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1 **Movements and site fidelity of killer whales (*Orcinus orca*) relative to seasonal**
2 **and long-term shifts in herring (*Clupea harengus*) distribution**

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Abstract

Predators specialising on migratory prey that frequently change migration route face the challenge of finding prey with an unpredictable distribution. Here, we used photo-identification data to investigate whether killer whales observed in herring overwintering and spawning grounds off Iceland follow herring year-round, as previously proposed, and have the ability to adapt to long-term changes in herring distribution. Of 327 identified whales seen more than once, 45% were seen in both grounds, and were thus presumed herring-specialists, likely following herring year-round, while others were only seen on one of the grounds, possibly following herring to unsampled grounds or moving to other locations and exploiting different prey. High seasonal site fidelity to herring grounds, long-term site fidelity to herring spawning grounds, and matches of individual whales between past and recently occupied herring overwintering grounds showed an ability to adapt to long-term changes in prey distribution as well as diversity of movement patterns which are maintained over time, likely as socially-learned traditions. Such population structuring shows that the movement patterns and foraging ecology of herring-eating killer whales are more complex than previously assumed and must be taken into account in future population assessments. Identifying the factors driving these differences in movements and resource use will be relevant towards our understanding of how prey predictability may drive specialization in this and other top predator species.

Keywords: movements, distribution shifts, photo-identification, predator-prey relationship, prey specialisation

Introduction

Animals often adopt complex movement strategies to utilize patchy and unpredictable environments, and research into these strategies is key to understanding population ecology, potential gene and information flow and population structure (e.g., Stevick et al. 2006; Musiani et al. 2007). Food resources likely drive the movements of predators (e.g., Sveegaard et al. 2012). Understanding the movement ecology of top predators is therefore essential for understanding the dynamics of the ecosystem, given their potential impacts on food webs through top-down regulation of prey (Myers et al. 2007). The distribution of prey may itself change, for example, due to natural factors or climate change (Perry et al. 2005). Variations in preferred prey abundance can affect the prey consumed by predators as well as their movement patterns and distribution (e.g., Weinrich et al. 1997). Over short time-scales of hours and days, movement patterns can be determined by food availability (e.g., Jaquet and Whitehead 1999; Whitehead 2003), following the principle of the ideal free distribution (Kacelnik et al., 1992). Over longer time-scales, movements can be more broadly constrained by life-history requirements and access to resources (e.g., migrations between feeding and breeding grounds; Calambokidis et al. 2001). Movement strategies may also differ between sexes within a population (e.g., Dufault et al. 1999; Whitehead 2003) or between social units (e.g., Whitehead and Rendell 2004; Lusseau et al. 2006). Identifying the behavioural and environmental factors governing movements and site fidelity is key to understanding the ecological role of predators and for effective conservation and management of both predator and prey populations.

Killer whales (*Orcinus orca*) are top marine predators with a cosmopolitan distribution (Forney and Wade 2006). Movement patterns vary across spatial scales

67 ((Andrews et al. 2008; Matthews et al. 2011; Durban and Pitman 2012; Matkin et al.
68 2012; Fearnbach et al. 2014;), and can even span thousands of km, as demonstrated
69 by long-range photographic matches (e.g., Dahlheim et al. 2008; Goley and Straley
70 1994; Eisert et al. 2015) and satellite tags (e.g., Matthews et al. 2011, Durban and
71 Pitman 2012). Movements appear to be at least seasonally linked to foraging
72 strategies and prey specialisations (Nichol and Shackleton 1996), or habitat
73 availability (Matthews et al. 2011), although physiological maintenance may explain
74 some large-scale movements from cold to subtropical waters (Durban and Pitman
75 2012). At a fine scale, movements and habitat use may differ between sympatric
76 populations (Matkin et al. 2012) and social groups (Hauser et al. 2007; Fearnbach et
77 al. 2014).

78 Early studies in the Northeast Atlantic suggested that the distribution of killer
79 whales changed seasonally in some locations, concurrent with changes in the
80 distribution of lipid-rich fish species (Bloch and Lockyer 1988; Sigurjónsson et al.
81 1988; Similä et al. 1996; Luque et al. 2006; Foote et al. 2010). In Norway and Iceland,
82 killer whales are thought to specialise on Atlantic herring (*Clupea harengus*) and
83 follow its movements year-round (Sigurjónsson et al. 1988; Similä et al. 1996). In the
84 Northeast Atlantic, the herring stock undergoes large changes in distribution
85 throughout the year as it migrates between overwintering, feeding and spawning
86 grounds (Holst et al. 2004). Over longer time-scales, changes in herring migration
87 routes occur, particularly in the location of overwintering grounds (Dommasnes et al.
88 1994; Dragesund et al. 1997; Óskarsson et al. 2009). Rather than adopting the same
89 migration pattern as older cohorts, a recruiting year class may adopt a new migration
90 route that it tends to repeat in subsequent years, establishing a new overwintering,
91 feeding or spawning ground (Corten 2002). Proposed drivers for these shifts in

92 distribution of herring stocks include climate, prey availability and predator-prey
93 interactions (Fernö et al. 1998; Corten 2001; Holst et al. 2004). Demography,
94 specifically the ratio between first-time and repeat spawners, appears to play a key
95 role in the establishment of new wintering areas (Huse et al. 2010). In addition,
96 herring stocks have undergone large changes in abundance over the last century,
97 either naturally or due to overfishing (Jakobsson et al. 1969; Dragesund et al. 1997;
98 Jakobsson and Stefánsson 1999; Toresen and Østvedt 2000). Such changes in
99 distribution and availability to some degree make herring an unpredictable prey
100 resource. If feeding exclusively on herring, killer whales have had to adapt to episodic
101 shifts in prey availability and distribution to potentially unpredictable locations.

102 The movements of killer whales in Norway support year-round specialisation on
103 the Norwegian spring-spawning stock of herring (Similä et al. 1996; Stenersen and
104 Similä 2004; Foote et al. 2010), although not all whales appear to be herring-
105 specialists (Vongraven and Bisther 2014). In Iceland, at least some individuals travel
106 seasonally to other locations and exploit higher trophic-level prey (Foote et al. 2010;
107 Deecke et al. 2011; Samarra and Foote 2015; Samarra et al. 2017b). Although killer
108 whales have long been known to occur frequently in Icelandic coastal waters
109 (Sæmundsson 1939; Sigurjónsson et al. 1988; Víkingsson 2004), limited dedicated
110 research of this population has meant that there is still relatively little knowledge of
111 population structure, foraging ecology and movement patterns. Although some
112 research has been conducted to understand whether killer whales follow the Icelandic
113 summer-spawning (ISS) herring using photo-identifications, the data were largely
114 collected over non-overlapping time periods and only 11 individuals were seen
115 travelling between separate grounds (Foote et al. 2010). In addition, since the 1980s
116 the main ISS herring overwintering grounds changed from East to West Iceland

(Óskarsson et al. 2009; ICES 2016) and it is unknown if individual killer whales have been able to adapt to these changes in herring distribution.

Here, we use photographic identifications of killer whales collected over a 7-year period in herring overwintering and spawning grounds in Iceland, during winter and summer, respectively, to investigate seasonal movements following the year-round migration of herring. We then use a previously-collected photographic dataset (1981-2007) from the same spawning grounds, but different overwintering grounds, to investigate long-term site fidelity and the ability of killer whales to adjust movement patterns in relation to long-term changes in prey distribution. We hypothesise that if killer whales occurring in coastal Icelandic waters are herring specialists, they should follow the herring migration year-round and adapt their movements to shifts in the distribution of their prey. This study therefore aims to increase our understanding of the movement and foraging ecology of herring-eating killer whales, while expanding current knowledge of population structure of Icelandic killer whales to contribute to effective conservation and management strategies.

Material and methods

Study area and data collection

Research was conducted during winter months in 5 field seasons (between 2011 and 2015, see below) in Grundarfjörður and Kolgrafafjörður, two fjords that formed part of an overwintering ground of the ISS herring in West Iceland (Figure 1A, ICES 2014) and around Vestmannaeyjar during summer months in 6 field seasons (between 2008 and 2015, see below), a traditional ISS herring spawning ground in South Iceland (Figure 1B, Jakobsson and Stefánsson 1999). Photographs were collected from dedicated research platforms, which consisted mainly of small research boats,

but also included land-based observations, observations from fish survey cruises and from whale-watch boats. During each field effort, research was generally conducted from 1-2 research boats each with at least one photographer. On fish survey cruises, photos were taken by a dedicated photographer whenever whales approached the vessel. On whale-watch boats, most photos were taken by research assistants and additional photos were obtained from guides and passengers. Effort varied depending primarily on weather, the data collection platform (dedicated research vs. whale-watch boat) and, in the case of whale-watch boats, the frequency of trips conducted (Table 1).

Winters were considered as the months from November to March, as this was the period when overwintering herring could be found within the fjords, and therefore spanned 2 years. Thus, for example, the winter of 2010/11 refers to the period between November 2010 and March 2011. Photographs from a herring survey cruise were collected in Breiðafjörður between the 29th November and the 2nd December 2012. Photographs from dedicated research efforts were collected in February-March 2013 to 2015 in Grundarfjörður and Kolgrafafjörður and in July 2008 to 2010 and 2013 to 2015 in Vestmannaeyjar, respectively. Photographs opportunistically collected and provided by whale-watch guides, colleagues and members of the public were collected in Grundarfjörður and Kolgrafafjörður in the winters of 2010/11 to 2014/15 (Table 1). Generally, whale-watch and dedicated research vessels worked with different whale groups, but over the course of a day could encounter the same whales. Thus, an encounter was defined as a day in which killer whales were sighted and could be identified, regardless of platform or how often individuals were seen throughout the day.

Photo-identification

Killer whales were approached and photographed for photo-identification (Bigg 1982), using a variety of digital single-lens reflex cameras and lenses. Photographs of killer whales taken from dedicated research boats were typically of the left sides of animals including dorsal fin and saddle patch (the lightly coloured area below and behind the dorsal fin). Pictures of the right side were also taken opportunistically. Both left and right side pictures were used for photo-identification purposes, however an individual was only added to the catalogue if a high quality left-side picture existed. Photographs from whale-watch boats or fish survey cruises were taken opportunistically of both sides of the body. Killer whales were identified based on the size and shape of the dorsal fin, the presence of nicks and scars, saddle patch pattern, and body scars (Bigg 1982). Individuals were classified as ‘male’, ‘female’, ‘juvenile’ or ‘other’ based on body size and size and shape of the dorsal fin, since the year of birth was unknown. Males were mature or sub-adult individuals with distinctly taller dorsal fins (Heimlich-Boran 1986). Females were mature sized individuals seen consistently with a calf in echelon position and seen during most of the study period without changes in dorsal fin size, or matched to a previous catalogue held by the Marine Research Institute (see below) and without changes in dorsal fin size since the last sighting. Juveniles were identifiable individuals >1 year of age that had not reached mature size. Others were whales that appeared of mature size, but for which sex was impossible to determine, which could include juvenile males or adult females. For some whales from which biopsy samples were collected, sex was assigned by genetic analysis (Tavares, unpublished data).

Often large aggregations of killer whales were encountered and division of whales into social groups was difficult (Tavares et al. 2017). In addition, this

information was not always available for opportunistic data collected aboard whale-watch vessels and provided by collaborators, guides or members of the public. Due to the observed fluidity in the social structure of this population (Tavares et al. 2017), all analyses were conducted treating each individual independently of its potential social group. However, it is likely that if whales form stable, long-term groups, the movements of sets of individuals identified in this study will be correlated. All photographs taken were first viewed by a human observer to select those that were deemed usable based on a judgement of photographic quality and distinctiveness of the identifying features of the individual, following a quality assessment based on the method of Friday et al. (2000). Photographs of high quality or where animal features were highly distinctive, such that they could be identified regardless of photographic quality, were analysed. To avoid false positives, a match was confirmed only when at least three clear distinctive features were present in two photographs. For each encounter, the best identification picture of each individual was chosen. Each individual was assigned a unique identification number and added to a catalogue of individuals sighted in Iceland (Samarra et al, 2017a). We then compiled all sightings for each individual into an encounter history to analyse individual re-sightings over time and across locations.

Seasonal movements between herring overwintering and spawning grounds

To investigate recent (2008-2015) killer whale movements between herring overwintering and spawning grounds, we used maximum likelihood methods, which account for a non-uniform and non-random spatial and temporal effort distribution in the dataset by using the photo-identifications as a proxy of effort, to investigate re-sighting probabilities (Whitehead 2001). This method permits the use of

217 opportunistically collected individual-identification data. Analysis of lagged
218 identification rates (i.e., the probability of reidentifying an individual after various
219 time lags, Whitehead 2001) was used to estimate the probability that an individual
220 sighted in one area at time t would be re-sighted in the same or another area at time
221 $t+\Delta t$ (Whitehead 2001). Only a single identification of each individual within a
222 sampling period set to one day was considered. If permanent emigration or mortality
223 occur, the lagged identification rates would typically fall as a function of time lag,
224 whereas if individuals return to an area after leaving (re-immigration) the lagged
225 identification rate may fall and then rise with time lag. If individuals moved between
226 areas, we would expect a non-zero probability of being identified in a different area at
227 time $t+\Delta t$. We fitted models to the data and chose the best-fit model as that which
228 minimised the quasi Akaike's Information Criterion (QAIC, see Whitehead 2007).

229 In addition, transition probabilities between areas were estimated, providing the
230 probability that an individual moves from one area to another between sampling
231 periods (Whitehead 2001). Transition probabilities within one area were also
232 estimated, which provide the probability that an individual is resighted in a study area
233 one sampling period later (Whitehead 2001). For this analysis, sampling period was
234 set to season, so that seasonal movements could be investigated. All analyses were
235 carried out using the program SOCPROG 2.7 (Whitehead 2009).

236 Within each season we also calculated the 'occurrence' of whales, defined as the
237 number of days in which an individual was photographed per season, and the
238 'occupancy', defined as the number of days elapsed from first to last sighting within
239 each season (see Weinrich et al. 1997). For both metrics we calculated the mean value
240 per season across all individuals, excluding individuals that were not seen in that
241 particular season. For each individual that was sighted in more than one season we

also estimated the maximum number of years between re-identifications. In this case 0.5 represented sightings in successive seasons (e.g., seen in winter and the following summer) and 1 represented sightings during the same season but in different years (e.g., seen in summer 2008 and again in summer 2009).

Finally, individuals were assigned a movement pattern as: 1) following herring, if identified at least once in both herring overwintering and spawning grounds or; 2) seen only seasonally, if identified only in herring overwintering or spawning grounds. Because an individual would only have to be identified once across 5 sampling seasons in herring overwintering grounds and 6 sampling seasons in herring spawning grounds included in this study, these broad and inclusive criteria should account for infrequently-seen individuals that follow herring year-round.

Comparison to previous identification data

Photo-identification of killer whales in Iceland started in 1981 (Sigurjónsson et al. 1988) and photographs collected since have been compiled in a catalogue coordinated by the Marine and Freshwater Research Institute (hereafter referred to as the MFRI catalogue; Foote et al. 2010) including each individual's sighting history. The MFRI catalogue contained 316 individuals identified in the winter (October to February) between 1981 and 1999 in the overwintering grounds of ISS herring, with the majority of sightings occurring in East Iceland (Figure 1). It also included a total of 101 individuals identified in the summer (May to August) between 1997 and 2007 in herring spawning grounds off Vestmannaeyjar (Figure 1). Only sightings for which the date and location were known and where individuals were photo-identified and a catalogue picture existed were included. All individuals were included in the

comparison, even if only a right side catalogue picture was available (31 out of 316 individuals).

To investigate if killer whales sighted in past herring overwintering grounds in East Iceland (hereafter termed past herring overwintering grounds) were resighted in recently occupied herring overwintering grounds off West Iceland (hereafter termed recent herring overwintering grounds), we compared all individuals photo-identified in ISS herring overwintering grounds off West Iceland between the winters of 2010/11 and 2014/15 with the MFRI catalogue, regardless of sighting frequency. To investigate long-term site fidelity to herring spawning grounds we compared all individuals photo-identified occurring in ISS herring spawning grounds in Vestmannaeyjar between 2008 and 2015 with the MFRI catalogue, regardless of sighting frequency. For both analyses, only individuals presumed to be adults during the study period (2008-2015) were included, as juveniles would not have been born since the last sightings included in the MFRI catalogue, or would have been very young calves and thus unrecognisable. Only matches confirmed by two scorers were accepted.

Matching was not possible if photographs from the MFRI catalogue were of poor quality or did not cover the whole fin and saddle patch areas. Because a large number of changes in marks could make individuals unrecognisable or the photographic quality when first sighted was too poor to confirm a match, the lack of a match could represent false negatives (misses) and the re-identification was biased towards individuals that were already well-marked (with distinctive nicks, scars or saddle patch pattern) in the past.

Results

Since 2008, killer whales were encountered on 129 days in herring overwintering grounds and on 66 days in herring spawning grounds (Table 1). We identified a total of 376 individuals, including 123 (33%) males, 110 (29%) females, 62 (16%) juveniles and 81 (22%) others. Of these, 49 whales (17 males, 10 females, 2 juveniles and 20 others) were only seen once, most of which (77%) were sighted in herring overwintering grounds. In contrast, 327 individuals were recorded during two or more encounters, of which 76 (23%) were only seen in one year and 251 (77%) were re-sighted in multiple years. Of the 76 individuals only seen in one year, the majority (66%) were only seen in herring overwintering grounds, 21% were only seen in herring spawning grounds and 13% were seen in both locations. The total number of whales identified per season and year varied from a minimum of 11 (winter 2014/15) to a maximum of 248 (winter 2012/13, mean \pm standard deviation: $X \pm SD = 96.3 \pm 67.2$). In the winter, the total number of individuals identified per year varied between 11 (in 2014/15) and 248 (in 2012/13) with a mean \pm standard deviation of $X \pm SD = 100.6 \pm 94.2$ (Table 1); in the summer, the total number of individuals identified per year varied between 42 (in 2008) and 150 (in 2015), with a mean \pm standard deviation of $X \pm SD = 92.7 \pm 43.6$ (Table 1).

The number of identified individuals across all seasons and years tended to depend on the total number of days with killer whale encounters (Pearson's correlation = 0.82; t-value = 4.30; df = 9; P = 0.002), however this relationship was significant in winter (Pearson's correlation = 0.94; t-value = 4.65; df = 3; P = 0.02) but not in the summer (Pearson's correlation = 0.75; t-value = 2.26; df = 4; P = 0.09). Nevertheless, in winter the number of identified individuals could also vary between seasons with similar total number of days with killer whale encounters. For example, 248 individuals were identified in 53 encounter days in the winter 2012/13, while only

131 were identified in 45 encounter days in the winter of 2013/14 (Table 1). The discovery curve, showing the cumulative number of individuals identified over time, suggested that the rate of identification of new individuals increased markedly following the first winter field seasons, particularly that of the winter of 2012/13 (Figure 2). However, towards the end of the study period this rate levelled off suggesting a nearly complete coverage of the population in these study areas during the study period (Figure 2).

Seasonal movements between herring overwintering and spawning grounds

Using recent (2008-2015) photo-identification data collected in herring overwintering and spawning grounds, the lagged identification rate analysis showed non-zero probabilities of re-identification in different areas over time lags ranging up to approximately 6 years (Figure 3). This suggests that individuals use both herring overwintering and spawning grounds and move across both locations. However, the probability of an individual being re-sighted in an area different from its first sighting was lower than the probability of being sighted in the same area (Figure 3). Indeed, of the 327 individuals sighted in at least two encounters, 146 (45%) were observed moving between herring overwintering grounds and spawning grounds while the remaining 161 (55%) were only identified either in herring overwintering grounds ($n = 117$) or spawning grounds ($n = 64$). The lagged identification rate from a given area to another was low at time lags of 116 days, which generally represented the time lag between a winter and subsequent summer data collection period; at time lags of 172 days it increased, which generally represented the time lag between a summer and subsequent winter data collection period. The lagged identification rate then stabilized for the remainder of the study period suggesting similar rates between areas in

subsequent years. The model that best fitted the lagged identification rate from a given area to another, by minimising the QAIC, was a Migration model (Whitehead 2001), which estimated a mean residence time in an area of 61.5 days (95% CI: 35.5 – 108.0) and a population size of 347.7 (95% CI: 295.5 – 418.1).

Within a given area, the lagged identification rate dropped at time lags from 1 to 84 days, reaching its lowest value at approximately 252 days. This suggests that individuals stayed within an area seasonally but then left. The lagged identification rate then increased again around a time lag of 365 days, although to lower levels than at its maximum, and remained stable until the end of the study period, suggesting return to the same area in successive years (Figure 3). This suggests high site fidelity to an area but return was not complete. The model that best fitted the lagged identification rate within an area was one of Emigration with Re-Immigration (Whitehead 2001), supporting the seasonal movements of whales away from the area where they were first observed and subsequent return in the following years. The model estimated a mean residence time of 17.6 days (95% CI: 9.9 – 32.8) within a given study area, and a mean residence time out of the area of 15.1 days (95% CI: 9.1 – 26.9) and a mean number of individuals present at any given time in the study area of 87.1 (95% CI: 78.0 – 96.8).

High transition probabilities within both overwintering and spawning grounds (0.89 and 0.62, respectively) supported the high site fidelity suggested by the lagged identification rate (Table 2). Transition probabilities between areas were lower, suggesting that not all individuals moved between locations. Transition probabilities of approximately 0.4 were estimated from spawning grounds to overwintering grounds across seasons. Indeed, 66% of the total number of individuals found in spawning grounds also occurred in overwintering grounds (Table 2). Transition

probabilities from overwintering grounds to spawning grounds were lower (approximately 0.1) and a smaller proportion of the total number of individuals sighted in overwintering grounds also occurred in spawning grounds (48%; Table 2).

The mean ‘occurrence’ (or number of days in which an individual was photographed, as defined by Weinrich et al. 1997) per season varied from a minimum of 1.38 to a maximum of 4.27 in summer and a minimum of 1.11 to a maximum of 5.76 in winter (Table 3). Mean occurrence tended to be lower in seasons when the total number of days with killer whale encounters was also low, however the maximum occurrence never reached the maximum number of days with killer whale encounters (Table 3), i.e. no individuals were seen on every day of sampling. The mean ‘occupancy’ (or number of days elapsed from first to last sighting within each season, as defined by Weinrich et al. 1997) ranged from a minimum of 2.69 to a maximum of 15.51 in summer and a minimum of 5 to a maximum of 43.42 in the winter (Table 3). The maximum occupancy per season in both winter and summer was generally very close to the number of days between the first and last encounter of that season, suggesting that within each season at least some individuals stayed or regularly returned to the study area (Table 3). Finally, on average the maximum number of years between re-sightings of individuals that were sighted in more than one season varied between 1 and 4.5, with a mean of $X \pm SD = 1.96 \pm 0.7$ years.

Movements between past and recent herring overwintering grounds

The comparison of photo-identification data collected in this study (2008-2015) with data collected between 1981 and 1999 in the MFRI catalogue resulted in a total of 16 individuals re-identified between past and recent herring overwintering grounds (Figure 4A). This represented 5% of the 316 individuals identified in past herring

overwintering grounds and 5% of the 301 individuals identified in recent herring overwintering grounds. All matched whales were first re-identified in recent herring overwintering grounds between 2010 and 2013. Eight of the 16 whales matched between past and recent herring overwintering grounds were only seen in one year. Of these, two were seen only in the winter of 2011/12, and six were only seen in the winter of 2012/13. Overall, the largest number of whales were seen in the winter of 2012/13 ($n = 14$), which was also the winter with the largest number of days with killer whale encounters (Figure 5). Despite a similar number of days with killer whale encounters in the winter of 2013/14, only 4 of the 16 whales matched between past and recent herring overwintering grounds were re-sighted, but they were sighted often (Figure 5). Most of the 16 whales did not appear to follow herring year-round between sampled herring grounds, as they were only seen in recent herring overwintering grounds, but not in the spawning grounds off Vestmannaeyjar, with two exceptions. In the MFRI catalogue, however, both these whales had only been seen once and in the winter. In contrast, two whales that were previously identified both in herring overwintering and spawning grounds in the MFRI catalogue, were no longer seen in spawning grounds and were thus not classified as whales following herring year-round in the present study. The remaining 12 whales were only identified in herring overwintering grounds in both the MFRI catalogue and this study.

Long-term fidelity to herring spawning grounds

The comparison of photo-identifications collected in this study (2008-2015) with data collected between 1997 and 2007 in the MFRI catalogue resulted in a total of 27 individuals re-identified in herring spawning grounds (Figure 4B). This represented 27% of the total number of individuals identified in herring spawning grounds off

Vestmannaeyjar in the MFRI catalogue ($n = 101$) and 12% of the total number of individuals identified in the same location during our study ($n = 221$). In this study, most of those whales were first re-sighted in herring spawning grounds between the summers of 2008 and 2010. Only three whales were first re-sighted in the later summer season of 2014. Four of the 27 whales matched between past and current sighting data were only seen in one year. Of these, two were seen only in the summer of 2008, one was only seen in 2010 and the other in 2014. Overall, most whales were seen in every summer season (mean \pm standard deviation number of individuals seen per season: $X \pm SD = 14.7 \pm 4$, min = 8, max = 20), although at different sighting frequencies that tended to follow the total number of days with killer whale encounters per season (Figure 5). Ten of these 27 whales were sighted in both the herring spawning grounds and the overwintering grounds and were classified as following herring year-round. The remaining 17 whales were only seen in herring spawning grounds. In the MFRI catalogue, however, most whales ($n = 26$) were previously only sighted in herring spawning grounds. Only one of the 27 individuals was identified both in herring overwintering and spawning grounds in the MFRI catalogue. However, this whale was only seen once in the present study and only in the herring spawning grounds, thus it was not assigned to the group presumed to follow herring year-round.

Discussion

This study shows that killer whales observed in Icelandic coastal waters have a mosaic of movement patterns. Some individuals were identified in both overwintering and summer herring grounds, thus appearing to follow herring movements year-round, putatively comprising a herring-specialist community. However, other whales were

only seen seasonally either on herring overwintering or spawning grounds. Previous studies of killer whales occurring in Icelandic coastal waters had noted the presence of killer whales in areas consistent with herring overwintering or spawning areas (Sigurjónsson et al. 1988; Foote et al. 2010) and suggested that these whales may specialise in feeding on herring and follow the year-round movements of the ISS stock of Atlantic herring (Sigurjónsson et al. 1988). However, only a small proportion of killer whales had previously been matched between herring overwintering and spawning grounds (Foote et al. 2010) and there was a lack of repeated within-year photo-identification effort in different herring grounds to investigate if killer whales indeed follow herring year-round. In this study, we found that nearly half of the individuals sighted on more than one occasion (45%) were sighted in both herring overwintering and spawning grounds, while the remaining 55% were only sighted in one of those locations. Although sampling effort could have influenced our ability to identify individuals in different locations, given our broad and inclusive criteria for a whale to be considered as following herring (see Methods), even infrequently-seen individuals should have been included. These results suggest that killer whales occurring in Icelandic coastal waters for at least part of the year did not all follow the ISS stock of Atlantic herring year-round.

The discovery rate curve for photo-identified individuals suggests that we achieved a fairly complete coverage of the population within our study areas during the study period, though sighting frequency varied considerably between individuals. Some whales were only seen once suggesting they were occasional visitors to these waters. Although our study suggests high site fidelity to Iceland of some individuals, it is clear that for others, information on movements is scarce due to low re-sightability. Given Iceland's position in the Northeast Atlantic, it is plausible that

individuals with a predominantly offshore distribution occasionally pass within the study areas. Surveys suggest a large population of killer whales in offshore waters (Gunnlaugsson and Sigurjónsson 1990), however there is little information about the movements and population identity of these whales.

Lagged identification rates suggest that individuals first sighted in the winter were less likely to be re-sighted in summer than those first sighted in summer. This was also supported by higher transition probabilities of individual killer whales from herring spawning grounds to herring overwintering grounds than vice-versa. This may suggest that individuals sighted in herring spawning grounds are more likely to follow herring year-round than individuals sighted in herring overwintering grounds. In fact, stable isotope analysis of a subset of the individuals included in this study showed that whales sampled in summer, even those that were only sighted in herring spawning grounds, tended to have low nitrogen stable isotope values, consistent with a diet composed of herring (Samarra et al. 2017b). In contrast, some of the whales observed only in winter have been observed regularly travelling to northern Scotland in summer and include higher trophic prey in their diet (Samarra and Foote 2015; Samarra et al. 2017b). This suggests that whales with different movement patterns and foraging ecologies may tend to aggregate in herring overwintering grounds, while whales occurring in herring spawning grounds may tend to be more consistently putative herring specialists.

Site fidelity

Site fidelity to a given area was high and in general individual whales were more likely to be re-sighted in the same area than between different herring grounds. Within a season, ‘occurrence’ and ‘occupancy’ metrics (as defined by Weinrich et al. 1997)

suggested individuals tended to remain in the same area but were not seen every day, either being missed by the photographic effort or spending periods of a few days outside of the study area before returning. Occasional movements outside the main feeding area have also been reported in herring-eating killer whales in coastal waters off Norway (Stenersen and Similä 2004). Emigration from a given area was seasonal with some but not all whales returning the following year. Over long time scales, return to the same herring spawning grounds was supported by photographic matches between the previous sighting data in the MFRI catalogue and those collected during this study, suggesting some long-term site fidelity to spawning grounds.

The fact that not all whales were observed on herring spawning grounds around Vestmannaeyjar and that site fidelity to spawning grounds was high, and maintained over the long-term, suggests that killer whale individuals or groups may have preferences for visiting particular herring spawning grounds and these are maintained throughout their lifetime and possibly transferred to offspring via social learning. Cultural differences in movement patterns, with potential fitness consequences, have been shown in cetaceans (e.g., Whitehead and Rendell 2004; Valenzuela et al. 2012). Herring spread out across different spawning grounds in the summer (Jakobsson and Stefánsson 1999), thus only a proportion of the entire resource stock is available at each spawning ground. Spatial segregation may be expected under the ideal free distribution if the availability of prey cannot sustain large aggregations of whales, allowing killer whale groups to successfully exploit the less abundant prey resources at each location, while leading to other whales moving elsewhere. Site fidelity to spawning grounds could then develop if it were advantageous to feed in areas where individuals have accumulated knowledge on local prey resource distribution and prey behaviour (Samarra and Miller 2015).

516

517 *Adaptation to long-term changes in prey distribution*

518 The match of individuals to the previous overwintering grounds shows the ability
519 of at least some whales to adapt to long-term shifts in herring distribution. It is
520 possible that the low number of whales matched between past and recent herring
521 overwintering grounds reflect a true low number of whales that have adapted their
522 movements to changes in prey distribution, but we lack sufficient information on
523 actual numbers of whales which used each of those grounds to draw such conclusions.
524 Our ability to detect matches to whales sighted in past overwintering grounds was
525 undoubtedly biased towards those individuals that were already well-marked adult
526 whales when first sighted in the past. The gap between re-sightings could have been
527 as large as 30 years, due to the lack of a consistent long-term photo-identification
528 effort for this population prior to this study. Less clearly marked young animals only
529 sighted in the 1980s would most likely have very different markings at present
530 making a re-sighting very difficult. Indeed, the fact that the more recent (1997-2007)
531 photo-identification data in the MFRI catalogue from herring spawning grounds led to
532 a higher number of matches could be an indication of facilitated matches between
533 photo-identifications with shorter time intervals. In addition, given the lack of
534 knowledge on the population's survival rate and the unknown age of the whales in the
535 MFRI catalogue, it is impossible to estimate how many individuals might have
536 survived over that time period.

537 Most of the whales matched between past and recent overwintering grounds were
538 seen in early winter seasons, when the amount of prey available was high (ICES
539 2014). Although the total number of days with killer whale encounters was related to
540 the number of whales identified overall, it did not fully explain the variation in re-

identifications. Despite similar total number of days with killer whale encounters in the winters of 2012/13 and 2013/14, fewer individuals overall were re-sighted in 2013/14, which also corresponded to a decrease in the amount of herring available in the study area (ICES 2014). Thus, prey abundance may regulate the number of whales that visit an area and the amount of time they remain available for photo-identification, as predicted for the ideal free distribution. Similar fluctuations in killer whale sightings related with changes in herring abundance and distribution have also been suggested for Norway (Kuningas et al. 2013, 2014).

Most of the whales in our study matched to the photo-identification data collected in previous herring overwintering grounds (MFRI catalogue) were only re-sighted in the winter and were never seen in the herring summer-spawning grounds sampled in this study. Investigating the sighting history of those whales collected previously in the MFRI catalogue revealed that also between 1981 and 2007 these whales were only sighted in herring overwintering grounds and not in the spawning grounds of Vestmannaeyjar. Although it is possible that these individuals were simply missed, the similarity of the individuals' sighting history in both datasets strongly suggests that, if these whales follow the ISS herring stock year-round, they are consistently choosing spawning grounds other than Vestmannaeyjar. Indeed, stable isotope analyses suggest that some whales only seen seasonally exhibit similar stable isotopic signatures in comparison to putative herring-specialists (Samarra et al. 2017b), and thus likely also follow herring year-round, but to other locations. Indeed, the ISS herring has several overwintering and spawning grounds (ICES 2016, Jakobsson and Stefánsson 1999). Individuals that follow herring year-round could travel between any number of these locations, thus not always being available for photo-identification in our study, which only covered one overwintering and one spawning ground. In

addition, whales first identified in Iceland were later observed feeding upon North Sea herring off Shetland (Deecke et al. 2011), suggesting some whales may feed upon herring year-round but exploit other herring stocks.

Alternatively, seasonal occurrence could indicate that some whales are consistently only visiting herring overwintering grounds and not spawning grounds, possibly exploiting other prey at other times of the year. The fact that occasional visitors (only sighted once) and whales seen more than once but only in one year occur mostly in herring overwintering grounds, suggests that these may serve as a gathering of whales with diverse movement patterns, more so than herring spawning grounds. Indeed, some of the whales observed only in recent herring overwintering grounds have been identified in summer in West Iceland (Samarra, unpublished data), while others travel to northern Scotland in the summer (Deecke et al. 2011; Samarra and Foote 2015). This agrees with stable isotope studies suggesting more variability in niche width of whales sampled in herring overwintering than herring spawning grounds (see above; Samarra et al. 2017b). Because herring forms larger aggregations when overwintering in comparison to spawning (Holst et al. 2004), the larger diversity of whales visiting herring overwintering grounds could be prey-related. However, social reasons, such as increased opportunities for breeding (Matkin et al. 1997), cannot be ruled out as drivers of killer whales movements in this study.

Taken together, the seasonal and long-term site fidelity to herring grounds and the long-term consistency in movement patterns (i.e., following herring year-round or seen only seasonally) support individual or group differences that are maintained over large temporal scales and may be an example of socially-learned traditions in movement patterns.

Implications for population structure

The occurrence of killer whales in Icelandic waters has long been known (Sæmundsson 1939; Sigurjónsson et al. 1988; Víkingsson 2004), however few studies have directly attempted to estimate population size and structure. A synthesis of information on global killer whale abundance classified killer whales in Iceland as ‘common’ (Forney and Wade 2006). Using surveys of local fishermen and photo-identification, estimates of the minimum number of whales present in Icelandic coastal herring grounds in the 1980s were in the low hundreds (284 individuals in Sigurjónsson 1984; 143 individuals in Sigurjónsson et al. 1988). In contrast, shipboard surveys in offshore Icelandic waters and adjacent regions in 1987 reported a total of 175 killer whales distributed widely (Sigurjónsson and Gunnlaugsson 1989), resulting in an estimate of over 6,000 killer whales in the entire area (Gunnlaugsson and Sigurjónsson 1990). Finally, a study gathering opportunistic and short-term dedicated photo-identification effort on killer whales in Vestmannaeyjar, South Iceland, and in East Iceland, including part of the 143 individuals previously identified (Sigurjónsson et al. 1988), reported a total of 379 individuals identified between 1984 and 2007 (Foote et al. 2010). These earlier studies seem to suggest that although across a large oceanic area the numbers of killer whales in Icelandic and adjacent waters could be very large, the number of whales visiting coastal waters is an order of magnitude smaller.

Our photo-identification effort in this study revealed the presence of at least 376 individuals, supporting earlier suggestions of a smaller coastal population. It is possible that the relatively low number of matches ($n = 43$) to the MFRI catalogue included in this study is an indication of a larger population. However, given the limitations of the comparison (see above) such an assumption should be treated with

caution. Within this total number of individuals there were occasional visitors, which were only sighted once, suggesting that the number of whales frequently occurring in Icelandic coastal waters is even smaller. This suggests a smaller population than that estimated for herring-eating killer whales in Norway (731 individuals in 2003; Kuningas et al. 2014), which could be related to the amount of herring available. Prey availability can severely impact killer whale population demography (Ward et al. 2009; Ford et al. 2010; Esteban et al. 2016a). In Norway, years of high herring biomass coincided with an apparent increase in the number of new individuals, although food availability alone did not seem to fully explain this increase (Kuningas et al. 2014). Current estimates of the spawning stock biomass of ISS herring are approximately 300 thousand tonnes (ICES 2016), much smaller than the approximately 4 million tonnes of Norwegian spring-spawning herring (ICES 2015). Further work relating the abundance and occurrence of killer whales and herring is necessary to understand how this prey resource may affect and limit populations that exploit it and depend on it.

Our study suggests spatial structuring with different individuals or groups within the population exhibiting different movement patterns. In combination with studies on stable isotopes, these differences in individual movement patterns suggest a mosaic of foraging preferences (Samarra et al. 2017b). Importantly, such differences in movement patterns and feeding preferences are not reflected in social isolation (Tavares et al. 2017), thus suggesting that these differences may occur in the absence of reproductive isolation. Future research using genetic markers will be crucial to further assess the degree of gene flow and potential structuring within this population. Nevertheless, different movement patterns and feeding ecology will likely have fitness implications and expose individuals to different potential risk factors. Putative

herring-eating specialists will likely be more affected by fluctuations in distribution and availability of this prey than whales that only seasonally exploit it and appear to exhibit higher movement and foraging plasticity. Because observational data alone cannot accurately reflect their feeding ecology (Samarra et al. 2017b), complementary dietary information such as stable isotope and fatty acid analyses could play a key role in assessing what proportion of the population may be herring-specialists in the future. Estimating parameters such as population size, survival and reproductive rates, critical for the assessment of the status of a population, requires long-term datasets (e.g. Kuningas et al. 2014; Esteban et al. 2016b). In addition, effective conservation and management requires an understanding of modal and exceptional movement patterns over a range of timescales (Dufault et al. 1999). Thus, continued population monitoring and combined analyses of photo-identification, visual observations, chemical tracers and genetic markers will be required to assess the status of this population as well as long-term stability in movement patterns and dietary preferences. Knowledge of population status is crucial to monitor viability for conservation purposes, but segregation within a population has conservation implications, as smaller units are more vulnerable to depletion (Stevick et al. 2006). However, our study points to the complex nature of population assessment in this case. Sampling in ISS herring overwintering grounds may provide a wider coverage of the population, but is more likely to include individuals with different movement patterns and foraging ecology. On the other hand, sampling in ISS herring spawning grounds will more likely produce a reliable picture of the status of at least part of the putative herring-specialist community. Such sampling limitations within any given area should be taken into account in future studies. This study points to a complex population structure in herring-eating killer whales and similar studies in other herring grounds in

the wider Northeast Atlantic will be valuable to understand if such complexity is widespread to help our understanding of how prey predictability may affect ecological specialization in this species.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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Figures

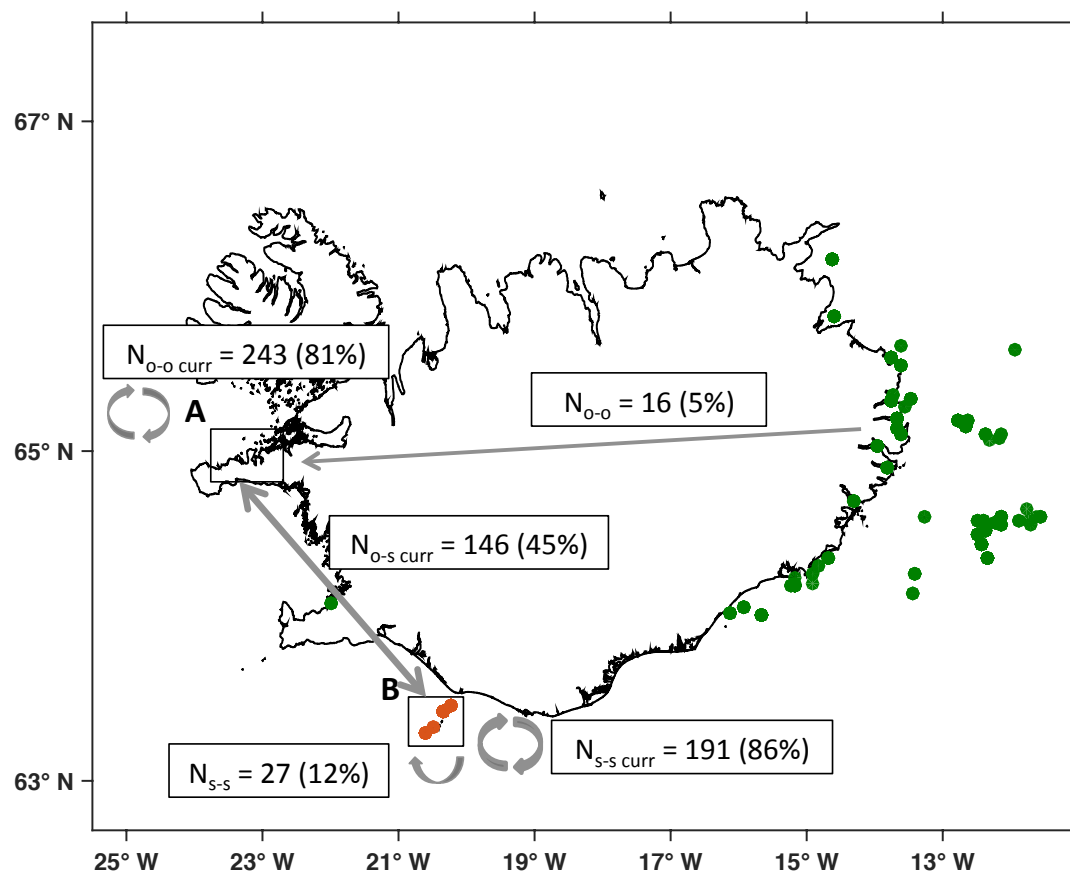


Fig. 1 Map of Iceland showing the approximate study locations where recent (2008-2015) killer whale photo-identification data were collected: A) recent herring overwintering grounds in the West of Iceland, including the fjords Grundarfjörður and Kolgrafafjörður and; B) herring spawning grounds off Vestmannaeyjar, in the South of Iceland. The locations of killer whale photo-identifications collected by previous effort for the MFRI catalogue, in herring spawning grounds off Vestmannaeyjar (red circles) and past herring overwintering grounds off East Iceland (green circles), are also shown. Arrows show the number of killer whales photographically matched between past and recent herring overwintering grounds (N_{o-o} and corresponding % of individual killer whales identified in recent herring overwintering grounds), between past and recent photo-identifications collected in the same herring spawning grounds off Vestmannaeyjar (N_{s-s} and corresponding % of individual killer whales identified in

recent herring spawning ground data), between recent (2008-2015) data collected in herring overwintering and spawning grounds (N_{o-s} and corresponding % of total individual killer whales identified more than once), re-sighted in recent herring overwintering grounds ($N_{o-o \text{ curr}}$ and corresponding % of total individual killer whales identified in recent herring overwintering grounds) and re-sighted in herring spawning grounds ($N_{s-s \text{ curr}}$ and corresponding % of total individual killer whales identified in recent herring spawning ground data). Only sightings for which location was known were plotted.

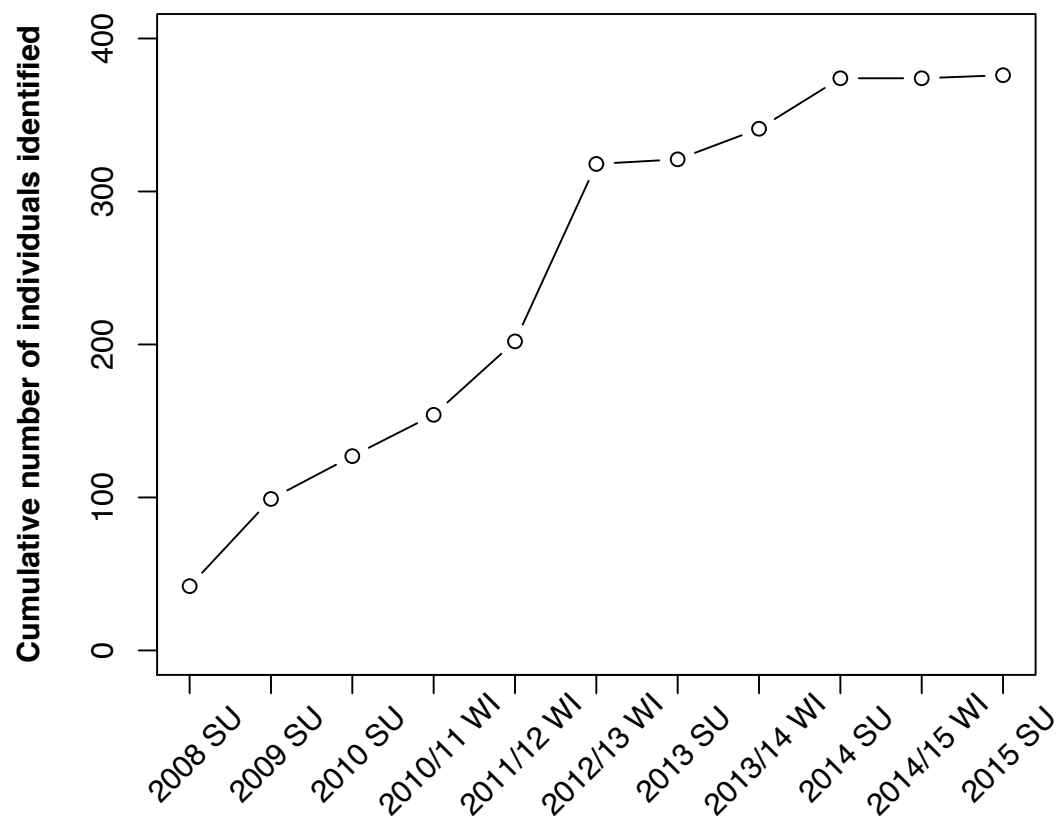


Fig. 2 Discovery curve of Icelandic killer whales by year and season where SU represents summer and WI represents winter. Winters are considered as the months of November to March and thus span across two years (e.g., the winter of 2010/11 represents the period between November 2010 and March 2011).

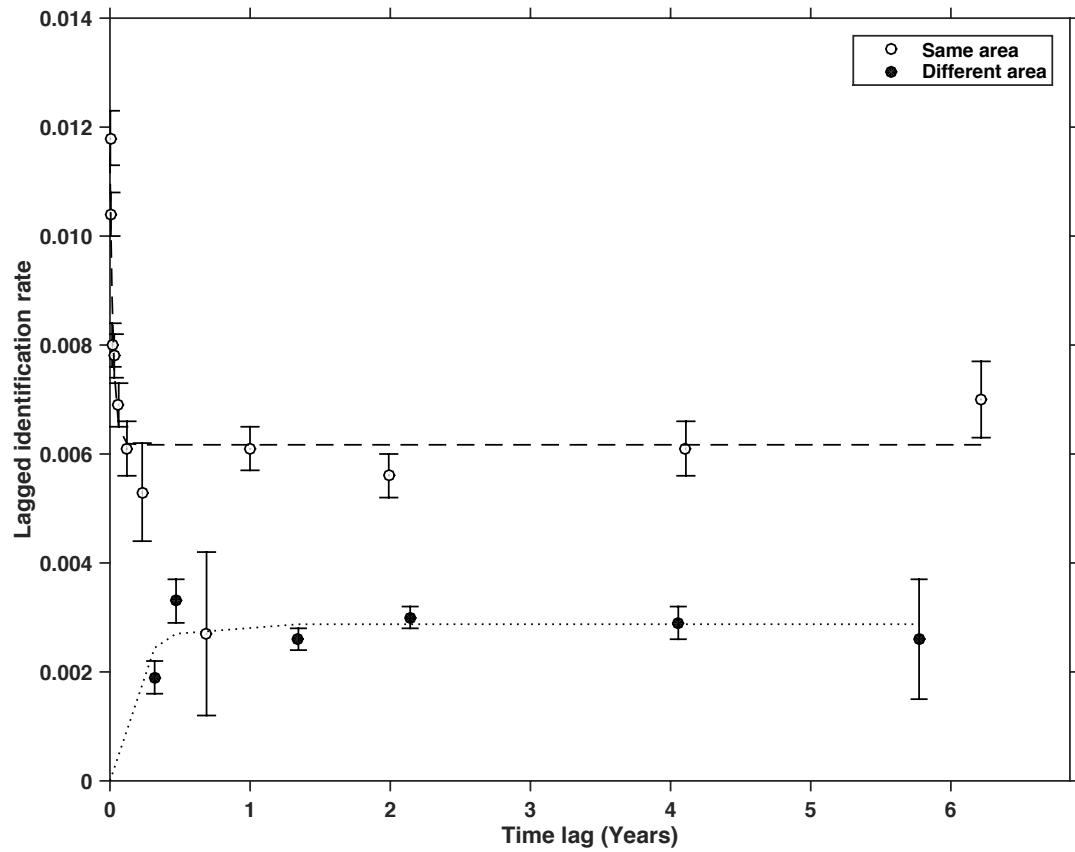


Fig. 3 Lagged identification rates (i.e., probability of reidentification after various time lags, see Whitehead 2001) of individual killer whales between and within herring overwintering and spawning grounds off Iceland. Error bars show jackknife standard errors. The best fitting model for the same area, corresponding to emigration with re-immigration, is represented by a dashed line, while the best fitting model for different areas, corresponding to migration, is represented by a dotted line.

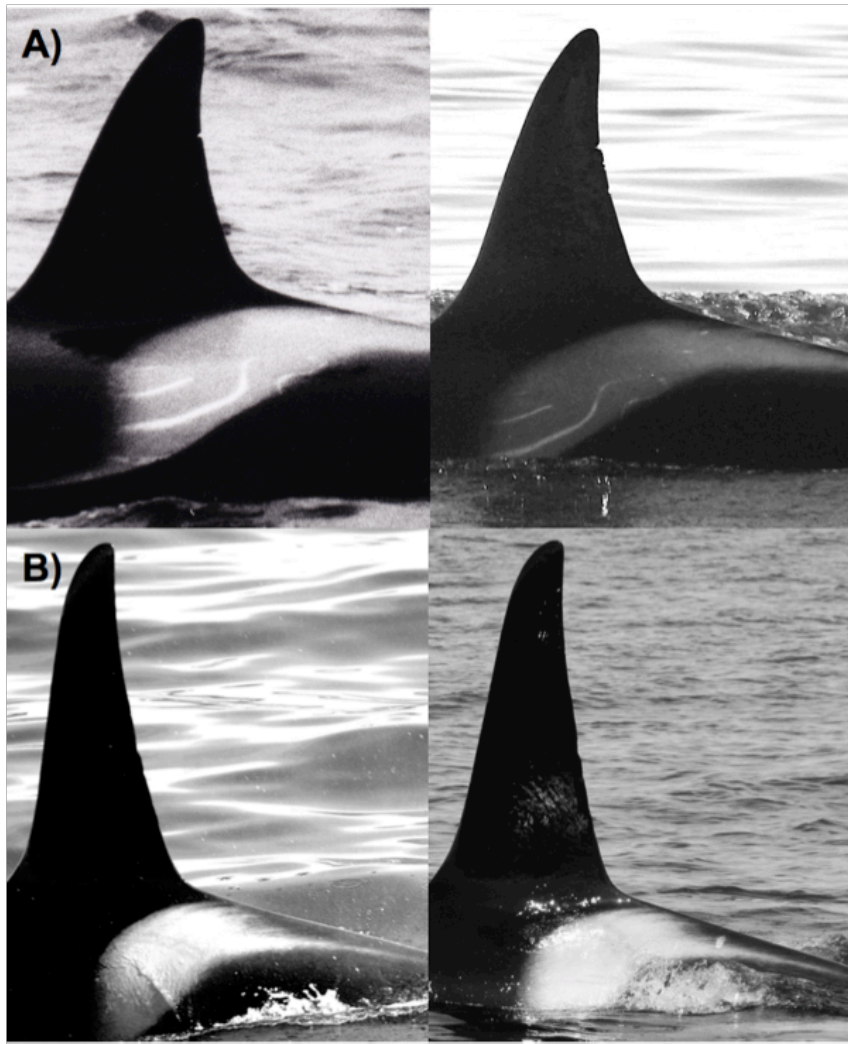


Fig. 4 Examples of photographic matches of Icelandic killer whales: A) IS084 matched between past (left, sighted in 1991) and recent (right, sighted in the winter 2012/13) herring overwintering grounds; B) IS059 matched between past (left, sighted in 1999) and recent (right, sighted in the summers of 2008, 2009 and 2010) spawning ground observations.

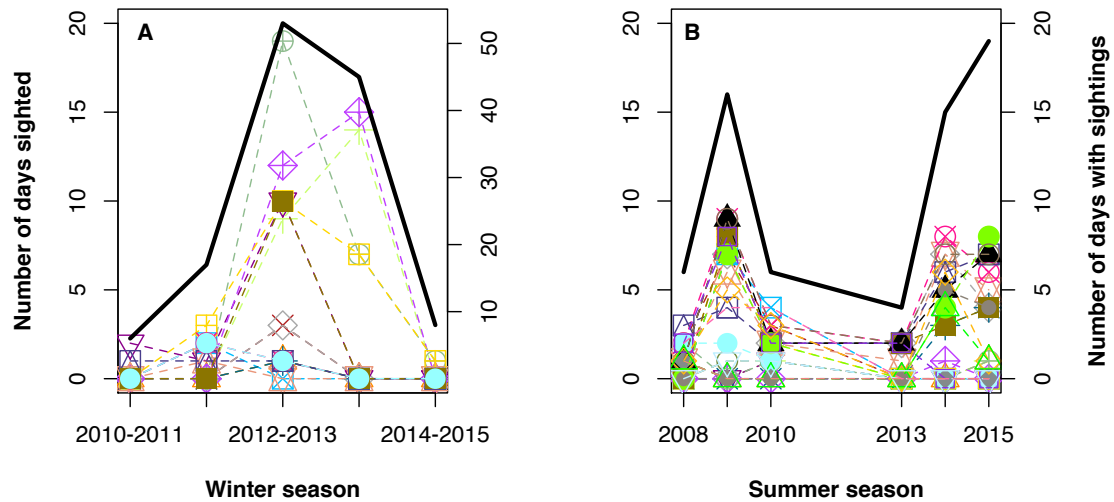


Fig. 5 Sighting frequency per season of Icelandic killer whales matched to the MFRI catalogue (1981-2007) during the study period (2008-2015): A) number of days sighted in recent herring overwintering grounds for each of the 16 killer whales matched to past herring overwintering grounds; B) number of days sighted for each of the 27 whales matched to the MFRI catalogue collected in the same herring spawning ground (1997-2007).. The sighting frequency of each individual whale for each season is represented by a coloured symbol and dashed line. The number of days with killer whale encounters per season is indicated by the thick black line. Note that in panel A, winters are considered as the months of November to March and thus span across two years (e.g., the winter of 2010/11 represents the period between November 2010 and March 2011).

Table 1. Summary of days with killer whale encounters in Icelandic waters. The number of encounters refers to the number of days with killer whale identifications and the number of IDs refers to the number of individually identified killer whales in each season.

Season/Location	Year	Field method	No. encounters	No. IDs
Summer/ Vestmannaeyjar (Herring spawning grounds)	2008	Research	6	42
	2009	“	16	83
	2010	“	6	97
	2013	“	4	50
	2014	“	15	150
	2015	“	19	134
Winter/ Grundarfjörður and Kolgrafafjörður (Herring overwintering grounds)	2010/11	Research	6	35
	2011/12	Whale-watch and Research	17	78
	2012/13	Whale-watch and Research	53	248
	2013/14	Whale-watch and Research	45	131
	2014/15	Whale-watch and Research	8	11

Table 2. Within and between area transition probabilities of Icelandic killer whales across seasons, including the total number of identified individuals in each area or resighted between areas across the entire study period.

From		To	
		Overwintering grounds	Spawning grounds
Overwintering grounds	<i>n</i>	301	146
	Transition probability	0.89	0.11
Spawning grounds	<i>n</i>	146	221
	Transition probability	0.38	0.62

Table 3. Mean, standard deviation, minimum and maximum individual occurrence (number of times each individual was seen, Weinrich et al. 1997) and occupancy

(number of days between first and last sighting of each individual, Weinrich et al. 1997) for Icelandic killer whales across all seasons. The number of days with killer whale encounters, and the number of days between the first and last encounter for each season are also provided.

Season/Year	Number of encounters (days)	Occurrence mean \pm SD [min-max] (days)	First-last encounter (days)	Occupancy mean \pm SD [min-max] (days)
Summer/2008	6	1.38 \pm 0.58 [1-3]	12	7.14 \pm 2.85 [1-11]
Summer/2009	16	4.27 \pm 2.82 [1-9]	22	10.30 \pm 5.46 [1-20]
Summer/2010	6	1.91 \pm 0.90 [1-4]	32	5.53 \pm 0.68 [1-32]
Summer/2013	4	1.56 \pm 0.58 [1-3]	12	2.69 \pm 2.75 [1-12]
Summer/2014	15	4.13 \pm 1.64 [1-8]	21	15.51 \pm 5.58 [1-21]
Summer/2015	19	3.49 \pm 2.35 [1-11]	22	10.56 \pm 5.72 [1-21]
Winter/2010/11	6	1.11 \pm 0.32 [1-2]	9	6.5 \pm 1 [5-7]
Winter/2011/12	17	1.65 \pm 0.85 [1-4]	42	16.25 \pm 13.59 [1-41]
Winter/2012/13	53	5.76 \pm 4.71 [1-23]	121	42.1 \pm 27.60 [1-120]
Winter/2013/14	45	3.81 \pm 4.01 [1-16]	99	43.42 \pm 23.43 [2-74]
Winter/2014/15	8	1.28 \pm 0.65 [1-3]	21	5 \pm 0 [5-5]