al. 2017). However, it is difficult to study these animals in the wild because they are highly mobile and not easily observable over long time periods, which has prevented the understanding of the mechanisms mediating these interactions (Wirsing et al. 2008; Syme et al. 2021). The increased use of animal-attached biologging tools (McIntyre 2014) allows continuous measurement of the behaviour of individual cetaceans, facilitating the study of behavioural interactions within and across cetacean species.

Acoustic communication plays a key role in interspecific interactions. Mobbing-like behaviours for example, are commonly associated with increased calling activity, which may serve a dual function: alerting and recruiting others (conspecifics and/or heterospecifics) for a social defence response, and deterring intruders or predators through intimidation (Bradbury and Vehrenkamp 2011). Sound travels efficiently underwater and is a major sensory modality for cetaceans. They use sound to communicate and to gain information from their environment, such as detecting the presence of other species (eavesdropping, Benti et al. 2021; Barluet De Beauchesne et al. 2022). Playback experiments have shown that cetaceans detect the sounds of potential predators, prey or competitors (Gannon et al. 2005; Curé et al. 2012, 2013, 2015, 2019; Benti et al. 2021; Pierry et al. 2023) and respond by exhibiting behavioural changes (Curé et al. 2015; Isojunno et al. 2016) including movement responses (Allen et al. 2014; Bowers et al. 2018; Benti et al. 2021), acoustic responses (Curé et al. 2013), changes in group organisation (Visser et al. 2016) and alteration of fitness-enhancing activities (Miller et al. 2022). Groups of Guiana dolphins (*Sotalia guianensis*), for example, reduce their time spent foraging, aggregate, and increase synchrony while moving away from playbacks of sounds from their potentially aggressive competitor, the Lahille's bottlenose dolphin (*Tursiops truncatus gephyreus*, Pierry et al.

2023). Bottlenose dolphins (*Tursiops truncatus*) on the other hand, respond to playbacks of sounds from their fish prey by turning towards the sound source and increasing their rate of echolocation (Gannon et al. 2005).

The killer whale (*Orcinus orca*) is the oceans' apex predator and a highly vocal species (Ford 1989). Local populations of killer whales are often highly specialised on a specific prey type, leading to the differentiation of several ecotypes, such as fish-eaters and mammal-eaters (Baird 2000). The acoustic behaviour of these ecotypes varies, with fish-eating killer whales being more vocally active during foraging, while mammal-eating killer whales mostly stay silent during hunts, likely to avoid detection by their prey (Ford 1989; Deecke et al. 2005; Simon et al. 2007; Samarra and Miller 2015). Indeed, many cetaceans show avoidance responses to playbacks of killer whale sounds (Cummings and Thompson 1971; Fish and Vania 1971; Tyack et al. 2011; Allen et al. 2014; Curé et al. 2015; Sivle et al. 2015; Benti et al. 2021). To date, the only species that are known to be attracted to killer whale sounds are the short-finned pilot whale (*Globicephala macrorhynchus*), the long-finned pilot whale (*G. melas*), and the humpback whale (*Megaptera novaeangliae*). Specifically, humpback whales feeding on herring (*Clupea harengus*) in Norway regularly form mixed-species associations with killer whales feeding on the same prey and approach sounds of these local herring-eating killer whales, likely to take advantage of feeding opportunities (Jourdain and Vongraven 2017; Benti et al. 2021). However, they avoid sounds of unfamiliar mammal-eating killer whales simulating potential predator presence (Curé et al. 2015; Benti et al. 2021). Long-finned pilot whales on the other hand, approach both fish- and mammal-eating killer whale sounds, potentially as a form of mobbing behaviour (Curé et al. 2012, 2019).

Interactions between long-finned pilot whales (hereafter pilot whales) and killer whales have been documented across the North Atlantic (Stenersen and Similä 2004; de Stephanis et al. 2014; Selbmann et al. 2022). In these interactions, pilot whales typically approach fish-eating killer whales, often at high speed and in large groups. The killer whales may tolerate the presence of pilot whales, respond to approaches by moving away at slow to moderate speeds, or at very high speeds as indicated by whales porpoising out of the water. Pilot whales may approach killer whales once or several times during an event (Selbmann et al. 2022). Playbacks of fish-eating killer whale and mammal-eating killer whale sounds led to strong attraction responses in pilot whales, but differences in behaviour show that pilot whales likely discriminate between the two stimuli (Curé et al. 2012, 2019). In response to mammal-eating killer whale sounds, pilot whales exhibited a cryptic approach strategy: they stopped foraging, tightened their groups and spent less time near the surface, while approaching the sound source, potentially to inspect and evaluate the threat level (Curé et al. 2019). When hearing fish-eating killer whales, pilot whale groups joined, increasing their overall group size and calling activity while approaching the sound source (Curé et al. 2012, 2019). The latter response is consistent with a mobbing-like behaviour towards a potential predator or perceived competitor (de Stephanis et al. 2014; Curé et al. 2019; Selbmann et al. 2022).

Although competition for prey could explain mobbing-like behaviour, there is little evidence for trophic niche overlap between killer whales and pilot whales in the locations where the interactions have been observed. In the Strait of Gibraltar, Spain, stable isotope niches of the two species were clearly segregated, indicating that they do not feed on the same prey (de Stephanis et al. 2014). In Iceland, killer whales are known to mostly feed on herring though variation in diet exists (Samarra et al. 2017a, 2018). Little is known about the diet of pilot whales around Iceland but stomach contents of a small sample of stranded animals indicate a diet based on squid (Sigurjónsson et al. 1993). Therefore, direct competition for food does not seem to be the driver of this interaction but possible spatial overlap in prey species habitat might still lead to competition for feeding areas. Predation of killer whales on pilot whales is rare (Jefferson et al. 1991) and only one attack was reported off Iceland, in 1987 (Donovan and Gunnlaugsson 1989). Thus, mobbing towards a competitor sharing the same habitat or to a low threat predator are currently the most likely explanations for pilot whale behaviour during these interactions (de Stephanis et al. 2014; Curé et al. 2019).

While playback experiments showed that the mobbing-like behaviour of pilot whales can be triggered by the detection of killer whale sounds (Curé et al. 2012, 2019), it remains unclear if and how the interaction can be also mediated in the other direction, i.e. by killer whales detecting pilot whale sounds and anticipating a potential interaction. An acoustic mechanism seems likely as killer whales have acute hearing across a range of frequencies, including those of pilot whale vocalisations (Hall and Johnson 1972; Szymanski et al. 1999; Branstetter et al. 2017). The variation of observed killer whale responses to the presence of pilot whales in their habitat (Selbmann et al. 2022) indicates that they may differentiate threat levels, but it is relatively unclear why this apex predator avoids a smaller, seemingly inferior aggressor. The large group sizes of approaching and actively vocalizing pilot whales may play a role (Stenersen and Similä 2004; Selbmann et al. 2022). The resulting cacophony of pilot whale sounds may either signal a high threat level to the killer whales, interfere with their own communication, or simply irritate them. The energetic cost of moving away at high speed coupled with potential loss of feeding opportunities, might impact killer whales, especially if these interactions occur repeatedly and over long time periods. Thus, detecting pilot whale sounds could help killer whales to anticipate and balance these costs by determining the most appropriate response ahead of time.

The aim of this study was to investigate whether the interaction between these two cetacean species might be acoustically shaped or driven, from both species' sides of the interaction. In particular, we tested the role of sounds produced by pilot whales in influencing the behaviour of killer whales by conducting playback experiments of pilot whale sounds to tagged killer whales. Experiments were conducted in a herring spawning ground where killer whales gather in large numbers during the summer months (Samarra et al. 2017c). Long-finned pilot whales are also regularly seen in the area and interactions between the two species have been observed (Selbmann et al. 2022). We hypothesized that killer whales would adjust their behaviour in response to pilot whale sounds to anticipate a flight. Specifically, we expected killer whales to 1) move away from the sound source and increase speed, 2) modify their own sound production to reduce detection and localisation by pilot whales, and 3) increase cohesion among, and synchrony with, group members.

2 Methods

The study was conducted in the waters around the Vestmannaeyjar archipelago in South Iceland in June-August 2021-2023. The general protocol included the following steps: 1) attaching a multi-sensor tag using suction cups to a killer whale, 2) post-tagging (recovery period) of at least 2 h, 3) start visual data collection of the tagged whale and its group, 3) conducting playback experiments consisting of 15-min duration pre-, during-, and post-playback periods, 4) cessation of visual data collection, 5) tag detachment and tag recovery.

A 6-m RHIB boat was first used for tagging and then to transmit the sound stimuli during the playback experiments (the ‘playback source boat’). Visual tracking and observational data collection during the playback experiment were conducted from a second (12-m) vessel, referred to as the ‘tracking boat’.

2.1 Tagging and behavioural data collection

Digital acoustic recording tags (Dtags, Johnson & Tyack, 2003) were attached to killer whales with suction cups, using a carbon fibre pole or pneumatic tag launcher (ARTS, Kleivane et al., 2022). Whales were tagged while feeding, slow travelling or milling. Only adults or large juveniles were targeted for tagging and males were tagged most often (Table 1), as their large size facilitates tagging and subsequent tracking. Killer whales showed no or only short-term responses (e.g. flinches) to tagging. Identification photographs of the tagged whale were taken and compared to an existing catalogue (Samarra et al. 2017b) to ensure that the same groups were not tagged in other experiments.

The tags were equipped with a pressure sensor, 3D magnetometer, 3D accelerometer (all sampling at 250 Hz), VHF transmitter, integrated GPS-ARGOS transceiver with snapshot GPS (F6G 134A, Lotek NZ Ltd), two hydrophones (240 kHz sampling rate). Approximate locations of the tagged whale were received from the GPS via ARGOS and the VHF beacon was used to pinpoint and track the tagged whale during experiments and to recover the tag after detachment. Dtags were programmed to release the next day (exact time dependent on weather forecast), at which point they automatically detached from the whale and floated while continuously transmitting VHF signals, allowing to locate and recover them.

Once a tag was attached to a whale, this tagged whale became the focal whale of the experiment. The tracking boat then joined the operation and started visual tracking of the tagged whale and its group. The location of the tagged whale was calculated based on the estimated distance from the tracking boat to the whale, the course-over-ground of the vessel, and the azimuth of the whale relative to the vessel’s heading measured by the observers using an angle board. This information was used in real-time to plot the track of the focal whale using the software Logger 2010 (International Fund for Animal Welfare, IFAW).

Visual observations of the surface behaviour of the focal whale and its group were collected from the tracking boat throughout the playback experiments. These behavioural observations followed the protocol described by Visser et al. (2014) and included group size, individual spacing, number of individuals in the focal area (200 m), milling index, and line swimming. The observations were recorded every two minutes or as soon as the tagged whale was visible again thereafter.

2.2 Playback experiments

Playback experiments started after a minimum 2 h recovery period following tag attachment. The playback protocol followed the same general approach previously used with other cetacean species (e.g. Curé et al. 2012, 2015, 2019). The playback source boat was positioned at 500-1000 m in front and 45-60° to the side of the focal whale's track. This position was specified by the tracking boat based upon the focal whale's real-time track.

The playback system consisted of a Tascam DR-40 or DR-40X recorder, a SONY XM-N502 amplifier, and a Lubell LL9162T underwater loudspeaker (frequency response: 0.2–20 kHz) submerged at 8 m depth. Sounds were projected into the water with the boat engine off and monitored using a calibrated hydrophone (Bruel & Kjaer 8104 amplified by a Bruel & Kjaer 2635 charge amplifier) attached at 1 m above the speaker and recording onto a Tascam DR-680MKII to ensure faithful playback.

Three types of acoustic stimuli were used for the playback experiments: long-finned pilot whale sounds, a broadband noise control and a 1-2 kHz upsweep control signal (example spectrograms in Figure S1, Supplementary material). Each stimulus had a duration of 15 minutes. Pilot whale sounds were natural sound sequences previously recorded in the study area using a towed hydrophone array or a Dtag. These recordings—accompanied by visual observations—indicated that pilot whales have higher call rates and produce more overlapped sounds when approaching killer whales during mobbing-like behaviours compared to in other contexts. Therefore, only sound sequences recorded in this distinct context were used as playback stimuli. Any potential killer whale calls, as well as surfacing noises on tag recordings were removed from the stimuli. Broadband noise control stimuli were created using periods without pilot whale sounds in the same recordings. These were amplified to the same averaged sound level as the pilot whale stimuli. The broadband noise control was used to test that killer whales would specifically respond to pilot whale sounds and not to any other sounds generated by the playback system. For both the pilot whale sounds and noise control stimulus types, three different versions, generated from recordings of different pilot whale groups, were used to reduce the risk of pseudoreplication (McGregor 1992). The upsweep control stimulus was composed of a 19 s, 1-2 kHz synthetic sound repeated without pause. This stimulus was used as a second control to test whether any frequency modulated sounds played by the playback system would trigger the same responses as the pilot whale sound stimulus. However, the use of this stimulus was ceased after the first year of field work to maximise data collection for the other two stimuli. As only two experiments were conducted with it, it was excluded from statistical analyses.

The playback level settings were adjusted at the start of each fieldwork season using a sound level meter (Bruel & Kjaer 2250) calibrated with the hydrophone (Bruel & Kjaer 8104) to transmit sound stimuli at a root-mean-square sound pressure level of 150 dB re 1 µPa, within the natural sound level range of pilot whales (Kok et al. 2020).

The timeline of each playback experiment consisted of three phases: a 15 min pre-exposure phase, 15 min of sound stimulus exposure, referred to as during-phase, and a 15 min post-exposure phase. Usually, each focal whale was subject to two experiments (with two types of stimuli) separated by a minimum of 15 minutes between the end of the first post-exposure phase and the start of the second pre-exposure phase. Stimulus types were presented in an alternating sequence to control for any potential order effect (Table 1).

2.3 Ethical statement

Tagging and experiments were approved by the Animal Welfare Ethics Committee at the University of St Andrews, and carried out in compliance with local regulations and under an institutional permit of the Marine and Freshwater Research Institute, Iceland.

2.4 Data processing

Pressure data from the Dtags were converted to depth, correcting for temperature effects. The body orientation of the whale was described in terms of pitch, roll and heading, which were based on acceleration and magnetic field strength (Johnson and Tyack 2003). Speed was calculated from flow noise in the 66-94 Hz band for depths greater than 5 m (Wensveen et al. 2015).

The horizontal track of the whale was estimated using a path reconstruction method, which combines dead-reckoning with the locations from visual sightings or GPS (offloaded from the tag after retrieval) to estimate location at one second intervals (Wensveen et al. 2015). Tag oo23_181b malfunctioned and we were unable to derive the body orientation of the whale from it. Therefore, the track of this whale was based upon linear interpolation between the visual and GPS positions. One large outlier in the GPS locations was identified using the sdafilter function (default speed threshold 2 m/s) of the argosfilter package (Freitas 2022) in R 4.3.0 (R Core Team 2023). This outlier was removed before track interpolation.

Audio recordings from the Dtags were inspected visually and aurally in the software Audacity version 3.3.3 (www.audacityteam.org). Spectrograms (Hann window, NFFT = 8192) were generated and killer whale calls and tail slaps were marked and given a quality rating of 1 (low), 2 (medium), or 3 (high) based on the perceived signal to noise ratio and overall clarity of the frequency contour. High-quality calls and tail slaps were considered to likely be produced by the tagged whale or a close by individual and thus used in further analyses. High-quality calls were classified to call type based on an existing catalogue (Selbmann et al. 2019, 2023). Calls that could not be assigned a call type were considered 'variable' or 'aberrant'. Variable calls are those that cannot be clearly assigned to a discrete category, while aberrant calls can be identified as belonging to a discrete category but show alterations in frequency or duration (Ford 1989). A custom Matlab (The MathWorks Inc. 2023) routine was used to display spectrograms and take measurements of the low frequency contour. Measurements were taken of the fundamental frequency at the start, middle, end, maximum and minimum points, as well as of the duration of the call (see Selbmann et al., 2020 for details).

2.5 State-dependent behavioural response

To identify potential changes in behaviour, hidden Markov models (HMMs) were applied to time series data derived from the high-resolution movement and acoustic data from the Dtags. HMMs identify the most likely underlying, non-observable (i.e. hidden) process. The states of the Markov chain can be interpreted as behavioural states and HMMs have been widely used to characterise animal movement data, including in cetaceans (e.g. DeRuiter et al. 2017; Quick et al. 2017; Isojunno et al. 2017; Wensveen et al. 2019; Tennessen et al. 2019; Southall et al. 2023). However, patterns identified by the these models may not relate to biologically meaningful behaviours and states may include multiple behaviours or the same behaviours may occur in more than one state (Patterson et al. 2017). Therefore, models need to be informed by knowledge on the behaviour of the study species and population.

We created a multivariate HMM with five variables at 5-minute resolution: step length, turning angle, mean depth, acoustic presence/absence of calls, and acoustic presence/absence of tail slaps. Step lengths and turning angles were calculated from the horizontal movement track. Mean depth were the mean depths of the whale over the 5-minute time intervals. The presence/absence of (one or more) calls and presence/absence of (one or more) tail slaps were extracted from the acoustic record of the tag. Icelandic killer whales have the highest calling rates when feeding and are mostly silent when travelling (Simon et al. 2007; Samarra and Miller 2015). During feeding on herring, killer whales also use underwater tail slaps to debilitate fish (Similä and Ugarte 1993; Simon et al. 2005). Therefore, calls and tail slap sounds can aid in the identification of behavioural states. Gamma distributions were used to model step length and mean depth. Turning angles were modelled as a von Mises distribution, and the presence/absence of calls and tail slaps as Bernoulli distributions.

A model with three states was selected over models with two or four states based on Akaike's Information Criterion (AIC) and biological interpretability. This 3-state model separated the data into a ‘travel’ state (state 1), a ‘feeding’ state (state 2), and a third state that likely included several behaviours, such as resting or socialising. State 3 was named ‘other’ following Simon et al. (2007). Assuming an avoidance response would involve a switch from the feeding or other state to the travelling state, we included a covariate ‘playback’ affecting state transitions to the travelling state. The playback covariate was a factor with three levels: Off (all periods without playback), Noise (noise control), PW (pilot whale sounds). We expected step length (and thus speed) to increase and calling to decrease in the travelling state, which was tested by incorporating the same covariate on the state-dependent observation distributions. Model-based estimates with 95% confidence intervals (CIs) were used for inference and the most likely state for each time step was predicted using the Viterbi algorithm. All analyses were conducted using the momentuHMM package (McClintock and Michelot 2021) in R 4.3.0 (R Core Team 2023).

As playbacks were 15 minutes long and the data were in 5-minute time steps, each sound exposure had a duration of three time steps. The 1-2 kHz upsweep control stimulus was pooled with the Off level (n = 1,443 data points), as a separate covariate level for this stimulus would consist of only six data points but would also increase the number of estimated parameters by two (one for each possible transition to the travelling state).

2.6 Horizontal movement response

We expected killer whales to move away from the pilot whale sound playback source, which was tested using a horizontal movement reaction score. This reaction score compares the observed horizontal track during playback to a projected course of the whale based on its direction of movement prior to the start of the playback (Curé et al. 2012). Similar to the approach used in the HMMs, a 5-minute time interval was chosen to create the projection. The reaction score is a relative measure; negative values represent an overall avoidance response, meaning the animal was farther at the end of playback compared to where it would have been if it would have kept its original course and average speed (projected position); while positive scores represent an attraction response as the animal position is closer to the source at the end of playback compared to the projected position. General Estimating Equations (GEEs) were used to analyse differences in the reaction scores between pilot whale and noise control stimuli, as they included repeated measures of the same individuals (details in the next section).

2.7 Acoustic and group behaviour responses

Several variables of group behaviour and acoustic responses were tested using GEEs. Here, we investigated changes between PRE_DUR and PRE_POST, i.e. changes between the 15-minute pre- and during-phases and changes between the pre- and post-phases. The change from the pre- to the during-phase captures the quantitative change occurring during the exposure, whereas the change from the pre- to the post-phase assesses whether a potential change that started during the exposure is prolonged over the post-phase or whether a change started during the post-phase rather than the during-phase. We expected killer whales might go silent in response to pilot whale sounds to avoid detection and thus investigated changes in the calling rate (number of calls corrected by focal group size). On the group behaviour level, we tested for changes in group size and organisation. We tested for changes in group size by looking at the mean number of individuals in the group of the tagged whale, and the maximum number of individuals in the focal area (200 m). To calculate the PRE_DUR and PRE_POST scores for calling, focal group size and individuals in the focal area, we subtracted the value of the pre-phase from the value of the during- or post-phase, respectively. Changes in group organisation were tested by investigating changes in the spacing between individuals, changes in line swimming (travelling on the same horizontal line) and changes in the milling index (heading into different directions). These variables were converted into reaction scores, which represent increases or decreases of the behavioural variables observed but do not represent absolute values.

To capture any potential tightening or spreading of the group members, individual spacing was recorded as a categorical value based on the distance in body lengths (BL) between the focal individual and the nearest individual. <1 BL is translated to a score -1 (very tight), 1-3 BL to a score 0 (tight), 3-15 BL to a score 1 (loose), >15 BL to a score 2 (very loose), and no other whales to a NA score because the animal was solitary. The maximum individual spacing score value was recorded for each 15 min phase. Milling and line swimming were recorded as present or absent. Given an absence of milling (all group members heading into the same direction) is the most common behaviour, we assessed whether there was at least one milling event recorded over each 15 min phase (Yes or No). Swimming on the same horizontal line was variable and therefore we assessed for each phase whether there was a majority of line swimming (Yes or No). The change scores PRE_DUR and PRE_POST for milling and line swimming were then obtained as follows: change from No over the pre-phase to Yes over the during- or the post-phase was given a score value of +1, whereas Yes to No was scored as -1. No change (No/No or Yes/Yes) was scored as 0 (no change).

In all GEEs the focal animal ID was used as a blocking unit to account for correlation between observations. We tested effects of the explanatory variables Stimulus (pilot whale, noise control), Order (1 or 2), Phase (PRE_DUR or PRE_POST), and an interaction term

Stimulus:Phase. Response variables were the horizontal movement reaction score, change in the number of calls, change in focal group size, change in individuals in the focal area, change in individual spacing, change in line swimming, and change in milling. For each response variable we first ran a full model with all explanatory variables and then selected models using backwards selection based on p-values given by an ANOVA (sequential Wald test, detailed methods in Curé et al., 2015). GEEs were run in R 4.3.0 (R Core Team 2023) using the geepack package (Højsgaard et al. 2006) and results were considered statistically significant at the 5% level.

3 Results

A total of eight tags were deployed on killer whales and 15 playback experiments were conducted: eight of pilot whale sounds, five of noise control, and two of the 1-2 kHz upsweep signals (Table 1). Generally, two experiments were conducted per tag deployment (one of pilot whale sounds and one with either the noise control or 1-2 kHz upsweep control), but for one deployment (oo23_181b) the second control experiment could not be conducted because of deteriorating weather conditions. Due to the low sample size the 1-2 kHz upsweep stimulus was not included in statistical analyses, but descriptive analyses of the responses are provided in sections 3.2-3.4.

Table1: Summary of Dtags deployed, and playback experiments conducted on killer whales in Iceland. Stimulus types are long-finned pilot whale sounds (PW), noise control (Noise), and 1-2 kHz upsweep control (Upsweep) and are given in chronological order. Individual ID is based on photo-identification from an existing catalogue (Samarra et al. 2017b). Age-sex class is given as female (F), male (M), or juvenile (J) at the time of tagging.

Tag ID	**Stimulus type**	**Stimulus version**	**Individual ID**	**Age-sex class**	**Deployment duration (hh:mm)**	**Playback start date and time**
oo21_184a	PW	1	IS064	F	19:54	2021-07-03 19:00:37
	Noise	1				2021-07-03 20:13:25
oo21_189a	Noise	2	IS406	F	17:26	2021-07-08 19:18:29
	PW	2				2021-07-08 20:19:38
oo21_199a	PW	3	IS118	M	17:03	2021-07-18 19:27:03
	Upsweep	NA				2021-07-18 20:26:56
oo21_202b	Upsweep	NA	IS273	M	17:28	2021-07-21 20:41:07
	PW	1				2021-07-21 21:57:11
oo22_228a	PW	2	-	J	04:38	2022-08-16 18:54:51
	Noise	2				2022-08-16 20:04:08
oo23_181a	Noise	3	IS291	M	24:46	2023-06-30 18:54:07
	PW	3				2023-06-30 20:14:20
oo23_181b	PW	1	IS401	M	23:59	2023-01-07 11:53:29
oo23_188a	PW	3	IS003	M	21:09	2023-07-08 10:15:30
	Noise	3				2023-07-08 11:36:51

3.1 State-dependent behavioural response

The fitted hidden Markov model had three states (Figures 1 and 2): state 1, labelled 'travel', was characterised by fast, directed horizontal movement, shallow to intermediate dive depths, and low probabilities of calling and tail slaps; state 2, labelled 'feeding', was characterised by slow, undirected horizontal movement, deep dives and high probabilities of calling and tail slaps; and state 3, named 'other', represented slow, undirected horizontal movement at shallow dive depth and intermediate probabilities of calling and tail slaps. The third state (other) was most commonly assigned (53%), followed by travelling (31%) and feeding (16%), but these percentages substantially varied among the individuals (Figure 1f). The model fitted the data well, but some autocorrelation remained in the residuals for step length, mean depth and presence/absence of calls (Figures 1, S2, supplementary material).

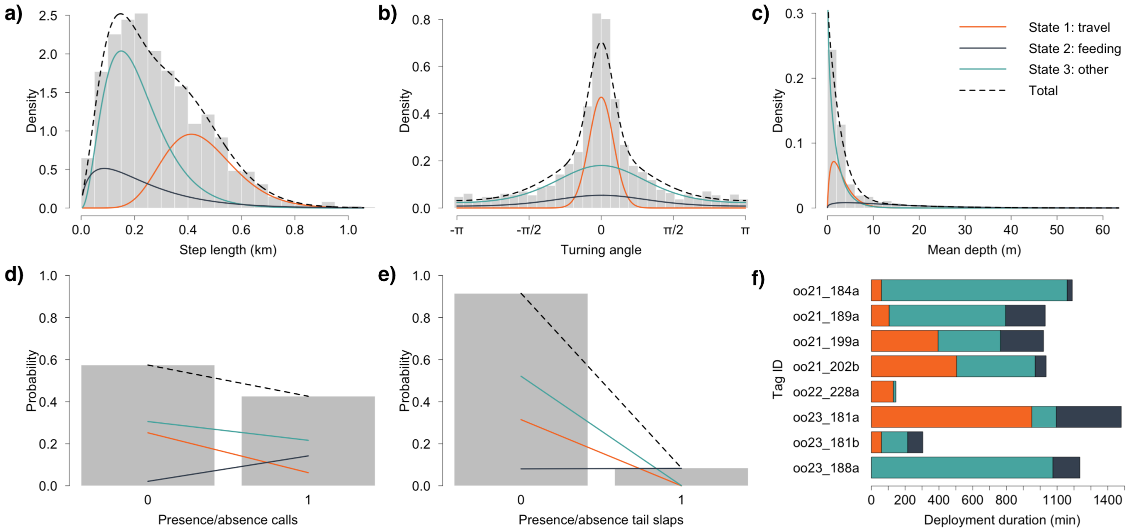

Figure 1: Summary of the hidden Markov model fitted to behavioural data from killer whales. Fitted state dependent distributions for a) step length, b) turning angle, c) mean depth, d) presence/absence of calls, e) presence/absence of tail slaps, and time spent in each state per tag deployment (f). State 1 (travel) is indicated in orange, state 2 (feeding) in dark blue, state 3 (other) in turquoise, and the summed density distribution is shown as a black dashed line.

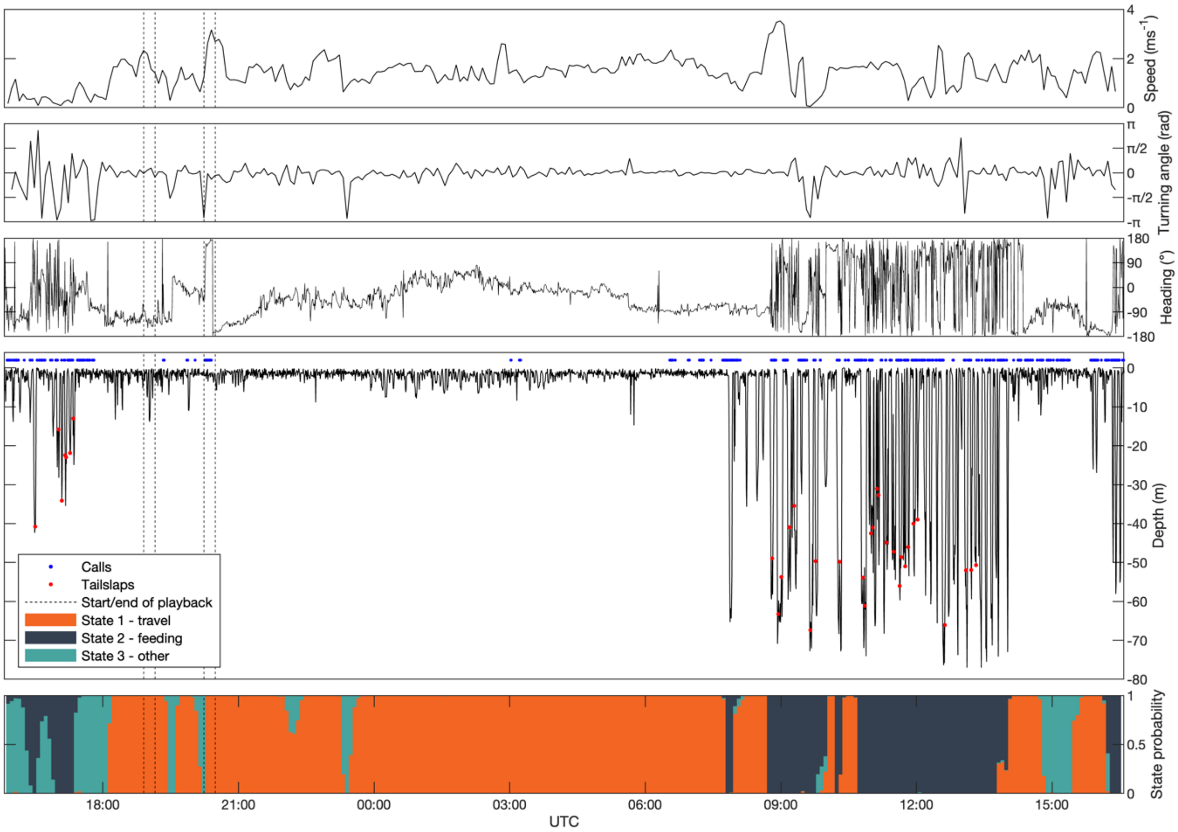

Figure 2: Example timeseries data obtained from a Dtag deployment on a killer whale exposed to noise control (first playback) and pilot whale sounds (second playback). Panels show (top to bottom): forward speed (m/s) calculated from step length, horizontal turning angle (radians), heading (degrees re North), depth (m), and the probability of being in each of the three states predicted by the HMM. State 1 (travel) is indicated in orange, state 2 (feeding) in blue and state 3 (other) in turquoise. The dive profile includes tail slaps and calls, shown as red and blue dots respectively. The start and end times of each playback are indicated with a dotted line. Speed, turning angle, and state probabilities are plotted in 5-minute steps as used in the HMM, the heading and depth are shown at 30 s time resolution.

The probability of switching from the other state (#3) to the travelling state (#1) was significantly increased for both pilot whale sound and noise control playbacks compared to periods without playback (Figure 3b). This transition probability was predicted to increase from 0.04 (CI: 0.03 - 0.06) when there was no playback to 0.19 (CI: 0.06 - 0.46) during pilot whale sounds and 0.29 (CI: 0.06 - 0.74) during noise control. Switching from the feeding state (#2) to the travelling state (#1) was not affected by the playback (Figure 3a), but the feeding state was rarely assigned to time periods immediately before, or during, a playback.

Within the travelling state, the horizontal step lengths were significantly longer during pilot whale sound playback (estimate: 0.80 km, CI: 0.70 - 0.90) compared to during noise control (estimate: 0.49 km, CI: 0.41 - 0.57) or when there was no playback (estimate: 0.45 km, CI: 0.44 - 0.47, Figure 3c). This reflects an increase in mean horizontal speed from 1.5 m/s for periods without playback to 2.7 m/s during playback of pilot whale sounds.

Call presence in the travelling state was similar for pilot whale sound playbacks compared to noise control playbacks or non-playback periods (Figure 3d). The probability of calling was predicted to be 0.25 (CI: -0.06 - 0.56) during pilot whale sound playback compared to 0.20 (CI: 0.16 - 0.24) when there was no playback and 0.09 (CI: -0.08 - 0.27) during playback of the noise control (Figure 3d).

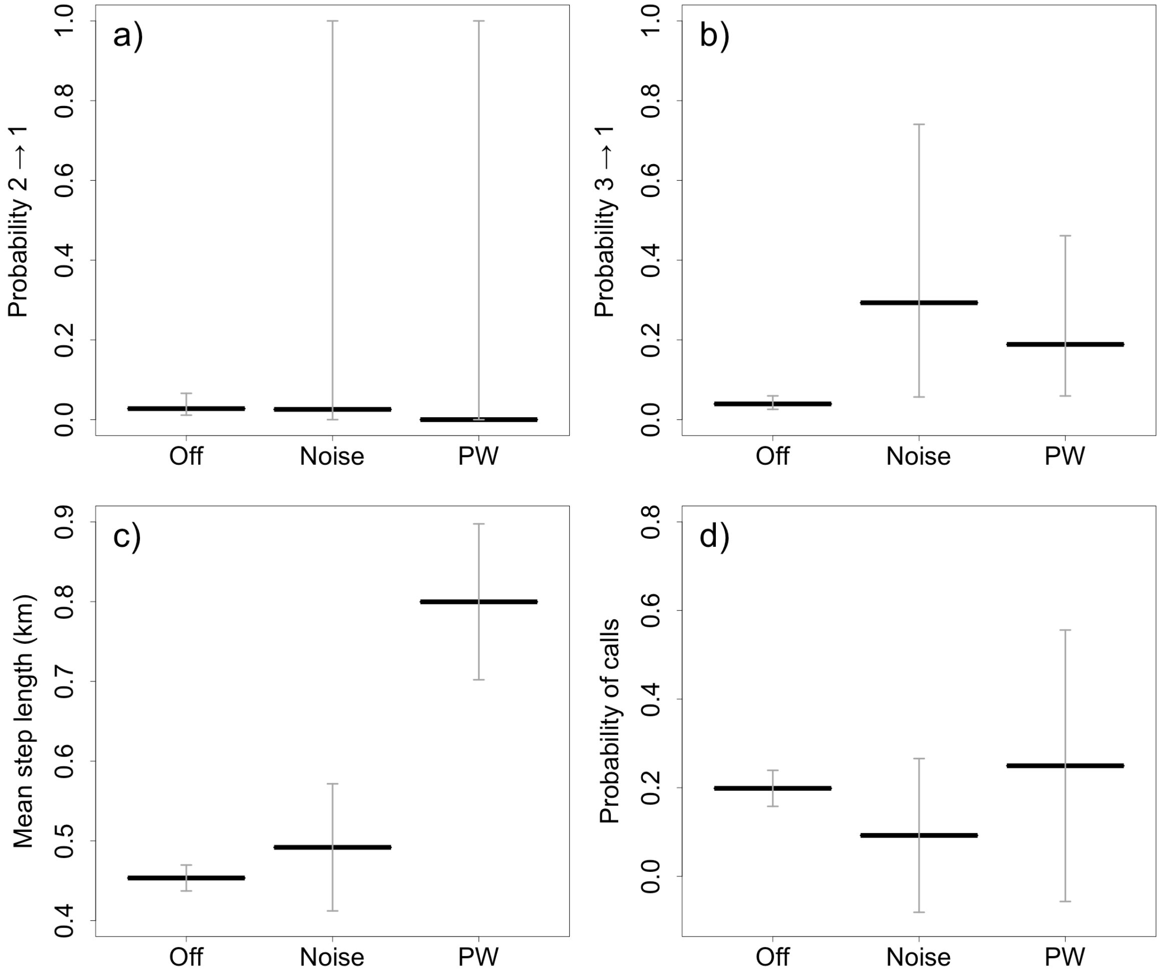

Figure 3: HMM-based predictions of behavioural changes of killer whales in response to pilot whale (PW, n = 24 data points from 8 experiments) and noise control (Noise, n = 15 data points from 5 experiments) sounds compared to non-playback periods (Off, n = 1,449 data points from times without playback including 6 with upsweep control): estimated transition probabilities from a) state 2 (feeding) to state 1 (travel) and b) state 3 (other) to state 1 (travel); c) mean step length (km) in the travelling state; and d) probability of calling in the travelling state. Error bars indicate 95% confidence intervals.

3.2 Horizontal movement responses

The pilot whale stimulus and the second playback generally had the lowest (i.e. most negative, indicating avoidance) horizontal movement reaction scores (Figure 4). The best GEE retained the explanatory variables Stimulus and Order, and both had a significant effect on the movement reaction scores (Stimulus: p = 0.02; Order: p = 0.004, Table 2). The mean horizontal movement reaction score was -82.2 (SD = 106.0) for pilot whale sound playbacks and -25.5 (SD = 88.5) for noise control playbacks. The mean value for the noise control playback was particularly influenced by the score for one individual (oo21_184a) and would have been positive without this data point. This individual did not show a clear turn away from the sound source, but the late start of the experiment led to a negative reaction score (Figure S3, supplementary material).

Four out of eight tagged whales tested with pilot whale sounds were judged to change direction away from the source during the playback (Figures S3-S10, supplementary material). Two whales (oo21_199a, oo23_188a) were already moving away from the source when the playback began and kept swimming away, one increasing its speed. Another two tagged whales (oo21_189a, oo22_228a) did not make a clear turn away from the sound source but both increased speed, which moved them past the sound source. In contrast, four of the five whales tested with the noise control did not show a clear response to the playback and only one whale showed a clear turn away from the sound source (oo22_228a). Another one (oo21_184a) slightly increased speed, while the other tagged whales decreased speed or showed no changes. In both experiments with the 1-2 kHz upsweep a turn away from the sound source was observed (oo21_199a, oo21_202b, Figures S5 and S6, Supplementary material), which is reflected in slightly negative horizontal movement reaction scores (Figure 4).

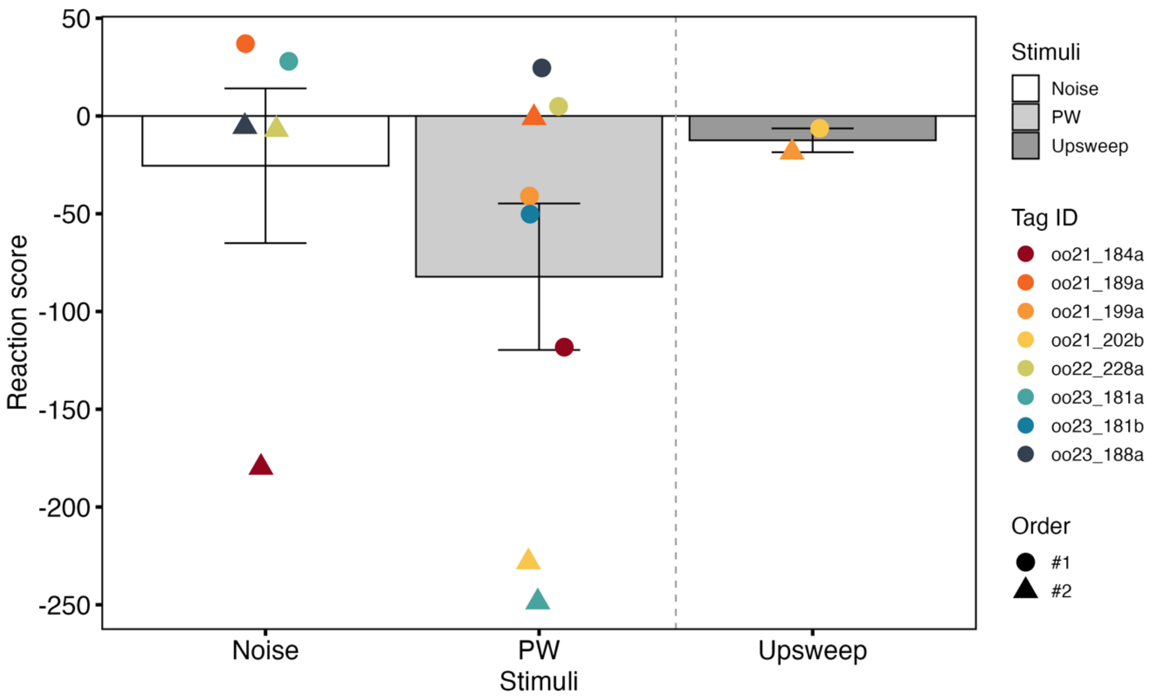

Figure 4: Predicted mean (± one standard error) horizontal movement reaction score of killer whales during noise control (white), pilot whale (light grey) and 1-2 kHz upsweep control (dark grey) sound playbacks. Individual data points are overlayed and coloured by tag deployment. The order of the experiment is shown as a circle (first playback) or triangle (second playback). Note that 1-2 kHz upsweep control playbacks were not included in the GEE.

*Table 2: Summary of the results of the best fitting General Estimating Equation (GEE) for killer whales tested using pilot whale sound and noise control stimuli. GEEs were selected based on p-values below 0.05 in the ANOVA tables (Table S1, Supplementary material). Results show the response variable coefficients, which represent the difference between explanatory variable levels. The reference levels for the explanatory variables were: Noise for Sitmulus, first order for Order, and change PRE_DUR for Phase. If the fitted model had an interaction term (Stimulus:Phase), only the p-value and coefficient for the interaction term could be interpreted. P-values are marked * at a significance level <0.05.*

Response variable	**Explanatory variable (reference level)**	**Response variable coefficient ± SE**	**Wald test statistic**	**p-value**
Horizontal movement	Stimulus (Noise)	-82.1 ± 35.5	5.4	0.02*
	Order (first)	-112.8 ± 39.5	8.2	0.004*
Number of calls	Stimulus (Noise)	0.2 ± 3.6	0	0.96
	Phase (PRE_DUR)	2 ± 1.6	1.5	0.22
	Stimulus:Phase (Noise :PRE_DUR)	-6.4 ± 2.2	8.2	0.004*
Individual spacing	Stimulus (Noise)	-0.7 ± 0.2	8.1	0.004*
	Order (first)	-0.5 ± 0.2	4.7	0.03*
Line swimming	Stimulus (Noise)	0.4 ± 0.1	7.8	0.005*
	Phase (PRE_DUR)	-0.3 ± 0.1	6.4	0.01*
Milling	Stimulus (Noise)	-0.5 ± 0.4	1.2	0.28
	Phase (PRE_DUR)	-0.4 ± 0.2	3.3	0.07
	Stimulus:Phase (Noise:PRE_DUR)	0.7 ± 0.3	5.9	0.02*

3.3 Acoustic responses

The total number of high-quality calls recorded was 284 in the eight pilot whale sound playbacks (n_{pre} = 49, n_{during} = 220, n_{post} = 15), 123 for the five noise control playbacks (n_{pre} = 22, n_{during} = 22, n_{post} = 79), and 115 for the two upsweep control playbacks (n_{pre} = 46, n_{during} = 42, n_{post} = 27). The mean number of calls adjusted for group size was 4.6 calls/individual in the pre-phases of the pilot whale sound playbacks, 4.7 calls/individual in the during-phases, and 0.2 calls/individual in the post-phases. The small difference between the mean number of calls/individual in the pre- and the during-phase was primarily due to one experiment (oo23_181b) with a high number of calls in the pre-phase, but in most experiments killer whales either increased their number of calls or showed only small changes in the during-phase (Figure 5). In the post-phase, five out of eight whales did not make any calls, and the other three whales produced only a few sounds. For the noise control playback, the mean number of calls adjusted for group size was 0.9 calls/individual in the pre-phases, 0.7 in the during-phases, and 2.8 in the post-phases. Most of these calls (n = 109) stem from one experiment (oo23_188a) and in the others whales were either silent and stayed silent or made just a few calls (Figure 5). For the upsweep control playbacks, a mean of 7.7 calls/individual were recorded in the pre-phase, 8.2 calls/individual in the during phases, and 4.0 calls/individual in the post-phases. The selected GEE retained Stimulus, Phase and the interaction Stimulus:Phase as explanatory variables and predicted a reduction in call production in the post-phase compared to the pre-phase when the playback was of pilot whale sounds (Stimulus:Phase: $p < 0.01$, Table 2, Figure 5).

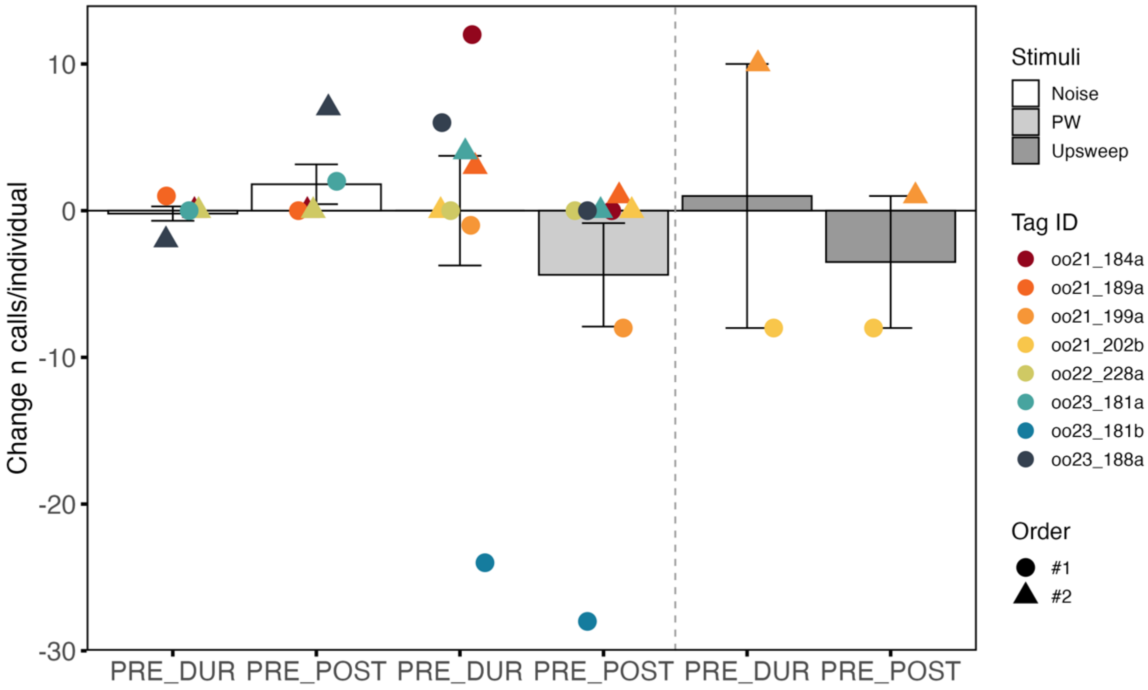

Figure 5: Mean changes in calling rates of killer whales in response to noise control (white), pilot whale (light grey) and 1-2 kHz upsweep control (dark grey) sound playbacks. Individual data points are overlayed and coloured by tag deployment. The order of the experiment is shown as a circle (first playback) or triangle (second playback). Error bars indicate the standard error. Note that 1-2 kHz upsweep control playbacks were not included in the GEE

Measurements of the fundamental frequency and duration of calls were taken of a total of 249 calls for pilot whale sound playbacks ($n_{pre} = 40$, $n_{during} = 195$, $n_{post} = 14$), 103 for calls for noise control playbacks ($n_{pre} = 17$, $n_{during} = 20$, $n_{post} = 66$), and 96 for upsweep control playbacks ($n_{pre} = 43$, $n_{during} = 29$, $n_{post} = 24$). Measurements of the mid, end, and maximum frequencies showed an increase in the during-phase for the pilot whale and noise control stimuli, as did the duration of calls for the noise control playbacks (Figure S11, supplementary material). These increases might be driven by individual differences between tag deployments or call types used, however, not enough calls from different experiments were recorded in the pre-phases to make statistical comparisons.

In total, 21 different call types and subtypes were recorded in the pre-, during- and post-phases of the experiments (Figure S12, supplementary material). For pilot whale sound playbacks, 9 different call types were recorded in the pre-phases, which increased to 11 in the during-phases, 5 of which were the same as in the pre-phases. In the post-phases 6 call types were recorded, all except one of them being also recorded in the previous two phases. Aberrant calls were only recorded in the during-phases, as was a high proportion of variable calls. The low number of calls recorded in noise control playbacks was reflected in only 4 call types being present (1 in the pre-phases, 3 in the during-phases, 3 in the post-phases), with no aberrant or variable call types being recorded. During the upsweep control playbacks, a total of 10 call types (9 in the pre-phases, 4 in the during-phases, 5 in the post-phases) as well as variable calls were recorded.

3.4 Group behaviour responses

The best GEEs for the mean number of individuals in the focal group as well as the maximum number of individuals in the focal area did not retain any of the explanatory variables, indicating no significant difference, although both tended to increase during pilot whale sound compared to noise control playbacks (Figure 6a and b). Group organisation, on the other hand, showed several significant changes between pilot whale and noise control playbacks. The spacing between individuals decreased significantly during playback of pilot whale sounds (Stimulus: $p = 0.004$, Table 2, Figure 6c) and during the second playback (Order: $p = 0.03$, Table 2). Killer whales also showed a horizontally lined-up geometry more often in response to pilot whale sounds compared to noise control playbacks (Stimulus: $p = 0.005$, Table 2, Figure 6d) and this effect reduced during the post-phase (Phase: $p = 0.01$, Table 2). Milling on the other hand, was observed less frequently only during pilot whale sound playback and over the post-phase of the noise control playback (Stimulus:Phase: $p = 0.02$, Table 2, Figure 6e). During playbacks of the upsweep control, individuals increased their spacing but no changes were observed in line swimming or milling (Figure 6).

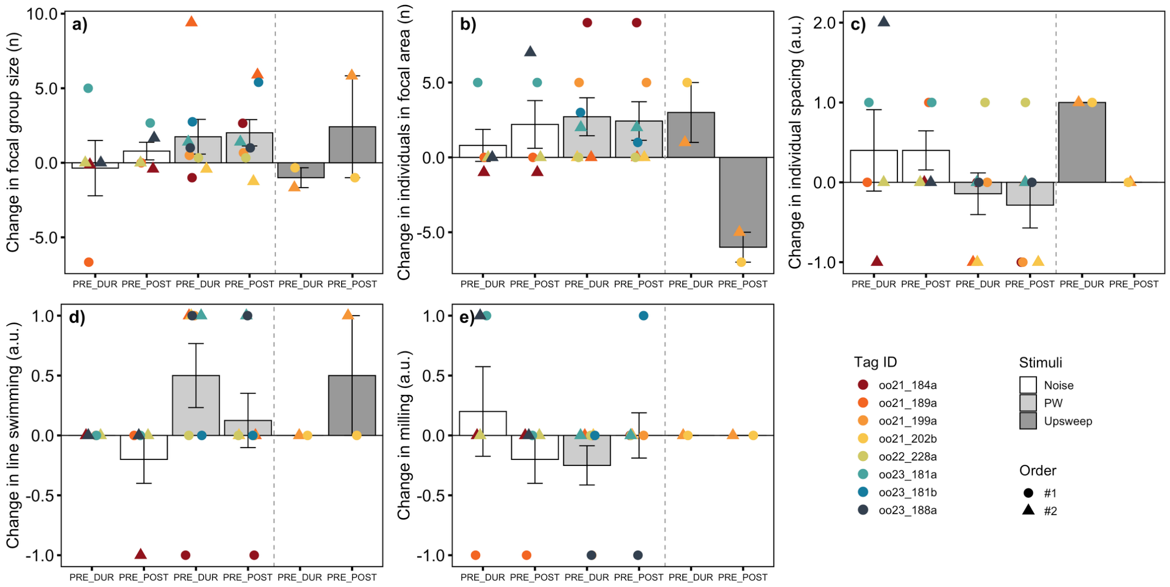

Figure 6: Mean changes in group behaviour parameters observed in killer whales in response noise control (white), to pilot whale sound (light grey) and 1-2 kHz upsweep control (dark grey) sound playbacks: a) mean number of animals in the focal group, b) maximum number of individuals in the focal area (200 m), reaction scores (arbitrary unit) of c) maximum spacing between individuals, d) line swimming, and e) milling. Individual data points are overlayed and coloured by tag deployment. The order of the experiment is shown as a circle (first playback) or triangle (second playback). Error bars indicate the standard error. Note that 1-2 kHz upsweep control playbacks were not included in the GEEs.

Discussion

Interspecific interactions between cetaceans have been observed widely but are often poorly understood and mechanisms remain unclear. Our results indicate that killer whales show an avoidance response to the sounds of pilot whales. This response is marked by a switch to travelling behaviour, increased speed and directed movement away from the sound source. Killer whales initially increased calling rates at the start of the playback but then became silent. They adjusted their group behaviour to increase cohesion, by tightening the spacing between individuals, aligning side by side and all moving in the same direction. These results are consistent with observations of real interactions, where killer whales avoid pilot whales and sometimes flee at high speed (Stenersen and Similä 2004; de Stephanis et al. 2014; Selbmann et al. 2022). As previous work demonstrated that pilot whales are attracted to killer whale sounds (Curé et al. 2012, 2019), our study demonstrates that acoustic signalling can mediate these interspecific interactions in both directions.

This study is, to our knowledge, the first to conduct playbacks of heterospecific sounds to killer whales and clearly shows their behavioural sensitivity to acoustic signals or cues from other species. In a few of our experiments, a weak response to the noise control sounds was recorded. Killer whales have a sophisticated acoustic communication system, consisting of echolocation clicks, burst-pulse calls and whistles that aids their prey detection and social communication (Ford 1989). For example, playbacks of conspecific sounds have shown that killer whales respond differently to playbacks of calls from their own compared to other pods (Filatova et al. 2011). Therefore, it is consistent that they also use sounds from other species to make decisions on behaviour.

The movement response observed here is consistent with avoidance responses by killer whales to naval sonar. As in our experiments, killer whales that were experimentally exposed to sonar typically switched to a travelling behaviour, with directed movement away from the sound source and increases in speed (Miller et al. 2012, 2014). Avoiding a potential perceived threat by moving away (i.e. negative phonotaxis) is a common threat-response across taxa, as has been shown in birds, terrestrial and marine mammals (Caro 2005). In cetaceans, playbacks of killer whale and/or sonar sounds led to movement away from the sounds source in sperm whales (*Physeter macrocephalus*, Curé et al. 2016), minke whales (*Balaenoptera acutorostrata*, Kvadsheim et al. 2017), humpback whales (*Megaptera novaeangliae*, Curé et al. 2015; Wensveen et al. 2017; Benti et al. 2021), blue whales (*Balaenoptera musculus*, Goldbogen et al. 2013), and several beaked whale species (Ziphiidae family, (Tyack et al. 2011; DeRuiter et al. 2013b; Stimpert et al. 2014; Miller et al. 2015; Wensveen et al. 2019). In many cases this movement away was accompanied by increases in speed (DeRuiter et al. 2013b; Stimpert et al. 2014; Curé et al. 2015; Kvadsheim et al. 2017; Wensveen et al. 2019), and reflected in behaviour state changes, such as cessation of feeding (Isojunno et al. 2016, 2017b; DeRuiter et al. 2017). The movement responses observed in our study likely reflect an aversive response in killer whales, demonstrating that they perceive pilot whale sounds as a potential threat.

Based on our observations in the field and responses of other cetaceans to threatening acoustic stimuli (e.g. Fish and Vania 1971; Deruiter et al. 2013a), we had expected killer whales to go silent in response to pilot whale sound playbacks in order to avoid detection or localisation by pilot whales or as part of the switch to a travelling state, during which Icelandic killer whales tend to be silent (Simon et al. 2007). However, we found that the probability of call production in the travelling state was comparatively high during pilot whale sound playbacks and significant decreases in calling rate were only detected in the post-phase. In several experiments, there was an initial increase in calling during the playback, followed by a decrease and often total cessation of calling. The initial increase in calling contained a large proportion of variable calls and some aberrant calls, the latter not being recorded during other phases of the experiments. We also observed increases in call frequency but could not confirm whether these were true changes in call features, individual differences or related to changes in call type usage. Similar responses were observed during controlled sonar exposure experiments, where killer whales showed changes in call frequency as well as initial increases in call rate, with more variable and aberrant calls, followed by a decrease in calling (Samarra et al. in review). Samarra et al. suggested that such a two-step response may be a way to coordinate behaviour in the group before moving away. It is likely that at the start of an interaction there is little benefit in going quiet as pilot whales would have already detected and localised killer whales at this point and it might instead be advantageous to alert conspecifics and coordinate behaviour. Alternatively, the increase in calling rate we observed might also be linked to the tightening of the group during exposure, which could have led to more individuals vocalising in close proximity to the tagged whale and thus more high-quality calls being detected. However, we also observed increases in frequency, variable and aberrant calls, which are thought to indicate excitement (Ford 1989). Thus, alarming conspecifics is a plausible function of this response.

The fact that no significant increases in focal group size or individuals in the area were observed, suggests that alarming conspecifics did not lead to recruitment of other groups. Predation risk is thought to be a major reason for group living across taxa (Ward and Webster 2016) and several species show grouping responses to perceived threats (Curé et al. 2013, 2019; Visser et al. 2016; Pierry et al. 2023). However, large groups may be more conspicuous and if part of the strategy of killer whales avoiding pilot whales involves minimizing attention, then increasing group size may be disadvantageous. We did observe a tightening of the group and more synchronised behaviours, such as line swimming and reduced milling. Part of the alignment of the group and reduction in milling is likely due to a change to travel behaviour, which includes more directed movement. Nevertheless, synchronisation is an important threat response in many group-living species (Bode et al. 2010; Prokopenko et al. 2024) and reduction of spacing was observed, for example, in long-finned pilot whales approaching killer whale sounds (Visser et al. 2016; Curé et al. 2019), as well as in several baleen whales in response to killer whale attacks (Ford and Reeves 2008). Killer whales exposed to sonar also responded with tightening of the group and increased synchrony (Miller et al. 2014). Tightening and synchronised movement have several benefits, such as reduced individual vulnerability, confusion of an attacker, as well as rapid information transmission to aid collective response (Krause and Ruxton 2002; Couzin 2018).

Under the risk-disturbance hypothesis, animals respond similarly to human disturbance and predation threat stimuli, based on the trade-off between the perceived risk and the reduction of fitness-enhancing activities (Frid and Dill 2002). Recent comparisons across cetacean species confirmed that responses to a high-level predation threat represented by mammal-eating killer whale sound playback are closely correlated to responses to perceived risk from sonar and depend on whether the species typically exhibit fight- or flight-behaviour (Miller et al. 2022). The responses we observed from killer whales to pilot whale sound playback indicate that either they perceive them as a relatively high-level threat, or that cost of avoidance is low. If killer whales perceive pilot whales as a threat, it remains unclear why. Despite interactions being observed in several locations and over several years, physical attacks or predation of pilot whales on killer whales has never been reported (Stenersen and Similä 2004; de Stephanis et al. 2014; Selbmann et al. 2022). Larger group sizes of pilot whales led to stronger responses by killer whales, suggesting that group size could play a role (Selbmann et al. 2022). In our experiments, responses rarely seemed to last much beyond the end of the playback. Often, killer whales reduced speed again immediately, stopped moving away from the sound source and the group returned to less aligned swimming behaviour within the 15-minute post-phase. Only once were killer whales in a feeding behaviour state directly before the start of the playback. While they immediately stopped feeding in response to the pilot whale sounds, they resumed relatively soon after the second playback of the experiment had finished (oo21_199a, Figure S5, Supplementary material). The area where experiments were conducted is a known herring spawning ground (Jakobsson and Stefánsson 1999) and during the summer herring is abundant but patchily distributed. Killer whales never left the general area in response to a playback, indicating that a short-term avoidance may be of little cost to them as they might be able to easily locate new feeding locations. In observations of interactions pilot whales eventually abort a pursuit and the two species often remain a few hundred meters apart until either the pilot whales leave the area or approach again (Selbmann et al. 2022). This demonstrates that these interactions are complex, and while individual responses may be of little costs to the killer whales it remains unclear what the cumulative effect of disturbance by repeated approaches is.

Unlike in reports of interactions (Selbmann et al. 2022) we never observed killer whales surfacing at very high speed (porpoising) during our playback experiments. This could indicate that the killer whales realised that the simulated group of pilot whales was not approaching or following them. It also illustrates that detecting the acoustic signals of pilot whales early on might help killer whales adjust their behaviour in time to avoid energetically costly behaviour such as porpoising. Response thresholds are likely influenced by several factors. These could be the context of the playback (Goldbogen et al. 2013; Friedlaender et al. 2016; DeRuiter et al. 2017), such as their group size, current behaviour, prey availability, or presence of calves; or information within the acoustic signals of the pilot whales, such as number of individuals, threat level, distance, or movement direction. Indeed, we observed some variation in the levels of responsiveness. For example, weaker or no responses were recorded in the two playbacks of one of the three pilot whale sound stimuli (version 2). Pilot whales increased calling rates in response to killer whale sounds (Visser et al. 2016; Curé et al. 2019) and we were careful to select recordings for our stimuli that were collected during observations of mobbing-like approaches of pilot whales to killer whales. Closer inspection of the stimuli revealed that version 2 had slight differences in the energy distribution across frequencies compared to the other two stimuli, which could indicate for example, the use of different call types. The observed variation in the response indicates that killer whales may perceive subtle variations in the sounds of pilot whales and mirrors the variation observed in responses to real pilot whale approaches (Selbmann et al. 2022). Future experiments using stimuli from pilot whales in different behaviour states (e.g. during socialising, which might be more neutral for killer whales) and from other populations could clarify whether killer whales respond to any pilot whale sounds. In addition, playback experiments on killer whales in different behavioural or prey contexts could help determine variation in response thresholds and the potential costs of avoidance, which would have implications for predictions of the impacts of these interactions for killer whales.

Two playbacks of a 1-2 kHz upsweep were conducted in 2021 but not statistically analysed due to the small sample size. This signal is representative of a continuous active sonar (CAS) signal that navies use at a much higher source level. The difference in this sonar type compared to previously tested conventional pulsed active sonar (PAS) is that there is no pause between individual sonar pings, which could lead to different types or severity of responses in cetaceans (Isojunno et al. 2020; Curé et al. 2021). The movement and acoustic responses we observed during the two 1-2 kHz upsweep playbacks were similar to those observed during previous controlled exposure experiments with sonar signals (Miller et al. 2012, 2014) and to the responses observed to pilot whale sounds in this study. However, on the group behaviour level differences were observed. For example, individual spacing increased during exposure to the upsweep signal, contrasting with the group tightening observed in response to the pilot whale sound playback. This shows that killer whales do not exhibit all same behavioural components in response to pilot whale sounds and to the 1-2 kHz upsweep control, which indicates that they are able to discriminate between pilot whales and a synthetic modulated sound in the same frequency range and adjust their behaviour according to the type of perceived threat.

In summary, our results demonstrate that killer whales exhibit a clear aversive response to long-finned pilot whales sounds, consisting of an avoidance response and increase in group cohesion. In combination with results of previous studies on pilot whales (Curé et al. 2012, 2019), this shows that interactions between the two species are acoustically mediated in both directions by detecting, and responding to, each other’s calls. The response of killer whales encompassed their movement, acoustic and social behaviour. While individual responses did not seem to extend much beyond the end of the sound exposure, cumulative long-term impacts of the interactions between killer and pilot whales remain unknown. Killer whales may abandon feeding events and expend high amounts of energy during avoidance, which could have energetic consequences. Repeated interactions between the species may also lead to changes in behaviour and habitat use, which could have population level effects that cascade down the food chain. While our study clearly demonstrates the behavioural mechanism of the interaction, potential drivers still remain unclear and future research on the trophic ecology, site fidelity and habitat use of both species could help to better understand whether competition or an anti-predator strategy are responsible. In many animal species, the severity of responses to human disturbance is assessed in comparison to anti-predator responses, which typically represent a reference response to a natural high-level threat (Frid and Dill 2002; Curé et al. 2016; Harris et al. 2018; Miller et al. 2022). Our results provide such a yardstick for the killer whale as an alternative to the risk-disturbance hypothesis that cannot be applied to this top predator species and help to interpret and predict human impacts on this species.

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References

Allen AN, Schanze JJ, Solow AR, Tyack PL (2014) Analysis of a Blainville's beaked whale's movement response to playback of killer whale vocalizations. *Marine Mammal Science* 30:154–168. doi: 10.1111/mms.12028

Baird RW (2000) The killer whale: Foraging specialisations and group hunting. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean Societies. The University of Chicago Press, Chicago, pp 127–153

Barluet De Beauchesne L, Massenet M, Oudejans MG, Kok ACM, Visser F, Curé C (2022) Friend or foe: Risso's dolphins eavesdrop on conspecific sounds to induce or avoid intra-specific interaction. *Animal Cognition* 25:287–296. doi: 10.1007/s10071-021-01535-y

Begon M, Townsend CR (2021) Ecology: From individuals to ecosystems. Wiley

Benti B, Miller P, Biuw M, Curé C (2021) Indication that the behavioural responses of humpback whales to killer whale sounds are influenced by trophic relationships. *Marine Ecology Progress* Series 660:217–232. doi: 10.3354/meps13592

Bode NWF, Faria JJ, Franks DW, Krause J, Wood AJ (2010) How perceived threat increases synchronization in collectively moving animal groups. *Proceedings of the Royal Society B: Biological Sciences* 277:3065–3070. doi: 10.1098/rspb.2010.0855

Bowers MT, Friedlaender AS, Janik VM, Nowacek DP, Quick NJ, Southall BL, Read AJ (2018) Selective reactions to different killer whale call categories in two delphinid species. *Journal of Experimental Biology* 221:1–12. doi: 10.1242/jeb.162479

Bradbury JW, Vehrenkamp SL (2011) Principles of animal communication. Sinauer Associates, Inc., Sunderland

Branstetter BK, St. Leger J, Acton D, Stewart J, Houser D, Finneran JJ, Jenkins K (2017) Killer whale (*Orcinus orca*) behavioral audiograms. *Journal of the Acoustical Society of America* 141:2387–2398. doi: 10.1121/1.4979116

Carlson NV, Griesser M (2022) Mobbing in animals: a thorough review and proposed future directions. In: Advances in the Study of Behavior. Academic Press, pp 1–41

Caro T (2005) Antipredator defenses in birds and mammals. University of Chicago Press

Cotter MP, Maldini D, Jefferson TA (2012) “Porpicide” in California: Killing of harbor porpoises (*Phocoena phocoena*) by coastal bottlenose dolphins (*Tursiops truncatus*). Marine Mammal Science 28:1–15. doi: 10.1111/j.1748-7692.2011.00474.x

Couzin ID (2018) Synchronization: The Key to Effective Communication in Animal Collectives. *Trends in Cognitive Sciences* 22:844–846. doi: 10.1016/j.tics.2018.08.001

Cummings WC, Thompson PO (1971) Gray whales, *Eschrichtius robustus*, avoid the underwater sounds of killer whales, *Orcinus orca*. *Fishery Bulletin* 69:525–530.

Curé C, Antunes R, Samarra F, Alves AC, Visser F, Kvadsheim PH, Miller PJO (2012) Pilot whales attracted to killer whale sounds: Acoustically-mediated interspecific interactions in cetaceans. *Plos One* 7:e52201. doi: 10.1371/journal.pone.0052201

Curé C, Antunes R, Alves AC, Visser F, Kvadsheim PH, Miller PJO (2013) Responses of male sperm whales (*Physeter macrocephalus*) to killer whale sounds: Implications for anti-predator strategies. *Scientific Reports* 3:1–7. doi: 10.1038/srep01579

Curé C, Sivle LD, Visser F, Wensveen PJ, Isojunno S, Harris CM, Kvadsheim PH, Lam FPA, Miller PJO (2015) Predator sound playbacks reveal strong avoidance responses in a fight strategist baleen whale. *Marine Ecology Progress Series* 526:267–282. doi: 10.3354/meps11231

Curé C, Isojunno S, Visser F, Wensveen PJ, Sivle LD, Kvadsheim PH, Lam FA, Miller PJO (2016) Biological significance of sperm whale responses to sonar: comparison with anti-predator responses. *Endangered Species Research* 31:89–102. doi: 10.3354/esr00748

Curé C, Isojunno S, Vester H, Visser F, Oudejans MG, Biassoni N, Massenet M, Wensveen PJ, Sivle LD, Tyack PL, Miller PJOM (2019) Discrimination between feeding sounds of fish and mammal eating killer whale ecotypes by long-finned pilot whales. *Animal Cognition* 22:863–882. doi: 10.1007/s10071-019-01282-1

Curé C, Isojunno S, Siemensma ML, Wensveen PJ, Buisson C, Sivle LD, Benti B, Roland R, Kvadsheim PH, Lam F-PA, Miller PJO (2021) Severity Scoring of Behavioral Responses of Sperm Whales (*Physeter macrocephalus*) to Novel Continuous versus Conventional Pulsed Active Sonar. *Journal of Marine Science and Engineering* 9:444. doi: 10.3390/jmse9040444

Curio E (1978) The Adaptive Significance of Avian Mobbing I. Teleonomic Hypotheses and Predictions. *Zeitschrift für Tierpsychologie* 48:175–183. doi: 10.1111/j.1439-0310.1978.tb00254.x

de Stephanis R, Giménez J, Esteban R, Gauffier P, García-Tiscar S, Sinding MHS, Verborgh P (2014) Mobbing-like behavior by pilot whales towards killer whales: a response to resource competition or perceived predation risk? *Acta Ethologica* 18:69–78. doi: 10.1007/s10211-014-0189-1

Deecke VB, Ford JKB, Slater PJB (2005) The vocal behaviour of mammal-eating killer whales: Communicating with costly calls. *Animal Behaviour* 69:395–405. doi: 10.1016/j.anbehav.2004.04.014

DeRuiter SL, Boyd IL, Claridge DE, Clark CW, Gagnon C, Southall BL, Tyack PL (2013a) Delphinid whistle production and call matching during playback of simulated military sonar. *Marine Mammal Science* 29:E46–E59. doi: 10.1111/j.1748-7692.2012.00587.x

DeRuiter SL, Southall BL, Calambokidis J, Zimmer WMX, Sadykova D, Falcone EA, Friedlaender AS, Joseph JE, Moretti D, Schorr GS, Thomas L, Tyack PL (2013b) First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. *Biology Letters* 9: 201302234. doi: 10.1098/rsbl.2013.0223

DeRuiter SL, Langrock R, Skirbutas T, Goldbogen JA, Calambokidis J, Friedlaender AS, Southall BL (2017) A multivariate mixed hidden markov model for blue whale behaviour and responses to sound exposure. *Annals of Applied Statistics* 11:362–392. doi: 10.1214/16-AOAS1008

Donovan GP, Gunnlaugsson T (1989) North Atlantic sightings survey 1987: report of the aerial survey off Iceland. *Report to the International Whaling Commission* 39:437-441

Driscoll I, Manser M, Thornton A (2022) Function of meerkats' mobbing-like response to secondary predator cues: recruitment not teaching. *Animal Behaviour* 194:111–126. doi: 10.1016/j.anbehav.2022.09.019

Filatova OA, Fedutin ID, Burdin AM, Hoyt E (2011) Responses of Kamchatkan fish-eating killer whales to playbacks of conspecific calls. *Marine Mammal Science* 27:1–17. doi: 10.1111/j.1748-7692.2010.00433.x

Fish JF, Vania JS (1971) Killer whale, *Orcinus orca*, sounds repel white whale, *Delphinapterus leucas*. *Fishery Bulletin* 69:531–535.

Ford JKB (1989) Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Canadian Journal of Zoology* 67:727–745. doi: 10.1139/z89-105

Ford JKB, Reeves RR (2008) Fight or flight: antipredator strategies of baleen whales. *Mammal Review* 38:50–86. doi: 10.1111/j.1365-2907.2008.00118.x

Freitas F Carla (2022) argosfilter: Argos Locations Filter.

Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6:11. doi: 10.5751/ES-00404-060111

Friedlaender AS, Hazen EL, Goldbogen JA, Stimpert AK, Calambokidis J, Southall BL (2016) Prey-mediated behavioral responses of feeding blue whales in controlled sound exposure experiments. *Ecological Applications* 26:1075–1085. doi: 10.1002/15-0783

Gannon DP, Barros NB, Nowacek DP, Read AJ, Waples DM, Wells RS (2005) Prey detection by bottlenose dolphins, *Tursiops truncatus*: An experimental test of the passive listening hypothesis. *Animal Behaviour* 69:709–720. doi: 10.1016/j.anbehav.2004.06.020

Goldbogen JA, Southall BL, DeRuiter SL, Calambokidis J, Friedlaender AS, Hazen EL, Falcone EA, Schorr GS, Douglas A, Moretti DJ, Kyburg C, McKenna MF, Tyack PL (2013) Blue whales respond to simulated mid-frequency military sonar. *Proceedings of the Royal Society B: Biological Sciences* 280:20130657. doi: 10.1098/rspb.2013.0657

Hall JD, Johnson CS (1972) Auditory Thresholds of a Killer Whale *Orcinus orca* Linnaeus. *Journal of the Acoustical Society of America* 51:515–517. doi: 10.1121/1.1912871

Harris CM, Thomas L, Falcone EA, Hildebrand J, Houser D, Kvadsheim PH, Lam FPA, Miller PJO, Moretti DJ, Read AJ, Slabbekoorn H, Southall BL, Tyack PL, Wartzok D, Janik VM (2018) Marine mammals and sonar: Dose-response studies, the risk-disturbance hypothesis and the role of exposure context. *Journal of Applied Ecology* 55:396–404. doi: 10.1111/1365-2664.12955

Højsgaard S, Halekoh U, Yan J (2006) The R Package geepack for Generalized Estimating Equations. Journal of Statistical Software 15:1–11. doi: 10.18637/jss.v015.i02

Isojunno S, Curé C, Kvadsheim PH, Lam FPA, Tyack PL, Wensveen PJ, Miller PJOM (2016) Sperm whales reduce foraging effort during exposure to 1-2 kHz sonar and killer whale sounds. *Ecological Applications* 26:77–93. doi: 10.1890/15-0040.1/suppinfo

Isojunno S, Sadykova D, DeRuiter S, Curé C, Visser F, Thomas L, Miller PJO, Harris CM (2017a) Individual, ecological, and anthropogenic influences on activity budgets of long-finned pilot whales. *Ecosphere* 8:e02044. doi: 10.1002/ecs2.2044

Isojunno S, Sadykova D, Deruiter S, Cure C, Visser F, Thomas L, Miller PJO, Harris CM (2017b) Individual, ecological, and anthropogenic influences on activity budgets of long-finned pilot whales. *Ecosphere*. doi: 10.1002/ecs2.2044

Isojunno S, Wensveen PJ, Lam F-PA, Kvadsheim PH, Von Benda-Beckmann AM, Martín López LM, Kleivane L, Siegal EM, Miller PJO (2020) When the noise goes on: received sound energy predicts sperm whale responses to both intermittent and continuous navy sonar. *Journal of Experimental Biology* 223:jeb219741. doi: 10.1242/jeb.219741

Jakobsson J, Stefánsson G (1999) Management of summer-spawning herring off Iceland. *ICES Journal of Marine Science* 56:827–833. doi: 10.1006/jmsc.1999.0542

Jefferson T, Stacey P, Baird R (1991) A review of Killer whale interactions with other marine mammals. *Mammal Review* 21:151–180. doi: 10.1111/j.1365-2907.1991.tb00291.x

Johnson MP, Tyack PL (2003) A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering* 28:3–12. doi: 10.1109/JOE.2002.808212

Jourdain E, Vongraven D (2017) Humpback whale (*Megaptera novaeangliae*) and killer whale (*Orcinus orca*) feeding aggregations for foraging on herring (*Clupea harengus*) in Northern Norway. *Mammalian Biology* 86:27–32. doi: 10.1016/j.mambio.2017.03.006

Kleivane L, Kvadsheim PH, Bocconcelli A, Øien N, Miller PJO (2022) Equipment to tag, track and collect biopsies from whales and dolphins: the ARTS, DFHorten and LKDart systems. *Animal Biotelemetry* 10:32. doi: 10.1186/s40317-022-00303-0

Kok ACM, Van Kolfshoten L, Campbell JA, Von Benda-Beckmann AM, Miller PJO, Slabbekoorn H, Visser F (2020) Diving apart together: Call propagation in diving long-finned pilot whales. *Journal of Experimental Biology* 223: jeb207878. doi: 10.1242/jeb.207878

Koper RP, Plön S (2016) Interspecific interactions between cetacean species in Algoa Bay, South Africa. *Aquatic Mammals* 42:454–461. doi: 10.1578/AM.42.4.2016.454

Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, Oxford

Kvadsheim PH, DeRuiter S, Sivle LD, Goldbogen J, Roland-Hansen R, Miller PJO, Lam FPA, Calambokidis J, Friedlaender A, Visser F, Tyack PL, Kleivane L, Southall B (2017) Avoidance responses of minke whales to 1–4 kHz naval sonar. *Marine Pollution Bulletin* 121:60–68. doi: 10.1016/j.marpolbul.2017.05.037

McClintock BT, Michelot T (2021) momentuHMM: R package for analysis of telemetry data using generalized multivariate hidden Markov models of animal movement.

McGregor PK (1992) Playback and studies of animal communication. Plenum Press, New York

McIntyre T (2014) Trends in tagging of marine mammals: a review of marine mammal biologging studies. *African Journal of Marine Science* 36:409–422. doi: 10.2989/1814232X.2014.976655

Miller PJO, Kvadsheim PH, Lam FPA, Wensveen PJ, Antunes R, Alves AC, Visser F, Kleivane L, Tyack PL, Sivle LD (2012) The Severity of behavioral changes observed during experimental exposures of killer (*Orcinus orca*), long-finned pilot (*Globicephala melas*), and sperm (*Physeter macrocephalus*) whales to naval sonar. *Aquatic Mammals* 38:362–401. doi: 10.1578/AM.38.4.2012.362

Miller PJO, Antunes RN, Wensveen PJ, Samarra FIP, Catarina Alves A, Tyack PL, Kvadsheim PH, Kleivane L, Lam F-PA, Ainslie MA, Thomas L (2014) Dose-response relationships for the onset of avoidance of sonar by free-ranging killer whales. *Journal of the Acoustical Society of America* 135:975–993. doi: 10.1121/1.4861346

Miller PJO, Kvadsheim PH, Lam FPA, Tyack PL, Curé C, DeRuiter SL, Kleivane L, Sivle LD, Van Ijsselmuide SP, Visser F, Wensveen PJ, Von Benda-Beckmann AM, Martín López LM, Narazaki T, Hooker SK (2015) First indications that northern bottlenose whales are sensitive to behavioural disturbance from anthropogenic noise. *Royal Society Open Science* 2: 140484. doi: 10.1098/rsos.140484

Miller PJO, Isojunno S, Siegal E, Lam F-PA, Kvadsheim PH, Curé C (2022) Behavioral responses to predatory sounds predict sensitivity of cetaceans to anthropogenic noise within a soundscape of fear. *Proceedings of the National Academy of Sciences* 119:e2114932119. doi: 10.1073/pnas.2114932119

Palacios DM, Mate BR (2006) Attack By False Killer Whales (*Pseudorca crassidens*) on Sperm Whales (*Physeter macrocephalus*) in the Galápagos Islands. *Marine Mammal Science* 12:582–587. doi: 10.1111/j.1748-7692.1996.tb00070.x

Patterson TA, Parton A, Langrock R, Blackwell PG, Thomas L, King R (2017) Statistical modelling of individual animal movement: an overview of key methods and a discussion of practical challenges. *AStA Advances in Statistical Analysis* 101:399–438. doi: 10.1007/s10182-017-0302-7

Pierry JC, Wedekin LL, Flores PAC, Rossi-Santos MR, Daura-Jorge FG (2023) Escape response of Guiana dolphins to bottlenose dolphin playback. *Journal of Experimental Marine Biology and Ecology* 566:151925. doi: 10.1016/j.jembe.2023.151925

Pitman RL, Deecke VB, Gabriele CM, Srinivasan M, Black N, Denkinger J, Durban JW, Mathews EA, Matkin DR, Neilson JL, Schulman-Janiger A, Shearwater D, Stap P, Ternullo R (2017) Humpback whales interfering when mammal-eating killer whales attack other species: Mobbing behavior and interspecific altruism? *Marine Mammal Science* 33:7–58. doi: 10.1111/mms.12343

Prokopenko CM, Ellington EH, Robitaille A, Aubin JA, Balluffi-Fry J, Laforge M, Webber QMR, Zabihi-Seissan S, Vander Wal E (2024) Friends because of foes: synchronous movement within predator–prey domains. *Philosophical Transactions of the Royal Society B: Biological Sciences* 379:20230374. doi: 10.1098/rstb.2023.0374

Quick NJ, Isojunno S, Sadykova D, Bowers M, Nowacek DP, Read AJ (2017) Hidden Markov models reveal complexity in the diving behaviour of short-finned pilot whales. *Scientific Reports* 7:45765. doi: 10.1038/srep45765

R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Samarra F, Vighi M, Aguilar A, Víkingsson G (2017a) Intra-population variation in isotopic niche in herring-eating killer whales off Iceland. *Marine Ecology Progress Series* 564:199–210. doi: 10.3354/meps11998

Samarra FIP, Miller PJO (2015) Prey-induced behavioural plasticity of herring-eating killer whales. *Marine Biology* 162:809–821. doi: 10.1007/s00227-015-2626-8

Samarra FIP, Tavares SB, Miller PJO, Víkingsson GA (2017b) Killer whales of Iceland 2016-2015. Report to the Marine and Freshwater Research Institute. Marine and Freshwater Research Institute, Iceland

Samarra FIP, Tavares SB, Béesau J, Deecke VB, Fennell A, Miller PJO, Pétursson H, Sigurjónsson J, Víkingsson GA (2017c) Movements and site fidelity of killer whales (*Orcinus orca*) relative to seasonal and long-term shifts in herring (*Clupea harengus*) distribution. *Marine Biology* 164:159. doi: 10.1007/s00227-017-3187-9

Samarra FIP, Bassoi M, Béesau J, Elíasdóttir MÓ, Gunnarsson K, Mrusczok M-T, Rasmussen M, Rempel JN, Thorvaldsson B, Víkingsson GA (2018) Prey of killer whales (*Orcinus orca*) in Iceland. *Plos One* 13:e0207287. doi: 10.1371/journal.pone.0207287

Selbmann A, Deecke VB, Fedutin ID, Filatova OA, Miller PJO, Samarra FIP (2019) A catalogue of pulsed calls produced by killer whales (*Orcinus orca*) in Iceland 2008-2016. Report to the Marine and Freshwater Research Institute. Marine and Freshwater Research Institute, Iceland

Selbmann A, Deecke VB, Fedutin ID, Filatova OA, Miller PJO, Svavarsson J, Samarra FIP (2020) A comparison of Northeast Atlantic killer whale (*Orcinus orca*) stereotyped call repertoires. *Marine Mammal Science* 37:268-289. doi: 10.1111/mms.12750

Selbmann A, Basran CJ, Bertulli CG, Hudson T, Mrusczok M-T, Rasmussen MH, Rempel JN, Scott J, Svavarsson J, Wensveen PJ, Whittaker M, Samarra FIP (2022) Occurrence of long-finned pilot whales (*Globicephala melas*) and killer whales (*Orcinus orca*) in Icelandic coastal waters and their interspecific interactions. *Acta Ethologica* 25:141–154. doi: 10.1007/s10211-022-00394-1

Selbmann A, Deecke VB, Filatova OA, Fedutin ID, Miller PJO, Simon M, Bowles AE, Lyrholm T, Lacey C, Magnúsdóttir EE, Maunder W, Wensveen PJ, Svavarsson J, Samarra FIP (2023) Call type repertoire of killer whales (*Orcinus orca*) in Iceland and its variation across regions. *Marine Mammal Science* 39:1136–1160. doi: 10.1111/mms.13039

Sigurjónsson J, Víkingsson G, Lockyer C (1993) Two mass strandings of pilot whales (*Globicephala melas*) on the coast of Iceland. Report to the International Whaling Commission Special Issue 14:407–423.

Similä T, Ugarte F (1993) Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology* 71:1494–1499. doi: 10.1139/z93-210

Simon M, Wahlberg M, Ugarte F, Miller LA (2005) Acoustic characteristics of underwater tail slaps used by Norwegian and Icelandic killer whales (*Orcinus orca*) to debilitate herring (*Clupea harengus*). *Journal of Experimental Biology* 208:2459–2466. doi: 10.1242/jeb.01619

Simon M, McGregor PK, Ugarte F (2007) The relationship between the acoustic behaviour and surface activity of killer whales (*Orcinus orca*) that feed on herring (*Clupea harengus*). *Acta Ethologica* 10:47–53. doi: 10.1007/s10211-007-0029-7

Sivle LD, Kvadsheim PH, Curé C, Isojunno S, Wensveen PJ, Lam FPA, Visser F, Kleivane L, Tyack PL, Harris CM, Miller PJO (2015) Severity of expert-identified behavioural responses of humpback whale, minke whale, and northern bottlenose whale to naval sonar. *Aquatic Mammals* 41:469–502. doi: 10.1578/AM.41.4.2015.469

Southall BL, Allen AN, Calambokidis J, Casey C, DeRuiter SL, Fregosi S, Friedlaender AS, Goldbogen JA, Harris CM, Hazen EL, Popov V, Stimpert AK (2023) Behavioural responses of fin whales to military mid-frequency active sonar. *Royal Society Open Science* 10:231775. doi: 10.1098/rsos.231775

Stenersen J, Similä T (2004) Norwegian killer whales. Tringa Forlag, Henningsvær

Stimpert AK, Deruiter SL, Southall BL, Moretti DJ, Falcone EA, Goldbogen JA, Friedlaender A, Schorr GS, Calambokidis J (2014) Acoustic and foraging behavior of a Baird's beaked whale, *Berardius bairdii*, exposed to simulated sonar. *Scientific Reports* 4:7031. doi: 10.1038/srep07031

Syme J, Kiszka JJ, Parra GJ (2021) Dynamics of Cetacean Mixed-Species Groups: A Review and Conceptual Framework for Assessing Their Functional Significance. *Frontiers in Marine Science* 8:678173. doi: 10.3389/fmars.2021.678173

Szymanski MD, Bain DE, Kiehl K, Pennington S, Wong S, Henry KR (1999) Killer whale (*Orcinus orca*) hearing: Auditory brainstem response and behavioral audiograms. *Journal of the Acoustical Society of America* 106:1134–1141. doi: 10.1121/1.427121

Tennessen JB, Holt MM, Ward EJ, Hanson MB, Emmons CK, Giles DA, Hogan JT (2019) Hidden Markov models reveal temporal patterns and sex differences in killer whale behavior. *Scientific Reports* 9:14951. doi: 10.1038/s41598-019-50942-2

The MathWorks Inc. (2023) MATLAB.

Tyack PL, Zimmer WMX, Moretti D, Southall BL, Claridge DE, Durban JW, Clark CW, D'Amico A, DiMarzio N, Jarvis S, McCarthy E, Morrissey R, Ward J, Boyd IL (2011) Beaked whales respond to simulated and actual navy sonar. *Plos One* 6: e17009. doi: 10.1371/journal.pone.0017009

Visser F, Miller PJO, Antunes RN, Oudejans MG, Mackenzie ML, Aoki K, Lam FPA, Kvadsheim PH, Huisman J, Tyack PL (2014) The social context of individual foraging behaviour in long-finned pilot whales (*Globicephala melas*). *Behaviour* 151:1453–1477. doi: 10.1163/1568539X-00003195

Visser F, Curé C, Kvadsheim PH, Lam FPA, Tyack PL, Miller PJO (2016) Disturbance-specific social responses in long-finned pilot whales, *Globicephala melas*. *Scientific Reports* 6:1–11. doi: 10.1038/srep28641

Ward A, Webster M (2016) Sociality: The Behaviour of Group-Living Animals. Springer Cham

Weller DW, Würsig B, Whitehead H, Norris JC, Lynn SK, Davis RW, Clauss N, Brown P (1996) Observations of an Interaction Between Sperm Whales and Short-Finned

Pilot Whales in the Gulf of Mexico. *Marine Mammal Science* 12:588–594. doi: 10.1111/j.1748-7692.1996.tb00071.x

Wensveen PJ, Thomas L, Miller PJO (2015) A path reconstruction method integrating dead-reckoning and position fixes applied to humpback whales. *Movement Ecology* 3:31. doi: 10.1186/s40462-015-0061-6

Wensveen PJ, Kvadsheim PH, Lam F-PA, Von Benda-Beckmann AM, Sivle LD, Visser F, Curé C, Tyack PL, Miller PJO (2017) Lack of behavioural responses of humpback whales (*Megaptera novaeangliae*) indicate limited effectiveness of sonar mitigation. *Journal of Experimental Biology* 220:4150–4161. doi: 10.1242/jeb.161232

Wensveen PJ, Isojunno S, Hansen RR, von Benda-Beckmann AM, Kleivane L, van IJsselmuide S, Lam FPA, Kvadsheim PH, DeRuiter SL, Curé C, Narazaki T, Tyack PL, Miller PJO (2019) Northern bottlenose whales in a pristine environment respond strongly to close and distant navy sonar signals. *Proceedings of the Royal Society B: Biological Sciences* 286:20182592. doi: 10.1098/rspb.2018.2592

Wirsing AJ, Heithaus MR, Frid A, Dill LM (2008) Seascapes of fear: Evaluating sublethal predator effects experienced and generated by marine mammals. *Marine Mammal Science* 24:1–15. doi: 10.1111/j.1748-7692.2007.00167.x

Supplementary material

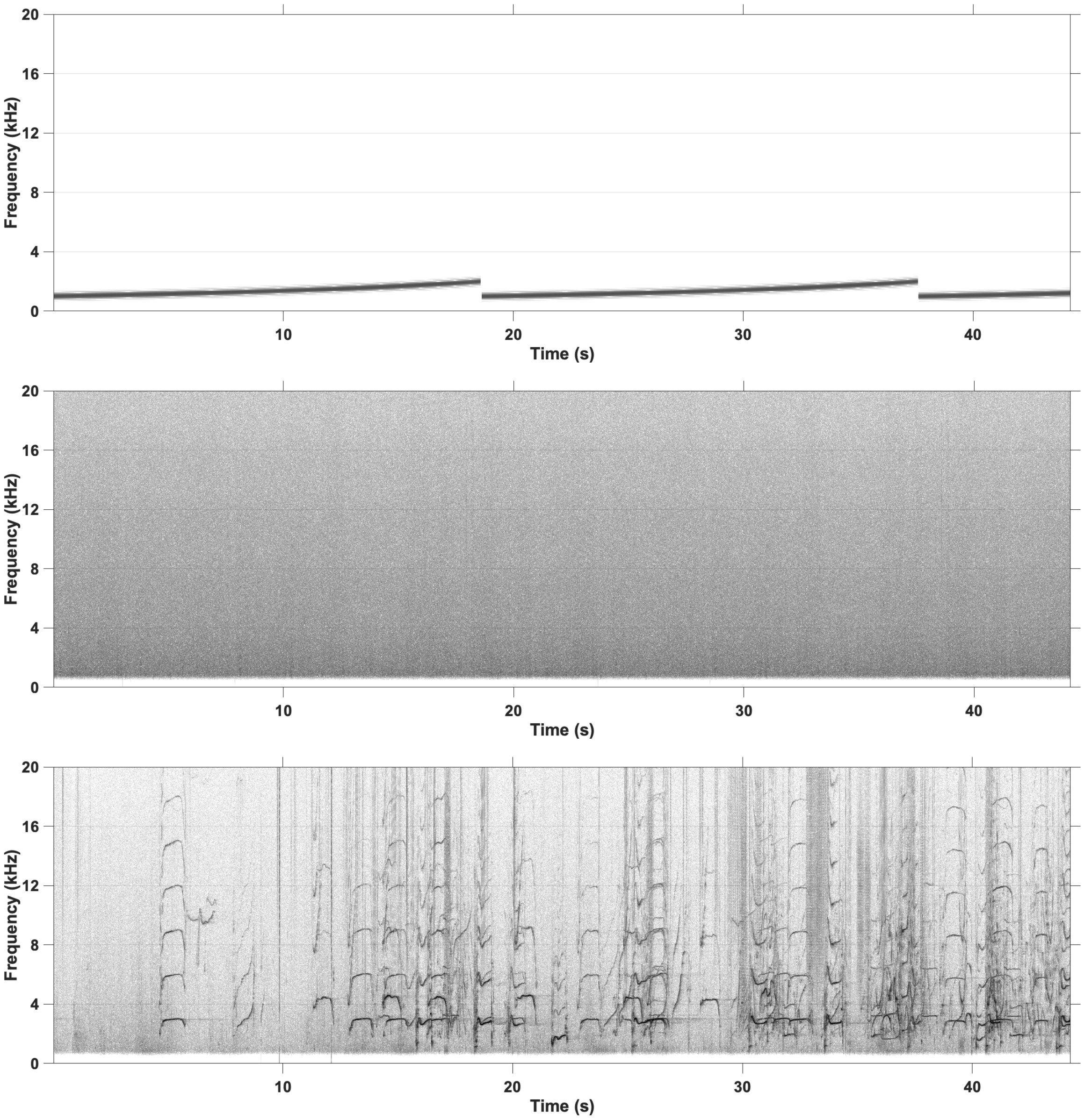


Figure S1: Example spectrograms of the sound stimuli used. Long-finned pilot whale sounds (top), noise control (middle), and 1-2 kHz upsweep control (bottom). Recordings sampled at 44.1 kHz. Spectrogram parameters: Hann window; 87.5% overlap; FFT size: 4096.

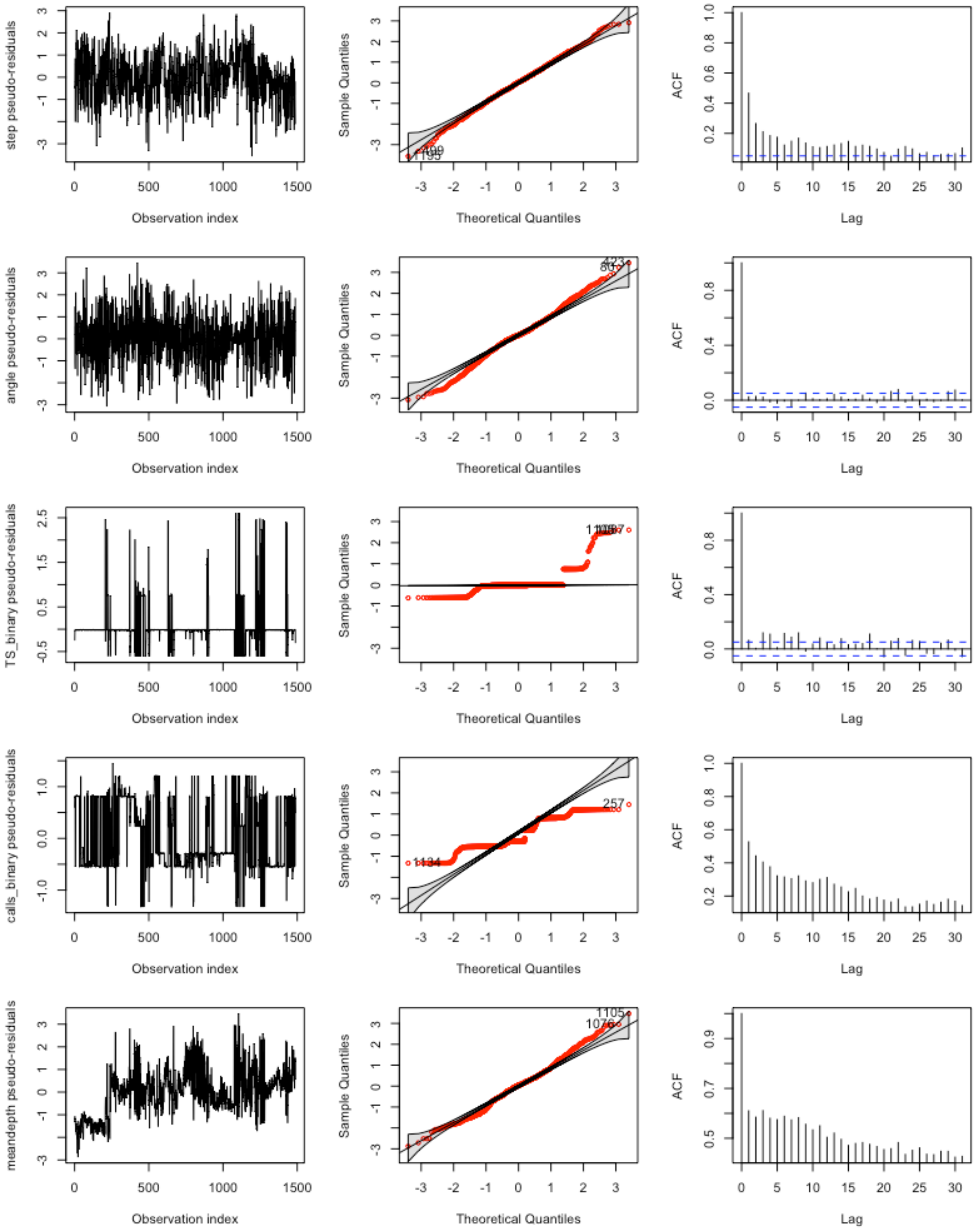


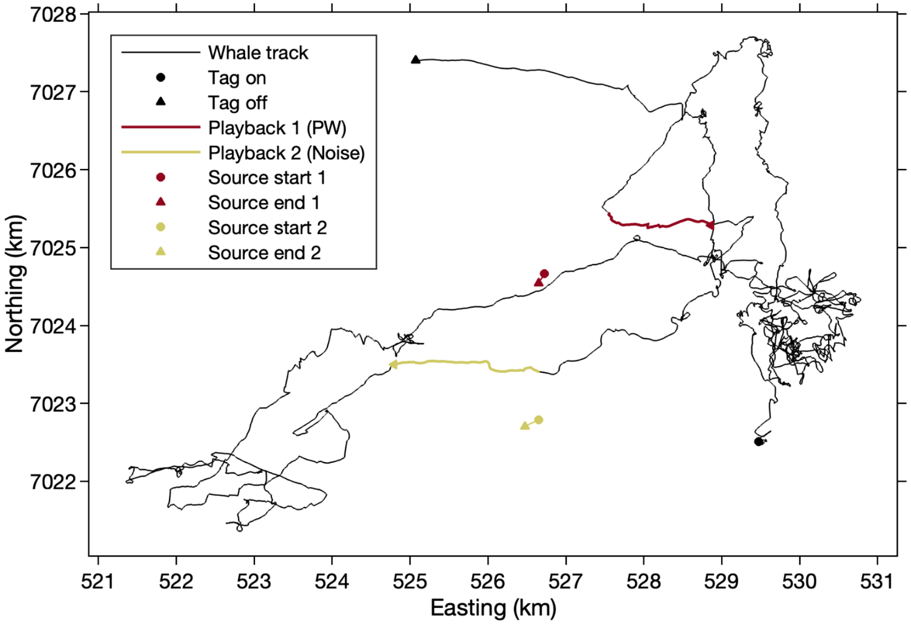
Figure S2: Timeseries, quantile-quantile, and autocorrelation function (ACF) plots of the pseudo-residuals for step lengths, turning angles, tail slaps, calls, and mean depth for the baseline hidden Markov model fitted to data from killer whales.

Figures S3-S10: Reconstructed tracks (left) and movement parameter time series (right) for all whales. Tracks show the entire track of the whale and the positions of the playback source boat. The track is highlighted in colour during playback times. Movement parameters shown are (from top to bottom): forward speed (m/s) calculated from step length, horizontal turning angle (radians), heading (degrees re North), depth (m). Depth includes dots for calls (blue) and tail slaps (red). The bottom panel shows the probability of being in each of the three states predicted by the HMM. State 1 (travel) is indicated in orange, state 2 (feeding) in blue and state 3 (other) in turquoise. The start and end times of each playback are indicated with a dotted line. Speed, turning angle, and state probabilities are plotted in 5-minute steps as used in the HMM, the heading and depth are shown at 30 s time resolution.

Figure S3

oo21_184a

Note: the turn before the start of playback 1 actually occurred right at the start of the playback (see heading data). The discrepancy in the track is likely due to error associated with visual locations and the path reconstruction method aiming to match positions and tracks.



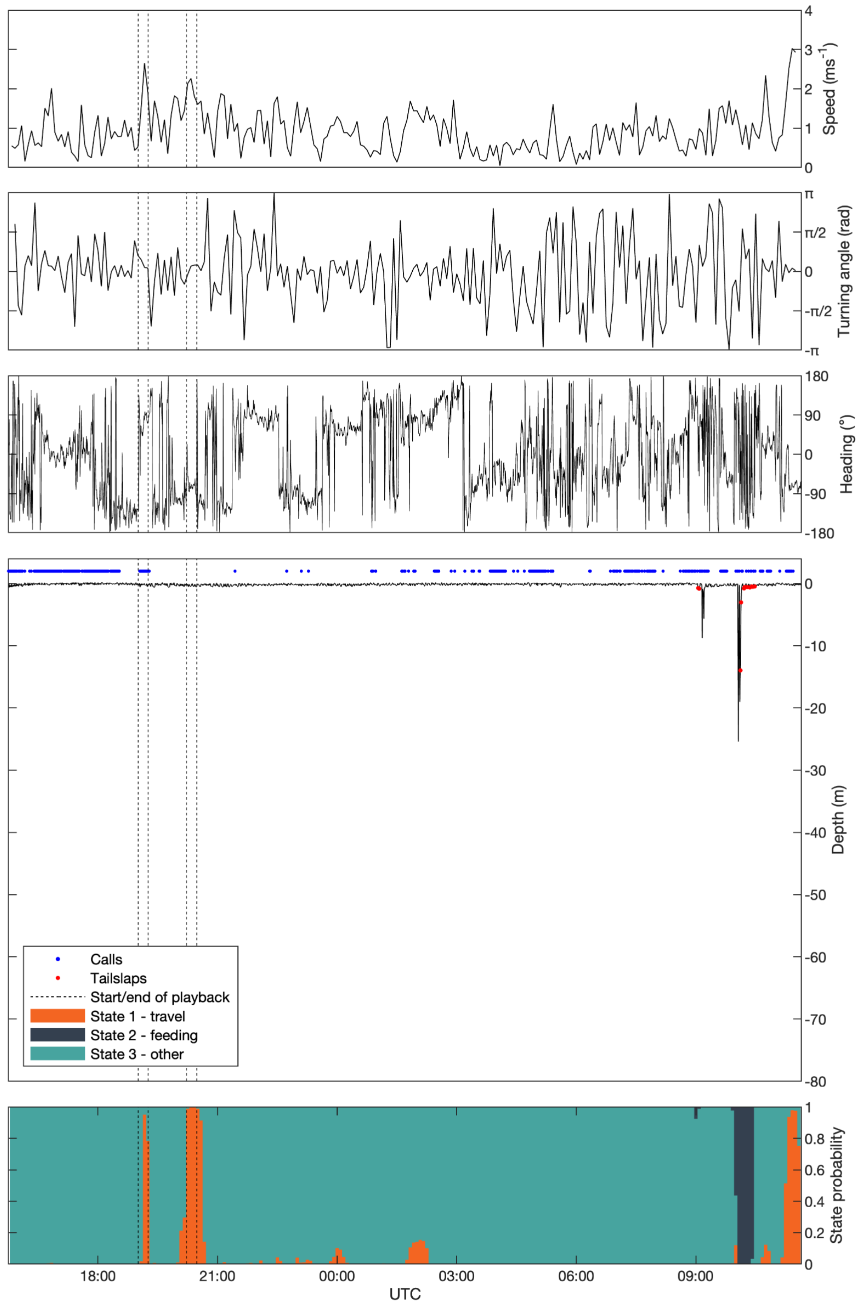


Figure S4

oo21_189a

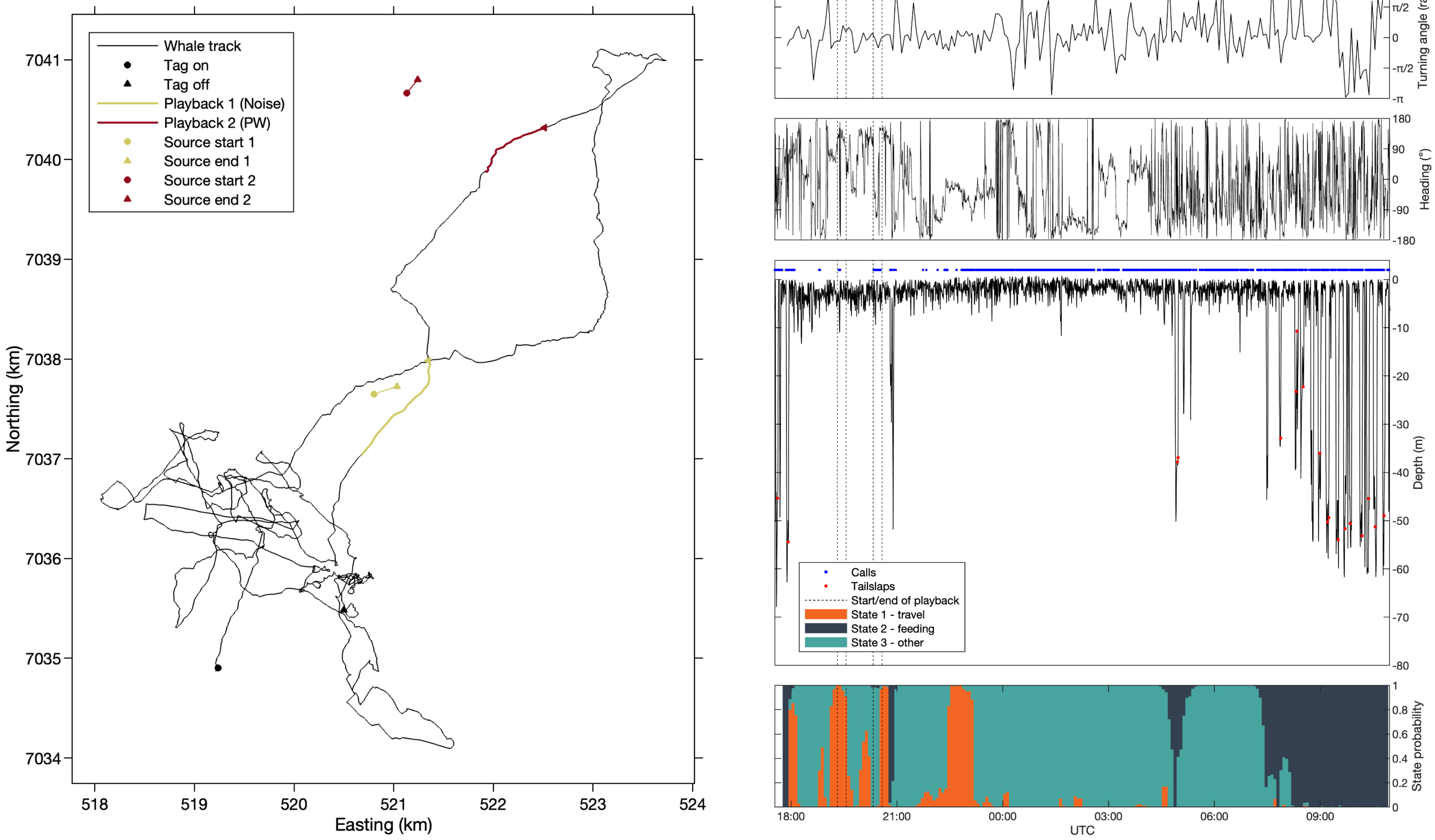


Figure S5 oo21_199a

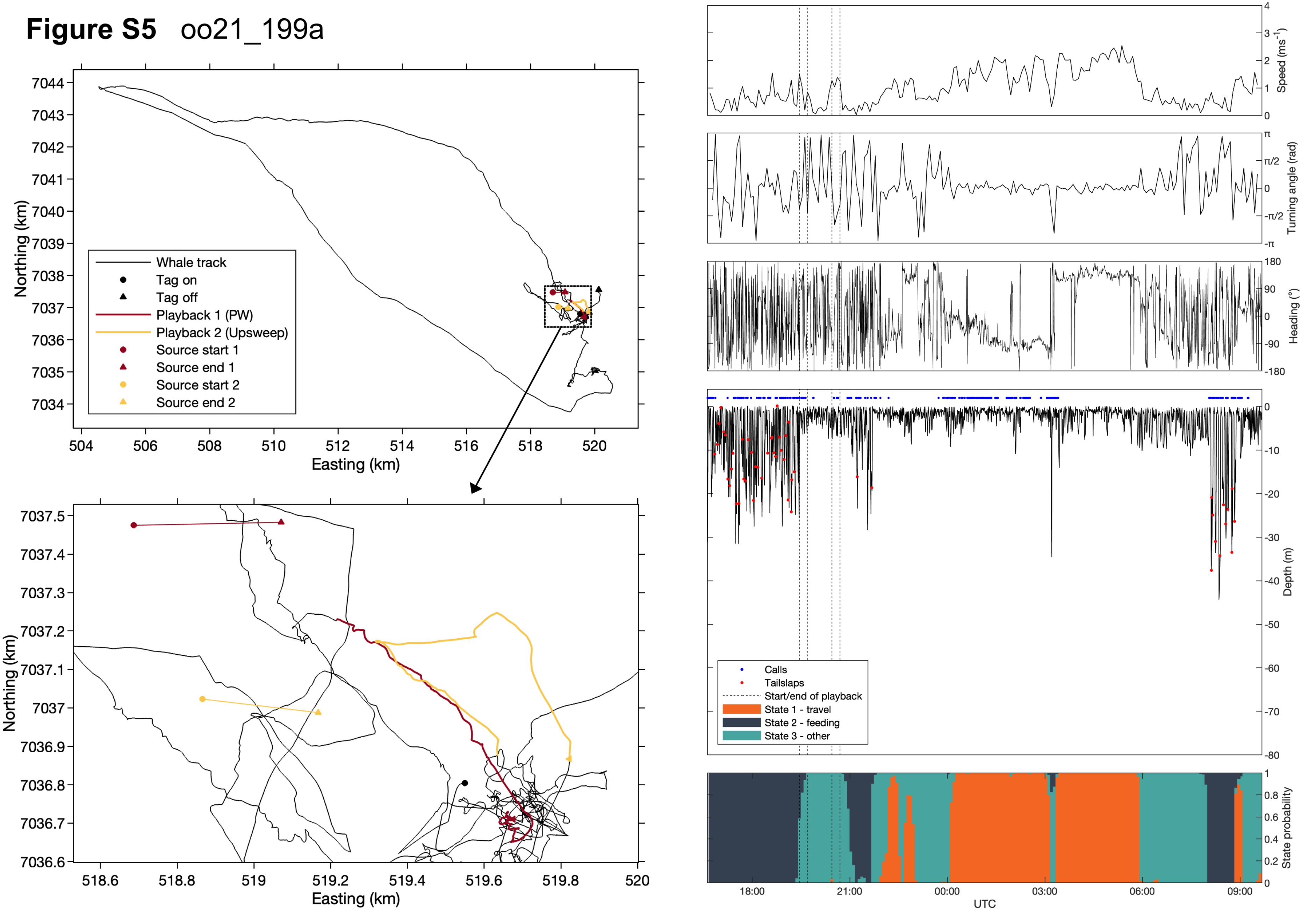


Figure S6 oo21_202b

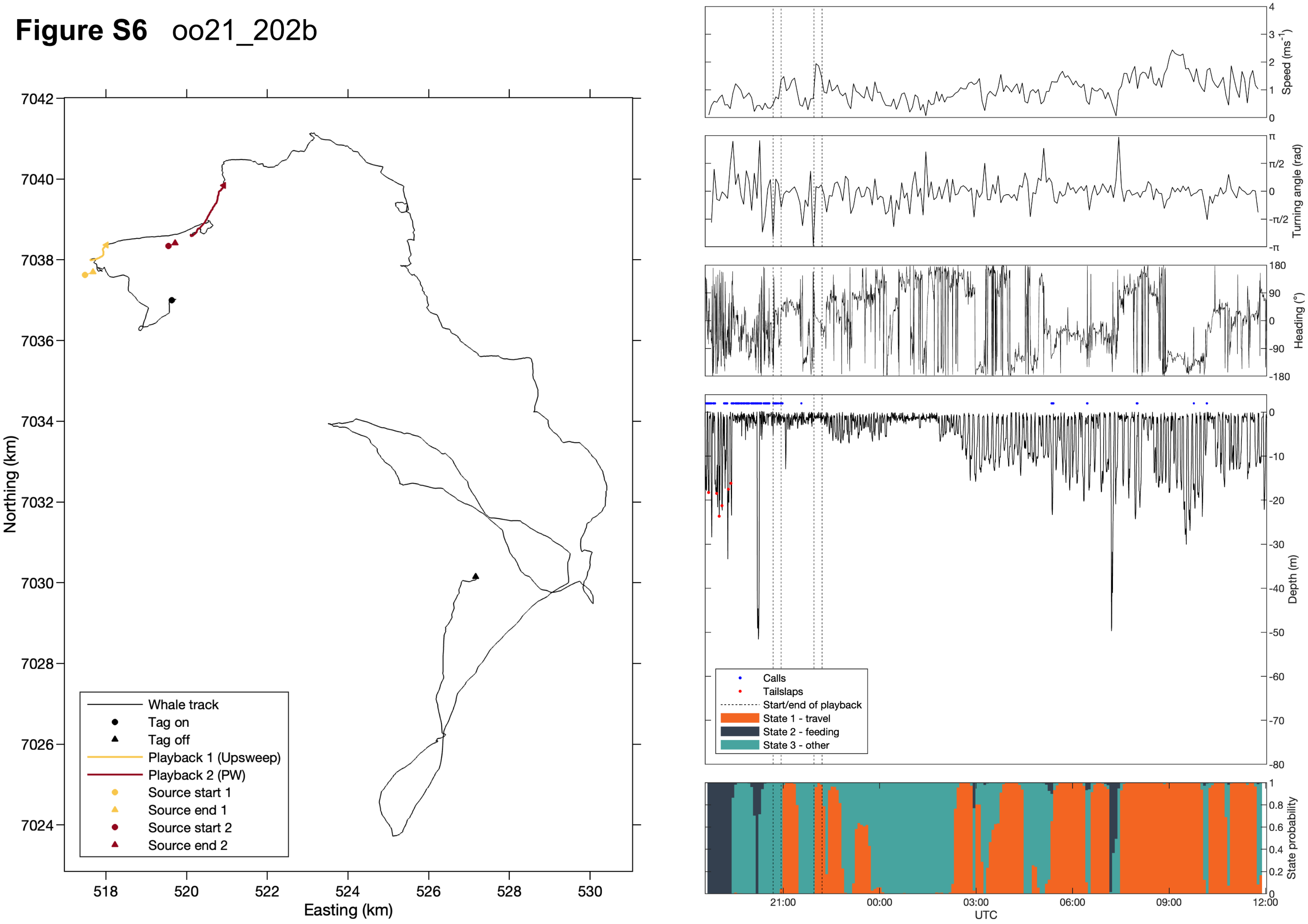
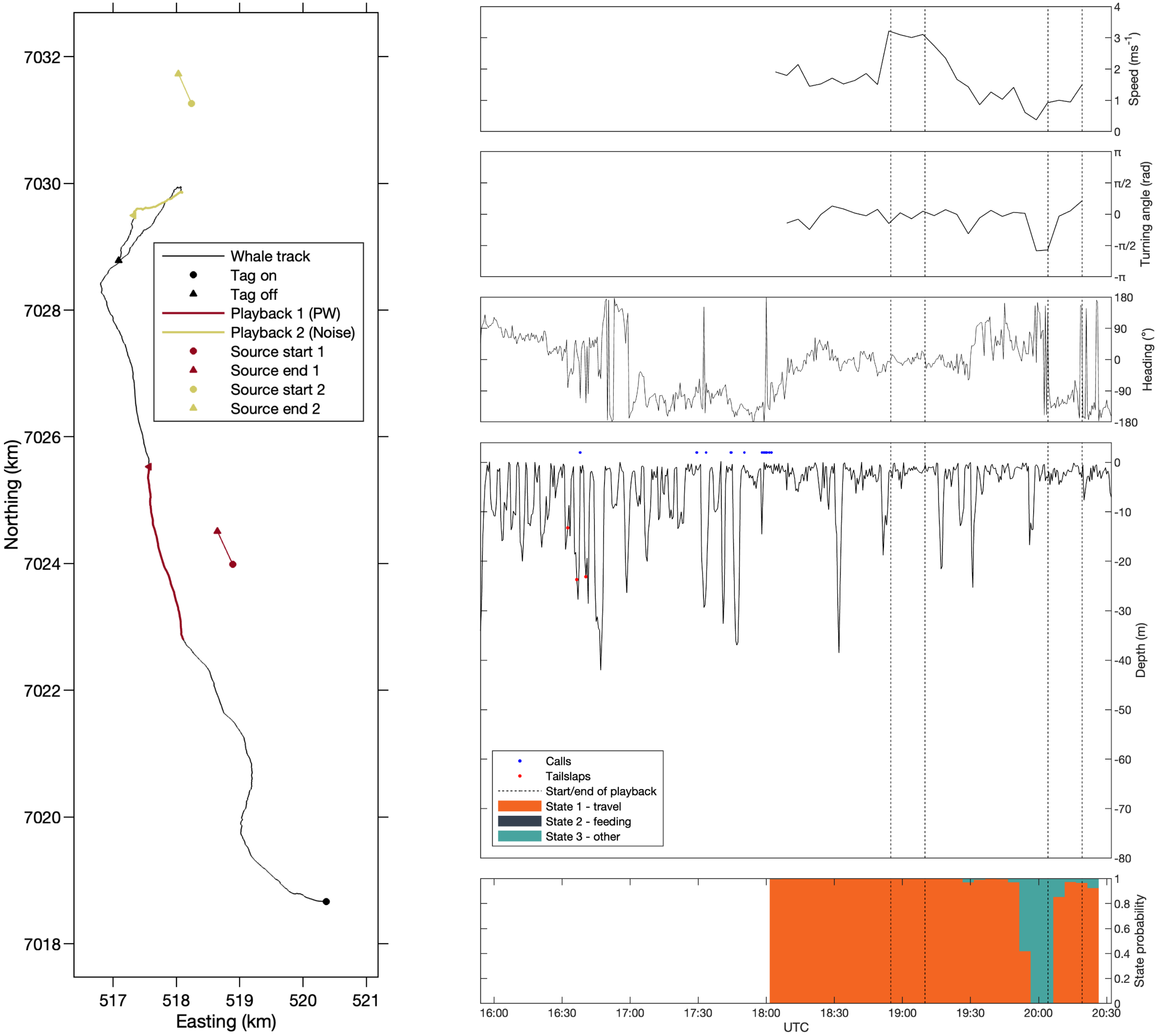


Figure S7

oo22_228a



Note: no GPS data were received during the tag deployment. Therefore, only visual sightings were used in the track reconstruction. Those were only available for part of the deployment time. Tag on/off times in the track refer to start/end of this track.

Figure S8 oo23_181a

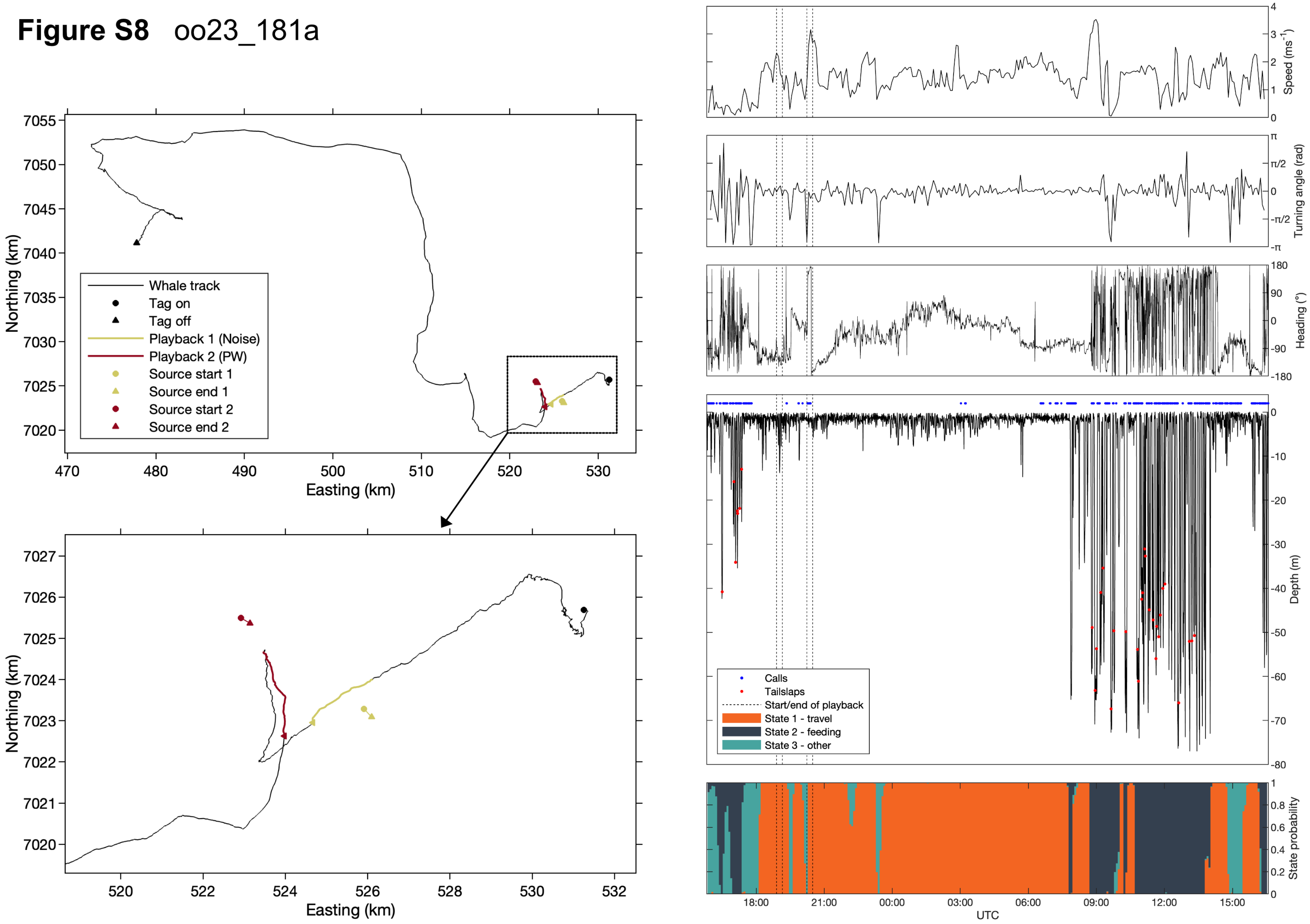
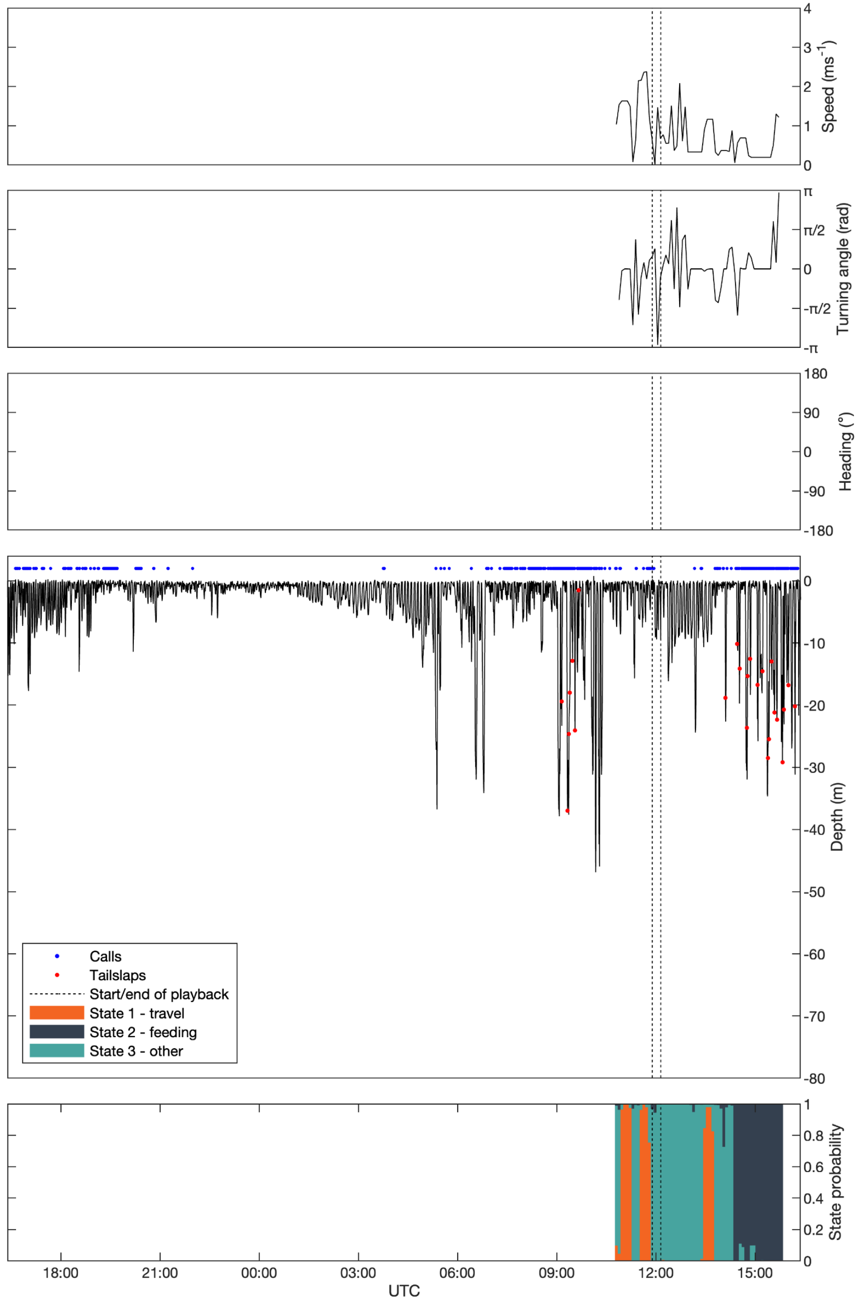


Figure S9

oo23_181b



Note: tag malfunctioned and we were unable to derive the body orientation from it. Therefore no heading data shown. Track is based on linear interpolation between the visual and Fastloc-GPS positions. Tag on/off times in the track refer to start/end of this track.

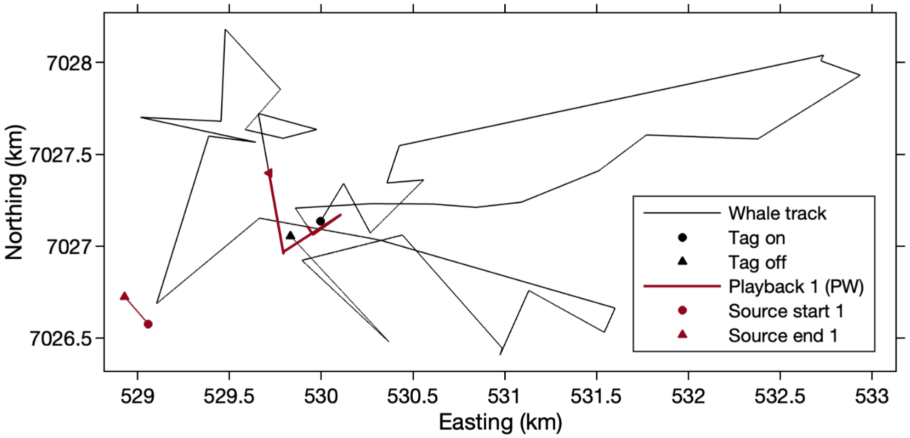
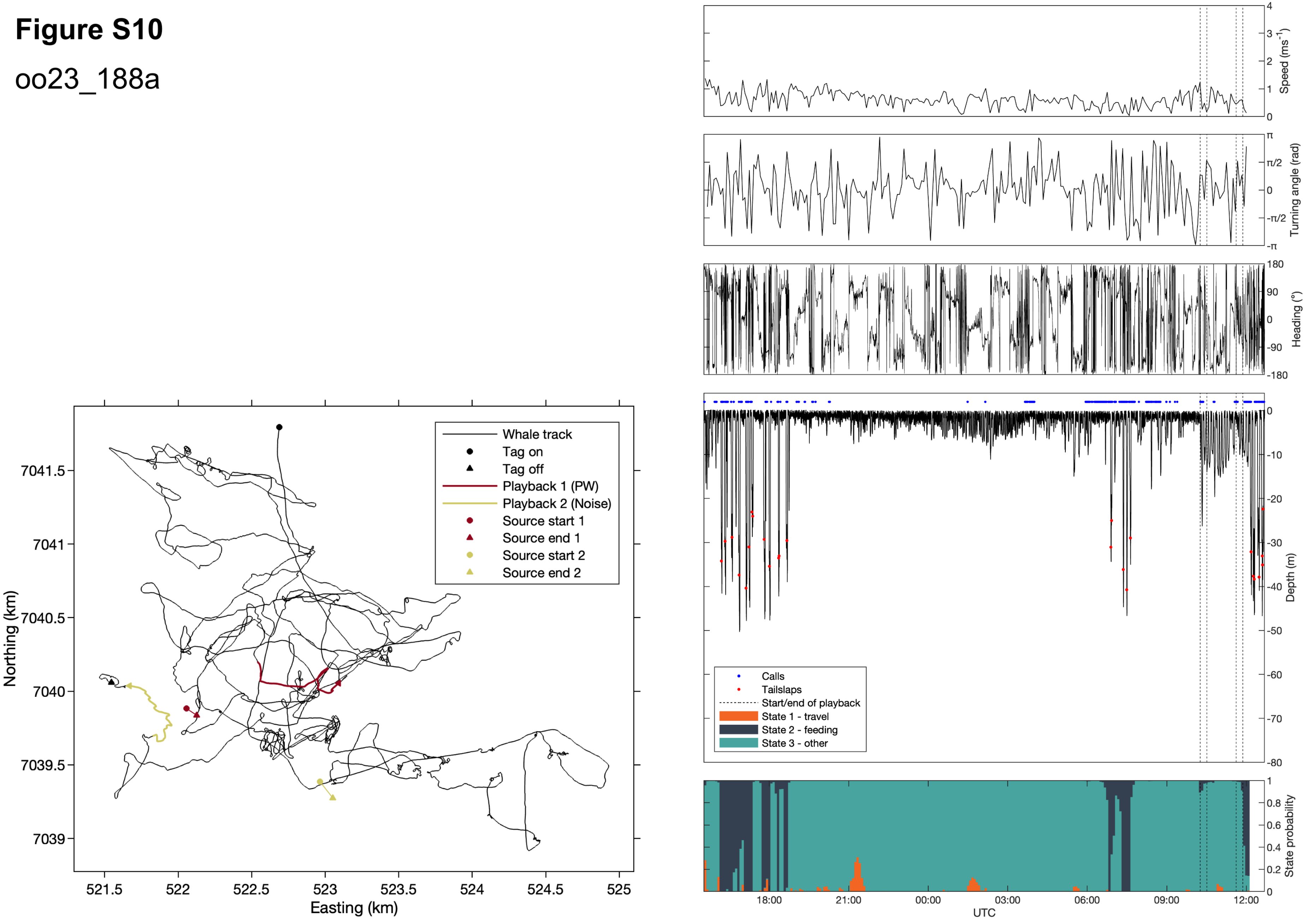


Figure S10

oo23_188a



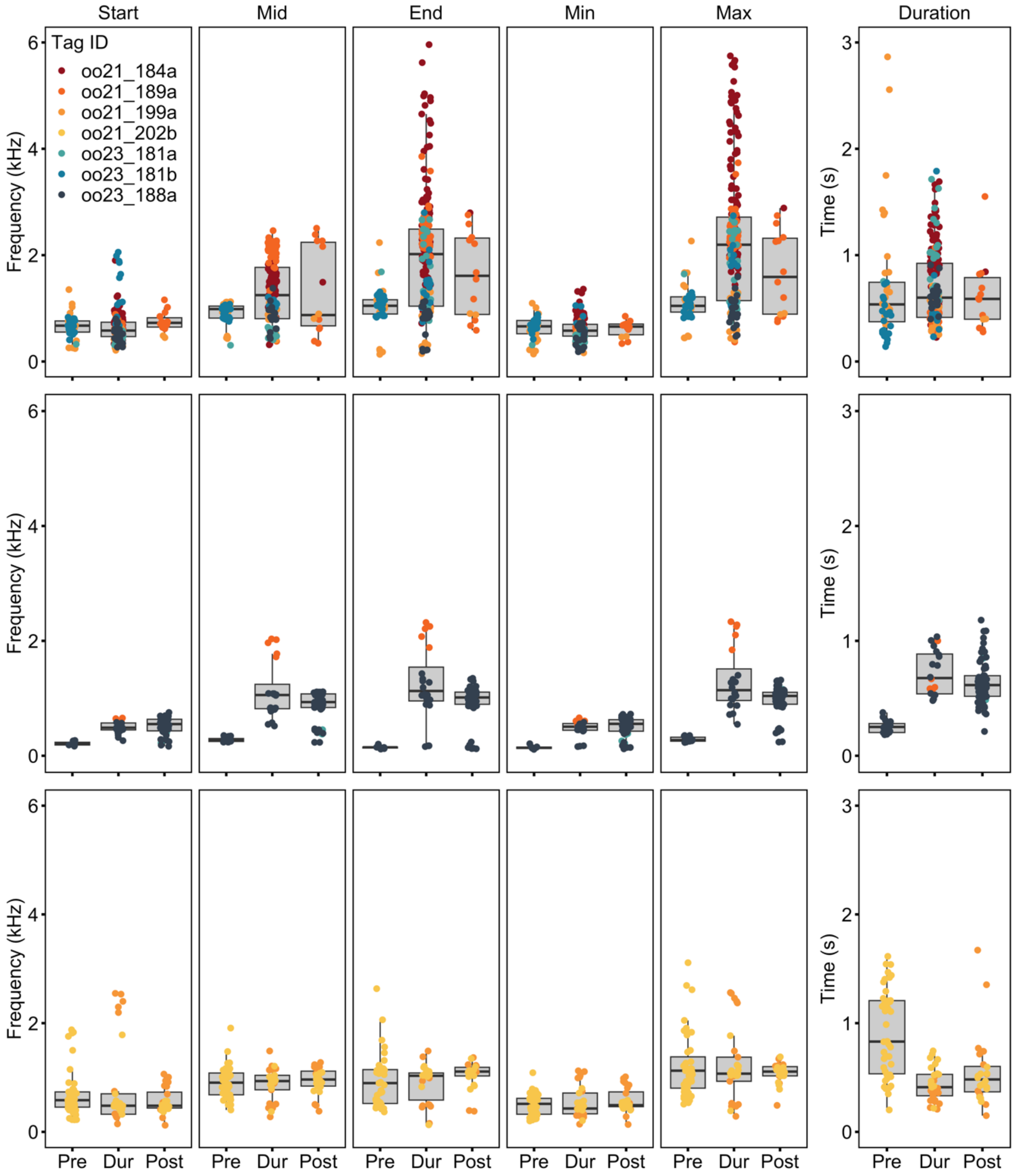


Figure S11: Measurements of frequency and time parameters taken from killer whale calls recorded before (Pre), during (Dur) and after (Post) playbacks of pilot whale sounds (top), noise control (middle), and 1-2 kHz upsweep control (bottom). Boxplots show the interquartile range, with the median indicated by a horizontal line and whiskers extending to 1.5 times the interquartile range. Individual data points are overlaid as dots and coloured by tag. All measurements for the noise and upsweep control playbacks came from very few tags. The pre-phase and post-phases of the pilot whale playbacks were also represented by a few tags. Therefore, no further statistical analysis was undertaken.

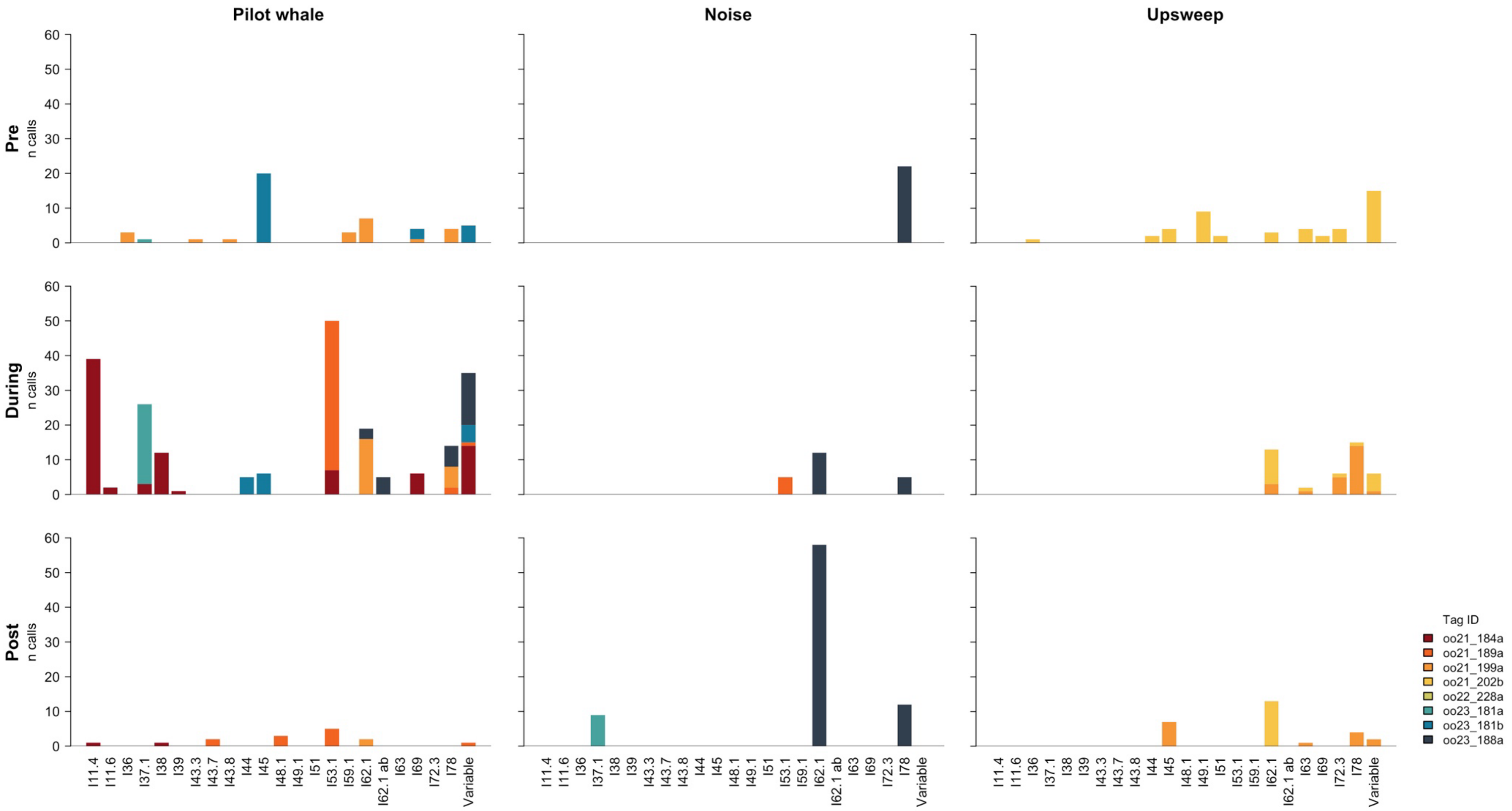


Figure S12: Call types recorded during pilot whale sound (left), noise control (middle), and 1-2 kHz upsweep control (right) playbacks. The number of calls for each call type is given for the pre- (top), during- (middle) and post-phase (bottom). Bars are coloured by tag. ab refers to aberrant version of a call type.

*Table S1: Results of the ANOVA (sequential Wald test) for the best fitting General Estimating Equation (GEE) showing the contribution of each explanatory variable retained to the final fitted GEE for each response variable. The full model included the explanatory variables Stimulus, Order, Phase and an interaction term Stimulus:Phase. The full model for the response variable horizontal movement reaction score did not include the explanatory variable Phase. P-values are marked * at a significance level <0.05.*

Response variable	**Explanatory variable**	χ^2	**p-value**
Horizontal movement	Stimulus	5.36	0.02*
	Order	8.15	0.004*
Number of calls	Stimulus	0.79	0.38
	Phase	3.76	0.05
	Stimulus:Phase	8.15	0.004*
Individual spacing	Stimulus	8.10	0.004*
	Order	4.65	0.03*
Line swimming	Stimulus	7.77	0.01*
	Phase	6.44	0.01*
Milling	Stimulus	0.15	0.70
	Phase	<0.01	1.00
	Stimulus:Phase	5.91	0.02*