Observations of movement and site fidelity of white-beaked dolphins (*Lagenorhynchus albirostris*) in Icelandic coastal waters using photo-identification

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ABSTRACT

The white-beaked dolphin (*Lagenorhynchus albirostris*) is the most commonly sighted delphinid species in Icelandic coastal waters. However, little is known about the species' abundance, site fidelity and movements throughout its range. Photo-identification studies were conducted from April–October (2002–10) during whalewatching operations in Faxaflói and Skjálfandi bays on the southwest and northeast coasts of Iceland, respectively. Minimum abundance, annual site fidelity and movement between bays were calculated. A total of 154 and 52 individuals were identified in Faxaflói and Skjálfandi bays, respectively. The annual re-sighting rate was 21.4% in Faxaflói bay while only one individual was re-sighted in Skjálfandi bay (1.7%). A total of five dolphins (2.3%) were matched between Faxaflói and Skjálfandi bays with the period between re-sightings ranging from 272 to 821 days (mean 28.16 days, SD = 5.94). Low site fidelity rates observed likely signify a much larger home range than the present study area, into either other coastal or offshore zones, or alternatively may be explained by a large natural population size and/or the opportunistic nature of sampling during this study. Therefore, expansion of the study area is required. The matches between bays suggest that white-beaked dolphins inhabit a large-scale coastal range of the Icelandic coast and can be considered highly mobile and transient possibly due to scarce and patchy resources. Alternatively it could be due to a large population size.

KEYWORDS: WHITE-BEAKED DOLPHIN; PHOTO-ID; SITE FIDELITY; MOVEMENTS; NORTH ATLANTIC; ICELAND; NORTHERN HEMISPHERE

INTRODUCTION

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The white-beaked dolphin (*Lagenorhynchus albirostris*) is endemic to the North Atlantic (Kinze *et al.*, 1997; Northridge *et al.*, 1997; Reeves *et al.*, 1999) and present in Icelandic coastal waters all year round (Magnúsdóttir, 2007). Although white-beaked dolphins have been studied in Icelandic waters (e.g. Bertulli *et al.*, 2012; Rasmussen *et al.*, 2013; Rasmussen and Miller, 2002), there has been insufficient data to fully understand their abundance and habitat use.

Higher occurrences of white-beaked dolphins have been observed on the southwest coast, on the northeast coast and on the southeast coast, based on aerial surveys conducted from 1986 to 2001 covering Icelandic coastal waters (Gunnlaugsson et al., 1988; Pike et al., 2009). Based upon opportunistic sightings from whalewatching boats, whitebeaked dolphins are routinely found in the southwest as the second most common species encountered; common minke whales (Balaenoptera acutorostrata) are the most sighted species (Bertulli, 2010). In the northeast they are the third most commonly sighted species in the Skjálfandi bay (hereafter 'Skjálfandi'); the most sighted species is the humpback whale (Megaptera novaeangliae) and the second most sighted is the common minke whale (Cecchetti, 2006), with a reported increase of sightings from 2004 to 2007 (Cooper, 2007). On the west coast of Iceland, sightings have also been reported (whalewatching operator, Láki Tours⁵). The east coast of Iceland remains inadequately surveyed.

The only available abundance estimate (Pike *et al.*, 2009) for white-beaked dolphins in Icelandic waters dates back to 2001 (NASS surveys conducted from 1986–2001), resulting in an estimated 31,653 animals (95% CI: 17,679–56,672).

Previous studies indicate site fidelity (Bertulli, 2010) and movement patterns of white-beaked dolphins in Icelandic waters spanning *ca*. 300km or greater (Rasmussen *et al.*, 2013; Tetley *et al.*, 2006).

The aim of this paper is to present opportunistic data on residency patterns (inter-annual site fidelity), observed movements between two Icelandic bays, Faxaflói Bay (southwest, hereafter 'Faxaflói') and Skjálfandi (northeast) and to evaluate the minimum abundance of white-beaked dolphin using photo-identification in these two study areas.

MATERIALS AND METHODS

Study area

Faxaflói (64°24'N, 22°00'W) and Skjálfandi (66°05'N, 17°33'W) are two relatively wide bays respectively located on the southwest and northeast coast of Iceland, approximately 600km apart from each other (see Fig. 1). Faxaflói is *ca*. 50km long and 90km wide (Stefansson and Guðmundsson, 1978; Stefánsson *et al.*, 1987) and covers about 4,400km². Skjálfandi is about 25km long and 10km wide (Gíslason, 2004) and covers about 1,100km² (Bertulli *et al.*, 2012). Both bays were used as locations to collect data because of the predictable seasonal occurrence of dolphins close to the shore in relatively high numbers and

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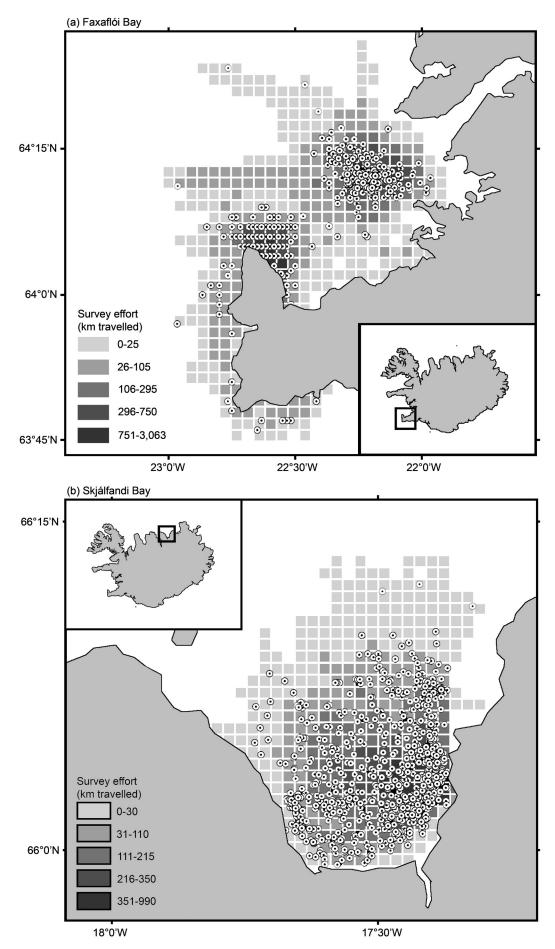


Fig. 1. Location of white-beaked dolphin sightings from 2002 to 2010 in Faxaflói (Top) and in Skjálfandi (Bottom). Searching effort (expressed in km travelled) using whale-watching vessels and white-beaked dolphin sightings (white circles) are shown.

for the presence of whalewatching operations giving multiple tours daily.

Data collection

Photo-identification was undertaken from April-September (2002-10) from two whalewatching boats based in Faxaflói, Reykjavik, and from May-October (2002-10) from three boats in Skjálfandi, Húsavík, Iceland. The whalewatching tours were generally conducted between the hours of 9:00 and 21:00 (at least three trips were scheduled daily lasting approximately three hours) across mainly the spring and summer seasons. Due to the high latitude of the study sites, daylight lasts between approximately 7:00-20:00 hours in April and September, and ca. 5:00-22:00 hours in May and August with almost constant daylight from mid-June till early July (see US Naval Observatory Astronomical Applications Department website⁶). Non-systematic boat surveys based on whalewatching boats in Beaufort sea states of zero to three were conducted in both bays. Observations were collected from the roof of the wheelhouse (5-8m above sea level in Faxaflói, 2.7 to 4.5m in Skjálfandi) of two vessels (length 25-26m) in Faxaflói and three vessels (length 20-25m) in Skjálfandi. Every 15 minutes data forms were used to enter environmental data (sea state, swell, visibility and glare), the vessel position (GPS) was recorded at 5-min intervals. Throughout the surveys there were specific cues utilised to detect animals, including the occurrence of bird feeding flocks and/or feeding whales (often associated with the presence of dolphins) and direct animal observations, either from their surfacing bodies or from their tall and curved dorsal fins. At times the location of animals was reported from other vessels operating in the same area.

At each dolphin sighting, the following information was recorded: species, time, position, environmental conditions, behaviour, and group size/composition (see Bertulli, 2010). Encounter duration was ultimately dependent on the captain's decision to stay with the animals or leave the area (Bertulli *et al.*, 2013). When possible, the vessel would run parallel to the dolphin group, allowing researchers to systematically photograph the whole surfacing pattern of each individual, including the dorsal fin (primary feature used). Secondary features such as the dorsum, flanks and peduncle carrying skin lesions were also used (e.g. Bertulli *et al.*, 2012).

In order to obtain an impartial estimate of the amount of animals encountered, an attempt was made to photo-identify every dolphin within each group without giving preference to obviously marked over unmarked individuals (Currey *et al.*, 2008; Gormley *et al.*, 2005; Williams *et al.*, 1993).

A range of digital cameras were used in both study areas with zoom lenses ranging from 55–200mm to 70–300mm for Faxaflói and from 28–135mm to 40–150mm for Skjálfandi. Images were taken in both JPG (300 pixel/inch) and RAW formats. The number of photographers varied from one to four, usually the principle investigator (CB) and three assistants, who were stationed 360° around the survey vessel in Faxaflói. In Skjálfandi, surveys were conducted by one or two teams, with a total of six different investigators being involved (on rotation) in data collection, also covering an area of 360° around the survey vessel.

Photo-identification analysis

Each photo-identification picture was allocated a quality rating (Q) from Q1 to Q6 (Q6 being the highest), taking into consideration focus, exposure, angle and proportion of the frame occupied by the body of the animal. The Q-value attributed to each image was not dependent of the marks visible on each individual. Only images rated $Q \ge 5$ were considered good enough for the analysis (Elwen et al., 2009; Gowans and Whitehead, 2001; Rosso et al., 2011). Considering the distinctiveness of each image, only distinctive and very distinctive dorsal fins were used in the analysis (Zaeschmar et al., 2014). In order to identify individual white-beaked dolphins from photographs, a previously adopted classification was used (Tscherter and Morris, 2005) which used dorsal fin edge marks (DEMs) as primary features and body marks as secondary features (but these were solely used in addition to DEMs). In fact, due to the lack of studies on the stability over time of secondary features (such as skin marks in white-beaked dolphins) only individuals marked on the fin (DEM) were used for the analysis. Notches have already proven to be reliable permanent marks in other dolphin species (Auger-Méthé and Whitehead, 2007; Rosso et al., 2011; Wilson et al., 1999).

Analysis was only carried out on adult individuals. All images were viewed using Adobe *Photoshop CS2/CS3* imaging software to identify unique permanent markings. Photographs were sorted into chronological order of collection, allowing researchers to detect the evolution of skin marks over time, making them a valid support to DEMs and therefore confirming the identity of different individuals. Additionally, during the matching process a single qualified person was responsible to quality-grade each photoidentification image which was also systematically evaluated by up to two people (i.e. CB or MHR) throughout each field season (Davies *et al.*, 2001; Sears *et al.*, 1990).

Data analysis

Three independent analyses were carried out: (1) estimate of minimum abundance (minimum number of individuals identified in each study area); (2) *'annual re-sighting proportion'* (the proportion of individual dolphins identified in more than one year among all years of study); and (3) matching of individual dolphins between Faxaflói and Skjálfandi bays. A *'re-sighting proportion'* is defined as the number of animals re-sighted in multiple years in both areas divided by the total number of individuals identified in these areas (Bertulli *et al.*, 2013).

The shortest distance between the two bays for the annual re-sighted white-beaked dolphins identified was determined using the 'ruler' tool provided by *Garmin MapSource* (version 6.14) as the direct route by sea (avoiding land) between Reykjavik (Faxaflói) and Húsavík (Skjálfandi) following Bertulli *et al.* (2013).

To describe the white-beaked dolphins visiting the Faxaflói and Skjálfandi study areas the word 'population' was used with no genetic or absolute abundance associations (Weir *et al.*, 2008; de Boer *et al.*, 2013).

Table 1

Survey effort for white-beaked dolphin surveys conducted in: (a) Faxaflói between March and November 1999 to 2010; and in (b) Skjálfandi between May and October 2002 to 2010. N/A = data not available. During the years 2005 in Faxaflói and 2003 in Skjálfandi, photo-IDs were not collected. Effort data was also not recorded in 2002 in Skjálfandi.

Study period	Survey effort (days)	Survey effort (trips)	Survey effort (hours)	Observation (days)	Observation (trips)	Observation (hours)	
(a) Faxaflói							
2002	105	134	402	94	112	336	
2003	119	163	489	94	119	357	
2004	135	188	564	99	130	390	
2005	191	401	1203	98	127	381	
2006	69	130	390	53	75	225	
2007	77	167	311.34	42	62	123.13	
2008	102	198	395.43	65	96	180.42	
2009	85	172	354.25	46	61	130.34	
2010	79	143	254.34	43	55	97.10	
Total	962	1,696	4,364.16	634	837	2,220.47	
(b) Skjálfandi	i						
2002	N/A	N/A	N/A	N/A	N/A	N/A	
2003	48	51	156.03	15	15	42.42	
2004	28	28	99.21	12	12	33.20	
2005	71	75	192.17	45	46	125.19	
2006	79	84	198.48	29	29	65.10	
2007	105	105	257.31	36	36	89.14	
2008	103	110	280.28	28	29	73.06	
2009	103	132	286.11	24	34	84.31	
2010	115	181	353.37	58	77	185.20	
Total	652	766	1,803.23	247	278	699.42	

RESULTS

Photo-identification effort and white-beaked dolphin encounters

Between April 2002 and October 2010, 881 (54.6%) days were spent observing white-beaked dolphins in both study areas, with a total of 837 tours in Faxaflói and 278 in Skjálfandi (Table 1). Dolphin encounters were distributed throughout the surveyed coastline, with particular clusters of sightings in the Garður (64°4'0"N 22°38'0"W) and Kollafjörður (62°7'6"N, 6°54'20"W) areas in Faxaflói and in the inner coastal part of Skjálfandi (Fig. 1).

In the Faxaflói area the number of surveys where whitebeaked dolphins were sighted seem to show an increase until 2004, then a drastic decrease in numbers (with the exception of the year 2008 which shows the highest number of tours in that area when dolphins were encountered since the year 2006). Conversely, in Skjálfandi, surveys showed an increase in numbers almost every other year (see Table 1).

Minimum abundance

A total of 524 high quality colour digital photographs were analysed (n = 415 in Faxaflói, n = 109 in Skjálfandi). As a result, a total of 154 individuals could be identified in Faxaflói, 52 in Skjálfandi and 5 individuals in both bays (Fig. 2).

Of the 211 individual dolphins identified in both areas in Faxaflói, 56 (35.2%) were left side identifications, 55 (34.6%) were right side identifications and 43 (27.0%) where both sides were identified. In Skjálfandi 23 (44.2%) were left side identifications, 18 (34.6%) were right side and 11 (21.2%) both sides. The 5 individuals photographed in both bays consisted of 1 right side identification (20.0%) and 4 both sides (80.0%).

Overall, in both study sites the cumulative number of identified individuals ('rate of discovery' curve) of whitebeaked dolphins did not decrease (Fig. 2). The number of photo-identified images collected counted an overall average

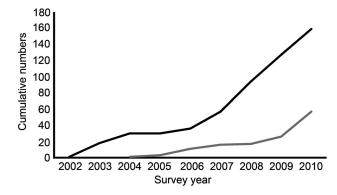


Fig. 2. The Discovery curve is established by plotting the cumulative number of newly marked (DEM) identified and catalogued white-beaked dolphins each year, in Faxaflói from 2002 to 2010 (black line) and in Skjálfandi from 2004 to 2010 (grey line) inclusive.

of $3.75 \pm 2.89 \ (\pm \text{SD})$ new white-beaked dolphins per day (every year) in Faxaflói and $2.97 \pm 1.86 \ (\pm \text{SD})$ in Skjálfandi.

Annual re-sighting proportion

The annual re-sighting proportion was 21.4% (n = 34) in Faxaflói, with the majority of identified dolphins observed only one year (n = 125, 78.6%), followed by 31 individuals recorded two years (19.5%), and 3 seen for three years (1.9%) between April and September 2002 to 2010 (Fig. 3). Of the 34 animals re-sighted annually, 21 (61.8%) were resighted in consecutive years; the highest number was resighted between 2007 and 2010. Only one individual (DEM57) was inter-annually re-sighted in Skjálfandi (annual proportion of 1.7%), this individual was first sighted in 2007 and then re-sighted in 2010.

Overlap between the Faxaflói and Skjálfandi whitebeaked dolphin 'populations'

Both photo-identified catalogues include images of 211 distinctive individuals (n = 154 in Faxaflói, n = 52 in

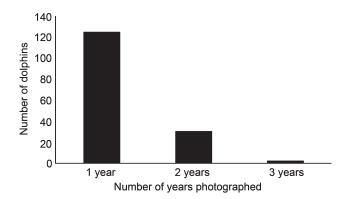


Fig. 3. Distribution of annual re-capture frequencies between years for all white-beaked dolphins identified in Faxaflói between April and October 2002 to 2010.

Skjálfandi) and five of these have been seen in both areas. This equates to an overall *re-sighting proportion* of 2.4%. Of the five re-sighted dolphins, three (60.0%) were first identified in Faxaflói and two (40.0%) in Skjálfandi. The time between re-sightings ranged from 272 to 821 days (mean of 411.20 days, SD = 230.43) (Table 2). The observed distances between re-sightings ranging from Faxaflói to Skjálfandi are *ca*. 600 km.

DISCUSSION

Minimum abundance

Stable conclusions on abundance and site fidelity are predictably restricted by the use of opportunistic platforms. However, despite its opportunistic nature, this study has given an insight into the population of white-beaked dolphins occurring on the SW and NE coasts of Iceland. Photoidentification indicates there were at least 211 individuals using the Faxaflói and Skjálfandi areas from 2002 to 2010. The absence of a plateau in the 'discovery' curve suggests that the white-beaked dolphins found are likely part of a larger population, as is confirmed by systematic aerial surveys which have reported a relative abundance of around thirty thousand animals in Icelandic coastal waters (Pike et al., 2009). Additionally, by 2010 the 'discovery' curve for both areas was still ascending, indicating that further photoidentification effort is still required within these waters. This may be important as the study area of Faxaflói surveyed was only a small part of the whole bay. Lastly, an analysis on group size estimates and numbers of photo-identification images would also offer clarification on the proportion of individuals identified during each encounter and consequently also help to explain the minimum abundance estimates found in this study.

There are currently three other existing photo-identification catalogues of white-beaked dolphins: one with 20 photoidentified individuals collected during the summer 2001–10 (Caroline Weir, unpublished data) in Aberdeenshire waters Scotland, one curated by MARINELife, in which eighty individuals were documented between 2007 and 2012 (Brereton, pers. comm.) in Lyme Bay and surrounding waters off south-west England and another detailing 26 identifications collected between 2003 and 2012 (by MARINELife; Kitching, pers. comm.) along the Northumberland coast of England. In comparison to these other white-beaked dolphin catalogues, the photo-identification results provided in this study represent the largest existing photo-identification catalogue of white-beaked dolphins in the North Atlantic.

The most successful identification criteria used for individual dolphins has proven to be notches which are prominent markings with a low gain and loss rate (Auger-Méthé *et al.*, 2010; Auger-Méthé and Whitehead, 2007; Gowans and Whitehead, 2001). To be able to use their body marks, an accurate analysis of their stability over time needs to be conducted in order to know whether these marks can robustly be used to identify individuals (Auger-Méthé *et al.*, 2010). In the present study, several different body marks (summarised by Bertulli *et al.*, 2012) were used as secondary features with the identification of DEMs. However, individuals identified by using only these secondary features were not included in the final abundance estimates (Berghan *et al.*, 2008).

An unbiased estimate of minimum abundance was ensured by using excellent quality images (Q \geq 5) as well as high distinctiveness of each dorsal fin (Nicholson *et al.*, 2012). Misidentifications (e.g. false positive and negative errors) were avoided by considering only notches on the dorsal fin as long-lasting and stable identification features. The data set has shown that photo-identification can be a useful technique for the individual recognition of white-beaked dolphins in the coastal waters of Iceland if a strict quality controlled protocol is followed. However, photoidentification can be important in not only obtaining accurate estimates of abundance and survival rates but also study of social interactions and health status of a species, for which photographic quality rules can be relaxed.

Annual re-sighting proportion

Dolphin habitat use (i.e. site fidelity) can be altered by both food availability and predation risk (Heithaus and Dill, 2002). Thus, it is beneficial for a dolphin species to reside in a small area if the food is plentiful and is therefore easily located (Baird *et al.*, 2008); if the food becomes scarce, the size of its home-range might increase (e.g. Defran *et al.*, 1999; Silva *et al.*, 2008).

As an indication of this, three individuals (DEM62, DEM93, DEM163) out of the five re-sighted between

Table 2								
Summary of white-beaked dolphin sightings and re-sightings between Faxaflói and Skjálfandi.								

No. animals identified	ID-name	1 st sighting date Faxaflói	Lat.	Long.	1 st sighting date Skjálfandi	Lat	Long	Time (days)
1	DEM62	29/07/2009	64.174	-22.394	19/06/2010	66.098	-17.611	325
2	DEM93	16/05/2008	64.206	-22.042	15/08/2010	66.040	-17.519	821
3	DEM65	16/07/2007	64.250	-22.000	03/08/2006	66.072	-17.625	337
4	DEM174	09/05/2010	64.207	-22.294	10/08/2009	66.046	-17.4791	272
5	DEM163	16/08/2009	64.222	-22.265	13/06/2010	66.119	-17.392	301

Faxaflói and Skjálfandi were sighted in Skjálfandi for the first time in 2010 but they had previously shown site fidelity to the Faxaflói area during 2007–2009. Similarly, 37 dusky dolphins (*Lagenorhynchus obscurus*) in New Zealand waters showed residency off Kaikoura during summer and spring months, when they were also recorded venturing *ca*. 200 km further north in the Marlborough Sounds area during the winter (Markowitz, 2004; Markowitz *et al.*, 2004).

Overlap between the Faxaflói and Skjálfandi whitebeaked dolphin 'populations'

This study indicates that white-beaked dolphins inhabit a large-scale coastal range of the Iceland coastline. Dolphins are capable of performing seasonal migrations (e.g. Constantine, 1995; Markowitz *et al.*, 2004; Wood, 1998), mid-distance movements (around 300km; Bearzi *et al.*, 2010; Silva *et al.*, 2008) and long-distance movements (up to 650km; O'Brien *et al.*, 2009). Two more recent findings showed a short-beaked common dolphin (*Delphinus delphis*) mother and calf pair travelling at least 1,000km (Genov *et al.*, 2012), and common bottlenose dolphins covering a minimum distance of 1,277km between UK and Ireland (Robinson *et al.*, 2012).

The reasons for the continual change in distances travelled by the Icelandic white-beaked dolphins are not known. Previous studies suggest how changes in temperature and the occurrence of oceanographic events (e.g. el Niño) could encourage animals to expand their home ranges (e.g. Hansen and Defran, 1990; Neumann, 2001). Since 1997, gradual changes including increased temperature and salinity in the Icelandic marine ecosystem (Marine Research Institute, 2008; 2012) have resulted in visible alterations in distribution and abundance of many fish species (e.g. Astthórsson et al., 2007; as summarised by Björnsson and Pálsson, 2004; Gudmundsdottir and Sigurdsson, 2004; Vilhjálmsson et al., 1997), some of which [e.g. cod (Gadus morhua), haddock (Melanogrammus aeglefinus), herring (Clupea harengus) mackerel, (Scomber scombrus), and whiting (Merlangius merlangus)] are known to be part of the white-beaked dolphins' diet (Canning et al., 2008; Van Bree and Nijssen, 1964; Víkingsson and Ólafsdóttir, 2004). The recent findings of movements of individuals from the southwest to the northeast coast of Iceland could support these recent changes in the Icelandic coastal marine environment.

Evidence of long distance movements has been previously documented on two occasions in Icelandic waters. In 2006, Tetley et al. (2006) reported a white-beaked dolphin sighted twice, 361km apart, in only 6 days. In the same year, a male white-beaked dolphin was tagged with a satellite transmitter in Faxaflói (Rasmussen et al., 2013) and was found to be travelling back and forth between the south and the west coasts, covering a total minimum distance of 5,280km. Opportunistic photo-identification images taken on the west coast of Iceland on 22 June 2008 were re-matched with a photo-identified individual (DEM184) which was photographed on 1 August 2010 in Faxaflói. More photographs taken on 24 February 2012 on the west coast resulted in another rematch with an individual (DEM247, Q4 quality so not included in this analysis) previously identified in Faxaflói on 11 July 2011. When compared to

these photo-identifications and to the satellite tagged dolphin data, the present study suggests that white-beaked dolphins in Icelandic waters reside in particular coastal areas, which they regularly explore. One of these areas might range between the southwest and northeast coast of Iceland.

To carefully review all results presented and assess the potential of this study in the long-term, a number of caveats should be highlighted regarding the methods adopted for this study. There were days when dolphins were sighted in the bay but photo-identification images were not collected due to the boats interest in other species (e.g. common minke whales, humpback whales) not associating with the dolphins at that time. White-beaked dolphins showing signs of disturbance and performing avoidance behaviour (e.g. frequent change of direction while surfacing, long dives, further re-surfacing) negated photo-identification being conducted.

Similarly to other 'core user' species, white-beaked dolphins in coastal Icelandic waters may exhibit site fidelity to an area, but they can also travel far through different geographical territories (e.g. Baird et al., 2008; Bearzi et al., 2010; Markowitz et al., 2004; Tezanos-Pinto, 2009; Wilson et al., 2004). The results of this study demonstrate the potential of photo-identification as a technique for studying long-distance movements of this species. A continual use of this technique is, therefore, recommended for future studies to facilitate further inter-regional collaboration between different research institutions in Iceland, and to improve current understanding of white-beaked dolphin abundance, movement patterns and distribution within the region. It is also suggested that an expansion of the area studied into other similar coastal areas on the west coast, could highlight an important connecting area between the southwest and the northeast territories. A focused, long-term, year-round study is needed to verify suggestions about dolphin movements as observed opportunistically from whalewatching boats.

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REFERENCES

- Astthórsson, O.S., Gislason, A. and Jonsson, S. 2007. Climate variability and the Icelandic marine ecosystem. *Deep-Sea Res. II* 54: 2456–77.
- Auger-Méthé, M., Marcoux, M. and Whitehead, H. 2010. Nicks and notches of the dorsal ridge: Promising mark types for the photo-identification of narwhals. *Mar. Mammal Sci.* 26(3): 663–78.
- Auger-Méthé, M. and Whitehead, H. 2007. The use of natural markings in studies of long-finned pilot whale (*Globicephala melas*). *Mar. Mammal Sci.* 23: 77–93.
- Baird, R.W., Webster, D.L., Hahaffy, S.D., McSweeney, D.J., Schorr, G.S. and Ligon, A.D. 2008. Site fidelity and association patterns in a deepwater dolphin: rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian Archipelago. *Mar. Mammal Sci.* 24(3): 535–53.
- Bearzi, G., Bonizzoni, S. and Gonzalvo, J. 2010. Mid-distance movements of common bottlenose dolphins in the coastal waters of Greece. *Journal* of *Ethology* 29: 369–74.
- Berghan, J., Algie, K.D., Stockin, K.A., Wiseman, N., Constantine, R., Tezanos-Pinto, G. and Mourõo, F. 2008. A preliminary photoidentification study of bottlenose dolphin (*Tursiops truncatus*) in Hauraki Gulf, New Zealand. NZ J. Mar. Freshwater Res. 42: 465–72.
- Bertulli, C. 2010. Minke whale (*Balaenoptera acutorostrata*) and whitebeaked dolphin (*Lagenorhynchus albirostris*) feeding behaviour in Flaxafloi bay, south west Iceland. Master's thesis, University of Iceland, Iceland. 239pp.
- Bertulli, C.G., Cecchetti, A., van Bressem, M.F. and van Waerebeek, K. 2012. Skin disorders in common minke whales and white-beaked dolphins off Iceland, a photographic assessment. *Journal of Marine Animals and their Ecology* 5(2): 29–40.
- Bertulli, C.G., Rasmussen, M.H. and Tetley, M.J. 2013. Photo-identification rate and wide-scale movement of common minke whales (*Balaenoptera* acutorostrata) in the coastal waters of Faxaflói and Skjálfandi Bays, Iceland. J. Cetacean Res. Manage 13(1): 39–45.
- Björnsson, H. and Pálsson, Ó.K. 2004. Distribution patterns and dynamics of fish stocks under recent climate change in Icelandic waters. *ICES CM* K:30. 27pp.
- Canning, S.J., Santos, M.B., Reid, R.J., Evans, P.G.H., Sabin, R.C. and Bailey, N. 2008. Seasonal distribution of white-beaked dolphins (*Lagenorhynchus albirostris*) in UK waters with new information on diet and habitat use. J. Mar. Biol. Assoc. U.K. 88(6): 1,159–66.
- Cecchetti, A. 2006. The spatial and temporal distribution of cetaceans within Skjálfandi bay, north-east Iceland. Master's thesis, University of Bangor, UK.
- Constantine, R. 1995. Monitoring the commercial swim-with-dolphin operations with the bottlenose dolphin (*Tursiops truncatus*) and common dolphin (*Delphinus delphis*) in the Bay of Islands, New Zealand. MSc thesis, University of Auckland, Auckland, New Zealand. 98pp.
- Cooper, D. 2007. Cetacean habitat modeling in Skjálfandi, Eyjafjörður and Öxarfjörður Bays, North East Iceland. MSc thesis, University of Wales, Bangor, England. 120 pp.
- Currey, R., Rowe, L.E., Dawson, S. and Slooten, E. 2008. Abundance and demography of bottlenose dolphins in Dusky Sound, New Zealand, inferred from dorsal fin photographs. *New Z. J. Mar. Fresh* 42: 439–49.
- Davies, J., Baxter, J., Bradley, M., Connor, D., Khan, J., Murray, E., Sanderson, W., Turnbull, C. and Vincent, M. 2001. *Marine Monitoring Handbook*. 405pp. ISBN 1 85716 550 0.
- De Boer, M.N., Clark, J., Leopond, M.F., Simmonds, M.-P., Reijnders, P.J.H. 2013. Photo-identification methods reveal seasonal and long-term site-fidelity of Risso's dolphins (*Grampus griseus*) in shallow waters (Cardigan Bay, Wales). Open J. Mar. Sci. 3: 66–75.
- Defran, R.H., Weller, D.W., Kelly, D.L. and Espinosa, M.A. 1999. Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the Southern Calfiornian Bight. *Mar. Mammal Sci.* 15(2): 381–93.
- Elwen, S.H., Reeb, D., Thornton, M. and Best, P.B. 2009. A population estimate of Heaviside's dolphins, *Cephalorhynchus heavisidii*, at the southern end of their range. *Mar. Mammal Sci.* 25(1): 107–24.
- Genov, T., Bearzi, G., Bonizzoni, S. and Tempesta, M. 2012. Long-distance movement of a lone short-beaked common dolphin (*Delphinus delphis*) in the central Mediterranean Sea. *Mar. Biol. Res.* 5(e9): 1–3.
- Gíslason, Á. 2004. Fish farming in Húsavík, Iceland. Arctic charr Tilapia – Atlantic halibut – Turbot. Report of the Húsavík Academic Center, Iceland. 82 pp.

- Gormley, A.M., Dawson, S.M., Slooten, E. and Brager, S. 2005. Capturerecapture estimates of Hector's dolphin abundance at Banks Peninsula, New Zealand. *Mar. Mammal Sci.* 21(2): 204–16.
- Gowans, S. and Whitehead, H. 2001. Photographic identification of northern bottlenose whales (*Hyperoodon ampullatus*): sources of heterogeneity from natural marks. *Mar. Mammal Sci.* 17: 76–93.
- Gudmundsdottir, A. and Sigurdsson, T. 2004. The autumn and winter fishery and distribution of the Icelandic summer-spawning herring during 1978– 2003. Marine Research Institute, Iceland, Report 104. 42pp.
- Gunnlaugsson, T., Sigurjónsson, J. and Donovan, G.P. 1988. Aerial survey of cetaceans in the coastal waters off Iceland, June–July 1986. *Rep. int. Whal. Commn* 38: 489–500.
- Hansen, L.J. and Defran, R.H. 1990. A comparison of photo-identification studies of California coastal bottlenose dolphins. *Rep. int. Whal. Commn* (special issue) 12: 101–04.
- Heithaus, M.R. and Dill, L.M. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecol.* 83: 480–91.
- Kinze, C.C., Addink, M., Smeenk, C., Garcia Hartmann, M., Richards, H.W., Sonntag, R. and Benke, H. 1997. The white-beaked dolphin (*Lagenorhynchus albirostris*) and the white-sided dolphin (*Lagenorhynchus acutus*) in the North and Baltic Seas: review of available information. *Rep. int. Whal. Commn* 47: 675–81.
- Magnúsdóttir, E. 2007. Year round distribution and abundance of whitebeaked dolphins (*Lagenorhynchus albirostris*) off the southwest coast of Iceland. M.Sc. thesis, University of Iceland, Reykjavik, Iceland. 149pp.
- Marine Research Institute. 2008. Þættir úr vistfræði sjávar 2007 / Environmental conditions in Icelandic waters 2007. Hafrannsóknastofnunin Fjölrit / MRI Technical Report. 139. 40pp.
- Marine Research Institute. 2012. Þættir úr vistfræði sjávar 2011 / Environmental conditions in Icelandic waters 2011. Hafrannsóknastofnunin Fjölrit / MRI Technical Report. 162. 51pp.
- Markowitz, T.M. 2004. Social organization of the New Zealand dusky dolphin. Ph.D thesis. Texas A&M University, USA. 278pp.
- Markowitz, T.M., Harlin, A.D., Würsig, B. and McFadden, C.J. 2004. Dusky dolphin foraging habitat: overlap with aquaculture in New Zealand. *Aquat. Conserv.* 14: 133–49.
- Neumann, D.R. 2001. Seasonal movements of short-beaked common dolphins (*Delphinus delphis*) in the north-western Bay of Plenty, New Zealand; Influence of sea surface temperatures and El Nino/La Nina. NZ J. Mar. Freshwater Res. 35: 371–74.
- Nicholson, K., Bejder, L., Allen, S.J., Krützen, M. and Pollock, J.H. 2012. Abundance, survival and temporary emigration of bottlenose dolphins (*Tursiops sp.*) off Useless Loop in the western gulf of Shark Bay, Western Australia. *Mar. Freshw. Res.* 63: 1,059–68.
- Northridge, S., Tasker, M. and Webb, A. 1997. White-beaked, Lagenorhynchus albirostris and Atlantic white-sided dolphin, L. acutus distributions in northwest European and US North Atlantic waters. Rep. int. Whal. Commn 47: 797–805.
- O'Brien, J.M., Berrow, S.D., Ryan, C., McGrath, D., O'Connor, I. and Pesante, G. 2009. A note on long-distance matches of bottlenose dolphins (*Tursiops truncatus*) around the Irish coast using photo-identification. J. Cetacean Res. Manage. 11: 69–74.
- Pike, D.G., Paxton, C.G.M., Gunnlaugsson, T. and Víkingsson, G.A. 2009. Trends in the distribution and abundance of cetaceans from aerial surveys in Icelandic coastal waters, 1986–2001. *NAMMCO Sci. Pub.* 7: 117–42.
- Rasmussen, M.H., Akamatsu, T., Teilmann, J., Víkingsson, G. and Miller, L.A. 2013. Biosonar, diving and movements of two tagged white-beaked dolphins in Icelandic waters. *Deep-Sea Res. II* 88–89: 97–105.
- Rasmussen, M.H. and Miller, L. 2002. Whistles and clicks from whitebeaked dolphins, *Lagenorhynchus albirostris* recorded in Faxaflói Bay. *Aquat. Mamm.* 28: 78–89.
- Reeves, R.R., Brownell, R.L., Kinze, C.C., Smeenk, C. and Lien, J. 1999.
 White-beaked dolphin *Lagenorhynchus albirostris* (Gray, 1828). pp.1–30. *In*: Ridgway, S.H. and Harrison, R. (eds). *Handbook of Marine Mammals*. Academic Press, London.
- Robinson, K.P., O'Brien, J.M., Berrow, S.D., Cheney, B., Costa, M., Eisfeld, S.M., Haberlin, D., Mandelberg, L., O'Donovan, M., Oudejans, M.G., Ryan, C., Stevick, P.T., Thompson, P.M. and Whooley, P. 2012. Discrete or not so discrete: long distance movements by coastal bottlenose dolphins in UK and Irish waters. *J. Cetacean Res. Manage* 12(3): 365–71.
- Rosso, M., Ballardini, M., Moulins, A. and Würtz, M. 2011. Natural markings of Cuvier's beaked whale *Ziphius cavirostris* in the Mediterranean Sea. *Afr. J. Mar. Sc.* 33(1): 45–57.
- Sears, R., Williamson, J.M., Wenzel, F.W., Bérubé, M., Gendron, D. and Jones, P. 1990. Photographic identification of the blue whale (*Balaenoptera musculus*) in the Gulf of St. Lawrence, Canada. *Rep. int. Whal. Commn (special issue)* 12: 335–42.
- Silva, A.M., Prieto, R., Magalhaes, S., Seabru, M.I., Santos, R.S. and Hammond, P.S. 2008. Ranging patterns of bottlenose dolphins living in oceanic waters: implications for population structure. *Mar. Biol.* 156: 179–92.

- Stefansson, U. and Guðmundsson, G. 1978. The freshwater regime of Faxaflói, Southwest Iceland, and its relation to meteorological variables. *Est. Coast. Mar. Sci.* 6: 535–51.
- Stefánsson, U., Thórdardóttir, T. and Ólafsson, J. 1987. Comparison of season oxygen cycles and primary production in the Faxafloi region, southwest Iceland. *Deep-Sea-Res.* 34(5/6): 725–39.
- Tetley, M.J., Wald, E. and Björgvinsson, Á. 2006. White-beaked dolphin movements around Iceland: Evidence from photo-identification studies. Paper read at the Seventh American Cetacean Society Conference, Ventura, California.
- Tezanos-Pinto, G. 2009. Population structure, abundance and reproductive parameters of bottlenose dolphins (*Tursiops truncatus*) in the Bay of Islands (Northland, New Zealand), PhD thesis, University of Auckland, Auckland, New Zealand. 243pp.
- Tscherter, U. and Morris, C. 2005. Identifying a majority of minke whales (*Balaenoptera acutorostrata*) in the St. Lawrence based on the presence of dorsal fin edge marks. *In*: P.G.H. Evans and V. Ridoux (eds). *European Research on Cetaceans* 159. Proceedings of the 15th Annual Conference of the European Cetacean Society, La Rochelle, 2005.
- Van Bree, P.J.H. and Nijssen, H. 1964. On three specimens of Lagenorhynchus albirostris Gray, 1846 (Mammalia, Cetacea). Beaufortia 11: 85–93.
- Víkingsson, G. and Ólafsdóttir, D. 2004. Hnýðingur (white-beaked dolphin). pp.154–7. In: Hersteinsson, P. (eds). Íslensk spendýr (Icelandic Mammals). Vaka-Helgafell, Reykjavík, Iceland. [In Icelandic].
- Vilhjálmsson, H., Misrund, O.A., Arrhenius, F., Holst, J.C., Gislason, A., Gudmundsdóttir, A., Jacobsen, J.A., Krysov, A., Malmberg, S.A. and Reid, D. 1997. Report on surveys of the distribution, abundance

and migrations of the Norwegian spring-spawning herring, other pelagic fish and the environment of the Norwegian Sea and adjacent waters in late winter, spring and summer of 1997. ICES Council Meeting Papers Y:4. 34pp. [Available from *http://www.ices.dk*].

- Weir, C.R., Canning, S., Hepworth, K., Sim, I. and Stockin, K.A. 2008. A long-term opportunistic photo-identification study of bottlenose dolphins (*Tursiops truncatus*) off Aberdeen, United Kingdom: conservation value and limitations. *Aquat. Mamm.* 34(4): 436–47.
- Williams, J.A., Dawson, S.M. and Slooten, E. 1993. The abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Can. J. Zool.* 71: 2,080–88.
- Wilson, B., Hammond, P.S. and Thompson, P.M. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecol. Appl.* 9: 288–300.
- Wilson, B., Reid, R.J., Grellier, K., Thompson, P.M. and Hammond, P.S. 2004. Considering the temporal when managing the spatial: A population range expansion impacts protected areas based management for bottlenose dolphins. *Anim. Conserv.* 7: 331–38.
- Wood, C.J. 1998. Movement of bottlenose dolphins around the south-west coast of Britain. J. Zool. (Lond.) 246: 155–63.
- Würsig, B. and Würsig, M. 1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science* 198: 755–56.
- Zaeschmar, J.R., Visser, I.N., Fertl, D., Dwyer, S.L., Meissner, A.M. and Halliday, J. 2014. Occurrence of false killer whales (*Pseudorca crassidens*) and their association with common bottlenose dolphins (*Tursiops truncatus*) off northeastern New Zealand. *Mar. Mammal Sci.* 30(2): 594–608.