INTRODUCTION

Understanding the movements and distribution of top predators is important for effectively managing them and for understanding their impacts on local resources and ecosystems. In the Northeast Atlantic, particularly Norway and Iceland, killer whales Orcinus orca are reported to specialize on Atlantic herring Clupea harengus, following the year-round movements of the Norwegian spring-spawning herring and the Icelandic summer-spawning (ISS) herring stocks, respectively (Sigurjónsson et al. 1988, Similä et al. 1996). However, to date killer whale seasonal movements have only been investigated in Norwegian coastal waters (Similä et al. 1996).

Killer whales were believed to move between Iceland and Norway prior to the collapse of the Atlanto-Scandian herring in the 1960s (Jonsgård & Lyshoel 1970). However, photo-identification data have not revealed any movements post-collapse (Foote et al. 2010). In contrast, individually identified killer whales that were first observed in the herring overwintering grounds of Iceland were photographically recaptured several years later in Scotland, outside of the ISS herring distribution range (Foote et al. 2010). Because Northeast Atlantic killer whales had not been previ-
ously matched between such distant locations, and known movements occurred only within Icelandic waters, Norwegian waters, or around the British Isles (Similä et al. 1996, Foote et al. 2010), those photographic captures between Iceland and Scotland may have indicated a shift in the distribution of some individuals. However, there are few within-year comparisons across locations, impairs our understanding of seasonal movements of killer whales in the Northeast Atlantic.

Here, we investigated movements of individually identified killer whales between Iceland and Scotland using photo-identification data collected from both locations within the same years.

**MATERIALS AND METHODS**

We photographed killer whales in Iceland during the winters of 2012, 2013 and 2014 in Grundarfjörður and Kolgrafa fjörður (West Iceland) from dedicated research vessels, and we also obtained photographs from the public made from whale-watch boats (Fig. 1A). Both fjords were part of the overwintering grounds of the ISS her-ring stock during these years (ICES 2014). Winters were considered as the months from November to March, as this was the period when overwintering herring could be seen in the fjords, and therefore spanned 2 yr. For example, the winter of 2012−2013 refers to the period between November 2012 and end of March 2013. Effort varied among years: in the winter of 2011−2012, photographs were collected in 17 d of effort from whale-watch trips that took place in February−March 2012; the winter of 2012−2013 included a 3 d herring survey (29 Nov–1 Dec 2012), 45 d of effort in whale-watch trips in January−March and 23 d of effort in dedicated killer whale research cruises in February–March 2013; and the winter of 2013−2014 included 33 d of effort from whale-watch trips from January to March and 22 d of effort in dedicated killer whale research cruises in February–March 2014. There were a total of 39 d with confirmed matches in Iceland. All photographs from Scotland were provided by members of the public who observed killer whales from ferries, from whale-watch boats, or from the shore from April to August of 2011 to 2014 (total of 11 d with confirmed matches).

Killer whales were photographed using various digital single-lens reflex cameras and lenses, and individuals were identified based on the size and shape of the dorsal fin, the presence of nicks and scars, and patterns of their saddle patches and body scars (Bigg 1982). The best photo was chosen for each encounter (defined as a day with at least 1 killer whale sighting). Those photographs were then compared among days to assess re-sightings of whales by time and location. Photo quality was judged based upon contrast, focus, angle and an overall quality assessment, adapted from Friday et al. (2000). Photographs of high quality or where animal features were highly distinctive (i.e. so that they could be identified unambiguously for lower quality pictures) were used to maximize the amount of data available. To avoid false positives, we confirmed matches only when at least 3 distinct features were matched between 2 photographs.

**RESULTS**

Of the 6 whales that were originally identified in Iceland and previously linked to Scotland (see Foote et al. 2010), 5 were re-identified in Iceland between 2012 and 2014. We report those individuals here by their combined Iceland/Scotland ID numbers (from unpublished catalogues). One whale (ID 01/133) was not re-identified in Iceland.
Sighting frequency varied among whales. One whale (9479/122) was first photo-identified in the Icelandic herring overwintering grounds in 1995 and was next seen in the summer of 2009 feeding upon the North Sea herring stock approximately 5 km off-shore of Shetland (see Table 1 in Deecke et al. 2011). That whale was seen again in Iceland, in ISS herring overwintering grounds, once in March 2012 and twice in March 2013. However, there were no confirmed sightings of it in Scotland during the summers of 2011 to 2014 (Table 1).

Four other whales originally seen in Iceland and then photographed in the nearshore waters off Scotland (T-38/12, 997/19, IF-4/21 and 993/62; Beck et al. 2012) were re-identified in Iceland. Each of those made at least one intra-annual movement between Iceland and Scotland (Table 1). The whale that was seen most often was 997/19, probably because the conspicuous nick on her dorsal fin allowed for identification even in more distant photographs. All whales except T-38/12 were identified in at least 2 consecutive winters and were sighted frequently in the winters of 2012–2013 and 2013–2014 (Table 1). T-38/12 was seen only in the winter of 2012–2013. Two others (IS153 and IS244) were commonly seen in association with 997/19 in Iceland but had not been previously reported in Scotland. Those whales were confirmed in Scotland (Table 1), providing 2 additional photo-identification matches between these locations. The time between the first and last sighting within a season in Iceland was up to 113 d in the winter of 2012–2013 and up to 71 d in the winter of 2013–2014 (Table 2). However, whales were not seen every day during these periods; the longest interval between sightings within the same season was 63 d (no effort was made during 46 of these days).

There were fewer sightings in Scotland because they were entirely derived from pictures of 11 opportunistic encounters taken from shore or during recreational and whale-watch boat trips by the public (Table 1). In 2011, 997/19 was identified in April, May and July off Orkney, Scotland, with a time between first and last sighting of 50 d. In 2014, IS153 and 997/19 were identified in May and August off Orkney, with a time between first and last sighting of 92 d.

## DISCUSSION

Our results indicate that previously reported movements of killer whales between Iceland and Scotland are seasonal movements rather than permanent relocations. Individual killer whales were seen repeatedly moving between Iceland and Scotland, a distance of at least 1300 km, in several consecutive seasons. During winter, these whales were photo-identified over a period of up to 4 mo (December to March) at herring overwintering grounds in Iceland. Visual observations in Iceland (a total of 39 encounters) were of whales apparently feeding on herring, exhibiting the same behavior as other whales: with circular movements and birds flying above them and picking up clearly identifiable herring. The whales then travelled to Scotland in spring and summer
Killer whales that eat herring have been thought to specialize on specific herring stocks and therefore are thought to follow annual herring migrations (Sigurðsson et al. 1988, Similä et al. 1996). The movements from Iceland to Scotland suggest that some whales appear to be exploiting herring, a seasonally abundant resource during the winter when it is found in large aggregations (Óskarsson et al. 2009), but move away from the summer ISS herring spawning grounds (Jakobsson & Stefánsson 1999, our Fig. 1A) to exploit alternative stocks or other prey found in summer off Scotland. Site fidelity to both locations and the repeated observations of movements between Iceland and Scotland that we present here, in addition to previous observations (Foote et al. 2010), suggest that this has been a consistent pattern for some years for at least a few killer whales. Nevertheless, the fact that to date only a few whales have been matched between Iceland and Scotland (Foote et al. 2010, this study) suggests that the number of individuals repeatedly moving between these locations may be small.

In Iceland we observed killer whales consistently preying upon herring, whilst in Scotland one sighting collected during this study period suggested typical seal-hunting behavior (see video clip in the Supplement at www.int-res.com/articles/supp/b024p075_supp/). Additionally, a group containing 997/19, IF-4/21 and 993/62 was previously observed exhibiting behavior typical of that observed for seal-hunting groups (described in Deecke et al. 2011) during a group follow by ADF on 31 May 2008 off the coast of Shetland. Finally, an encounter off St Kilda, Scotland, on 1 July 2015 documented a group containing T-38/12 clearly predating on a seal (Figs. S1 & S2 in the Supplement). Switching between fish and marine mammal prey has previously been observed in Norway (Vongraven & Bisther 2014). Preying on whatever resources are most abundant at particular times or locations (i.e. a foraging generalist) might be the best tactic when those resources vary substantially in time and space. Herring stocks can undergo large changes in availability (e.g. Jakobsson & Stefánsson 1999); thus, specializing on a specific stock may not be an effective strategy. However, this would require the ability to shift between specialized feeding strategies adapted to different prey resources (Similä & Ugarte 1993, Deecke et al. 2011, Beck et al. 2012). Our understanding of the extent of behavioral plasticity in foraging strategies and to what extent killer whales may switch prey types requires future study, particularly combining seasonal behavioral observations and diet assessment in different feeding contexts.

This preliminary study, although based on only a few individuals, suggests diversity in seasonal movement patterns of killer whales observed on herring grounds. Our study suggests that not all whales feeding on herring will specialize on a particular stock, although others appear to do so (e.g. Similä et al. 1996). The individuals identified moving between Iceland and Scotland represent approximately 2% of the total number of individuals presently known from the Icelandic herring overwintering grounds and approximately 10% of the individuals identified in the nearshore waters of northeastern Scotland. Investigating the seasonal movements of a larger number of individuals will be key to evaluating the extent of this diversity and the effects of killer whale consumption on local prey resources. Recent substantial changes in the ecosystem of the Northeast Atlantic Ocean, such as changes in mackerel Scomber scombrus distribution (Astthorsson et al. 2012), which are a known prey of killer whales in some areas (Nettstead et al. 2014), emphasize the importance of knowing the dynamics of killer whale diet for understanding and predicting their responses to variations in the availability of various prey.

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