

Samarra, Filipa I.P., Tavares, Sara B., Béseau, Julie, Deecke, Volker B. ORCID: <https://orcid.org/0000-0003-2781-5915> , Fennell, Alexandra, Miller, Patrick J.O., Pétursson, Hlynur, Sigurjónsson, Johann and Víkingsson, Gisli 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 (8). Article:159.

Downloaded from: <http://insight.cumbria.ac.uk/id/eprint/3080/>

Usage of any items from the University of Cumbria's institutional repository 'Insight' must conform to the following fair usage guidelines.

Any item and its associated metadata held in the University of Cumbria's institutional repository Insight (unless stated otherwise on the metadata record) may be copied, displayed or performed, and stored in line with the JISC fair dealing guidelines (available [here](#)) for educational and not-for-profit activities

provided that

- the authors, title and full bibliographic details of the item are cited clearly when any part of the work is referred to verbally or in the written form
 - a hyperlink/URL to the original Insight record of that item is included in any citations of the work
- the content is not changed in any way
- all files required for usage of the item are kept together with the main item file.

You may not

- sell any part of an item
- refer to any part of an item without citation
- amend any item or contextualise it in a way that will impugn the creator's reputation
- remove or alter the copyright statement on an item.

The full policy can be found [here](#).

Alternatively contact the University of Cumbria Repository Editor by emailing insight@cumbria.ac.uk.

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

3

4 Samarra, F. I. P.^{1,2}, Tavares, S. B.², Béesau, J.², Deecke, V. B.³, Fennell, A.², Miller, P.
5 J. O.², Pétursson, H.¹, Sigurjónsson, J.¹ and Víkingsson, G. A.¹

6

7 (1) Marine and Freshwater Research Institute, Skúlagata 4, 101 Reykjavík, Iceland

8 (2) Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews,

9 St Andrews, Fife KY16 8LB, U.K.

10 (3) Centre for Wildlife Conservation, University of Cumbria, Rydal Road, Ambleside,

11 Cumbria, LA22 9BB, U.K.

12

13

14 Corresponding author: Filipa I. P. Samarra; Marine and Freshwater Research Institute,

15 Skúlagata 4, 101 Reykjavík, Iceland; email: fipsamarra@gmail.com; telephone: +354-

16 5752000; fax: +354-5752001

17 **Abstract**

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

38

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

41

42 **Introduction**

43 Animals often adopt complex movement strategies to utilize patchy and
44 unpredictable environments, and research into these strategies is key to understanding
45 population ecology, potential gene and information flow and population structure (e.g.,
46 Stevick et al. 2006; Musiani et al. 2007). Food resources likely drive the movements
47 of predators (e.g., Sveegaard et al. 2012). Understanding the movement ecology of
48 top predators is therefore essential for understanding the dynamics of the ecosystem,
49 given their potential impacts on food webs through top-down regulation of prey
50 (Myers et al. 2007). The distribution of prey may itself change, for example, due to
51 natural factors or climate change (Perry et al. 2005). Variations in preferred prey
52 abundance can affect the prey consumed by predators as well as their movement
53 patterns and distribution (e.g., Weinrich et al. 1997). Over short time-scales of hours
54 and days, movement patterns can be determined by food availability (e.g., Jaquet and
55 Whitehead 1999; Whitehead 2003), following the principle of the ideal free
56 distribution (Kacelnik et al., 1992). Over longer time-scales, movements can be more
57 broadly constrained by life-history requirements and access to resources (e.g.,
58 migrations between feeding and breeding grounds; Calambokidis et al. 2001).
59 Movement strategies may also differ between sexes within a population (e.g., Dufault
60 et al. 1999; Whitehead 2003) or between social units (e.g., Whitehead and Rendell
61 2004; Lusseau et al. 2006). Identifying the behavioural and environmental factors
62 governing movements and site fidelity is key to understanding the ecological role of
63 predators and for effective conservation and management of both predator and prey
64 populations.

65 Killer whales (*Orcinus orca*) are top marine predators with a cosmopolitan
66 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

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

119 Here, we use photographic identifications of killer whales collected over a 7-year
120 period in herring overwintering and spawning grounds in Iceland, during winter and
121 summer, respectively, to investigate seasonal movements following the year-round
122 migration of herring. We then use a previously-collected photographic dataset (1981-
123 2007) from the same spawning grounds, but different overwintering grounds, to
124 investigate long-term site fidelity and the ability of killer whales to adjust movement
125 patterns in relation to long-term changes in prey distribution. We hypothesise that if
126 killer whales occurring in coastal Icelandic waters are herring specialists, they should
127 follow the herring migration year-round and adapt their movements to shifts in the
128 distribution of their prey. This study therefore aims to increase our understanding of
129 the movement and foraging ecology of herring-eating killer whales, while expanding
130 current knowledge of population structure of Icelandic killer whales to contribute to
131 effective conservation and management strategies.

132

133 **Material and methods**

134 *Study area and data collection*

135 Research was conducted during winter months in 5 field seasons (between 2011
136 and 2015, see below) in Grundarfjörður and Kolgrafafjörður, two fjords that formed
137 part of an overwintering ground of the ISS herring in West Iceland (Figure 1A, ICES
138 2014) and around Vestmannaeyjar during summer months in 6 field seasons (between
139 2008 and 2015, see below), a traditional ISS herring spawning ground in South
140 Iceland (Figure 1B, Jakobsson and Stefánsson 1999). Photographs were collected
141 from dedicated research platforms, which consisted mainly of small research boats,

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

151 Winters were considered as the months from November to March, as this was the
152 period when overwintering herring could be found within the fjords, and therefore
153 spanned 2 years. Thus, for example, the winter of 2010/11 refers to the period
154 between November 2010 and March 2011. Photographs from a herring survey cruise
155 were collected in Breiðafjörður between the 29th November and the 2nd December
156 2012. Photographs from dedicated research efforts were collected in February-March
157 2013 to 2015 in Grundarfjörður and Kolgrafafjörður and in July 2008 to 2010 and
158 2013 to 2015 in Vestmannaeyjar, respectively. Photographs opportunistically
159 collected and provided by whale-watch guides, colleagues and members of the public
160 were collected in Grundarfjörður and Kolgrafafjörður in the winters of 2010/11 to
161 2014/15 (Table 1). Generally, whale-watch and dedicated research vessels worked
162 with different whale groups, but over the course of a day could encounter the same
163 whales. Thus, an encounter was defined as a day in which killer whales were sighted
164 and could be identified, regardless of platform or how often individuals were seen
165 throughout the day.

166

167 *Photo-identification*

168 Killer whales were approached and photographed for photo-identification (Bigg
169 1982), using a variety of digital single-lens reflex cameras and lenses. Photographs of
170 killer whales taken from dedicated research boats were typically of the left sides of
171 animals including dorsal fin and saddle patch (the lightly coloured area below and
172 behind the dorsal fin). Pictures of the right side were also taken opportunistically.
173 Both left and right side pictures were used for photo-identification purposes, however
174 an individual was only added to the catalogue if a high quality left-side picture existed.
175 Photographs from whale-watch boats or fish survey cruises were taken
176 opportunistically of both sides of the body. Killer whales were identified based on the
177 size and shape of the dorsal fin, the presence of nicks and scars, saddle patch pattern,
178 and body scars (Bigg 1982). Individuals were classified as ‘male’, ‘female’, ‘juvenile’
179 or ‘other’ based on body size and size and shape of the dorsal fin, since the year of
180 birth was unknown. Males were mature or sub-adult individuals with distinctly taller
181 dorsal fins (Heimlich-Boran 1986). Females were mature sized individuals seen
182 consistently with a calf in echelon position and seen during most of the study period
183 without changes in dorsal fin size, or matched to a previous catalogue held by the
184 Marine Research Institute (see below) and without changes in dorsal fin size since the
185 last sighting. Juveniles were identifiable individuals >1 year of age that had not
186 reached mature size. Others were whales that appeared of mature size, but for which
187 sex was impossible to determine, which could include juvenile males or adult females.
188 For some whales from which biopsy samples were collected, sex was assigned by
189 genetic analysis (Tavares, unpublished data).

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

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

210

211 *Seasonal movements between herring overwintering and spawning grounds*

212 To investigate recent (2008-2015) killer whale movements between herring
213 overwintering and spawning grounds, we used maximum likelihood methods, which
214 account for a non-uniform and non-random spatial and temporal effort distribution in
215 the dataset by using the photo-identifications as a proxy of effort, to investigate re-
216 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

242 also estimated the maximum number of years between re-identifications. In this case
243 0.5 represented sightings in successive seasons (e.g., seen in winter and the following
244 summer) and 1 represented sightings during the same season but in different years
245 (e.g., seen in summer 2008 and again in summer 2009).

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

253

254 *Comparison to previous identification data*

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

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

268 To investigate if killer whales sighted in past herring overwintering grounds in
269 East Iceland (hereafter termed past herring overwintering grounds) were resighted in
270 recently occupied herring overwintering grounds off West Iceland (hereafter termed
271 recent herring overwintering grounds), we compared all individuals photo-identified
272 in ISS herring overwintering grounds off West Iceland between the winters of
273 2010/11 and 2014/15 with the MFRI catalogue, regardless of sighting frequency. To
274 investigate long-term site fidelity to herring spawning grounds we compared all
275 individuals photo-identified occurring in ISS herring spawning grounds in
276 Vestmannaeyjar between 2008 and 2015 with the MFRI catalogue, regardless of
277 sighting frequency. For both analyses, only individuals presumed to be adults during
278 the study period (2008-2015) were included, as juveniles would not have been born
279 since the last sightings included in the MFRI catalogue, or would have been very
280 young calves and thus unrecognisable. Only matches confirmed by two scorers were
281 accepted.

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

289

290 **Results**

291 Since 2008, killer whales were encountered on 129 days in herring overwintering
292 grounds and on 66 days in herring spawning grounds (Table 1). We identified a total
293 of 376 individuals, including 123 (33%) males, 110 (29%) females, 62 (16%)
294 juveniles and 81 (22%) others. Of these, 49 whales (17 males, 10 females, 2 juveniles
295 and 20 others) were only seen once, most of which (77%) were sighted in herring
296 overwintering grounds. In contrast, 327 individuals were recorded during two or more
297 encounters, of which 76 (23%) were only seen in one year and 251 (77%) were re-
298 sighted in multiple years. Of the 76 individuals only seen in one year, the majority
299 (66%) were only seen in herring overwintering grounds, 21% were only seen in
300 herring spawning grounds and 13% were seen in both locations. The total number of
301 whales identified per season and year varied from a minimum of 11 (winter 2014/15)
302 to a maximum of 248 (winter 2012/13, mean \pm standard deviation: $X \pm SD = 96.3 \pm$
303 67.2). In the winter, the total number of individuals identified per year varied between
304 11 (in 2014/15) and 248 (in 2012/13) with a mean \pm standard deviation of $X \pm SD =$
305 100.6 ± 94.2 (Table 1); in the summer, the total number of individuals identified per
306 year varied between 42 (in 2008) and 150 (in 2015), with a mean \pm standard deviation
307 of $X \pm SD = 92.7 \pm 43.6$ (Table 1).

308 The number of identified individuals across all seasons and years tended to
309 depend on the total number of days with killer whale encounters (Pearson's
310 correlation = 0.82; t-value = 4.30; df = 9; P = 0.002), however this relationship was
311 significant in winter (Pearson's correlation = 0.94; t-value = 4.65; df = 3; P = 0.02)
312 but not in the summer (Pearson's correlation = 0.75; t-value = 2.26; df = 4; P = 0.09).
313 Nevertheless, in winter the number of identified individuals could also vary between
314 seasons with similar total number of days with killer whale encounters. For example,
315 248 individuals were identified in 53 encounter days in the winter 2012/13, while only

316 131 were identified in 45 encounter days in the winter of 2013/14 (Table 1). The
317 discovery curve, showing the cumulative number of individuals identified over time,
318 suggested that the rate of identification of new individuals increased markedly
319 following the first winter field seasons, particularly that of the winter of 2012/13
320 (Figure 2). However, towards the end of the study period this rate levelled off
321 suggesting a nearly complete coverage of the population in these study areas during
322 the study period (Figure 2).

323

324 *Seasonal movements between herring overwintering and spawning grounds*

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

341 subsequent years. The model that best fitted the lagged identification rate from a
342 given area to another, by minimising the QAIC, was a Migration model (Whitehead
343 2001), which estimated a mean residence time in an area of 61.5 days (95% CI: 35.5 –
344 108.0) and a population size of 347.7 (95% CI: 295.5 – 418.1).

345 Within a given area, the lagged identification rate dropped at time lags from 1 to
346 84 days, reaching its lowest value at approximately 252 days. This suggests that
347 individuals stayed within an area seasonally but then left. The lagged identification
348 rate then increased again around a time lag of 365 days, although to lower levels than
349 at its maximum, and remained stable until the end of the study period, suggesting
350 return to the same area in successive years (Figure 3). This suggests high site fidelity
351 to an area but return was not complete. The model that best fitted the lagged
352 identification rate within an area was one of Emigration with Re-Immigration
353 (Whitehead 2001), supporting the seasonal movements of whales away from the area
354 where they were first observed and subsequent return in the following years. The
355 model estimated a mean residence time of 17.6 days (95% CI: 9.9 – 32.8) within a
356 given study area, and a mean residence time out of the area of 15.1 days (95% CI: 9.1
357 – 26.9) and a mean number of individuals present at any given time in the study area
358 of 87.1 (95% CI: 78.0 – 96.8).

359 High transition probabilities within both overwintering and spawning grounds
360 (0.89 and 0.62, respectively) supported the high site fidelity suggested by the lagged
361 identification rate (Table 2). Transition probabilities between areas were lower,
362 suggesting that not all individuals moved between locations. Transition probabilities
363 of approximately 0.4 were estimated from spawning grounds to overwintering
364 grounds across seasons. Indeed, 66% of the total number of individuals found in
365 spawning grounds also occurred in overwintering grounds (Table 2). Transition

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

369 The mean ‘occurrence’ (or number of days in which an individual was
370 photographed, as defined by Weinrich et al. 1997) per season varied from a minimum
371 of 1.38 to a maximum of 4.27 in summer and a minimum of 1.11 to a maximum of
372 5.76 in winter (Table 3). Mean occurrence tended to be lower in seasons when the
373 total number of days with killer whale encounters was also low, however the
374 maximum occurrence never reached the maximum number of days with killer whale
375 encounters (Table 3), i.e. no individuals were seen on every day of sampling. The
376 mean ‘occupancy’ (or number of days elapsed from first to last sighting within each
377 season, as defined by Weinrich et al. 1997) ranged from a minimum of 2.69 to a
378 maximum of 15.51 in summer and a minimum of 5 to a maximum of 43.42 in the
379 winter (Table 3). The maximum occupancy per season in both winter and summer
380 was generally very close to the number of days between the first and last encounter of
381 that season, suggesting that within each season at least some individuals stayed or
382 regularly returned to the study area (Table 3). Finally, on average the maximum
383 number of years between re-sightings of individuals that were sighted in more than
384 one season varied between 1 and 4.5, with a mean of $X \pm SD = 1.96 \pm 0.7$ years.

385

386 *Movements between past and recent herring overwintering grounds*

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

391 overwintering grounds and 5% of the 301 individuals identified in recent herring
392 overwintering grounds. All matched whales were first re-identified in recent herring
393 overwintering grounds between 2010 and 2013. Eight of the 16 whales matched
394 between past and recent herring overwintering grounds were only seen in one year. Of
395 these, two were seen only in the winter of 2011/12, and six were only seen in the
396 winter of 2012/13. Overall, the largest number of whales were seen in the winter of
397 2012/13 ($n = 14$), which was also the winter with the largest number of days with
398 killer whale encounters (Figure 5). Despite a similar number of days with killer whale
399 encounters in the winter of 2013/14, only 4 of the 16 whales matched between past
400 and recent herring overwintering grounds were re-sighted, but they were sighted often
401 (Figure 5). Most of the 16 whales did not appear to follow herring year-round
402 between sampled herring grounds, as they were only seen in recent herring
403 overwintering grounds, but not in the spawning grounds off Vestmannaeyjar, with
404 two exceptions. In the MFRI catalogue, however, both these whales had only been
405 seen once and in the winter. In contrast, two whales that were previously identified
406 both in herring overwintering and spawning grounds in the MFRI catalogue, were no
407 longer seen in spawning grounds and were thus not classified as whales following
408 herring year-round in the present study. The remaining 12 whales were only identified
409 in herring overwintering grounds in both the MFRI catalogue and this study.

410

411 *Long-term fidelity to herring spawning grounds*

412 The comparison of photo-identifications collected in this study (2008-2015) with
413 data collected between 1997 and 2007 in the MFRI catalogue resulted in a total of 27
414 individuals re-identified in herring spawning grounds (Figure 4B). This represented
415 27% of the total number of individuals identified in herring spawning grounds off

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

435

436 **Discussion**

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

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

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

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

470 Lagged identification rates suggest that individuals first sighted in the winter
471 were less likely to be re-sighted in summer than those first sighted in summer. This
472 was also supported by higher transition probabilities of individual killer whales from
473 herring spawning grounds to herring overwintering grounds than vice-versa. This may
474 suggest that individuals sighted in herring spawning grounds are more likely to follow
475 herring year-round than individuals sighted in herring overwintering grounds. In fact,
476 stable isotope analysis of a subset of the individuals included in this study showed that
477 whales sampled in summer, even those that were only sighted in herring spawning
478 grounds, tended to have low nitrogen stable isotope values, consistent with a diet
479 composed of herring (Samarra et al. 2017b). In contrast, some of the whales observed
480 only in winter have been observed regularly travelling to northern Scotland in summer
481 and include higher trophic prey in their diet (Samarra and Foote 2015; Samarra et al.
482 2017b). This suggests that whales with different movement patterns and foraging
483 ecologies may tend to aggregate in herring overwintering grounds, while whales
484 occurring in herring spawning grounds may tend to be more consistently putative
485 herring specialists.

486

487 *Site fidelity*

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

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

500 The fact that not all whales were observed on herring spawning grounds around
501 Vestmannaeyjar and that site fidelity to spawning grounds was high, and maintained
502 over the long-term, suggests that killer whale individuals or groups may have
503 preferences for visiting particular herring spawning grounds and these are maintained
504 throughout their lifetime and possibly transferred to offspring via social learning.
505 Cultural differences in movement patterns, with potential fitness consequences, have
506 been shown in cetaceans (e.g., Whitehead and Rendell 2004; Valenzuela et al. 2012).
507 Herring spread out across different spawning grounds in the summer (Jakobsson and
508 Stefánsson 1999), thus only a proportion of the entire resource stock is available at
509 each spawning ground. Spatial segregation may be expected under the ideal free
510 distribution if the availability of prey cannot sustain large aggregations of whales,
511 allowing killer whale groups to successfully exploit the less abundant prey resources
512 at each location, while leading to other whales moving elsewhere. Site fidelity to
513 spawning grounds could then develop if it were advantageous to feed in areas where
514 individuals have accumulated knowledge on local prey resource distribution and prey
515 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-

541 identifications. Despite similar total number of days with killer whale encounters in
542 the winters of 2012/13 and 2013/14, fewer individuals overall were re-sighted in
543 2013/14, which also corresponded to a decrease in the amount of herring available in
544 the study area (ICES 2014). Thus, prey abundance may regulate the number of whales
545 that visit an area and the amount of time they remain available for photo-identification,
546 as predicted for the ideal free distribution. Similar fluctuations in killer whale
547 sightings related with changes in herring abundance and distribution have also been
548 suggested for Norway (Kuningas et al. 2013, 2014).

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

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

569 Alternatively, seasonal occurrence could indicate that some whales are
570 consistently only visiting herring overwintering grounds and not spawning grounds,
571 possibly exploiting other prey at other times of the year. The fact that occasional
572 visitors (only sighted once) and whales seen more than once but only in one year
573 occur mostly in herring overwintering grounds, suggests that these may serve as a
574 gathering of whales with diverse movement patterns, more so than herring spawning
575 grounds. Indeed, some of the whales observed only in recent herring overwintering
576 grounds have been identified in summer in West Iceland (Samarra, unpublished data),
577 while others travel to northern Scotland in the summer (Deecke et al. 2011; Samarra
578 and Foote 2015). This agrees with stable isotope studies suggesting more variability
579 in niche width of whales sampled in herring overwintering than herring spawning
580 grounds (see above; Samarra et al. 2017b). Because herring forms larger aggregations
581 when overwintering in comparison to spawning (Holst et al. 2004), the larger
582 diversity of whales visiting herring overwintering grounds could be prey-related.
583 However, social reasons, such as increased opportunities for breeding (Matkin et al.
584 1997), cannot be ruled out as drivers of killer whales movements in this study.

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

590

591 *Implications for population structure*

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

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

616 caution. Within this total number of individuals there were occasional visitors, which
617 were only sighted once, suggesting that the number of whales frequently occurring in
618 Icelandic coastal waters is even smaller. This suggests a smaller population than that
619 estimated for herring-eating killer whales in Norway (731 individuals in 2003;
620 Kuningas et al. 2014), which could be related to the amount of herring available. Prey
621 availability can severely impact killer whale population demography (Ward et al.
622 2009; Ford et al. 2010; Esteban et al. 2016a). In Norway, years of high herring
623 biomass coincided with an apparent increase in the number of new individuals,
624 although food availability alone did not seem to fully explain this increase (Kuningas
625 et al. 2014). Current estimates of the spawning stock biomass of ISS herring are
626 approximately 300 thousand tonnes (ICES 2016), much smaller than the
627 approximately 4 million tonnes of Norwegian spring-spawning herring (ICES 2015).
628 Further work relating the abundance and occurrence of killer whales and herring is
629 necessary to understand how this prey resource may affect and limit populations that
630 exploit it and depend on it.

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

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

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

669

670 **Acknowledgments**

671 We thank all volunteers, colleagues and students who helped with data collection
672 throughout the many field seasons, Annika Firmenich for help processing the
673 photographic data from 2008, and the Vestmannaeyjar Research Centre, particularly
674 Páll M. Jónsson, for logistical support. We are grateful to Láki Tours, particularly
675 Gísli Ólafsson, for allowing research assistants to join whale-watch trips to collect
676 photo-identification data and sharing sightings information in Grundarfjörður and
677 Kolgrafafjörður. Thanks are also due to Viking Tours and RibSafari for sharing
678 sightings information and allowing us to go onboard to collect data in Vestmannaeyjar.
679 We are grateful to Cathy Harlow and Alexa Kershaw from Discover the World, as
680 well Rob Lott, Baldur Thorvaldsson, Róbert Stefánsson, Stefán Á. Ragnarsson,
681 Vassili Papastavrou, Mike Hatcher, Dave Gibson, Kevin Tappenden and Neil
682 Woodward for kindly providing additional photographs, Malene Simon for providing
683 pictures collected in Vestmannaeyjar during earlier efforts as well as Eyþór Þórðarson,
684 Birgir Stefánsson and Tiu Similä. We thank Dr. Andrew Foote for very helpful
685 guidance on the previously collected data in Iceland, as well as providing useful
686 comments on a previous version of this manuscript. The manuscript furthermore
687 benefited from helpful comments by 3 anonymous reviewers. Funding was provided
688 by a Fundação para a Ciência e a Tecnologia doctoral scholarship (grant number
689 SFRH/BD/30303/2006), an Icelandic Research Fund (i. Rannsóknasjóður) START
690 Postdoctoral Fellowship (grant number 120248042), the National Geographic Society

691 Science and Exploration Europe (grant number GEFNE65-12) and a Russell Trust
692 Award (University of St. Andrews) to FIPS, the Office of Naval Research (grant
693 number N00014-08-10984) to PJOM, a Fundação para a Ciência e a Tecnologia
694 doctoral scholarship (grant number SFRH/BD/84714/2012) to SBT and support from
695 the BBC Natural History Unit and funding from a Full Doctorate Fellowship from
696 CNPq/Capes through the Science Without Borders Program, Marie-Curie Intra-
697 European Fellowship and Research and Scholarship Development Fund (University
698 of Cumbria) to VBD.

699

700 All applicable international, national, and/or institutional guidelines for the care and
701 use of animals were followed.

702

703 **Conflict of Interest**

704 The authors declare that they have no conflict of interest.

705

706 **References**

- 707 Andrews RD, Pitman RL and Balance LT (2008) Satellite tracking reveals distinct
708 movement patterns for Type B and Type C killer whales in the southern Ross Sea,
709 Antarctica. *Polar Biol* 31: 1461-1468
- 710 Bigg M (1982) An assessment of killer whale (*Orcinus orca*) stocks off Vancouver
711 Island, British Columbia. *Rep Int Whal Comm* 32: 655–666
- 712 Bloch D and Lockyer C (1988) Killer whales (*Orcinus orca*) in Faroese waters. *Rit*
713 *Fisk* 11: 55-64
- 714 Calambokidis J, Steiger GH, Straley JM, Herman LM, Cerchio S, Salden DR, Urbán
715 JR, Jacobsen JK, von Ziegesar O, Balcomb KC, Gabriele CM, Dahlheim ME,

716 Uchida S, Ellis G, Miyamura Y, de Guevara PLP, Yamaguchi M, Sato F, Mizroch
717 SA, Schlender L, Rasmussen K, Barlow J and Quinn II TJ (2001) Movements and
718 population structure of humpback whales in the North Pacific. *Mar Mamm Sci* 17:
719 769-794

720 Corten A (2001) Northern distribution of North Sea herring as a response to high
721 water temperatures and/or low food abundance. *Fish Res* 50: 189-204

722 Corten A (2002) The role of “conservatism” in herring migrations. *Rev Fish Biol and*
723 *Fish* 11: 339-361

724 Dahlheim ME, Schulman-Janiger A, Black N, Ternullo R, Ellifrit D and Balcomb KC
725 (2008) Eastern temperate North Pacific offshore killer whales (*Orcinus orca*):
726 occurrence, movements, and insights into feeding ecology. *Mar Mamm Sci* 24:
727 719-729

728 Deecke VB, Nykänen M, Foote AD and Janik VM (2011) Vocal behaviour and
729 feeding ecology of killer whales *Orcinus orca* around Shetland, UK. *Aquat Biol*
730 13: 79-88

731 Dommasnes A, Rey F and Røttingen I (1994) Reduced oxygen concentrations in
732 herring wintering areas. *ICES J Mar Sci* 51: 63-69

733 Dragesund O, Johannessen A and Ulltang Ø (1997) Variation in migration and
734 abundance of Norwegian spring-spawning herring (*Clupea harengus* L.). *Sarsia*
735 82: 97-105

736 Dufault S, Whitehead H and Dillon M (1999) An examination of the current
737 knowledge on the stock structure of sperm whales (*Physeter macrocephalus*)
738 worldwide. *J Cetacean Res Manage* 1: 1-10

739 Durban JW and Pitman RL (2012) Antarctic killer whales make rapid, round-trip
740 movements to subtropical waters: evidence for physiological maintenance
741 migrations? *Biol Lett* 8: 274-277

742 Eisert R, Ovsyanikova E, Visser I, Ensor P, Currey R and Sharp B (2015) Seasonal
743 site fidelity and movement of type-C killer whales between Antarctica and New
744 Zealand. *Rep Int Whal Comm [SC/66a/SM/9]*, 13 pp

745 Esteban R, Verborgh P, Gauffier P, Giménez J, Foote AD and de Stephanis R (2016a)
746 Maternal kinship and fisheries interaction influence killer whale social structure.
747 *Behav Ecol Sociobiol* 70: 111-122

748 Esteban R, Verborgh P, Gauffier P, Giménez J, Martín V, Pérez-Gil M, Tejedor M,
749 Almunia J, Jepson PD, García-Tiscar S, Barrett-Lennard LG, Guinet C, Foote AD
750 and de Stephanis R (2016b) Using a multi-disciplinary approach to identify a
751 critically endangered killer whale management unit. *Ecol Ind* 66: 291-300

752 Fearnbach H, Durban JW, Ellifrit DK, Waite JM, Matkin CO, Lunsford CR, Peterson
753 MJ, Barlow J and Wade PR (2014) Spatial and social connectivity of fish-eating
754 “Resident” killer whales (*Orcinus orca*) in the northern North Pacific. *Mar Biol*
755 161: 459-472

756 Fernö A, Pitcher TJ, Melle W, Nøttestad L, Mackinson S, Hollingworth C and
757 Misund OA (1998) The challenge of the herring in the Norwegian Sea: making
758 optimal collective spatial decisions. *Sarsia* 83: 149-167

759 Ford JKB, Ellis GM, Olesiuk PF and Balcomb KC (2010) Linking killer whale
760 survival and prey abundance: food limitation in the oceans’ apex predator? *Biol*
761 *Lett* 6: 139-142

762 Forney KA and Wade P (2006) Worldwide distribution and abundance of killer
763 whales. In: Estes JA, Brownell RL, DeMaster DP, Doak DF, Williams TM (eds)

764 Whales, Whaling, and Ecosystems. University of California Press, Berkeley, CA,
765 pp 145-162

766 Foote AD, Similä T, Vikingsson GA and Stevick PT (2010) Movement, site fidelity
767 and connectivity in a top marine predator, the killer whale. *Evol Ecol* 24: 803-814

768 Friday N, Smith TD, Stevick PT and Allen J (2000) Measurement of photographic
769 quality and individual distinctiveness for the photographic identification of
770 humpback whales, *Megaptera novaeangliae*. *Mar Mamm Sci* 16: 355–374

771 Goley PD and Straley JM (1994) Attack on gray whales (*Eschrichtius robustus*) in
772 Monterey Bay, California, by killer whales (*Orcinus orca*) previously identified in
773 Glacier Bay, Alaska. *Can J Zool* 72: 1528-1530

774 Gunnlaugsson T and Sigurjónsson J (1990) NASS-87: Estimation of abundance of
775 large cetaceans from observations made onboard Icelandic and Faroese survey
776 vessels. *Rep Int Whal Comm* 40: 571-580

777 Hauser DDW, Logsdon MG, Holmes EE, VanBlaricom GR and Osborne RW (2007)
778 Summer distribution patterns of southern resident killer whales *Orcinus orca*:
779 core areas and spatial segregation of social groups. *Mar Ecol Prog Ser* 351: 301-
780 310

781 Heimlich-Boran JR (1986) Photogrammetric analysis of growth in Puget Sound
782 *Orcinus orca*. In: Kirkevold BC, Lockard JS (eds) *Behavioral Biology of Killer*
783 *Whales*. Alan R Liss, New York NY, pp 97-111

784 Holst JC, Røttingen I and Melle W (2004) The herring. In: Skjoldal HR (ed) *The*
785 *Norwegian Sea Ecosystem*. Tapir Academic Press, Trondheim, pp 203–226

786 Huse G, Fernö A and Holst JC (2010) Establishment of new wintering areas in
787 herring co-occurs with peaks in the ‘first time/repeat spawner’ ratio. *Mar Ecol*
788 *Prog Ser* 409: 189-198

789 ICES (International Council for the Exploration of the Sea) (2014) Report of the
790 North-Western Working Group (NWWG), 24 April–1 May 2014. ICES CM
791 2014/ACOM: 07, ICES Headquarters, Copenhagen. 702 pp.

792 ICES (International Council for the Exploration of the Sea) (2015) Report of the
793 Working Group on Widely Distributed Species (WGWIDE), 25 August-31
794 August 2015. ICES CM2015/ACOM: 15, Pasaia, Spain 646 pp.

795 ICES (International Council for the Exploration of the Sea) (2016) Report of the
796 North-Western Working Group (NWWG), 27 April–4 May 2016. ICES CM
797 2016/ACOM: 08, ICES Headquarters, Copenhagen. 703 pp.

798 Jakobsson J, Vilhjálmsson H and Schopka SA (1969) On the biology of the Icelandic
799 herring stocks. Rit Fisk 4: 1-16

800 Jakobsson J and Stefánsson G (1999) Management of summer-spawning herring off
801 Iceland. ICES J Mar Sci 56: 827–833

802 Jaquet N and Whitehead H (1999) Movements, distribution and feeding success of
803 sperm whales in the Pacific Ocean, over scales of days and tens of kilometers.
804 Aquat Mamm 25: 1-13

805 Kacelnik A, Krebs JR and Bernstein C (1992) The ideal free distribution and predator
806 prey populations. Trends Ecol Evol 7: 50-55

807 Kuningas S, Kvadsheim PH, Lam F-PA and Miller PJO (2013) Killer whale presence
808 in relation to naval sonar activity and prey abundance in northern Norway. ICES
809 J Mar Sci 70: 1287-1293

810 Kuningas S, Similä T and Hammond PS (2014) Population size, survival and
811 reproductive rates of northern Norwegian killer whales (*Orcinus orca*) in 1986-
812 2003. J Mar Biol Assoc UK 94: 1277-1291

813 Luque PL, Davis CG, Reid DG, Wang J and Pierce GJ (2006) Opportunistic sightings
814 of killer whales from Scottish pelagic trawlers fishing for mackerel and herring
815 off North Scotland (UK) between 2000 and 2006. *Aquat Living Resour* 19: 403-
816 410

817 Lusseau D, Wilson B, Hammond PS, Grellier K, Durban JW, Parsons KM, Barton TR
818 and Thompson PM (2006) Quantifying the influence of sociality on population
819 structure in bottlenose dolphins. *J Anim Ecol* 75: 14-24

820 Matkin CO, Matkin DR, Ellis GM, Saulitis E, McSweeney D (1997) Movements of
821 resident killer whales in Southeastern Alaska and Prince William Sound, Alaska.
822 *Marine Mammal Science* 13:469-475

823 Matkin CO, Durban JW, Saulitis EL, Andrews RD, Straley JM, Matkin DR and Ellis
824 GM (2012) Contrasting abundance and residency patterns of two sympatric
825 populations of transient killer whales (*Orcinus orca*) in the northern Gulf of
826 Alaska. *Fish Bull* 110: 143-155.

827 Matthews CJD, Luque SP, Petersen SD, Andrews RD and Ferguson SH (2011)
828 Satellite tracking of a killer whale (*Orcinus orca*) in the eastern Canadian Arctic
829 documents ice avoidance and rapid, long-distance movement into the North
830 Atlantic. *Polar Biol* 34: 1091-1096

831 Myers RA, Baum JK, Shepherd TD, Powers SP and Peterson CH (2007) Cascading
832 effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315:
833 1846-1850

834 Musiani M, Leonard JA, Cluff HD, Gates CC, Mariani S, Paquet PC, Vilà C and
835 Wayne RK (2007) Differentiation of tundra/taiga and boreal coniferous forest
836 wolves: genetics, coat colour and association with migratory caribou. *Mol Ecol*
837 16: 4149-4170

838 Nichol LM and Shackleton DM (1996) Seasonal movements and foraging behaviour
839 of northern resident killer whales (*Orcinus orca*) in relation to the inshore
840 distribution of salmon (*Oncorhynchus spp.*) in British Columbia. Can J Zool 74:
841 983-991

842 Óskarsson GJ, Gudmundsdottir A and Sigurdsson T (2009) Variation in spatial
843 distribution and migration of Icelandic summer-spawning herring. ICES J Mar Sci
844 66: 1762-1767

845 Perry AL, Low PJ, Ellis JR and Reynolds JD (2005) Climate change and distribution
846 shifts in marine fishes. Science 308: 1912-1915

847 Samarra FIP and Foote AD (2015) Seasonal movements of killer whales between
848 Iceland and Scotland. Aquat Biol 24: 75-79

849 Samarra FIP and Miller PJO (2015) Prey-induced behavioural plasticity of herring-
850 eating killer whales. Mar Biol 162: 809-821

851 Samarra FIP, Tavares S, Miller PJO and Víkingsson GA (2017a) Killer whales of
852 Iceland 2006-2015. Report of the Marine and Freshwater Research Institute HV
853 2017-005, ISSN 2298-9137.

854 Samarra FIP, Vighi M, Aguilar A and Víkingsson G (2017b) Intra-population
855 variation in isotopic niche in herring-eating killer whales. Mar Ecol Prog Ser 564:
856 199-210

857 Sigurjónsson J (1984) Killer whale census off Iceland during October 1982. Rep Int
858 Whal Comm 34: 609-612

859 Sigurjónsson J, Lyrholm T, Leatherwood S, Jónsson E and Víkingsson G (1988)
860 Photo-identification of killer whales, *Orcinus orca*, off Iceland, 1981 through 1986.
861 Rit Fisk 11: 99-114

862 Sigurjónsson J and Gunnlaugsson T (1989) NASS-87: Shipboard sightings surveys in
863 Icelandic and adjacent waters June-July 1987. Rep Int Whal Comm 39: 392-409

864 Similä T, Holst JC and Christensen I (1996) Occurrence and diet of killer whales in
865 northern Norway: seasonal patterns relative to the distribution and abundance of
866 Norwegian spring-spawning herring. Can J Fish Aquat Sci 53:769-779

867 Stenersen J and Similä T (2004) Norwegian killer whales. Tringa forlag. Henningsvær,
868 Norway

869 Stevick PT, Allen J, Clapham PJ, Katona SK, Larsen F, Lien J, Mattila DK, Palsbøll
870 PJ, Sears R, Sigurjónsson J, Smith TD, Víkingsson G, Øien N and Hammond PS
871 (2006) Population spatial structuring on the feeding grounds in North Atlantic
872 humpback whales (*Megaptera novaeangliae*). J Zool 270: 244-255

873 Sveegaard S, Andreassen H, Mouritsen KN, Jeppesen JP, Teilmann J and Kinze CC
874 (2012) Correlation between the seasonal distribution of harbour porpoises and
875 their prey in the Sound, Baltic Sea. Mar Biol 159: 1029-1037

876 Sæmundsson B (1939) Mammalia. The Zoology of Iceland, vol IV: 1–37

877 Tavares SB, Samarra FIP and Miller PJO (2017) A multilevel society of herring-
878 eating killer whales indicates adaptation to prey characteristics. Behav Ecol 28:
879 500-514

880 Toresen R and Østvedt OJ (2000) Variation in abundance of Norwegian spring-
881 spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and
882 the influence of climatic fluctuations. Fish Fish 1: 231-256

883 Valenzuela LO, Sironi M, Rowntree VJ and Seger J (2009) Isotopic and genetic
884 evidence for culturally inherited site fidelity to feeding grounds in southern right
885 whales. Mol Ecol 18: 782-791

- 886 Vikingsson GA (2004) Háhyrningur. In: Hersteinsson P (ed) Íslensk spendýr, Vaka-
887 Helgafell, Reykjavík, pp 166–171
- 888 Ward EJ, Holmes EE and Balcomb KC (2009) Quantifying the effects of prey
889 abundance on killer whale reproduction. *J Applied Ecol* 46:632-640
- 890 Weinrich M, Martin M, Griffiths R, Bove J and Schilling M (1997) A shift in
891 distribution of humpback whales, *Megaptera novaeangliae*, in response to prey in
892 the southern Gulf of Maine. *Fish Bull* 95: 826-836
- 893 Whitehead H (2001) Analysis of animal movement using opportunistic individual
894 identifications: application to sperm whales. *Ecology* 82: 1417-1432
- 895 Whitehead H (2003) Sperm whales: social evolution in the ocean. University of
896 Chicago Press, Chicago, 431 pp
- 897 Whitehead H (2007) Selection of models of lagged identification rates and lagged
898 association rates using AIC and QAIC. *Commun Stat B-Simul* 36:1233-1246
- 899 Whitehead H (2009) SOCPROG programs: analysing animal social structures. *Behav*
900 *Ecol Sociobiol* 63: 765-778
- 901 Whitehead H and Rendell L (2004) Movements, habitat use and feeding success of
902 cultural clans of South Pacific sperm whales. *J Anim Ecol* 73: 190-196

Figures

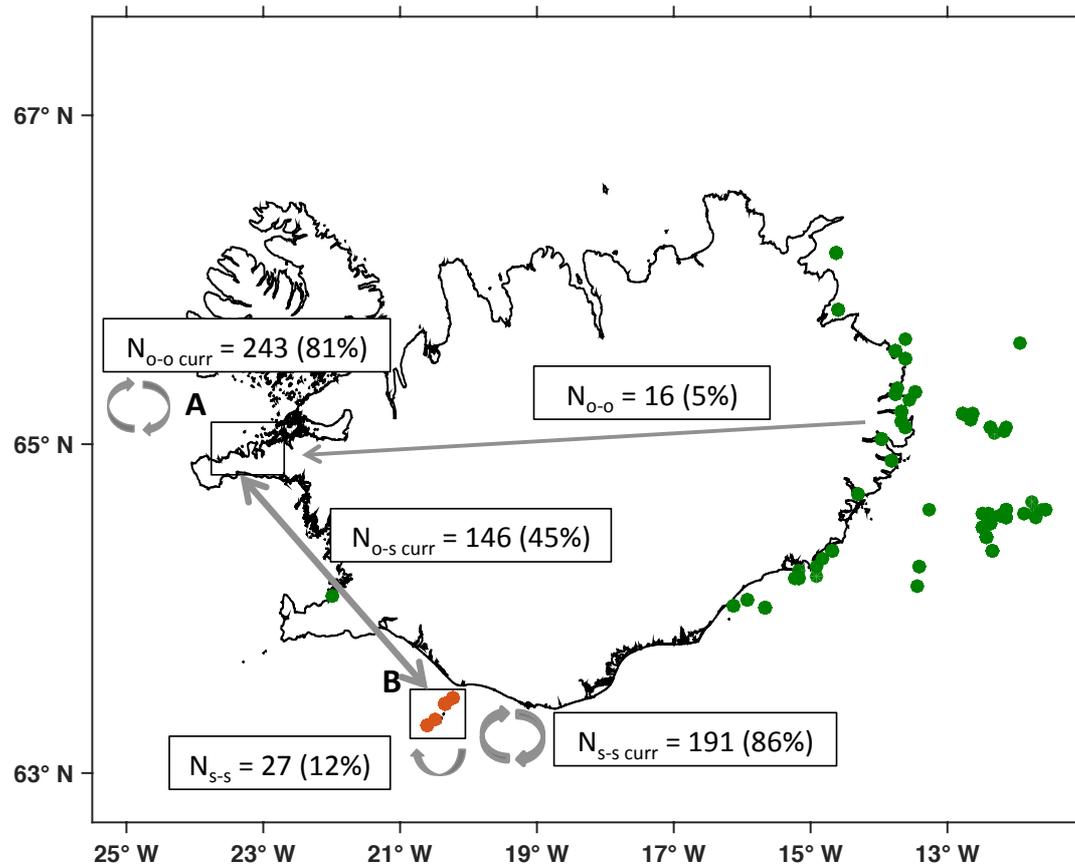


Fig. 1 Map of Iceland showing the approximate study locations where recent (2008-2015) killer whale photo-identification data were collected: A) recent herring overwintering grounds in the West of Iceland, including the fjords Grundarfjörður and Kolgrafafjörður and; B) herring spawning grounds off Vestmannaeyjar, 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.

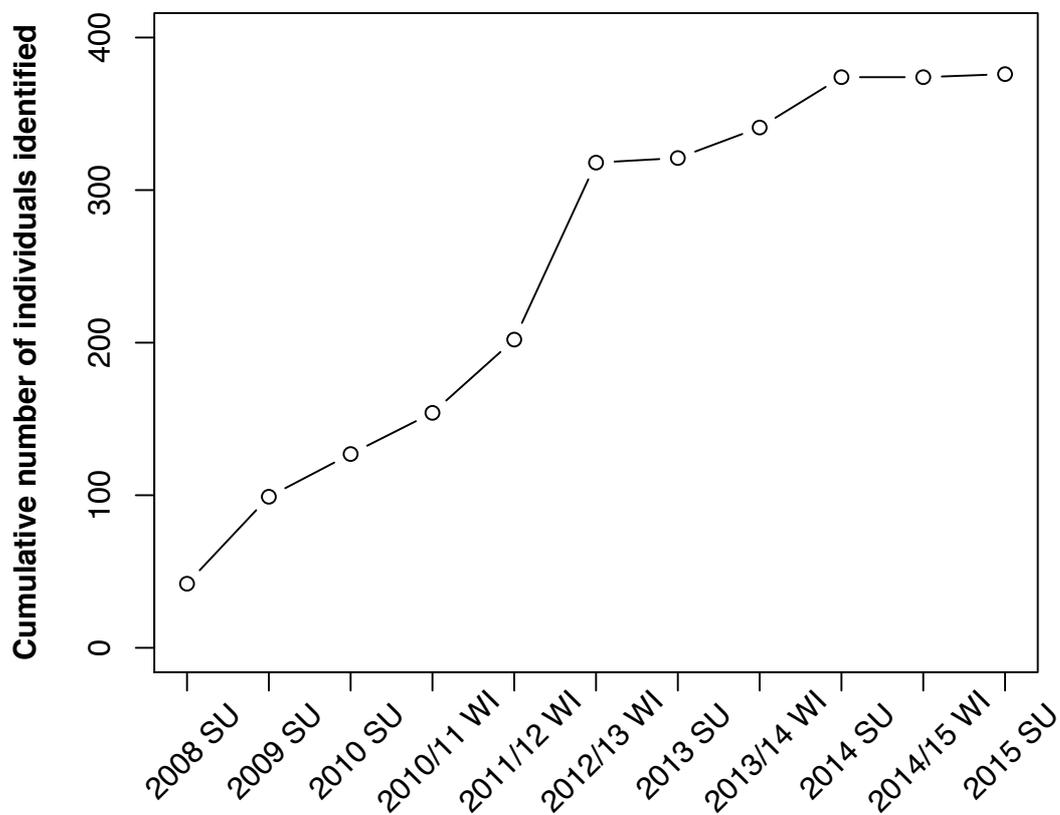


Fig. 2 Discovery curve of Icelandic killer whales by year and season where SU represents summer and WI represents winter. Winters are considered as the months of November to March and thus span across two years (e.g., the winter of 2010/11 represents the period between November 2010 and March 2011).

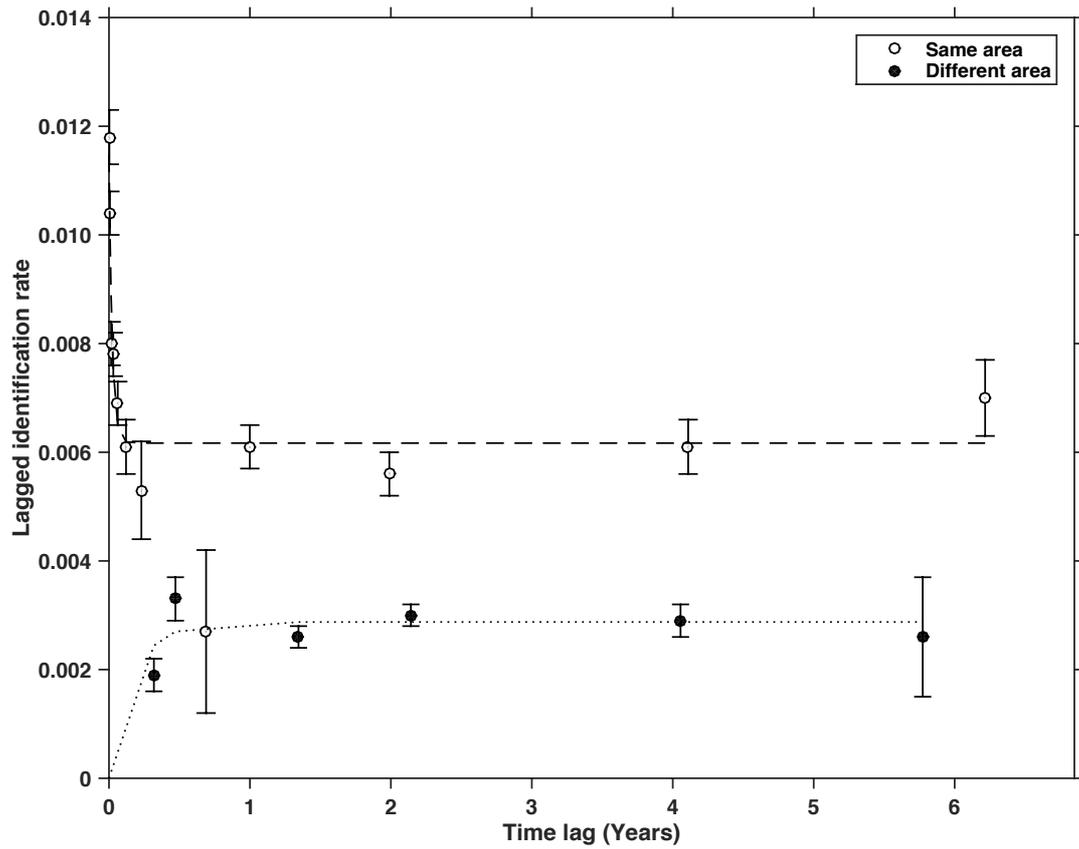


Fig. 3 Lagged identification rates (i.e., probability of reidentification after various time lags, see Whitehead 2001) of individual killer whales between and within herring overwintering and spawning grounds off Iceland. Error bars show jackknife standard errors. The best fitting model for the same 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.

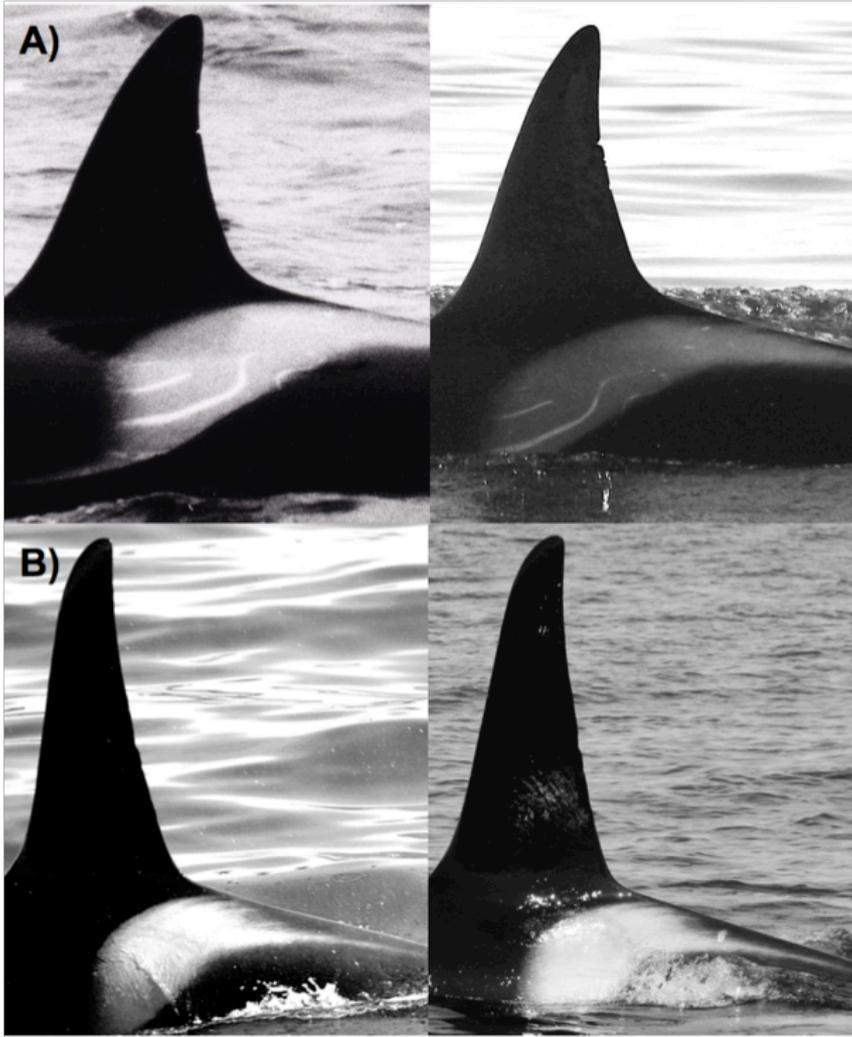


Fig. 4 Examples of photographic matches of Icelandic killer whales: A) IS084 matched between past (left, sighted in 1991) and recent (right, sighted in the winter 2012/13) herring overwintering grounds; B) IS059 matched between past (left, sighted in 1999) and recent (right, sighted in the summers of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

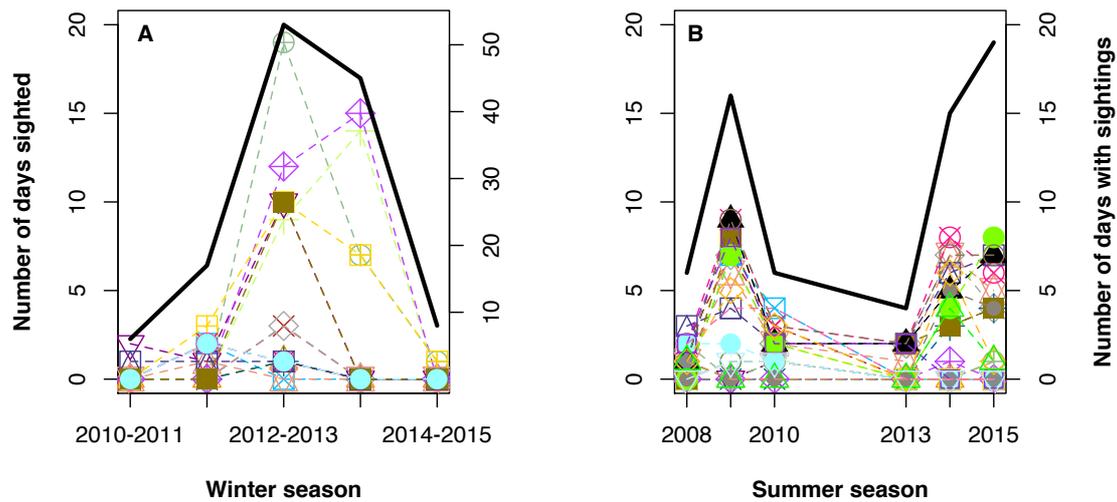


Fig. 5 Sighting frequency per season of Icelandic killer whales matched to the MFRI catalogue (1981-2007) during the study period (2008-2015): A) number of days sighted in recent herring overwintering grounds for each of the 16 killer whales matched to past herring overwintering grounds; B) number of 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±SD [min-max] (days)	First-last encounter (days)	Occupancy mean±SD [min-max] (days)
Summer/2008	6	1.38±0.58 [1-3]	12	7.14±2.85 [1-11]
Summer/2009	16	4.27±2.82 [1-9]	22	10.30±5.46 [1-20]
Summer/2010	6	1.91±0.90 [1-4]	32	5.53±0.68 [1-32]
Summer/2013	4	1.56±0.58 [1-3]	12	2.69±2.75 [1-12]
Summer/2014	15	4.13±1.64 [1-8]	21	15.51±5.58 [1-21]
Summer/2015	19	3.49±2.35 [1-11]	22	10.56±5.72 [1-21]
Winter/2010/11	6	1.11±0.32 [1-2]	9	6.5±1 [5-7]
Winter/2011/12	17	1.65±0.85 [1-4]	42	16.25±13.59 [1-41]
Winter/2012/13	53	5.76±4.71 [1-23]	121	42.1±27.60 [1-120]
Winter/2013/14	45	3.81±4.01 [1-16]	99	43.42±23.43 [2-74]
Winter/2014/15	8	1.28±0.65 [1-3]	21	5±0 [5-5]