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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**

3

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

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 29<sup>th</sup> November and the 2<sup>nd</sup> 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  $100.6 \pm 94.2$  (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

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699

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702

### 703 **Conflict of Interest**

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

705

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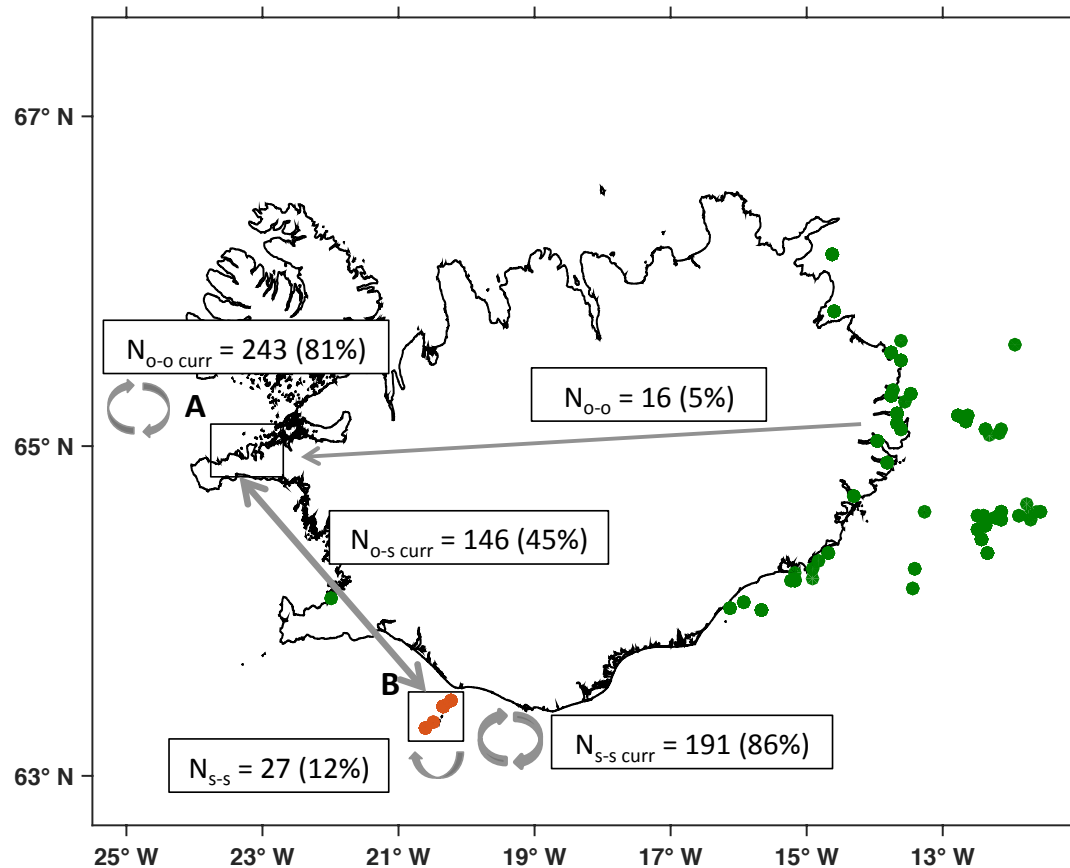
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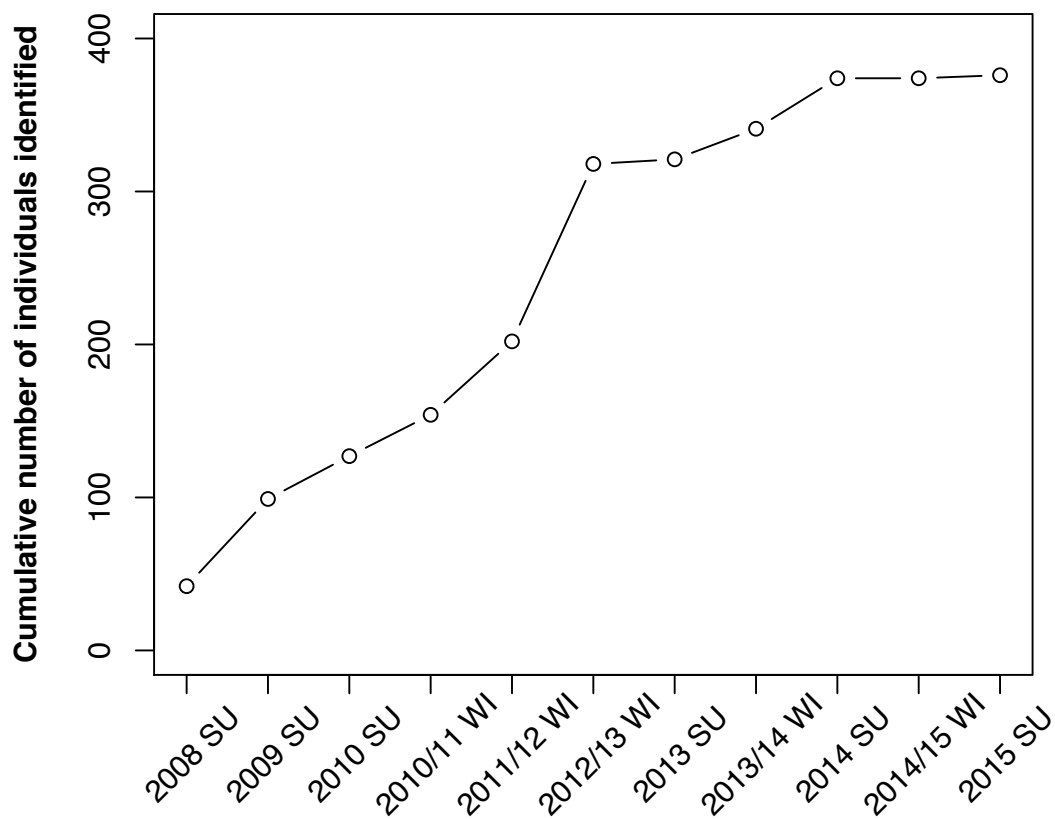
## Figures



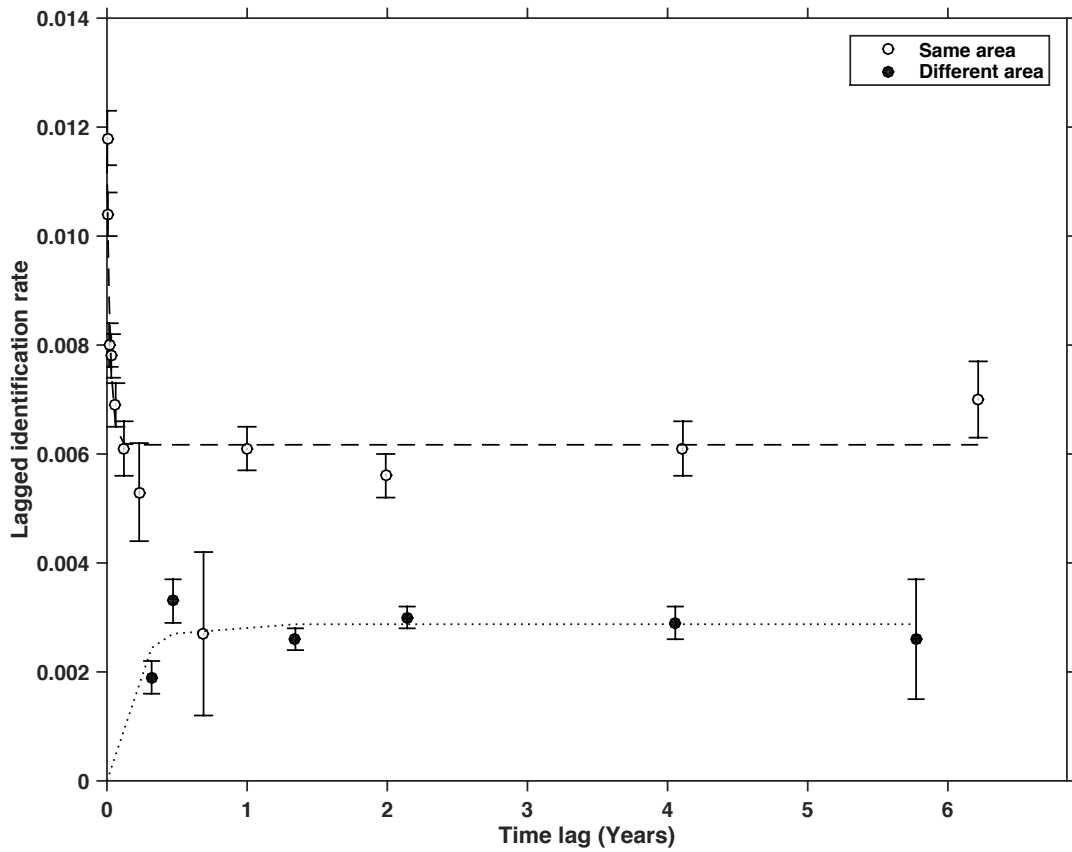
**Fig. 1** Map of Iceland showing the approximate study locations where recent (2008-2015) killer whale photo-identification data were collected: A) recent herring overwintering grounds in the West of Iceland, including the fjords Grundarfjörður and Kolgrafafjörður and; B) herring spawning grounds off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

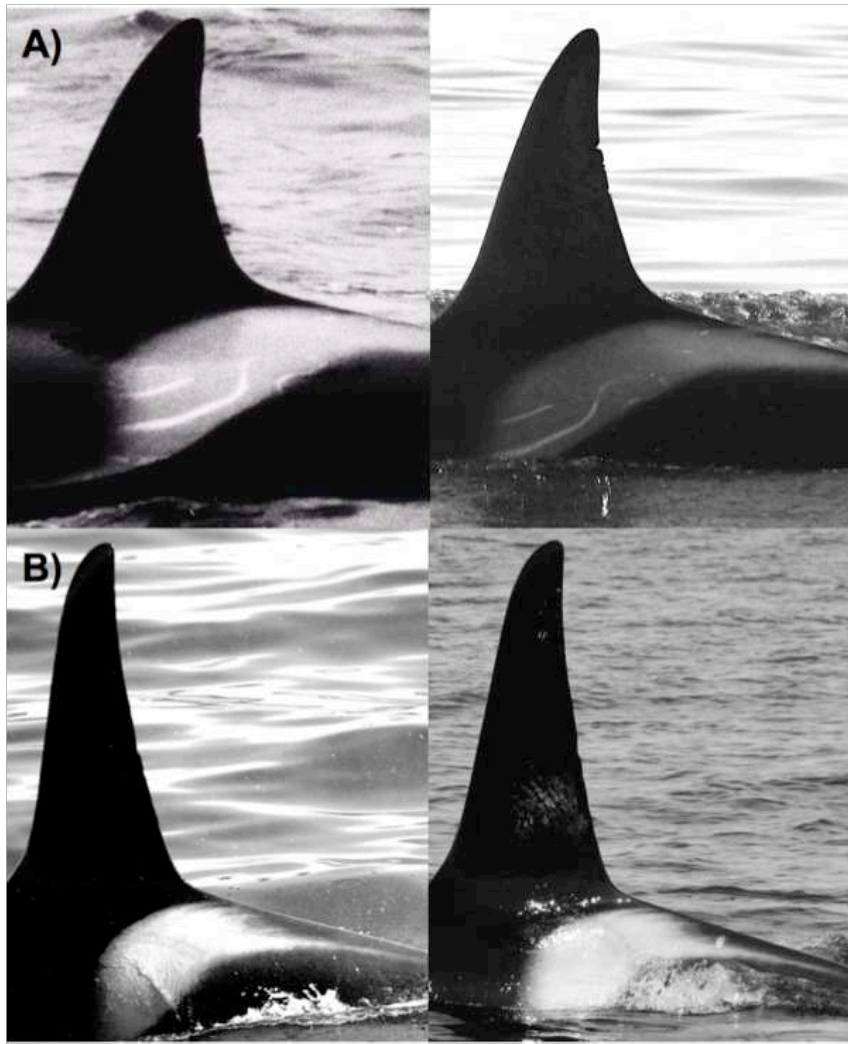




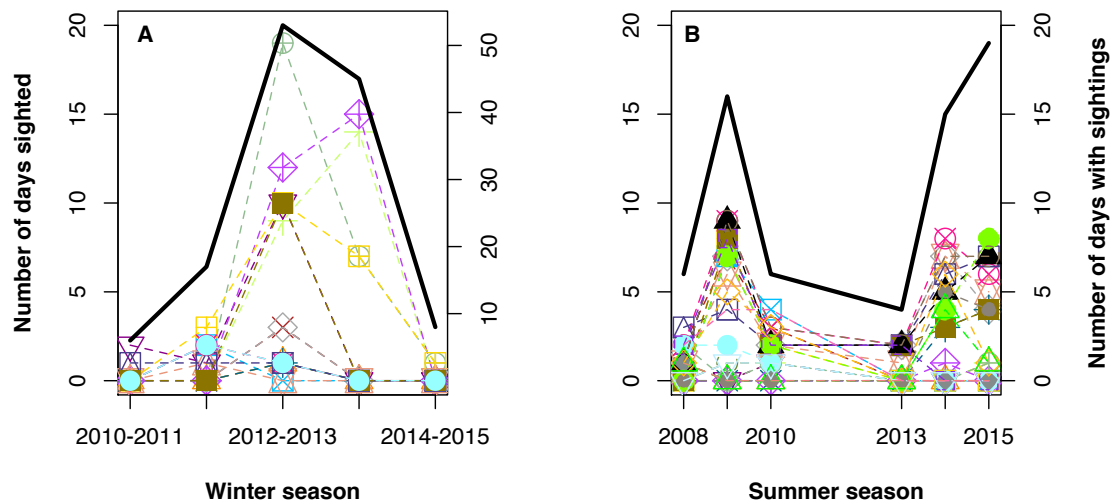
**Fig. 2** Discovery curve of Icelandic killer whales by year and season where SU represents summer and WI represents winter. Winters are considered as the months of November to March and thus span across two years (e.g., the winter of 2010/11 represents the period between November 2010 and March 2011).



**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±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]