The use of natural markings to study the demography and social structure of common minke whale (*Balaenoptera acutorostrata*) and white-beaked dolphin (*Lagenorhynchus albirostris*)

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Dissertation submitted in partial fulfillment of a
Philosophiae Doctor degree in Biology

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Abstract

The demography and social structure were investigated in a whale (common minke whale; *Balaenoptera acutorostrata*) and a dolphin species (white-beaked dolphin; *Lagenorhynchus albirostris*) that are both abundant yet poorly understood within Icelandic coastal waters. Analysis were conducted from 12 years (2002–2014) of photo-identification data collected from onboard whale-watching boats in Faxaflói and Skjálfandi with some additional images obtained from colleagues working in Breiðafjörður. Stranding reports from outside of Iceland were also used to better understand our knowledge on the occurrence of veterbral column deformities in white-beaked dolphins.

We first assessed the prevalence, abundance and rates of change of 28 naturally occurring mark types that could be used for capture-mark-recapture studies of both species. Results suggested fin and body injury marks were among the most accurate features to use for capture-mark-recapture studies as noted for other cetacean species. However, our results also suggested that cookie-cutter shark bites for common minke whales and fin patches for white-beaked dolphins could also be used due to their low loss rate, which was a novel realisation that will ultimately increase sample sizes for any database for both species.

We explored the occurrences of vertebral column deformities of white-beaked dolphins from free-ranging and stranded specimens across Europe. The results indicated that vertebral column deformities occur in this species and that some individuals can live with such anomalies for several months. Five white-beaked dolphins showed outwardly vertebral kyphosis, kyphoscoliosis or lordosis. Two of the free-ranging cases and two of the stranded specimens appeared to have an acquired disease, either as direct result of trauma, or indirect from trauma/wound and subsequent infection and bony proliferation, although we were unable to specifically identify the causes. These results represent a good starting point to understand occurrence and implications of vertebral column deformities in white-beaked dolphins from the eastern North Atlantic.

We analysed 823 images, and distinguished stage classes (adults, juveniles, calves and neonates) based on size and then colour components were described per stage class and ontogenetically. Results showed that the color components were useful in estimating maturity in white-beaked dolphins, a method that would benefit from the assessment of a geographically varied sample of freshly stranded specimens of known sex and age.

The social structure of white-beaked dolphins was described using a total of 489 sightings of identified white-beaked dolphin, which represented 35 adults sighted on five or more days. The results indicated a high social differentiation and permutation tests indicated that dolphins associated non-randomly, similar to other oceanic species of dolphins. Coefficients of associations were fluid and weak but association index values were in the range observed in other dolphin species. The association patters are best described as 'casual acquaintances'. Results expanded the latitudinal range for which social structure has been described for oceanic dolphin species and specifically one for which very little has been published.

Finally, the abundance and survival of common minke whales and white-beaked dolphins were estimated using capture-recapture methods, accounting for imperfect detection and transience. We estimated an average abundance of 226 (169-301) white-beaked dolphins in Faxaflói Bay; and 70 (53-93) minke whales in Faxaflói Bay and 18 (12–27) in Skjálfandi Bay. A weighted regression revealed a significant positive trend in abundance of common minke whales during over the 12-year period. We also found that apparent survival was constant over time for the white-beaked dolphin and minke whales in both bays. These are the first estimates of abundance for these species to use capture-recapture methods and the first estimates of abundance in over a decade.

Without an adequate understanding of the threats to a species as well as its demographics and social structure, the ability to inform stakeholders and future management decisions becomes somewhat limited. The results presented here give an important insight into the dynamics of Icelandic common minke whales and white-beaked dolphins providing valuable information, for the scientific community and for the local whale-watching operators. These findings also provide other researchers with new and improved methodologies that will be used for the same species in other areas.

Útdráttur

Rannsókn var gerð á stofnfræði og félagsgerð hvalategundanna hrefnu (*Balaenoptera acutorostrata*) og hnýðings (*Lagenorhynchus albirostris*). Báðar tegundirnar eru algengar í strandsjó við Ísland. Safn af ljósmyndum sem spannar 12 ár (2002–2014) var notað til greiningar. Ljósmyndirnar voru teknar á hvalaskoðunarbátum á Faxaflóa og Skjálfanda. Að auki fengust myndir frá samstarfsmönnum á Breiðafirði. Einnig voru strandaðir hnýðingar erlendis notaðir til að auka þekkingu á tilfellum þar sem hryggsúla hvalanna var afmynduð.

Fyrst var lagt mat á algengi, hlutfallslegan fjölda og breytingar á 28 gerðum af líkamseinkennum sem nýst gætu fyrir rannsóknir sem byggja á þekkjanlegum einstaklingum. Niðurstöður bentu til þess að áverkar á bakugga og líkama væru notadrýgstu sérkennin fyrir slíkar rannsóknir, líkt og greint hefur verið frá varðandi aðrar hvalategundir. Niðurstöðurnar benda einnig til þess að merki eftir hákarlabit geti verið nothæf hjá hrefnum og blettir á bakugga hjá hnýðingum þar eð þessi líkamseinkenni voru langvarandi. Þetta er ný uppgötvun sem mun leiða til þess að sýnastærðir aukast í hvers kyns rannsóknum sem byggjast á útlitseinkennum einstakra dýra.

Tilfelli afmyndunar hryggsúlu voru könnuð bæði hjá lifandi og dauðum hnýðingum víðs vegar að frá ströndum Evrópu. Niðurstöðurnar bentu til þess að afmyndun á hryggsúlu verði stundum hjá þessari tegund og sumir einstaklingar geti lifað með slíka afmyndun í nokkra mánuði. Herðakistilsmyndun á hrygg, kyphoscoliosis og lendasveigja voru greinileg hjá 5 hnýðingum. Tvö tilfelli greindust hjá lifandi hnýðingum og tvö hjá strönduðum einstaklingum þar sem hvalirnir virtust hafa fengið sjúkdóm sem hefur leitt til sýkingar og útvaxtar í beinum. Þetta virtist bein eða óbein afleiðing meiðsla, en ekki tókst að finna nákvæma orsök þessa. Þessar athuganir er góður upphafspunktur fyrir skilning á afmyndun hryggsúlna meðal hnýðinga í austanverðu Norður-Atlantshafi.

Greiningar voru gerðar á 823 ljósmyndum af hnýðingum, þeir flokkaðir í fullorðna, unga, kálfa og nýbura eftir stærð og litareinkennum hvers þroskastigs var lýst. Litareinkennin reynast góður mælikvarði til að meta þroskastig hvalanna. Bæta mætti þessa aðferð með því að athuga nýlega rekna hnýðinga á stærra svæði þar sem greina má bæði kyn og aldur með vissu.

Félagsgerð hnýðinga var könnuð með 489 athugunum á 35 þekktum einstaklingum sem sáust fimm eða fleiri daga. Niðurstöður bentu til þess að hnýðingar myndi ekki hópa á tilviljunarkenndan hátt frekar en aðrar höfrungategundir í hafinu. Mynstri félagstengsla er best lýst sem lauslegum kunningsskap.

Að lokum var stofnstærð og afkoma hrefnu og hnýðinga metin með aðferðum sem byggjast á greiningu einstaklinga, að teknu tilliti til ófullkominna greininga og varanleika á einkennum. Meðaltal stofnstærðarmats hnýðinga í Faxaflóa var 226 (169–301) og fyrir hrefnur 70 (53–93) á Faxaflóa og 18 (12–27) á Skjálfanda. Vegið aðhvarf sýndi marktæka fjölgun hrefnu á þessu 12 ára rannsóknatímabili. Einnig virtist afkoma vera stöðug yfir tímabilið fyrir bæði hnýðinga og hrefnur í flóunum báðum. Þetta er fyrsta stofnstærðarmat á þessum tveimur tegundum í meira en áratug þar sem notast er við aðferðir af þessu tagi.

Þær niðurstöður sem kynntar eru hér veita mikilvægan skilning á stofnbreytileika hrefnu og hnýðinga við Ísland. Þetta eru verðmætar upplýsingar fyrir vísindasamfélagið og hvalaskoðunarfyrirtæki á landinu og bjóða upp á endurbættar rannsóknaraðferðir fyrir tegundirnar á öðrum hafsvæðum.

To Oliver

..” but Nature, whose sweet rains fall on unjust and just alike, will have clefts in the rocks where I may hide, and secret valleys in whose silence I may weep undisturbed. She will hang the night with stars so that I may walk abroad in the darkness without stumbling, and send the wind over my footprints so that none may track me to my hurt: she will cleanse me in great waters, and with bitter herbs make me whole”. De Profundis – Oscar Wilde

List of publications

This thesis is based on the following papers. The papers will be referred in the text by their respective Romanic numerals.

- **Paper I:** Bertulli, C.B., Rasmussen, M.H. and Rosso, M. (2015). An assessment of the natural marking patterns used for photo-identification of common minke whales and white-beaked dolphins in Icelandic waters. *Journal of the Marine Association of the United Kingdom* 1-13. Doi:10.1017/S0025315415000284

- **Paper II:** Bertulli, C.B., Galatius, A., Kinze, C.C., Rasmussen, M.H., Deaville, R., Jepson, P., Vedder, E.J., Sánchez Contreras, G.J., Sabin, R.C. and A. Watson (2015) Vertebral column deformities in white-beaked dolphins from the eastern North Atlantic. *Diseases of Aquatic Organisms* 116:59-67.

- **Paper III:** Bertulli, C.B., Galatius, A., Kinze, C.C., Rasmussen, M.H., Keener, B. and Webber, M. Color patterns in white-beaked dolphins (*Lagenorhynchus albirostris*) from Iceland (submitted).

- **Paper IV:** Bertulli, C.B., Gero, S. and Rasmussen, M.H. Association patters of white-beaked dolphins *Lagenorhynchus albirostris* in Iceland: insights into social organization (manuscript in progress).

- **Paper V:** Bertulli, C.G., Guéry, L., McGinty, N., Suzuki, A., Brannan, N., Marques, T., Rasmussen, M.H. and Gimenez, O. Abundance and survival estimations of photographically identified humpback whales, white-beaked dolphins and common minke whales, in Icelandic coastal waters using capture recapture methods (submitted).

Other peer-reviewed papers published during the study period (not included in the thesis).

- **Bertulli, C.G.**, Tetley, M.J., Magnúsdóttir, E.E. and Rasmussen, M.H. 2015. Observations of movement and site fidelity of white-beaked dolphins (*Lagenorhynchus albirostris*) in Icelandic coastal waters using photo-identification. *Journal of Cetacean Research and Management,* 15:27-34.

- Christiansen, F., **Bertulli, C.G.**, Rasmussen, M.H. and Lusseau, D. (2015). Estimating cumulative exposure of wildlife to non-lethal disturbance using spatially explicit capture–recapture models. *The Journal of Wildlife Management*, doi: 10.1002/jwmg.836.

- **Bertulli, C.G.**, Leeney, R., Barreau, T. and Matassa, D.S. (2014). Can whale-watching and whaling co-exist? Tourist perceptions in Iceland. *Journal of Marine Biological Association of the United Kingdom*, doi:10.1017/S002531541400006X.

- **Bertulli, C.G.**, Rasmussen, M.H. and Tetley, M.J. (2013). Photo-identification rate and wide-scale movement of minke whales (*Balaenoptera acutorostrata*) in the coastal waters of Faxaflói and Skjálfandi Bays, Iceland. *Journal of Cetacean Research and Management*, 13(1):39-45.

- **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.

- Higby, L.K., Stafford, R. and **Bertulli, C.G.** (2012). An evaluation of ad-hoc presence only data in explaining patterns of distribution: cetacean sightings from whale-watching vessels. *International Journal of Zoology*, Article ID 428752, 5 pages. doi:10.1155/2012/428752.

Acknowledgements

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1 Introduction

1.1 The common minke whale

Common minke whales (*Balaenoptera acutorostrata* Lacépède 1804; hereafter 'minke whales') belong to the family *Balaenopteridae* whose members (knowns also as rorquals, Gill 1994) are the most numerous and varied among all baleen whales (Berta and Sumich 1999). Rorquals whales include humpback (*Megaptera novaeangliae*), blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis)*, Bryde's (*Balaenoptera edeni*), minke and Antarctic minke whale (*Balaenoptera bonaerensis*, Bannister 2002, Reeves *et al*. 2002). Minke whales are the smallest among all rorqual whales with adults ranging in size between 7.8 m (males) and 8.4 m (females; Víkingsson and Sigurjónsson 1998, Víkingsson 2004).

For a long time it was thought that only one species of minke whale existed. However, after studying the morphology and the genetics of this species, the existence of many geographically distinct subspecies was accepted (Christensen *et al*. 1990, Martinez and Pastene 1999, Born *et al*. 2003). In the northern hemisphere minke whales are divided into two subspecies, the North Atlantic minke whale (*Balaenoptera acutorostrata acutorostrata*) and the North Pacific minke whale (*Balaenoptera acutorostrata scammoni*) (Perrin *et al*. 2002).

A southern subspecies of the minke whale has been recognised: the Southern Hemisphere dwarf minke whale, genetically more closely related to the North Atlantic than to the North Pacific type (Perrin and Brownell 2002, Reeves *et al*. 2003).

The minke whale has a worldwide distribution, with sightings recorded in all oceans (Perrin *et al*. 2002). Minke whales are thought to follow the same general balaenopterid life history strategy of seasonal migration between summer feeding grounds and winter breeding grounds (Jonsgård 1966, Stewart and Leatherwood 1985, Christensen *et al*. 1990, Víkingsson and Heide-Jørgensen 2005).

1.1.1 The minke whale in Iceland: abundance, distribution and site fidelity

In Iceland, the minke whale (Fig. 1-1) is the most abundant baleen whale (Borchers *et al*. 2009, Pike *et al*. 2009a, Pike *et al*. 2009b, Hauksson *et al*. 2011, Pike *et al*. 2011). Details of the seasonal movements of this species to and from Icelandic waters are still unclear.

Figure 1-1 Minke whale photographed in Faxaflói Bay, off Reykjavík, Iceland, on August 11 2011. Photo credit: Chiara G. Bertulli/ University of Iceland.

Minke whales are more frequently sighted off the south-west coast of Iceland, in Faxaflói Bay, than off the north-east coast, in Skjálfandi Bay (Pike *et al.* 2009b). Minke whale sightings in Faxaflói generally increase around the end of March and peak during the months of July and August (Bertulli 2010, Salo 2004). However, at least from 2009 until the 2011 winter (November to March), whalewatching tours organised on the southwest coast found that not all individuals leave the area at the end of the summer (C. Bertulli, pers. obs.).

Despite indications of higher abundance in 2008, abundance of minke whales in the Icelandic continental shelf area has been considerably lower in recent years compared with 1987-2001. In fact, aerial surveys covering Icelandic coastal waters (inside the 600m depth contour) conducted to estimate minke whale abundance, as part of the North Atlantic Sighting Survey (NASS) (Gunnlaugsson *et al.* 1988, Pike *et al.* 2009b), yielded a population estimate of 43633 (95% CI:30148–63149) individuals in Icelandic shelf waters in 2001, 18262 individuals (95% CI: 7381–24919) in 2007, and 9588 (95% CI: 5274–14420) in 2009 (Pike *et al.* 2008, 2011; Borchers *et al.* 2009). In this species site fidelity was detected on the southwest coast (Faxaflói Bay off Reykjavík) and the northeast coast (Skjálfandi Bay off Húsavík), although the majority of individuals were re-sighted only once (Bertulli *et al.* 2013).

1.2 The white-beaked dolphin

The white-beaked dolphin (*Lagenorhynchus albirostris*) is endemic to the North Atlantic (Kinze *et al.* 1997, Northridge *et al.* 1997, Reeves *et al.* 1999) where it occurs mainly on the continental shelf and in semi-enclosed waters, notably the Gulf of St. Lawrence and the North Sea (Northridge *et al.* 1997, Kinze *et al.* 1997, Reeves *et al.* 1999).

The white-beaked dolphin belongs to the family *Delphinidae*. Five other dolphin species belong to the genus *Lagenorhynchus*; *i.e.*, *L. acutus*, *L.*

obliquidens, *L. cruciger*, *L. obscurus* and *L. australis.* However, the genus is acknowledged to be polyphyletic, with recent studies showing that the white-beaked dolphin is not closely related to most other species in the group (LeDuc *et al*. 1999, Harlin-Cognato and Honeycutt 2006, McGowen 2011).

1.2.1 The white-beaked dolphin in Iceland: abundance, distribution and site fidelity

White-beaked dolphins occur in Icelandic waters all year round (Magnúsdóttir 2007). On the southwest coast of Iceland, white-beaked dolphins are the second most frequently encountered species (Bertulli 2010) while in the northeast, they are the third most commonly sighted species (Cecchetti 2006).

In recent years (Fig. 1-2, Rasmussen and Miller 2002, Rasmussen *et al*. 2013) there are still large gaps in our knowledge with regard to abundance and habitat use.

Figure 1-2 White-beaked dolphins photographed in Faxaflói Bay, off Reykjavík, Iceland, on June 16, 2010. Photo credit: Chiara G. Bertulli/ University of Iceland.

The only available abundance estimate for white-beaked dolphins in Icelandic waters dates back to 2001 (NASS survey conducted in 1986–2001). An estimated number of 31,653 animals (95% CI:17,679–56,672) was reported (Pike *et al.* 2009a) although a minority of other dolphins species (*e.g.*, white-sided dolphins *Lagenorhynchus obliquidens*, and bottlenose dolphins *Tursiops truncatus*) were included in this dolphin category during the analysis.

Resightings of individuals suggest that white-beaked dolphins move long distances along the Icelandic coast and can be highly mobile and transient, possibly due to scarce and patchy resources (Bertulli *et al*. 2015). Tetley (2004) reported on a case of an individual re-sighted at a distance of 361 km in only 6 days. A male white-beaked dolphin, tagged with a satellite transmitter in 2006, was recorded covering large areas west of Iceland between the Westfjords and Faxaflói (Rasmussen *et al*. 2013). In 2004 an individually recognizable white-beaked dolphin was spotted both in Breiðafjörður and in Skjálfandi Bay (Tetley 2006) and in 2010 three individuals were seen both in Faxaflói and Skjálfandi (Bertulli 2010,

Bertulli *et al*. 2015), and One more individual was seen both in Breiðafjörður and Faxaflói (unpublished data).

In the Faxaflói Bay the white-beaked dolphin is primarily distributed, in an area approximately 10–12 nm west from Kollafjörður (Magnúsdóttir 2007, Bertulli 2010).

1.2.2 Association patterns in delphinids

The social structure is an important aspect of the biology of marine mammals and their place in the environment (Whitehead and Van Parijs 2010) and is also relevant for the management and conservation of species (Sutherland 1998, Whitehead *et al*. 2004, Lusseau 2005, Parra *et al*. 2011). Social structure is based primarily on how individuals interact with one another (Whitehead 2008a). It varies dynamically across different taxa and it influences population biology, behaviour, conservation, genetics, fitness, physiology, ecology and the transmission of diseases (Wilson 1975, Sutherland 1998, Altizer *et al*. 2003, Krutzen *et al*. 2003, Whitehead *et al*. 2004, Silk 2007, Archie *et al*. 2008). Studying social organization in cetaceans poses logistical and methodological challenges - whales and dolphins spend most of their time underwater (Mann 1999). Nevertheless such information has been collected from populations of killer whales (*Orcinus orca*) showing stable and long-lasting social bonds (Bigg 1982, Heimlich-Boran and Heimlich-Boran 1990, Bigg *et al*. 1990). In bottlenosed dolphins more temporary and changing associations within societies which vary regularly in composition have been observed (Würsig and Würsig 1977, Wells *et al*. 1987, Smolker *et al*. 1992, Connor *et al*. 2000). The differences in social structure among these two species are based on the presence or absence of preferred partners (Wells *et al*. 1987, Smolker *et al*. 1992) and they are affected by environmental parameters such as availability of food resources, predation risk (Wrangham and Rubenstein 1986) and by movement patterns (Bräger 2004). Social structure of oceanic species has been given very little attention in the literature (Pearson 2009, Mirimin *et al*. 2011) with no published records of association patterns in white-beaked dolphins at the time of writing.

1.2.3 Vertebral column deformities in delphinids

Axial deviations of the vertebral column have been reported in several delphinid species (*e.g*., Nutman and Kirk 1988, Wilson *et al*. 1997, Berghan and Visser 2000, Watson *et al*. 2004, Berrow and O'Brien 2006, Van Bressem *et al*. 2006, Bearzi *et al*. 2009, DeLynn *et al*. 2011, Robinson 2013). They can be classified as deformities arising from congenital causes (*e.g*., bottlenose dolphin with congenital scoliosis in DeLynn *et al*. 2011), or that have been acquired following trauma (*e.g.*, bottlenose dolphin with kyphosis due to conspecific aggression in Watson *et al.* 2004).

Such deformities are usually described within three categories (adapted from Noden and deLahunta 1985): (1) kyphosis – abnormal deviation of vertebral column in a sagittal plane when vertebrae are fixed to produce a curvature of the vertebral column with concavity on the ventral side; (2) lordosis – (opposite to kyphosis) abnormal deviation of vertebral column in a sagittal plane when vertebrae are fixed to produce a curvature of the vertebral column with concavity on the dorsal side; (3) scoliosis – abnormal deviation of vertebral column in a dorsal plane so the vertebrae are fixed to produce a lateral curvature, the possibilities are of either left or right-sided curvatures or both. These deformities are often present in varying combinations.

Although cases of kyphosis have been reported in white-beaked dolphins (Slijper 1936, van Assen 1975, Kompanje 1995), a review of vertebral column deformities in this species is not available.

1.3 Photo-identification studies

The Photo-ID technique, first developed in the 1970's (Würsig and Würsig 1977), allowed researchers to take photographs of natural markings occurring on whales and dolphins and to study them in their natural environment without disturbing them. Natural marks included the presence of missing part of the the dorsal fin on trailing and leading edges (Urian *et al*. 2014), scars and wounds (*e.g*., Lockyer and Morris 1990, Wilson *et al*. 1999), pigmentation patterns (*e.g*., Sears *et al*. 1990) or callosities (Payne 1986) on their bodies. Natural marks occurring on cetaceans can originate from parasites, predator attacks, interactions between conspecifics, anthropogenic activities and congenital conditions (*e.g*., Schaeff and Hamilton 1999, Rosso *et al*. 2011, Bertulli *et al*. 2012, Dwyer *et al*. 2014, McCordic *et al*. 2014). These markings are used for photoidentification techniques and capture-recapture (CR) models in order to estimate the population size and survival rates of cetacean species (*e.g*., Slooten *et al*. 1992, Durban *et al*. 2012, Nicholson *et al*. 2012). Markings are also used to investigate social interactions (*e.g*., Slooten *et al*. 1993, Gero *et al*. 2005, Parra *et al*. 2011), movement of individuals (*e.g.,* O'Brien *et al*. 2009, Bearzi *et al*. 2010, Robinson *et al*. 2012, Bertulli *et al*. 2013), to describe individual, ontogenetic and geographic variations in colouration patterns (*e.g*., Mitchell 1970, Tsutsui *et al*. 2001, Arnold *et al*. 2005, Rosso *et al*. 2008, Keener *et al*. 2011, Lodi and Borobia 2013) and to monitor the development of diseases in freeranging whales and dolphins (*e.g*., Van Bressem *et al*. 2003, Burdett Hart *et al*. 2010, Maldini *et al*. 2010).

Minke whales, although considered more difficult to study than some of the other baleen whale species such as the humpback, blue and right whales (*Eubalena glacialis*), have been successfully studied and photo-identified since 1980 (Dorsey 1983, Dorsey *et al*. 1990, Gill *et al*. 2000, Stern *et al*. 1990, Tscherter and Morris 2005, Anderwald 2009). The present study

follows several previous studies in which the successful identification of individuals was based upon dorsal fin edge marks (DEMs). The DEMs are the best traits for reliable reidentification of individuals. These nicks, notches or indentations can be identified even if only one side of the whale is photographed (Bertulli *et al*. 2013). The percentage of individuals (just over 50%) identified by distinctive large or small DEMs seen in a previous study off Iceland (Bertulli *et al*. 2013) is similar to values found in the San Juan Islands on the western coast of the USA (40.0%) by Dorsey *et al*. (1990) and around the Isle of Mull in Scotland (50%) by Gill *et al*. (2000). Body scars such as lesions, anthropogenic scars and marks supposedly left by parasites are thought to be less reliable than DEMs, although they have been used for minke whales in the San Juan Islands and Monterey Bay, California (Dorsey 1983, Dorsey *et al*. 1990, Stern *et al*. 1990) as a possible re-match mark for individuals (Baumgartner 2008, Anderwald 2009). Some individuals photographed in Iceland had the potential to be identified by their distinct dorsal fin shape (Bertulli *et al*. 2013) a trait that has been used in the Small Isles in Scotland (Anderwald 2009).

There are currently three existing photo-id catalogues of white-beaked dolphins; one including just 20 photo-identified individuals collected during the summer 2001-2010 in Aberdeenshire waters Scotland (Caroline Weir unpublished data), one curated by MARINELife, comprising 80 individuals collected between 2007 and 2012 in Lyme Bay and surrounding waters off south-west England (Brereton pers. comm.) and the third detailing 26 identifications collected between 2003 and 2012 along the Northumberland coast of England (by MARINELife, Kitching pers. comm.). In comparison to the other white-beaked dolphin catalogues, the photo-id results from Iceland (Bertulli *et al*. 2015) represent the largest existing photo-id catalogue of white-beaked dolphins in the North Atlantic.

The most successful identification criteria used for individual dolphins, have been proved to be notches which are promising mark types with low gain and loss rates (*e.g*., Gowans and Whitehead 2001, Auger-Méthé and Whitehead 2007, Auger-Méthé *et al*. 2010). In order to use body marks such as notches, an accurate analysis of their stability over time needs to be conducted in order to ascertain whether these marks could be used to discriminate between individuals (Auger-Méthé *et al*. 2010).

1.4 Study areas

This study (**Paper I, II, III, IV, V**) was conducted in Faxaflói Bay, southwest, Iceland and Skjálfandi Bay, northeast Iceland. A part of this study (**Paper III),** includes images provided by colleagues conducting fieldwork in Breiðafjörður (west, Iceland, Fig. 1-4).

1.4.1 Faxaflói Bay

Faxaflói Bay (Fig. 1-3) is a 50 x 105 km wide bay in southwestern Iceland, located between the peninsulas of Snæfellsnes and Reykjanes (64° 24'N23°00'W) (Stefansson and Guðmundsson 1978, Stefánsson *et al.* 1987). It is quite a shallow bay with depths of less than 20 meters mainly present in the eastern part of this bay. The majority (60%) of this bay has depths within 50 m with the remainder (~ 30%) within 50-100 m. The water inside the bay is saline and quite warm Atlantic water which originates from the North Atlantic Drift (Logmann *et al.* 2013); rivers are also flowing into the bay mainly from its eastern side (Stefánsson and Guðmundsson 1978).

Faxaflói Bay is also a known spawning, nursing and feeding ground for different species of fish such as sandeels (*Ammodytes* spp.) and cod (*Gadus morhua*; Grabowski *et al.* 2012, ICES 2005, Gunnarson *et al.* 2008) as well as zooplankton (*e.g.*, *Calanus finmarchicus*; Astthorsson and Gislason 1999).

A shallow bank, Syðra-Hraun, is located in the southern part of the bay (Gunnarsson *et al.* 2008). The bank has a rocky bottom, interrupted by gravel and sand (Thors 1977). In the sandy areas of Syðra-Hraun, sandeels are spawning and they are found in high numbers (Gunnarsson *et al.* 2008). These areas are important feeding grounds for both minke whales and white-beaked dolphins (Bertulli 2010).

1.4.2 Skjálfandi Bay

Skjálfandi Bay (Fig. 1-3) is a smaller bay, approximately 25 km wide at its mouth (Gíslason 2004), in northern Iceland (66°05'N; 17°33'W). The town of Húsavík (approximately 2,500 inhabitants) is located by the bay and serves as the main centre for activities within the bay (Einarsson 2009).

Skjálfandi Bay is characterized by shallow waters around the coast with the deepest point (240 m) on the northwest side, close to Flatey Island. The bay has steeper slopes in shallower areas, and is composed mainly of gravel/sand along the slope (Á. Björgvinsson pers. comm.). Sediments are transported into the bay by two freshwater rivers that enter on the south side of the bay and greatly influence its salinity (Gíslason 2004).

Sandeel, cod, capelin (*Mallotus villosus*) and herring (*Clupea harengus*) are the most common fish species found in the bay. Juvenile capelin migrate to the north coast of Iceland in the summer, following the currents, and are thought to represent the main food source for whales in the area (Magnússon and Pálsson 1991, Vilhjálmsson 1997, Hunt and Drinkwater 2005).
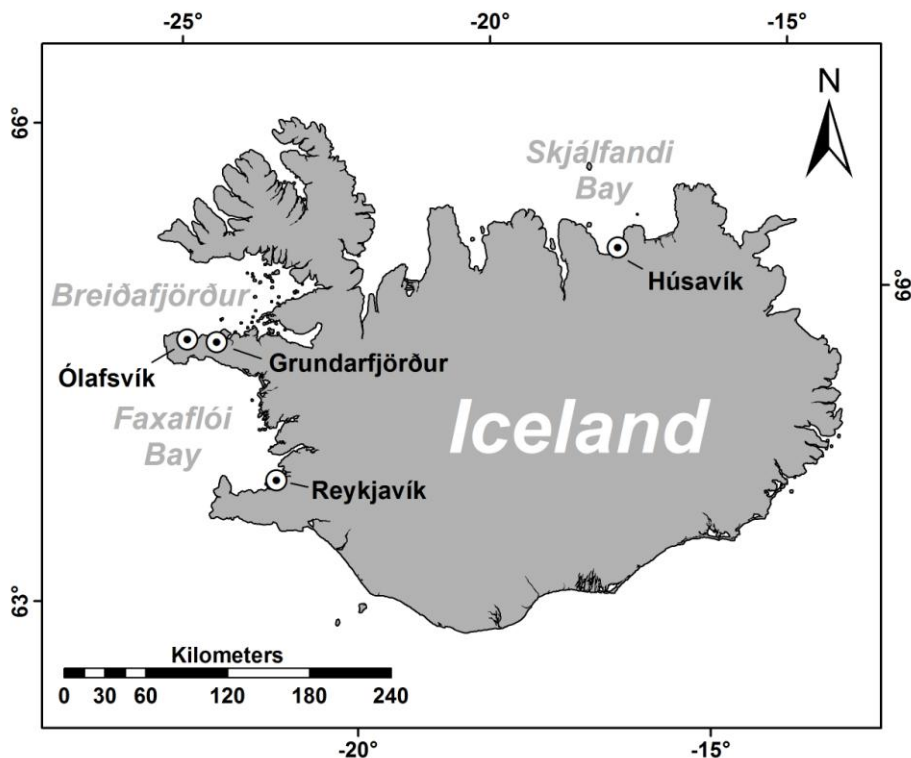
Figure 1-3 Map of Iceland showing locations of the study sites: Faxaflói Bay, Breiðafjörður, and Skjálfandi Bay. Map courtesy of M.J. Tetley.

1.5 Potential threats to Icelandic whales and dolphins

1.5.1 Marine boat traffic: whale-watching activities

The demand of people wanting to interact with wild animals has increased over the years (Duffus and Dearden 1990). Particular attention needs to be spent monitoring these activities since the exposure to human recreational activities can have long-term consequences for the targeted populations (Lusseau *et al*. 2006).

More than 100,000 tourists each year, 1 in 8 visitors, go whalewatching in Iceland (Hoyt 2001, O'Connor *et al*. 2009). Whale-watching has proven to be a business capable of producing both environmental and socio-economic benefits (Garrod and Fennell 2004, Cisneros-Montemayor *et al*. 2010, Parsons 2012). As whale-watching can also have negative effects on whales (Garrod and Fennell 2004, Parsons 2012), the careful management of this bourgeoning form of tourism is essential if it is to be sustainable. Whale-

watching operations do induce several short-term behavioural changes on cetaceans (summarized in Parsons 2012).

Over the last decade, there has been a considerable growth in whale-watching activities in Faxaflói and Skjálfandi Bay. Due to the coastal distribution and year-round presence of minke whales and white-beaked dolphins, these species are most frequently exposed to this tourism. Whale-watching activities distrupt feeding behaviour of minke whales in the Faxaflói Bay (Fig. 1-5, Christiansen *et al*. 2013) but do not seem to affect their survival (Christiansen *et al*. 2015).

Figure 1-5 Minke whale photographed in Faxaflói Bay, Reykjavík, on May 1 2011, while it was followed by a whale-watching boat in the area. Photo credit: Chiara G. Bertulli/ University of Iceland.

Whale-watching traffic was also found to affect white-beaked dolphin behaviour in Faxaflói Bay with an increasing number of whale-watching boats leading to a higher frequency of dolphin avoidance responses (Zezza 2014).

1.5.2   **Whaling and illegal hunting**

There are three forms of whaling as distinguished by the International Whaling Commission (IWC): those conducted for commercial, aboriginal subsistence and research purposes (Freeman 1993). Aboriginal subsistence whaling (ASW) was proposed in 1981 as whaling 'for purposes of local aboriginal consumption carried out by or on behalf of aboriginal, indigenous or native people who share strong community, familial, social and cultural ties related to a continuing traditional dependence on whaling and on the use of whales' (Donovan 1982), while commercial whaling is simply defined as any whaling, unrelated to research, which does not fit the aforementioned definition (Holt 1985). Several countries still practise either ASW or commercial whaling (Reeves 2002, WWF 2003, Corkeron 2007, Hoyt 2008), whilst the majority of industrial nations are opposed to whaling at a

commercial scale (Aron *et al*. 2000). Most of the whale stocks depleted in the past have yet to recover to pre-whaling levels (Brownell *et al*. 1989, Brownell 1995, Clapham *et al*. 1999, Aron *et al*. 2000, Clapham and Baker 2002, Alter *et al*. 2007). However, those who support whaling propose that sustainable harvests of some whale stocks are now possible (Aron *et al.* 2000), and some countries even argue that culling of marine mammals is necessary to reduce conflict with commercial fisheries and re-establish 'balance' in certain marine ecosystems (Lavigne 2003, Swartz and Pauly 2008).

In Iceland, whaling began around the 17th century when Basque hunters came to the region (Cunningham *et al*. 2012), with modern whaling starting around 1883 (Sigurjónsson 1988, Sigurjónsson and Gunnlaugsson 2006).

Whaling of minke whales was conducted on the Iceland continental shelf area in 1975 to 1985 and resumed in 2003 with scientific whaling and commercial whaling since 2007 (Marine Research Institute 2014). From 2008 to 2013 a total of 324 individuals were caught (Marine Research Institute 2014) in different bays around Iceland, with the majority of catches in the Faxaflói Bay.

Illegal catching of dolphins and porpoises also takes place in Iceland, as is evident by menus of some restaurant in downtown Reykjavík, or by the meat sold in the capital second-hand market (Kolaportið, Bertulli pers. commn.).

1.5.3 The Icelandic coastal marine ecosystem: recent changes

The abundance and spatial aggregation of whales and dolphins are regulated through bottom-up (environment and prey availablity) and top-down through direct (hunting) and indirect (shipping and fishing) effects (Greene and Pershing 2004, Benoit-Bird and McManus 2012). These often interact with each other to create unpredictable responses that due to their nature, are ultimately hard to forecast. Since 1996 gradual changes including increased temperature and salinity in the Icelandic marine ecosystem (Marine Research Institute 2008, 2012) were recorded in the north of Iceland, due to an increase flow of Atlantic water to this area, while similar increases were observed in the south (Malmberg and Valdimarsson 2003, Anon 2005, Jonsson and Valdimarsson 2005).

In the north, zooplankton biomass varied according to the water temperature, increasing during warmer years and decreasing during the cold ones (summarized in Astthorsson *et al*. 2007). The warm Atlantic water flowing to the north increased primary production and consequently creating more favourable conditions for the zooplankton (Astthorsson and Gislason 1998, Astthorsson and Vilhjalmsson 2002).

Increased water temperatures and salinity values also resulted in visible alterations in the distribution and abundance of many fish species (*e.g.*, Vilhjálmsson 1997, summarized in Björnsson and Pálsson 2004, Guðmundsdottir and Sigurðsson 2004, Astthorsson *et al*. 2007), some of which (*e.g.*, cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, herring *Clupea harengus*, mackerel *Scomber scombrus*, whiting *Merlangius merlangus*) are known to be part of the white-beaked dolphins' diet (van Bree and Nijssen 1964, Víkingsson and Ólafsdóttir 2004, Canning *et al*. 2008). Around the year 2005, the number of sand-eels (*Ammodytes marinus*), a favoured prey species of minke whales (Vikingsson *et al*. 2014), decreased dramatically in the southern and western Icelandic waters (Bogason and Lilliendahl 2009, Vikingsson *et al*. 2014). As a result many bird species have been affected in the area *e.g.*, puffin (*Fratercula arctica*), razorbill (*Alca torda*) and common guillemot (*Uria aalge*) (Bornaechea and Gardarsson 2006, Gardarsson 2006, Umhverfisráðuneytið 2011, Helgason 2012). The arctic tern (*Sterna paradisaea*) whose diet depends on the sand-eel, also experienced breeding failure in Iceland and recent studies conducted in the Snæfellsnes Peninsula recorded premature death in the young in some breeding areas between 2008 and 2011 (Vigfusdóttir *et al*. 2013). These species of seabirds often target the same food sources as the whale and dolphin species around Iceland and they are therefore a useful indicator of their food situation.

2 Aims

For management and conservation purposes of any population it is essential to gather information about demography, social structure, movement and distribution. Given the limited knowledge regarding these topics for the common minke whales and white-beaked dolphins occurring in Icelandic waters, this thesis attempts to redress this issue with the following objectives: (i) the identification of reliable natural occurring marks to produce unbiased abundance estimations of common minke whales and white-beaked dolphins in Iceland (**Paper I**), (ii) the occurrence of vertebral column deformities, their origins and their life implications in white-beaked dolphins (**Paper II**), (iii) the analysis of colour pattern components to use as tools to age white-beaked dolphins at sea (**Paper III**), (iv) the analysis of social structure in white-beaked dolphins to understand the biology of this species and its role in the Icelandic coastal marine environment (**Paper IV**), and (v) the estimation of abundance and survival in both common minke whales and white-beaked dolphins to manage and conserve both species (**Paper V**). While this work will undoubtedly improve on the current knowledge base for both species in Icelandic waters many of the findings from these papers will also be of interest to researchers that study these species in other areas. In particular, the methodologies outlined in **Paper I** and **III** where the newly developed procedures for identifying individuals can be used for populations of both species elsewhere.

2.1 Paper I

The aim of **Paper I** is to calculate abundance and prevalence of 28 mark types observed in minke whales and white-beaked dolphins photographed in Icelandic waters for 11 years (2002-2013) in order to identify reliable markings which could be suitable for capture-mark recapture studies. There is a current lack of knowledge regarding the basic demographic parameters of both species in Iceland and in other countries. In order to produce an unbiased estimation of both populations it is pivotal that the feasibility of individual identification by photo-identification is first ascertained.

Authors contribution. Provided data: CGB, MHR. Analysed the data: CGB, MR. Wrote the paper: CGB, MR (see 'List of Publications' for full list of co-author names).

2.2 Paper II

In **Paper II** we analysed five white-beaked dolphins with vertebral kyphosis, kyphoscoliosis or lordosis identified during a photo-identification survey of over 400 individuals (2002-2013) in Faxaflói and Skjálfandi Bays, Iceland. Three stranding reports from Denmark, The Netherlands and the United Kingdom were also analysed providing both external observation and post-mortem details of axial deviations of the vertebral column in this species. Although cases of kyphosis have been reported in white-beaked dolphins, a review of vertebral column deformities in this species is not available. Our data represent a starting point to understand vertebral column deformations and their implications in white-beaked dolphins from the eastern North Atlantic.

Authors contribution. Provided data: CGB, AG, CCK, MHR, RD, PJ, EJV, GJS, RS. Analysed the data: CGB, AG, RD, PJ, GKS, RCS, AW. Wrote the paper: CGB, AG, AW (see 'List of Publications' for full list of co-author names).

2.3 Paper III

In **Paper III** we use an extensive sample of photographs of free-ranging white-beaked dolphins collected in three areas around Iceland to describe the components that make up the color patterns and, where possible, ascribe them to ontogenetic variation, allowing us to discriminate between four age classes: adults, juveniles, calves and neonates. The body coloration of white-beaked dolphins is known to be highly variable and have natural complex pigmentation patterns. However, it has never been the topic of a formal study, only few studies have dealt with it, relying mainly on descriptions of dead specimens.

Authors contribution. Provided data: CGB, MHR. Analysed the data: CGB, AG, CCK, WK, MW. Wrote the paper: CGB, AG, CCK, WK, MW (see 'List of Publications' for full list of co-author names).

2.4 Paper IV

In **Paper IV** we quantitatively describe the association structure of white-beaked dolphins using photo-identification data collected from onboard whale-watching boats on the southwest (Faxaflói Bay) and northeast coasts (Skjálfandi Bay) of Iceland for 11 years (2002-2013). Specifically we tested for our observed patterns against a null of random associations, and further examined patterns of association over time and across habitat between the two bays. Specifically, we address the following two questions: 1) Are the association patterns of white-beaked dolphins non-random; 2) Do association patterns change over time. Our study allows us to expand as well the latitudinal range to study social structure of an oceanic species little attention has been given to and

no knowledge is available of in the literature. Addionally, tn the light of increased natural and anthropogenic disturbances in Icelandic waters our study on social structure it is important to assist management decisions.

Authors contribution. Provided data: CGB, MHR. Analysed the data: CGB, SG. Wrote the paper: CGB, SG (see 'List of Publications' for full list of co-author names).

2.5 Paper V

The aim for **Paper V** is to estimate abundance and survival while accounting for imperfect detection, using open capture-recapture models allowing the estimation of recapture probabilities to correct counts of individuals. These are the first estimates of abundance and survival of humpback whales, white-beaked dolphins and minke whales occurring in Icelandic coastal-shelf waters via an individual-based monitoring using capture-recapture methods, which can be used to inform and develop future sustainable conservation management practices in Iceland for these species.

Authors contribution. Provided data: CGB, MHR. Analysed the data: CGB, LG, NG, AS NB, TM, OG. Wrote the paper: CGB, LG, NG, OG, NB (see 'List of Publications' for full list of co-author names).

3 Material and Methods

3.1 Photo-identification

3.1.1 Photo-id classification system

The photo-identification technique was used in all papers (**Papers I-V**). ID-images of individual minke whales and white-beaked dolphins were collected from onboard whale-watching boats operating in Reykjavík, Húsavík (**Paper I**, **II**, **III**, **IV**), Grundafjörður and Ólafsvík (**Paper III**). Digital cameras were mainly equipped with 70–300 mm lenses (AF-S VR Nikkor lens f/4.5–5.6 IF-ED), with photographers placed on the roof of the wheelhouse (5–8 m above sea level in Faxaflói Bay, 2.7–4.5 m in Skjálfandi Bay) of each boat. When possible the vessel would be manoeuvred parallel to the whale or dolphin group encountered, allowing researchers to photograph both sides of each individual, including fin, dorsum, flanks and peduncle (Agler *et al*. 1990, Würsig and Jefferson 1990). In order to obtain an unbiased estimation of the number of animals with re-identifiable marks in each mark class, whales and dolphins were photographed without making any distinction of their mark status (Williams *et al.* 1993, Gormley *et al.* 2005, Currey *et al.* 2008).

Identification to individuals was undertaken using the classification system developed by Tscherter and Morris (2005). Initial sorting of acceptable quality photographs involved searching for the presence of indentations or 'nicks' on the dorsal fin, usually on the trailing edge; these are known as dorsal fin edge marks or DEMs. The position of these markings on the fin was further compared with the general fin shape and any additional body marks and scars to further reduce the likelihood that two different whales were identified as one. If no nicks were obvious from the photographs, individuals were classified using remaining distinctive fin shapes and body marks where available. However, in **Paper V**, considering minke whales and white-beaked dolphins, dorsal fin outline marks (*e.g.,* notch and distinct notch on trailing and leading edges as well as protruding piece of tissue) were used as the primary feature to identify all animals, while body marks as secondary features (see **Paper I** for the list of 'body marks'). In **Paper V** a third species was included in the analyses, the humpback whale, although it is not part of this study. Humpback whales were identified using pigmentation pattern on the ventral side of their flukes and/or presence of notches in the fluke edge. When a photo of a marked dorsal fin of a humpback whale was available it was used as a secondary feature as well.

Only photo-id images of adult individuals were analysed. All images were viewed using Adobe *Photoshop CS2/CS3* imaging software to identify unique permanent markings. Photos were matched in chronological order of collection allowing researchers to detect the evolution of skin marks over time making them usable secondary features to support DEMs and confirming the identity of different individuals. Additionally, during the matching process the quality-grading of the photo-ID images was limited to a single qualified person, and periodically graded by more than one person (C.B. or M.H.R.) throughout all the field seasons (*e.g.*, Sears *et al*. 1990).

3.1.2 Image quality rating (Q) and distinctiveness

Each photo-identification picture was assigned a quality rating (Q) from the lowest Q1 to the highest Q6, considering focus, exposure, angle and proportion of the frame occupied by the body of the animal. The Q-value of each image was independent of the marks visible on each individual. Only images rated Q $\geq$ 5 were considered for the analysis (Gowans and Whitehead 2001, Elwen *et al*. 2009, Rosso *et al*. 2011) in **Paper I**, **Paper III**, **Paper V**. In **Paper II** and **Paper IV** images rated Q$\geq$4 were used.

To assess the distinctiveness of each fin a grading system was used (scale from 1 to 4 with 1-*very distinctive*, 2-*distinctive*, 3-*slightly distinctive*, 4-*not distinctive*) and only *distinctive* and *very distinctive* fins were incorporated in the analysis (Zaeschmar *et al*. 2014).

3.2 Mark prevalence, abundance and change (gain and loss rates)

Mark prevalence, abundance and rate of change were calculated in **Paper I**. In order to describe mark types, photos in the database were analysed chronologically. Mark prevalence and abundance were assessed using 200 randomly selected images per species similar to Gowans and Whitehead (2001) and Auger-Méthé and Whitehead (2007). The size of each mark was calculated using ImageJ software (http://rsb.info.nih.gov/ij; *e.g.*, Fearnbach *et al*. 2011) and available estimates of dorsal height (G. Vikingsson and S.D. Halldórsson, Marine Research Institute, Reykjavík, unpublished data) and their shape, location and colour were also defined.

A total of 28 mark types were identified and then classified into nine categories based on morphological features:

(1) Fin outline: Marks occurring on the leading and trailing edge of the fin were included in this category. Notches, missing pieces of tissue (Würsig and Würsig 1977) were defined as <1 cm in size. Those >1 cm and located on the trailing edge were defined as distinct notches (Dufault and Whitehead 1993); if located on the leading edge they were defined as LE Distinct notches. Any protruding

piece of tissue (Auger-Méthé and Whitehead 2007) were also part of this category since they occurred along the outline of the fin.

(2) Body and fin pigmentation: This category included mottled pigmentation (Sears *et al.* 1990), speckling (Arnold *et al.* 2005, Krzyszczyk and Mann 2012), hypo-pigmentation comprising highly pigmented patches typical of immature white-beaked dolphins, and patches of pigment on the fin. White patches resemble those described by Webber (1987) in his work on dusky dolphins (*Lagenorhynchus obscurus*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) and described as 'a zone of light coloration found on the dorsal fin of some *Lagenorhynchus*'. Grey patches only appeared on the fin and/or base of the fin although without histological and microbiological examination it was not possible to know if they were phenotypical features like the white patches or infections.

(3) Patches: White or black marks, either circular or irregular (Auger-Méthé and Whitehead 2007, Gomez-Salazar *et al.* 2011) occurred on all observed body parts and were included in this category.

(4) Bite marks: Bite marks from cookie-cutter sharks (*Isistius* spp.) and lamprey (*Petromyzon marinus*) (Dorsey *et al.* 1990, Moore *et al.* 2003, Nichols and Tscherter 2011, Samarra *et al.* 2012) were included in this category.

(5) Linear marks: This category included fine scrapes (<1 cm) or medium scrapes (>1 cm) (Rosso *et al.* 2011). Scrape thickness was measured using ImageJ with a scale of reference determined previously in the study area for minke whales (28.8 cm fin height) and white-beaked dolphins (25.3 cm fin height; G. Vikingsson and S.D. Halldorsson, unpublished data). Tooth-rake produced by white-beaked dolphins (Ross and Wilson 1996, Haelters and Everhaarts 2011) and lamprey skidding bite marks (parallel light grey marks; Pike 1951, Bertulli *et al.* 2012, Ólafsdóttir and Shinn 2013) were also included in this category.

(6) Injuries: Large wounds from natural causes (*e.g.*, predator attacks) and from anthropogenic causes (*e.g.*, net entanglement and propeller but excluding notches on the leading edge of the fin) were included in this category following Bertulli *et al.* (2012). Measurements of tooth-rake mark interstices were within the range of 25 mm and 32 mm of killer whales (Craighead George *et al.* 1994, Visser 1999). This category also included major body indentations (Luksenburg 2014), amputation and fin deformation (Van Waerebeek *et al.* 2007, Higdon and Snow 2009, Mansur *et al.* 2012, 'dorsal fin bend', Luksenburg 2014).

(7) Cutaneous elevation: Skin elevations including blisters and nodules of un-known origin, as described by Bertulli *et al.* (2012), were part of this category.

(8) Infectious lesions: Tattoo like, wart-like and herpes-like lesions were included in this category based on their macroscopic appearance following Bertulli *et al*. (2012).

(9) Miscellaneous: This category was used to classify all other marks lacking diagnostic features of the previously described categories (Auger-Méthé and Whitehead 2007, Auger-Méthé *et al*. 2010).

For each mark type the following parameters were calculated: (1) the total number of occurrences for each mark n_i: i is the type of mark; (2) mark prevalence p_i: frequency of individuals with the i mark; (3) mark severity l_i: mean number of marks of i type only on individual with i occurrences; (4) relative portion r_i of each mark type to the total amount of marks R; and (5) mark abundance a_i: mean number of the i mark per individual. Standard deviations were calculated for mark severity and mark abundance.

To assess changes in mark abundance and prevalence, all individuals in a photograph (same body side) in at least 2 consecutive years were selected. If numerous images were available for each year the highest quality frame was randomly chosen (Gowans and Whitehead 2001). Photographs of sequential years were compared for presence or absence of each mark. Images containing marks below the water line and therefore not visible were not used in the analysis (Rosso *et al*. 2011). Individuals photographed during gapped bins of consecutive years (*e.g.*, 2008–2009, 2011–2013) were analysed separately and only for the consecutive year bins (Dufault and Whitehead 1995). To avoid pseudoreplication when both left and right sides were photographed during consecutive years, only the side with the highest number of marks was included in the analysis. Formulas to estimate gain and loss rates, 'whale years' as well as 'whale years of available marks' (WYAM) were calculated following Auger-Méthé and Whitehead (2007). Marks showing no losses over the duration of the study were considered reliable marks for analysis (Gowans and Whitehead 2001).

3.3 Capture mark-recapture

We used the year as a time unit (*e.g.*, Silva *et al*. 2009), whereby each year was made of 3 to 12 months. A standard Cormack-Jolly-Seber (CJS) open-population model (*e.g.*, Lebreton *et al*. 1992) was used with two different parameters, namely the recapture (p) and survival (ϕ) probabilities. We considered constant or time effects on these parameters, which resulted in four different models: (1) both ϕ and p were constant over time; (2) ϕ was constant and p was time-dependent; (3) ϕ was time-dependent and p was constant; and (4) both parameters were time-dependent. RMark (Laake 2013) was used to fit these CR models and estimate survival whilst accounting for detectability of less than one. Program U-CARE (Choquet *et al*. 2009) was used to assess the quality of fit of CJS models to the photo-id

CR data (Pradel *et al*. 2005). We detected a transient effect for both populations of minke whales (see Results section). Therefore a transient effect was incorporated in the models following Pradel *et al.* (1997). Specifically, we used a two-age class on survival and considered the age in CR analysis as the time passed since the animal was first sighted. Individuals that were sighted only once were part of the first age-class while all the others were part of the second (*e.g*., Ramp *et al*. 2006, Madon *et al*. 2012). The proportion of transients was estimated and the abundance estimate amended accordingly (Madon *et al*. 2012). To determine the most parsimonious model, the model with the lowest AICc score (Akaike Information Criterion corrected for small sample sizes; *e.g.,* Burnham and Anderson 2002) was selected. The selected model was then used in a bootstrap procedure (with 500 iterations) to calculate the mean and 95% confidence interval for population size (*e.g*., Cubaynes *et al*. 2010). To assess trends in abundance, we performed weighted linear regressions of the estimated parameters over time, using the inverse of the squared bootstrapped standard deviation as the model weights.

The minke whale data from both Faxaflói and Skjálfandi Bay were used; each bay was considered separately to calculate abundance. Two individual whales (DEM72 and DEM217) were identified in both bays but due to the low number of exchanges (DEM72 sighted four times; DEM217 sighted seven times), they could not be used to estimate movement probabilities in multisite CR models (*e.g*., Lebreton *et al*. 2009). These two individuals were sighted more often in the Faxaflói Bay area, and were thus considered as part of the Faxaflói Bay population. The white-beaked dolphins data from only Faxaflói Bay were used, since only three individual dolphins were resighted in Skjálfandi Bay between years. Similarly, the humpback whale data from only Skjálfandi Bay were used, since only five individuals were resighted in Faxaflói Bay between years.

3.4 Group composition

Group composition was calculated in **Paper III** and **IV**. The white-beaked dolphins photographed were assigned to one of four age classes (adult, juvenile, calf and neonate, see Results) by estimating the relative body length of each individual, and by association with conspecifics. Adult: length ranges from 2.4-3.1 m (Kinze 2002, Dong *et al.* 2006, Galatius *et al.* 2013). Juvenile: about 2/3 to 3/4 of adult length, swimming independently or associated with an adult (Bearzi *et al.* 1997, Karczmaski 1999, Mann and Smuts 1999). In a sample of white-beaked dolphins from the North Sea, sexual maturity was attained at total lengths between 2.30- 2.55 m in males and 2.32- 2.38 m in females (Galatius *et al.* 2013), while Jansen *et al.* (2010, 2013) reported that immature individuals from Dutch waters measured between 1.70- 2.10 m. Calf: less than 1/3 of adult length and consistently escorted by an adult (Shane

1990, Karczmarski 1999, Karczmarski *et al.* 1999, Constantine 2001). Neonate: less than 1/2 of an adult length, usually with fetal folds or pale fetal lines resulting from the folds (Bearzi *et al.* 1997, Stockin *et al.* 2009), predominantly swimming in echelon position by an adult's mid-lateral flank, Gubbins *et al.* 1999); reported to be 1.1-1.2 m in length (Fraser 1974, Collet and Duguy 1981, Kinze 2009).

In **Paper III** it was difficult in the field to distinguish between neonates and very young calves without fetal lines, so the latter were lumped into the neonate age class. Adult males are generally larger than females (Reeves *et al.* 1999, Kinze 2002, Galatius *et al.* 2013), however, their lengths overlap (*e.g.,* Galatius *et al*. (2013) reported total body lengths of 22 sexually mature males as 2.52-2.90 m, and 17 mature females as 2.42-2.65 m). Therefore, it was not possible to positively determine the sex of most dolphins photographed, and this study does not attempt to describe differences in coloration between males and females of any age class.

In **Paper IV** sub-adult dolphins could not be feasibly distinguished from juveniles because they were similar in appearance and behavior, so they were lumped with the juvenile age class. Calves and neonates were excluded from the analysis, juveniles were discarded unless they carried along any of the dorsal fin and/or injury marks mentioned above.

3.5 Association patterns: SOCPROG

Individuals were considered as part of the same group if they were no more than 100m away from each other and coordinating their movement and behavior (Wells *et al*. 1987, Shane 1990). When larger groups were encountered their size was estimated by counting each group separately (Bearzi *et al.* 1997). Best estimates of group size were estimated *in situ* by an observer during each sighting and when groups were large and animals were actively moving around the vessel, it was estimated by at least two people located in different places on board, and the obtained mean of the best estimate was recorded (*e.g*., Chilvers and Corkeron 2002).

Dolphins were considered associated when identified within the same group with a sampling interval of 1 day in order to account for potential demographic effects (Whitehead 2008a). Only dolphins that were sampled ≥5 times were including in analyses. All analyses were performed using SOCPROG 2.5 (Whitehead 2009).

The half-weight-index (HWI; Cairns and Schwager 1987, Ginsberg and Young 1992) was used to quantify the proportion of time a pair of dolphins spends associating (Whitehead 2008a). It was chosen as Cairns and Schwager (1987) suggested it accounts for bias when a pair is more likely to be observed separate than when together, as is often the case in photo-identification studies. However, considering that estimated relationship

measures might contain an error because in real life the time a pair spends together might be different (Whitehead 2008b), we wanted to test how accurate it was to use these estimated measure to build up models and social representations. Thus, the correlation coefficient (r) and social differentiation (S) were calculated using formulas and Poisson and likelihood approximation methods proposed by Whitehead (2008a, b). r indicates the accuracy of association measures used to construct social structures with models and S indicates the variability of a social system, from homogenous to very well differentiated (Whitehead 2008a).

The null hypothesis stated that there were no preferred associates or avoidances given the number of groups in which each animal was seen during each sampling period (Chilvers and Corkeron 2002, Whitehead 2008a). This hypothesis was tested using Whitehead's (2009) variation of the permutation test by Bejder *et al*. (1998). Association data were permuted 25000 times until *p* value stabilized.

The cophenetic correlation coefficient (CCC) was estimated, with values ≥ 0.8, generally indicating there are clustering in the population and that the created dendrograms accurately represented the complexity of the white-beaked dolphin social structure (Whitehead 2008a). Modularity was assessed with values ≥0.3 suggesting the population is well divided (Newman 2004). Coefficients of associations were classified according to Quintana-Rizzo and Wells (2001) as low 0.01–0.20, medium–low 0.21–0.40, medium 0.41–0.60, medium–high 0.61–0.80 and high 0.81–1.

In order to study how a dyadic association changes over time, lagged association rates (LAR) were estimated (Whitehead 1995) using individuals associating ≥2 times. Additionally, to interpret them null association rates were used, representing the expected LAR values if animals associated randomly (*e.g*., no preferred associates) (Whitehead 2008a, 2009). Lagged and null association rates were standardized (SLAR, Whitehead 1995) since during this study it was not possible to properly photo-identified all individuals in each encountered group (Gowans *et al*. 2001, Karczmarski *et al*. 2005). Precision of the estimated lagged association rates was performed using the temporal jackknife procedure (Sokal and Rohlf 1995) implemented in SOCPROG 2.5 and standard errors were created (Efron and Gong 1983) similarly to previous studies on cetaceans (*e.g*., Gowans *et al*. 2001, Karczmarski *et al*. 2005, Wiszniewski *et al*. 2009). We fit models to the observed SLARs (Whitehead 1995, Whitehead 2008a) using maximum likelihood technique including 1) constant companions, who are permanently together, (2) casual acquaintances, who associate for some time, disassociate, and possibly re-associate later, (3) constant companions and casual acquaintances and (4) two levels of casual acquaintances who associate and disassociate at two different time scales. The best model fit model was selected by the lowest quasi Akaike Information Criterion (QAIC) value

(Burnham and Anderson 1998; Whitehead 2007). The difference in QAIC values (ΔQAIC) between the best-fit model and the others indicate the level of support: strong support (0-2), some support (4-7) and no support (>10) (Burnham and Andersen 2002).

3.6 Vertebral column deformities

Data and photographs of vertebral column deformities in free-ranging white-beaked dolphins were collected during an 11-year photo-identification study (2002-2013) in **Paper II**. Such deformities are usually described within three categories (adapted from Noden and deLahunta 1985): (1) kyphosis – abnormal deviation of vertebral column in a sagittal plane when vertebrae are fixed to produce a curvature of the vertebral column with concavity on the ventral side; (2) lordosis – (opposite to kyphosis) abnormal deviation of vertebral column in a sagittal plane when vertebrae are fixed to produce a curvature of the vertebral column with concavity on the dorsal side; (3) scoliosis – abnormal deviation of vertebral column in a dorsal plane so the vertebrae are fixed to produce a lateral curvature, possibilities of left and/or right-sided curvatures. These deformities are often present in varying combinations.

Stranded cases from outside Icelandic waters were collected through the e-mailing list MARMAM (Marine Mammals Research and Conservation Discussion) in 2013. Images and post-mortem report information were shared by the UK Cetacean Strandings Investigation Programme at the Zoological Society of London (Case # 6) and the Seal Rehabilitation and Research Centre in Pieterburen (Case # 7), The Netherlands. A full necropsy was not conducted for Case # 8, although the specimen was measured and examined at the Fisheries and Maritime Museum in Esbjerg, Denmark, by Thyge Jensen (1949-2014) and Svend Tougaard. The vertebrae from Case # 6 were assembled by the Natural History Museum in London after being prepared by manual de-fleshing followed by non-chemical, cold water maceration. Standard anatomical nomenclature and directional terminology was used based on *Nomina Anatomica Veterinaria* (International Committee on Veterinary Gross Anatomical Nomenclature 2012).

4 Results and discussion

4.1 Paper I

In **Paper I** a total of 28 mark types wered described which were contained in a randomly selected sample of images for minke whales and white-beaked dolphins.

In the minke whale subsample a total of 24 mark types were distinguished and categorized into nine different mark categories. From the subsample of 200 minke whale images 21 mark types (Fig. 4-1) were considered. The most prevalent marks encountered were cookie-cutter bite, notch and lamprey bite and the most abundant marks were herpes-like and blisters. Herpes-like lesions and black marks were the most severe mark types. In the white-beaked dolphin subsample a total of 22 mark types were distinguished and categorized into nine different mark categories . From the subsample of 200 white-beaked dolphins images, the same amount of mark types were considered (Fig. 4-2). The most prevalent marks were notch, fin patches and fine scrape and the most abundant were black marks and fine scrapes. Blister lesions and tattoolike were the most severe mark types.

Figure 4-1 The twenty-four mark types described in minke whales: (a) ans—antagonistic scars; (b) hl—herpes-like; (c) n—notch, ln—leading notch, bm—black marks; (d) dn—distinct notch, m—mottling; (e) wm—white marks, lb—lamprey bite; (f) w— wound; (g) a—amputation, sk—skidding; (h) cb—cookie bite, m—miscellaneous; (i) pp—protruding piece; (j) bi—back indentation; (k) ldn—leading distinct notch; (l) fp—fin patches, fs—fine scrape; (m) wl—wart-like; (n) d—deformation, b—blisters, (o) as—anthropogenic scars; (p) ms—medium scrape. (Page 42).

Figure 4-2 The twenty-two mark types described in white-beaked dolphins: (a) n—notch, bi—back indentation; (b) a—amputation, fp—fin patches; (c) fs—fine scrape, tl—tattoo-like; tr—tooth-rake; (d) pp—protruding piece; (e) sk—skidding, bm—black mark; (f) d—deformation; (g) dn—distinct notch, ln—leading notch; (h) w—wound; (i) lb—lamprey bite-like; (j) b—blisters, ans—antagonistic scars; (k) wm—white mark; (l) m—miscellaneous; (m) as—anthropogenic scars; (n) hp—hypo-pigmentation, sp—speckling. (Page 43).
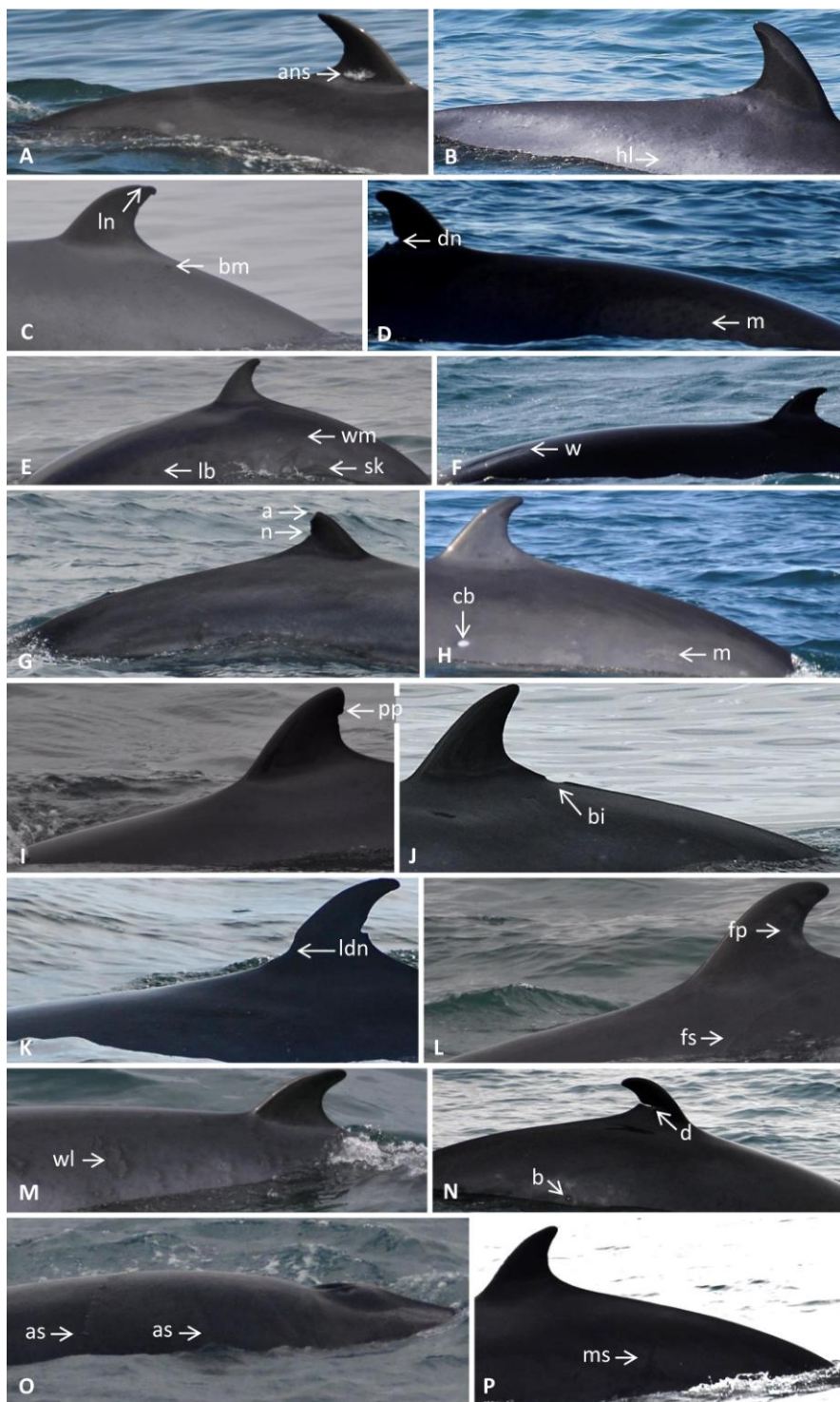
For minke whales, seven mark types demonstrated no loss during a total of 110 whale years of available marks: notch, leading notch, distinct notch, protruding piece of tissue, wound, back indentation and amputation. However, the marks with higher WYAM were notch, leading notch and distinct notch. Ten mark types showed gains with time. For white-beaked dolphins thirteen mark types demonstrated a loss rate of zero: notch, leading notch, distinct notch, protruding piece of tissue, hypopigmentation, white mark, lamprey bite, wound, antagonistic and anthropogenic marks, back indentation, amputation and tattoo-like lesion. Marks with the highest WYAM were notch, distinct notch and amputation. Three individuals showed gains of notches over time, with one notch being acquired from one year to the next (Fig. 4-3).
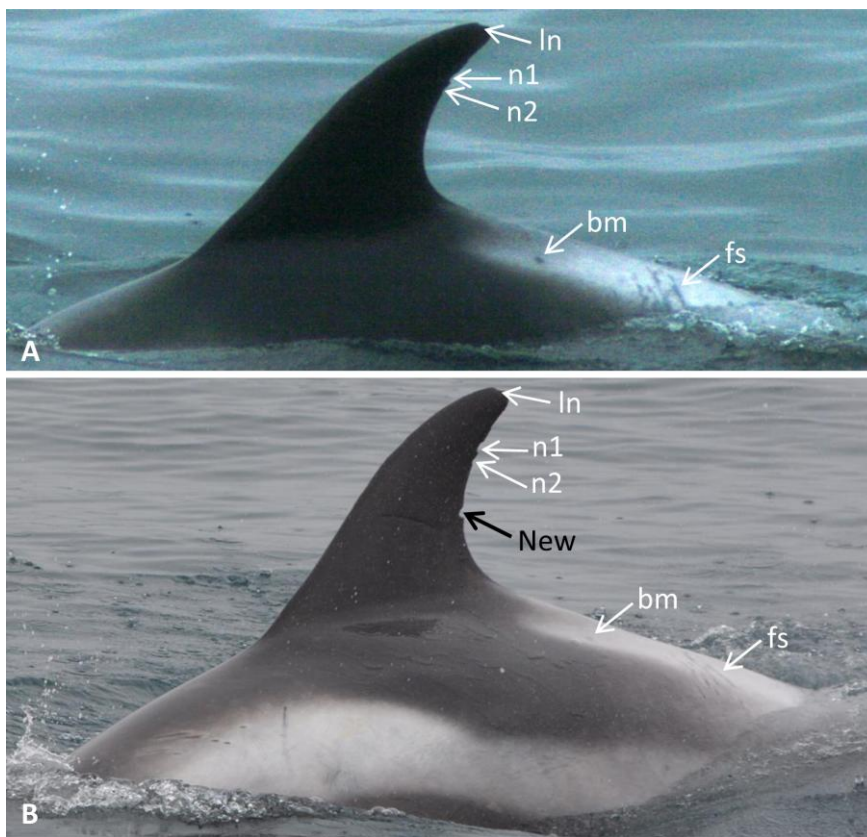
Figure 4-3 White-beaked dolphin DEM79 photographed in 2009 and in 2010: (a) - (nl) nick on leading edge, (n1) (n2) nicks on trailing edge, (bm) black mark, (fs) fine scrapes; (b) - same marks visible with the addition of a new nick mid posterior on the trailing edge (New).

Our findings confirm that fin and injury marks are among the most accurate features to use for capture-recapture studies as noted for other cetacean species (Lockyer and Morris 1990, Scott *et al*. 1990, Wilson *et al*. 1999, Auger-Méthé and Whitehead 2007). We also suggest including cookie-

cutter shark bites for minke whales and fin patches for white-beaked dolphins due to their low loss rate.

The use of cookie-cutter bite marks in minke whale photoidentification studies may increase the amount of identified individuals by ~ 28%. The use of fin patches in photo-identification studies for white-beaked dolphins could increase the amount of identified individuals ~ 5% rate. These two mark types were amongst the most prevalent in both species, so their addition will be pivotal in increasing the power of analysis conducted using photo-identification data obtaining more accurate population estimates.

4.2 Paper II

Cases of white-beaked dolphins with axial deviations suggestive of vertebral column deformities were observed from 2002 to 2013, as presented in **Paper II**, as well as three stranded cases from outside of Iceland (Denmark, The Netherlands and the United Kingdom).
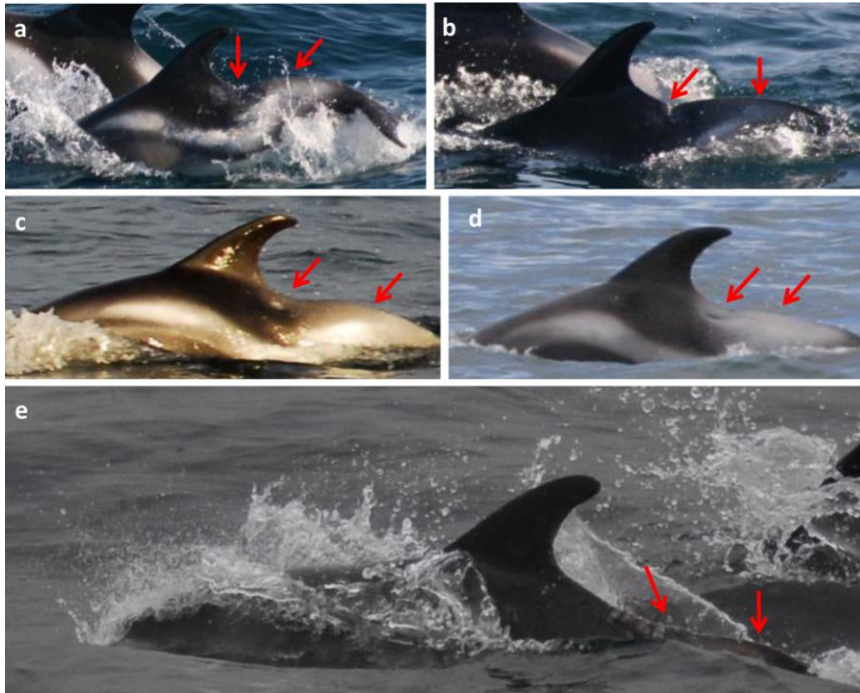
Figure 4-4 Six cases of kyphosis and lordosis collected in Icelandic waters: (a,b) juvenile white-beaked dolphins with lordosis followed by kyphosis photographed in Skjálfandi Bay, Cases # 1 and 2, photo credits: Zoe Burr/ University of Iceland; (c) juvenile white-beaked dolphin with lordosis followed by kyphosis photographed in Faxaflói Bay, Case # 3, photo credit: Meggie Hudspith/University of Iceland; (d) adult white-beaked dolphin with kyphosis photographed in Skjálfandi Bay, Case # 4, photo credit: Húsavík Whale Museum; (e) juvenile white-beaked dolphin with lordosis followed by kyphosis photographed in Faxaflói Bay, Case # 5, photo credit: Sarah Lawrence/ University of Iceland.

Two of the free-ranging cases (Fig. 4-4a,b) and two of the stranded specimens (Fig. 4-5) appeared to have an acquired disease, either as direct result of trauma, or indirect from trauma/wound and subsequent infection and bony proliferation, although we were unable to specifically identify the causes.
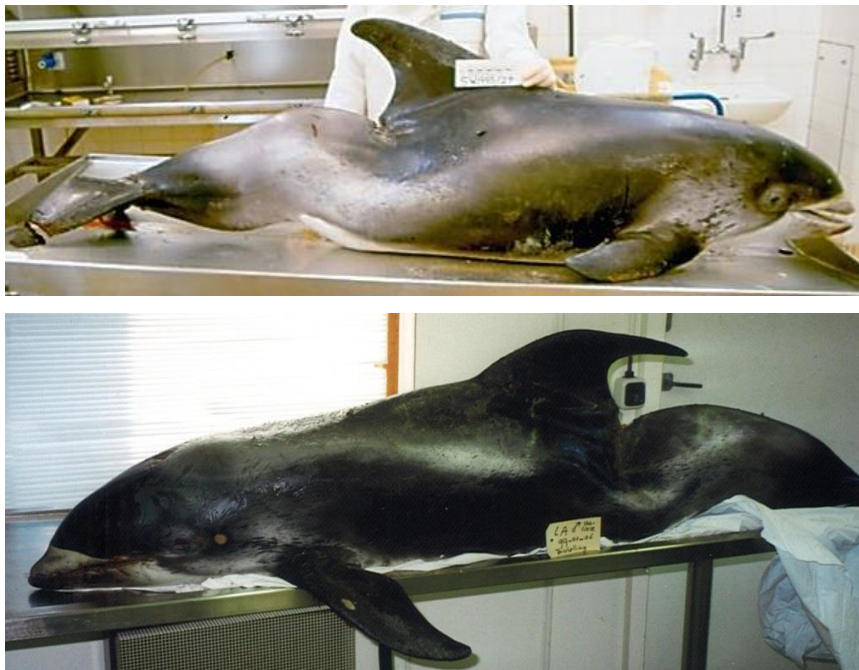
Figure 4-5 (a) Juvenile male white-beaked dolphin (TBL 173 cm) with kyphoscoliosis stranded on England coast, Case # 6, with detail of wound at caudal base of fin; (b) Juvenile male white-beaked dolphin (TBL 184 cm) with kyphosis stranded on the Dutch island of Terschelling, Case # 7, with wound caudal to the fin and visible kyphotic hump.

Our results indicate that vertebral column deformities occur in white-beaked dolphins and that some individuals may live with such anomalies for several months. Our data represent a starting point to understand vertebral column deformations and their implications in white-beaked dolphins from the eastern North Atlantic. We recommend for future necropsy cases to conduct macro - and microscopic evaluation of muscle from both sides of the deformed region, in order to assess chronic or acute conditions related to the vertebral deformations and cause of death.

4.3 Paper III

In **Paper III** we analyzed pigmentation characteristics of white-beaked dolphins and describe 25 color pattern components and their ontogenetic variation, allowing us to discriminate between four stage classes: adults,

juveniles, calves and neonates (Fig. 4-6). For the 25 components described, we used seven terms previously applied to white-beaked dolphins and 12 previously applied to other dolphin species. In addition, we proposed six new terms: mouth band, post-ocular crescent, semi-circular head blaze, peduncular ridge stripe, lateral patch and umbilical patch. We used 408 images in the first dataset capturing 571 individual white-beaked dolphins that showed one or more color pattern components. We assigned them to the following age classes: 437 adults, 109 juveniles, 14 calves, and 11 neonates. Quantities presented for the occurrence frequencies of the 25 color pattern components are based on these 571 individuals, with the exception of the fin patch, for which we used the photo-identified second dataset of 415 marked dolphins.

Figure 4-6 Age classes: adult, juvenile, calf and neonate. Photo credits: C.G. Bertulli/University of Iceland (A) and C. Schmidt/Húsavík Whale Museum (B).

Our results showed that adults were identified by any of several diagnostic features including fully-developed blowhole chevron, completely filled-in post-ocular crescent, continuous dorsal flank blaze, flank patch, peduncular saddle, dark gray abdominal field, beak blaze of dark gray color with white or pink tip, and flipper stripe as a demarcation line between the white throat chevron and the gray post-ocular crescent. One surprising result was that, despite its common name, only 7.1% of adult white-beaked dolphins had a

pure white beak—a feature much more frequently seen in immature animals. Juveniles and calves were identified by the presence of any of three color components: speckling, semi-circular head blaze and lateral patch. Juveniles were unique in having the semi-circular head blaze and light gray beak blaze, while only calves showed a gray beak blaze and a yellow film on the abdominal field. Neonates were distinguished by yellow-tinging on the beak blaze, helmet, and on the small, dull-colored precursors of the thoracic field, lateral patch and post-ocular crescent, as well as by the usual presence of fetal folds.

This study is the first to review the complex color patterns in the white-beaked dolphin, distinguish stage classes (adults, juveniles, calves and neonates) by suites of color pattern components, and describe their ontogenetic variation. Future studies utilizing stranded specimens of known age and maturity would allow confirmation of these findings, and possibly reveal new age class-specific components, as well as sexually dimorphic differences not discussed in this study. Geographical variation could be investigated by comparing large image datasets and stranded animals from different parts of the North Atlantic.

4.4 Paper IV

Photo-identification images collected over a 11-year study (2002-2013) were used to describe the social organization and patterns of association of white-beaked dolphins for the first time in **Paper IV**. A total of 489 white-beaked dolphins were photo-identified, 292 solely photographed in Faxaflói, 173 in Skjálfandi. There were also 24 'core users' (*i.e.*, frequent users, Tezanos-Pinto 2009), individuals photographed in both bays, moving between them during the study period. A total of 1119 dolphin groups (n=610 in Faxaflói, n=509 in Skjálfandi) were encountered. Photo-id images quality rated Q4 or higher were taken for 26% (n=297) of these groups. A total of 22% (n=64) of these groups had 50% or more individuals identified within each group.

Group size estimates varied between one and 300 individuals in Faxaflói with an overall mean group size of 7.9 (SD=16.23, n=610) and with the majority (87%) of the groups observed consisted of ≤10 dolphins. In Skjálfandi, estimates varied between one and 150 individuals with an overall mean group size of 10.0 (SD=16.43, n=509) and with groups of ≤10 dolphins observed most frequently (79%). With regard to group composition, all groups included adults and only 12% included immatures in Faxaflói and 28% in Skjálfandi.

A total of 35 adult white-beaked dolphins were sighted five or more times and they were used to analyze the association patterns. The estimate of social differentiation, CV of true association indices, (S±SE=1.830±0.369)

close to one indicated that the associations were very varied. The estimate of correlation between true and estimated association indices using Poisson approximation was equal to 0.692 (SE=0.033, SE's from bootstrap with 1000 replications). With the likelihood method a value of 0.3 was obtained. Data on associations were randomly permuted 25000 times when p-values stabilized and the resulting SD (observed mean=0.1, random mean=0.07, p=1.000) values of the real data were significantly higher compared to the random proving associations among individuals are not random but preferred and/or avoided during the 11 years of study. Additionally, the SDs of non-zero association indices were higher in the observed data (SDo=0.13503) compared to the random data (SDr=0.05158), indicating companionships that persist across sampling periods. The proportion of non-zero association indices was higher for random data (0.24474) indicating the presence of avoidance among some individuals.

The cophenetic correlation coefficient (CCC) of the average-linkage clustering dendrogram was estimated to be 0.846 indicating that it represents well the association data of white-beaked dolphins in the present study. Maximum modularity (type 1; when controlling for gregariousness, Q=0.36639) with an association index of 0.061 generated seven different clusters (mean±SD=5.0±2.38 individuals, range=2-9) (Fig. 4-7). Additionally, the overall association index resulting from HWI had a mean of 0.39 (SD=0.21) and the coefficients of associations (COA) were for the majority low (37%, n=13), followed by moderate-low and moderate (each 23%, n=8) and moderate-high (17%, n=6). There was one dyad with the highest COA (=0.8) made of 'core-users' DEM199-DEM154.
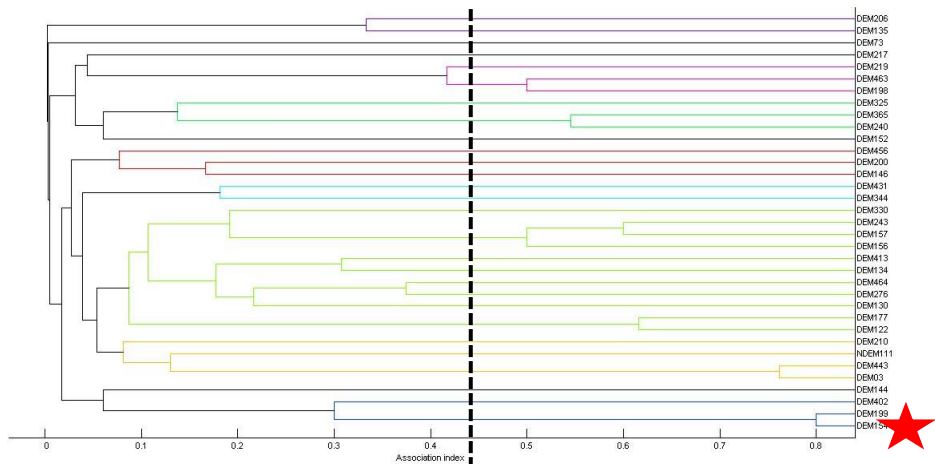
Figure 4-7 Dendrogram of the hierarchical cluster analysis using average linkage for 35 photo-identified individual white-beaked dolphins off Iceland. The star symbol indicates the strongest association. CCC=0.85. The dashed line indicates cluster division occurs at AI = 0.39 (modularity = 0.366).

The best model which represented the association patterns of our data were of 'casual acquaintances' (Fig. 4-8). The lagged association rate showed a rapid decrease after 10 days, a final drop at around 450 days steadily declining and falling below the null association rate on two occasions, the first one at around 1120 days (~ 3 years). The error bar dropped below the null association rate at around 1000 days. The association rate persisted above the null rate for at least 1200 days (~ 3 years) as shown by the standardized lagged association rate (SLAR, Fig. 4-8). 'Two level of casual acquaintances' (SLAR4, see **Paper IV**, Table 2) shows a very similar curve (red line, Fig. 4-8) and a ΔQAIC of 2.62 suggesting some support.
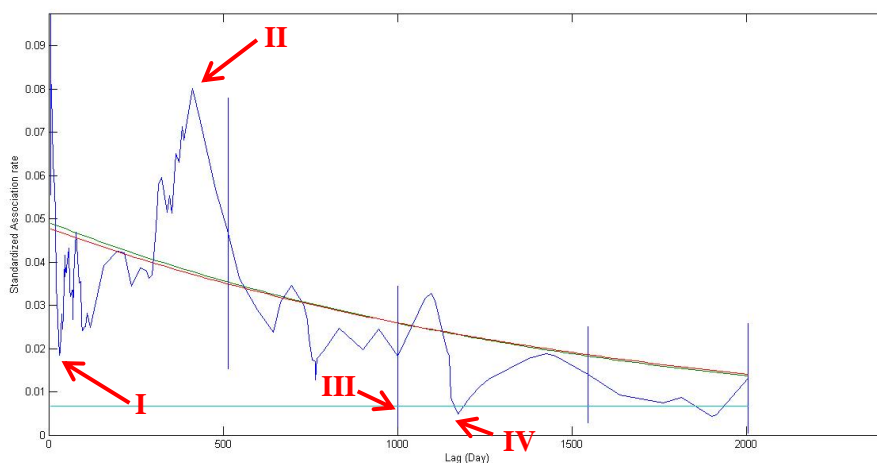
Figure 4-8 SLARs for white-beaked dolphins sighted off Iceland with a moving average of 400 associations. Vertical bars indicate approximate standard errors calculating using the temporal jackknife method. The best fitting models were 'casual acquaintances' (green line) and 'two levels of casual acquaintances' (red line). Light blue line is The null association rate (violet line) is the lagged association rate expected if individuals were associating at random. Red arrows indicate: (I) first drop ~10 days, (II) peak ~450 days, (III) error bar drops below null ~1000 days and (IV) data drop below null ~1200 days.

The observed mean group size of white-beaked dolphins recorded during this study were similar to those found in other coastal white-beaked dolphin populations (Weir and Stockin 2001, Canning *et al*. 2008, Weir *et al*. 2008, Weir *et al*. 2009, Fall and Mette-Skern-Mauritzen 2014). The estimates recorded in Faxaflói (mean±SD; mean=7.9 ± 16.23) were comparable with mean group sizes in Scotland (mean=7.7; Weir and Stockin 2001, Weir *et al*. 2008, Weir *et al*. 2009) and the Barents Sea (mean=8.0; Fall and Mette-Skern-Mauritzen 2014), while the Skjálfandi estimates (mean=10.0 ± 16.43) were similar to those recorded in the Gulf of St. Lawrence and Halifax (mean=8.6, Kinglsey and Reeves 1998, mean=9.1, Simard *et al*. 2006) but larger than the others. Overall, in this study larger group sizes were recorded

compared to those collected in Iceland in previous years (e.g., mean group size 6.3 95% CI 5.6-7.1, Pike *et al*. 2009a) and compared to strandings data from the UK and Ireland (mean=4.2, SD=2.77; Canning *et al*. 2008). Previous studies suggested that cetacean group size varies according to predation pressure, ocean climate variation, food availability, interspecific competition and habitat type (*e.g.*, Connor *et al*. 1998, Ersts and Rosembaum 2003, Lusseau *et al*. 2004, Gowans *et al*. 2007, Parra *et al*. 2011). In Iceland small (7.9 in Faxaflói) to moderate group sizes (10 in Skjálfandi, Acevedo-Gutiérrez 2002) could be a reflection of a low predation risk and patchy food resources. In Icelandic waters, predators to white-beaked dolphins are killer whales which are sighted few times every year crossing the whale-watching grounds in Faxaflói and Skjálfandi. Killer whale tooth-rake marks on white-beaked dolphins were only photographed on 5 individuals (Bertulli *et al*., 2012, 2015). The distribution and abundance of many fish species was altered after 1995 by changes in temperature and salinity in the Icelandic marine ecosystem, on the south, west and north coasts (Vikingsson *et al*. 2015). Some of these fish species (*e.g.*, Vilhjálmsson 1997, summarized in Björnsson and Pálsson 2004, Guðmundsdottir and Sigurðsson 2004, Astthorsson *et al*. 2007) are known to be part of the white-beaked dolphins' diet (van Bree and Nijssen 1964, Víkingsson and Ólafsdóttir 2004, Canning *et al*. 2008). Similarly to white-beaked dolphins, dusky dolphins (*Lagenorhynchus obscurus*) in Admiralty Bay, New Zealand, have similar mean group size (7.9±6.0, Pearson 2009) to the Faxaflói individuals and low occurrence of predators. It was suggested prey availability and female estrous are the main factors influencing grouping for this species.

Results indicated white-beaked dolphins in Icelandic coastal waters live in a differentiated society associating non-randomly with one another like other dolphin species (*e.g.*, Parra *et al*. 2011, Augusto *et al*. 2012, Louis *et al*. 2015). Similarly to oceanic delphinids (*e.g.*, dusky dolphins, Commerson's dolphins, spinner dolphins, common dolphins *Delphinus* sp., Atlantic bottlenose dolphins) they live in fission-fusion societies, have few preferred associations and have mainly weak bonds with one another (Bruno *et al*. 2004, Markowitz 2004, Karczmarski *et al*. 2005, Viricel *et al*. 2008, Pearson 2008, Coscarella *et al*. 2011, Augusto *et al.* 2012, Elliser and Herzing 2014, Martinho *et al*. 2014, Stockin *et al*. 2014).

Avoidance among some individuals was detected in this study. With information on sex, maturity and genetic structure of the identified individuals, it might be possible to further understand this finding.

In this study, white-beaked dolphins in Icelandic waters showed coefficient of associations which were highly fluid and with few long-term bonds (weak associations) similarly to other dolphin communities (Rogan *et al*. 2000, Quintana-Rizzo and Wells 2001, Chilvers and Corkeron 2002, Keith *et al*.

2002, Mourão 2006, Coscarella *et al*. 2011, Louis *et al*. 2015). Coefficients of association can be influenced by population size, with the smaller the population the larger the coefficient, but also by grouping patterns (Whitehead 2008a). In Icelandic coastal waters white-beaked dolphin are part of a large population (>30,000 individuals, Pike *et al*. 2009) and they are forming small to moderate sized groups, so the type of associations they establish are the results of both population and group size.

The association patters of white-beaked dolphins inhabiting the coastal waters of Faxaflói and Skjálfandi are best described as 'casual acquaintances', which is similar to the bottlenose population in the Sado Estuary (Augusto *et al*. 2012) and Sétubal Bay (Martinho *et al*. 2014), Portugal. Casual acquaintances is also the best fit model for associations in humpback dolphins in Cleveland Bay, Australia (Parra *et al*. 2011) and Pacific humpback-dolphins in the coastal waters surrounding Hong Kong, China (Dungan *et al*. 2012). The SLAR association rate showed an initial drastic decline after approximately 10 days, then the lagged association rate went up again until around 450 days (roughly 1 year; between 2002-2003, Fig. 4.8) to then decline once again. A fall in the SLAR might suggest that individuals after associating for a certain period of time (*e.g.*, 10 days) separated, possibly due to death or movement of the individuals outside of the identified population (*e.g.*, 'emigration', Whitehead 2008a). Declines in the SLAR could also be a reflection of the effort spent collecting data, where interruptions in the data collection *e.g.*, winter months from 2002-2011 in Faxaflói, and all years in Skjálfandi are when the curve falls; photo-id data not collected in the year 2005 in Faxaflói. The second fall in the SLAR curve suggested the majority of associations between individuals did not seem to last longer than a year. This second decrease could be due to emigration and re-immigration, as we have a population of identified individuals where some reside in our study areas while others are occasionally transiting out. In a previous study (Bertulli *et al*. 2015) a movement of white-beaked dolphins between both our study sites (*i.e.*, Faxaflói and Skjálfandi) was detected. This movement suggested individual dolphins to be highly mobile and transient, inhabiting large-scale coastal range of the Icelandic coast, possibly due to scarce and patchy resources or to its large population size (Bertulli *et al*. 2015). Photo-identification data (2002-2013) collected on this species also showed a low 'inter-annual re-sighting proportion' (18.3%) and 'intra-annual re-sighting proportion' (19.2%), and a 'rate of discovery' curve that continued to rise steadily (Bertulli *et al.* 2015). At around 1000 (around 3 years; after 2004) and 1600 days (4 years; year 2006) the error bars dropped below the null association rate with a first drop of the SLAR. It is likely that this fall reflected a stop in data collection during the year 2005. The error bar crossing the null association rate which was found in this study it was recorded in other studies (Ottensmeyer and Whitehead 2003, Beck *et al*. 2012). A similar scenario appears in Argentina with Commerson's dolphins where 13 marked individuals associated for 15 days before disassociating (Coscarella *et al*. 2011).

4.5 **Paper V**

In **Paper V** we calculated the first estimates using CR methods of survival and abundance of photographically identified white-beaked dolphins and minke whales.
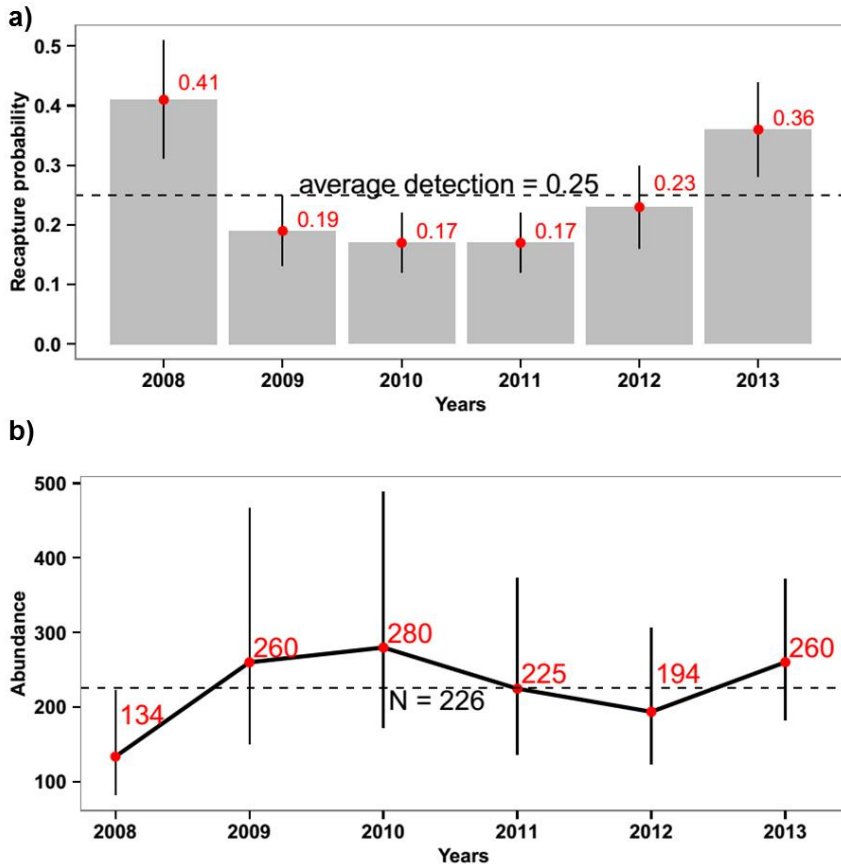
Figure 4-9 (a) Estimates of recapture probability for adult white-beaked dolphins in Faxaflói Bay, with 95% confidence intervals (vertical bars); (b) Estimates of abundance for adult white-beaked dolphins in Faxaflói Bay, with 95% confidence intervals (vertical bars).

From May 2002 to September 2013, a total of 283 individual adult white-beaked dolphins were photo-identified during these surveys, with 36% (n=103) of individuals photographed more than once and 24% (n=67) photographed across multiple years. Please check **Paper V**, Table 2b, for information about the number of marked, newly sighted and total number of resighted humpback whales per year. In Faxaflói Bay, the test of transience was not significant (TEST 3.SR, χ^2=5.8, df=6, *P*=0.45), and we found that the CJS model fitted the data well (χ^2=25, df=21, *P*=0.25). The best CJS model

retained constant survival and time-dependent recapture probability (see **Paper V**, Table 3). The estimated constant survival was 0.75 (0.67–0.82). The highest detection probability was recorded in 2008 (0.41, SE=0.10) and the lowest in 2010 (0.17, SE=0.05), with an overall estimate of 0.25 (SE=0.03, Fig. 4-9a). On average, we estimated a total abundance of 226 white-beaked dolphins in Faxaflói Bay (169–301). The annual abundance varied from 134 whales in 2008 (82–223) to 280 in 2010 (172–489, Fig. 4-9b). We did not find a linear effect of time in abundance estimates (adjusted r^2=-0.123, P=0.539). Due to low recapture rates, reliable abundance estimates could not be obtained for the first five years (2002-2007).
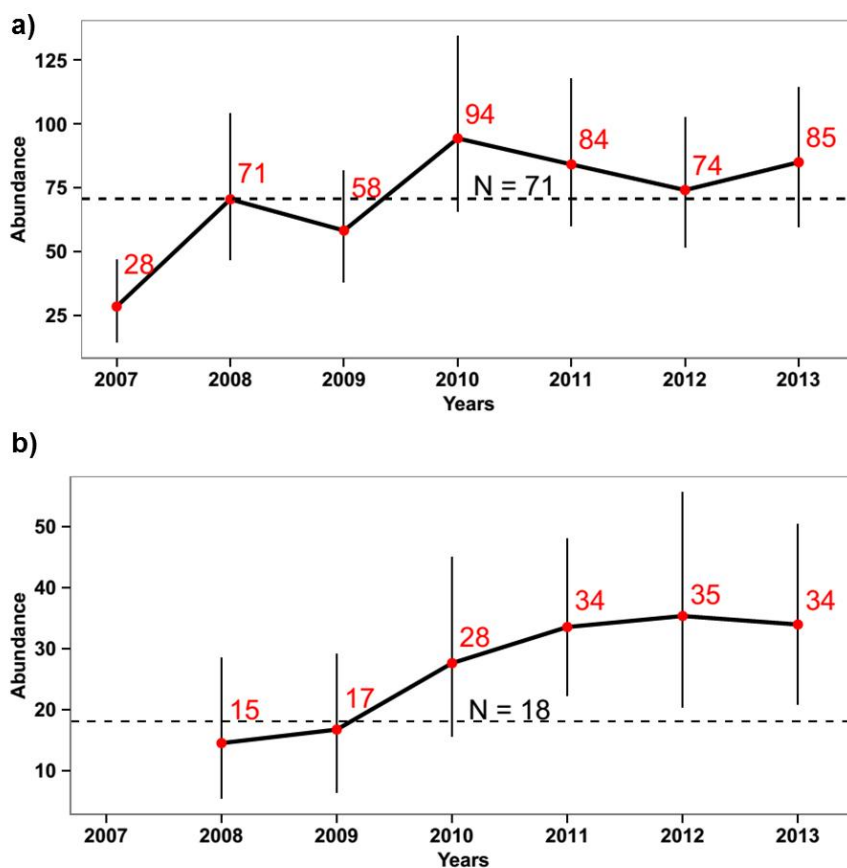
Figure 4-10 (a) Estimates of abundance for adult minke whales in Faxaflói Bay, with 95% confidence intervals (vertical bars); (b) Estimates of abundance for adult minke whales in Skjálfandi Bay, with 95% confidence intervals (vertical bars). The gray fitted straight line represents the linear trend in abundance.

From May 2007 to December 2013, a total of 667 days (2417 sightings) were spent using whale-watching boats to collect photo-identification

images in the coastal waters of Faxaflói Bay, southwest Iceland. A total of 206 individual adult minke whales were photo-identified during these surveys, with 46% (n=95) of individuals photographed more than once and 33% (n=68) photographed across multiple years. Table 2c provides information about the number of marked, newly detected and total number of resighted minke whales per year in Faxaflói Bay, showing that the cumulative number of identified individuals ('in catalogue' in Table 2c) of minke whales did not decrease with time in the study area. In Faxaflói Bay, the test of transience was significant (TEST 3.SR, $\chi 2$=25, df=5, P<0.001). Once a transient effect was accounted for, the CJS model fit the data well ($\chi 2$=6.3, df=11, P=0.85). The best model retained a transient effect on survival and constant recapture probability (Table 3). The average proportion of transients in the photo-identified minke whales was 46% (32%-58%). The estimated survival was estimated at 0.86 (0.76–0.93) for resident individuals. A constant recapture probability was estimated at 0.48 (0.39–0.57). On average, we estimated a total abundance of 71 minke whales in Faxaflói Bay (53–93). The annual abundances varied from a low 28 whales in 2007 (14–47) to a high 94 in 2010 (66–135, Fig. 4-10a). We detected a significant positive time trend in abundance estimates (adjusted r2=0.627, =0.021).

From May 2001 to September 2013, a total of 656 days (1442 sightings) were spent using whale-watching boats to collect photo-identification images in the coastal waters of Skjálfandi Bay, northeast Iceland. A total of 44 individual adult humpback whales were photo-identified during these surveys, with 52% (n=23) of individuals photographed more than once and 48% (n=21) photographed across multiple years. Please check **Paper V**, Table 2c for information about the number of marked, newly captured and total number of recaptured humpback whales per year, showing that the cumulative number of identified individuals ('in catalogue' in Table 2c) of humpback whales did not decrease with time in the study area. In Skjálfandi Bay, the test of transience was significant (TEST 3.SR, χ^2=15.2, df=6, P=0.02). Once a transient effect was incorporated, the CJS model fit the data well (χ^2=15.4, df=18, P=0.63). The best CJS model retained a transient effect on survival and constant recapture probability (see **Paper V**, Table 3). The average proportion of transients in the photo-identified minke whales was estimated 24% (0.1%-46%), with substantial uncertainty due to the low number of individuals in the dataset and imprecise survival estimates. The estimated survival for resident individuals was 0.97 (0.71–1.00). A constant recapture probability was estimated equal to 0.49 (0.37–0.61). On average, we estimated a total abundance of 18 minke whales in Skjálfandi Bay (12–27). The annual abundance varied from 15 whales in 2008 (5–29) to 35 in 2012 (21–50, Fig. 4.10b). We detected a significant positive time trend in the abundance estimates (adjusted r^2=0.830, P=0.007). Due to low detection

rates, reliable abundance estimates could not be obtained for the first six years (2001-2007).

This study presents the first abundance and survival estimates using CR for humpback whales, white-beaked dolphins and minke whales inhabiting the Icelandic coastal waters of Faxaflói and Skjálfandi Bays.

The results in this study showed the presence of transience for minke whales in both Faxaflói and Skjálfandi. Generally, transience introduces heterogeneity in a population with some animals being capturable (*i.e.*, the 'residents') while others have a null probability of being recaptured (*i.e.*, the 'transients'). By correcting our population size estimates by the proportion of transients, the abundance estimate obtained did not carry biases (*i.e.*, overestimation). The transient effect detected in this study could not be interpreted as an effect of true age (*e.g.*, a difference in survival between young and adults) since only adults were used in this study. It has been suggested that transience could be a result of heterogeneity in the sampling effort (Silva *et al*. 2009, Madon *et al*. 2012). In **Paper V**, Table 1, a lower sampling effort is visible in the year 2008 for minke whales in Faxaflói and in 2003-2004 for the same species in Skjálfandi. It is unlikely though that the observed transience was caused by so few years out of 7 of data collected for minke. The transient effect could be also sex-specific. A recent study demonstrated female humpback whales in New Caledonia are more prone to be transient than males during the breeding season (Madon *et al*. 2012), which was attributed to females' relatively more elusive behavior (Smith *et al*. 1999, Garrigue *et al*. 2004, Madon 2010) and shorter residency times (Palsbøll *et al*. 1997, Craig *et al*. 2001). Assessing the sex-ratio in minke whales could inform us about the transiency we found in this species and possibly help in providing more accurate demographic estimates for Iceland. Previous studies conducted in Iceland report of a minke whale (DEM217) migrating (ca. 600 km) between southwest (Faxaflói) and northeast (Skjálfandi) (Bertulli *et al*. 2013) while the present study yielded a similar case (DEM72). A larger sample of data and from more geographical areas are needed before drawing firm conclusions about site fidelity, movements and residents vs. transients in Icelandic waters.

A significant positive trend in abundance was detected for two species: humpback and minke whales. For minke whales, this datum could suggest possible partial recovery of this species on the southwest coast (Faxaflói), where it was reported to be declining since 2007 in southern and western waters (Borchers *et al*. 2009, Pike *et al*. 2009b, 2011, Víkingsson *et al*. 2015). The abundance of humpback whales showed an increase from 1986 to 2001 before reaching a plateau in 2000 (Pike *et al*. 2009b, Víkingsson *et al*. 2015). Therefore, the positive trend in abundance we found could be continuing this existing trend.

A number of caveats should be mentioned with respect to the methods employed for this study. There might have been some temporary emigration meaning there were individuals who were not available for capture (Nicholson *et al*. 2012). Temporary emigration might have also occurred due to uneven sampling of the study areas (*e.g*., data collection was dependent on whale-watching tours or due to non-dedicated efforts) or due to some individuals with home ranges within each bay that extended beyond areas of survey effort. As a consequence, our abundance estimates could have been biased towards lower range estimates (*e.g*., Read *et al*. 2003). Usually, in such situations, a robust design approach is adopted to account for temporary emigration (*e.g*., Nicholson *et al*. 2012, Daura-Jorge *et al*. 2013, Smith *et al*. 2013). The Pollock's closed robust design (Pollock 1982, Kendall *et al.* 1997) could be used in the future pending some modifications to the sampling protocol. In particular, future research could be conducted in other bays on the west and east coasts of Iceland that would provide further knowledge on patterns of distribution and movement of whales and dolphins. This would be very helpful in redesigning how to distribute future photographic effort using CR techniques.

The estimated overall survival rate for humpback whales (0.50, [0.40–0.60]) in this study was similar to estimates of resident Southeastern Pacific humpback whales from Ecuador (0.45, [0.32–0.58], Felix *et al*. 2011). In general, however, humpback whale apparent survival estimates are much higher (*e.g*., Barlow and Clapham 1997, Calambokidis and Barlow 2004, Felix *et al*. 2011). White-beaked dolphin survival rates in this study (0.75 [0.67–0.82]) were similar to Hector's dolphins in New Zealand (0.77, Slooten *et al*. 1992, 0.72, Gormley *et al.* 2005) but overall lower than most of values reported in other dolphin studies (*e.g*., Lockyer *et al*. 1988, Currey *et al*. 2009, Mansur *et al*. 2011, Fearnbach *et al*. 2012, Nicholson *et al*. 2012, Pusineri *et al*. 2014, Tyne *et al*. 2014). The ecological features of each study site could have influenced differences between these values (Currey *et al*. 2009). Survival estimates for resident minke whales in both bays (Faxaflói Bay: 0.86 [0.76–0.93]; Skjálfandi Bay: 0.97 [0.71–1.00]) are similar to other reported whale survival estimates (*e.g*., Barlow and Clapham 1997, Calambokidis and Barlow 2004, Felix *et al*. 2011). Ryan *et al*. (2014) suggested that lower estimates could reflect an outward migration (*e.g*., temporary or permanent migration). Here, we estimated 'apparent' survival, *i.e*., the product of true survival and the study area site fidelity (Lebreton *et al*. 1992). 'Apparent' survival is underestimated, than when compared to the true survival, unless permanent emigration equals zero. Additionally, if the study area is contained within a wider area, this can induce bias in survival estimates (Gilroy *et al*. 2012). Future analyses could resort to recently developed methods to infer true survival, such as kernel models (Gilroy *et al*. 2012) or spatially-explicit CR models (Schaub and Royle 2013). Alternatively, Felix *et al*. (2011) argued that lower survival

estimates might be caused by a 'transient effect'. In our case, failing to detect transience for humpback whales could be due to a lack of statistical power. The lower survival rates for humpback whales and white-beaked dolphin could also be the result of the overlap of our study areas with fishing activities. Whale-watching activities do not appear to affect adult minke whale survival in Faxaflói (Christiansen *et al*. 2015). However, Christiansen *et al*. (2015) also proposed to investigate into the overall exposure of whales to whale-watching, which might show a significant effect on whales. Whaling of minke whales was conducted in the Iceland continental shelf area between 1975 and 1985, and resumed in 2003 until the present time (Marine Research Institute 2014). From 2008 to 2013, a total of 324 individuals were caught (Marine Research Institute 2014) in different bays around Iceland, with the majority of catches in Faxaflói. In the future, we recommend the use of CR models allowing the incorporation of cause-specific death (*e.g*., Koons *et al*. 2014) – *i.e*., taking whaling into account – to disentangle natural mortality from human-induced mortality. Lastly, according to findings in other locations outside of Iceland (Kasuya and March 1984, Ramp *et al*. 2010), survival rates in whales and dolphins are sex-dependent; regrettably, sex could not be reliably determined for all minke whales, humpback whales and white-beaked dolphins used in the analyses for this study. Future studies assessing sex among whales and dolphins occurring in Icelandic coastal waters could clarify if these differences explain the low survival values obtained in this study.

In this study, the time-varying recapture probability estimates of humpback whales and white-beaked dolphins could be a result of differences in sampling effort, type of vessels used, survey equipment used, variations in individual patterns of residency (*e.g*., site fidelity: Silva *et al*. 2009, Straley *et al*. 2009, Cantor *et al*. 2012, Alves *et al*. 2014), or environmental conditions. The low recapture probability for white-beaked dolphins suggests low site fidelity, with a high proportion of non-resident individuals and migration of dolphins between Faxaflói Bay and outside areas (Bertulli *et al*. 2015). All humpback whales did not perform the fluking-out behavior observed in this species before a deep-dive during sightings, which could explain the differences in recapture probabilities obtained for humpback whales, as observed in other populations (*e.g.*, Straley *et al*. 2009).

Other sources of bias that can be introduced into abundance and survival estimates include 'trap dependence' effects. 'Trap dependence' *lato sensu* occurs when the detection of individuals is different depending on whether or not it was detected before (Pradel 1993). We did not detect trap-dependence for any of our populations (TEST 2.CT for humpback whales: $\chi^2=3$, df=4, $P=0.56$; white-beaked dolphins $\chi^2=7$, df=5, $P=0.19$; minke whales-Faxaflói: $\chi^2=3$, df=4, $P=0.58$; minke whales-Skjálfandi $\chi^2=9$, df =7, $P=0.26$). The trap-dependence effect can have several explanations in the

photo-identification study context. For example, observer effects or species site fidelity (see review in Pradel and Sanz-Aguilar 2012). To the authors' knowledge, the impact of trap-dependence on the estimation of abundance in an open-population has only been investigated once in a study that showed to what extend abundance could be underestimated when detection events were correlated (Lenoël *et al.* submitted).

5 Conclusions and Perspectives

In **Paper I** we found that as it was previously noted for other cetacean species, the most stable and reliable natural marks were notches and injury marks. We also identified other mark types that should be used for future photo-identification projects on minke whales and white-beaked dolphins, such as cookie-cutter shark bites and fin patches. Since these marks were amongst the most prevalent in these species, their addition will significantly increase the number of identifiable animals and subsequently allow for more accurate estimates of population analysis.

In **Paper II** we found that vertebral column deformities occur in white-beaked dolphins and that some individuals may live with such anomalies for several months. With 426 identified white-beaked dolphins in Icelandic coastal waters (Bertulli, unpublished data) the overall prevalence of vertebral column deformities in this sample was 1.2%. However, an over- or under-identification of dolphins with deformities might have affected our results due to the lack of a formal Icelandic stranding network – a specimen with a deformity might not be regularly reported – and due to an increase in observed elusive behavior displayed by certain local individuals over the years (Bertulli pers. obs.). Prevalence of vertebral deformities varies among dolphin species and populations. Kyphosis and scoliokyphosis affected 0.18% (n= 545, 1990-1994) and 0.32% (n=314, 1985-1989) of long-beaked common dolphins *Delphinus capensis* in Peru, respectively (Van Bressem *et al.* 2006); whereas, axial conformational deformities in bottlenose dolphins from northeast Scotland was estimated at 4.9 % (Fig. 2i in Wilson *et al.* 1997). A better understanding of the aetiology of these vertebral column deformities will be facilitated through appropriate necropsy examination of future cases, especially a microscopic evaluation of the musculature either side of the deformed region(s).

In **Paper III** we found that each stage class (*e.g.*, adult, juvenile, calf and neonate) could be identified by the use of stage-class specific color components. Adults could be identified by fully-formed color components; they also have two unique beak blaze coloration patterns: dark gray with a white or pink tip, and a pure white beak occurring at a low frequency. Juveniles and calves could be recognized by the presence of speckling, semi-circular head blazes, and lateral patches. Calves showed a yellow film on the abdominal fields, and some had gray beaks. Neonates were identified by yellow-tinged areas on the helmets, flanks and behind the eyes (post-ocular crescents). Future studies utilizing stranded specimens of known age and maturity would allow confirmation of these findings, and possibly reveal new age class-specific components, as well as sexually dimorphic

differences not discussed in this study. Geographical variation could be investigated by comparing large image datasets and stranded animals from different parts of the North Atlantic.

In **Paper IV** we investigated the association patterns in white-beaked dolphins inhabiting Icelandic coastal waters. Results showed that they live in a fission-fusion society defined by a majority of moderate-low associations but showing preferred associations throughout the whole study period. The data collected in Iceland form a strong basis to understand the social structure of white-beaked dolphins and can be used as a guideline for further research. It is recommended to collect data from other sites around the Icelandic coastline covering the west and east areas in order to test the results presented here.

Paper V presented the first estimates of abundance and survival for minke whales and white-beaked dolphins occurring in Icelandic coastal-shelf waters using CR methods. In the future, we recommend enlarging the sampling area and collecting data from multiple sites to increase our knowledge on whales and dolphins' habitat use, residency patterns and movements.

Even though minke whales have a worldwide distribution, much of the current information on their biology and ecology remains inadequate. White-beaked dolphins are one of only a handful of smaller delphinids occurring in polar areas and the only one regularly sighted in Arctic waters. Although white-beaked dolphins have been studied in Icelandic waters, very limited knowledge is available on their abundance, distribution, movements and demography. In this study, the common minke whale and white-beaked dolphins are subject of one of the longest ongoing projects in Icelandic coastal waters (2002-2014). Natural occurring marks *e.g.*, fin and injury marks as well as cookie-cutter bite (for whales) and fin patches (for dolphins) have been identified as the most accurate features to use for capture-recapture studies on these species. Abundance estimates were produced showing positive trend over time for minke whales, with constant survival for both species. The occurrence of vertebral column deformities in white-beaked dolphins showed these anomalies occur in this species and that individuals can live with them for several months. The study of changing color characteristics of white-beaked dolphins with age usefully advances our knowledge on one aspect of ontogenetic morphological variation, with a detailed analysis of a large sample of photographs for the first time. Social structure was investigated for the first time, extending the latitudinal range of our knowledge of delphinid social structure by including an arctic species which is difficult to study.

Data on demography and social structure are the two most important piece of information to clarify the conservation status of common minke whales

and white-beaked dolphins at local and state levels. Therefore, the photo-identification studies in Faxaflói and Skjálfandi Bays should be continued to provide information on longer-term trends in population abundance for both species in Iceland. Additionally, long term photo-identification studies will allow more accurate data on social structure, distribution, habitat use, movement and demographic parameters to be gathered for these species.

For future studies we also recommend directing attention to the impacts of anthropogenic activities on coastally distributed common minke whales and white-beaked dolphins. Over the last decade there has been a considerable growth in whale-watching activities both on the southwest and northeast coasts of Iceland, with companies also operating year-round on the west coast. Due to the coastal distribution and year-round presence, the white-beaked dolphins are more frequently exposed to dolphin-watching tourism, as well as noise pollution created by increasing vessel traffic and a number of operations. In the light of these findings we recommend to continue conducting dedicated surveys to monitor the cumulative effect of whale-watching traffic. We also suggest testing experimentally the existing guidelines used by all whale-watching operators in the area to ensure biological relevance and to minimize the disturbance to both species.

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Paper I

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An assessment of the natural marking patterns used for photo-identification of common minke whales and white-beaked dolphins in Icelandic waters

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Authors contribution. Provided data: CGB, MHR. Analysed the data: CGB, MR. Wrote the paper: CGB, MR.

An assessment of the natural marking patterns used for photo-identification of common minke whales and white-beaked dolphins in Icelandic waters

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Natural marks occurring in cetaceans are used to measure population parameters, social structure and movements. However, the changeable nature of these marks can originate bias in these estimates. The aim of this work was to calculate abundance and prevalence of 28 mark types observed in common minke whales and white-beaked dolphins photographed in Icelandic waters for 11 years (2002–2013) in order to identify reliable markings which could be suitable for capture-mark-recapture studies. In the common minke whale subsample the most prevalent occurring marks were cookie-cutter shark bite, notch and lamprey bite, and herpes-like lesions and blisters were the most abundant. White-beaked dolphins had notch, fin patches and fine scrape as the most prevalent, and black mark and fine scrape were the most abundant. Loss and gain rates were also estimated resulting in eight mark types with no losses in common minke whales including fin outline and injury marks. In white-beaked dolphins there were 13 mark types with null loss rate among which there were notch, distinct notch and amputation. Our findings confirm that fin and injury marks are among the most accurate features to use for capture-mark-recapture studies as noted for other cetacean species. We also suggest including cookie-cutter shark bites for common minke whales and fin patches for white-beaked dolphins due to their low loss rate. These two mark types were amongst the most prevalent in both species, so their addition will be pivotal in increasing the power of analysis conducted using photo-identification data obtaining more accurate population estimates.

Keywords: natural mark, photo-identification, common minke whale, *Balaenoptera acutorostrata*, white-beaked dolphin, *Lagenorhynchus albirostris*, mark rate

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INTRODUCTION

Natural marks occurring on cetaceans can originate from parasites, predator attacks, conspecifics, anthropogenic activities and congenital conditions (e.g. Schaeff & Hamilton, 1999; Rosso *et al.*, 2011; Bertulli *et al.*, 2012; Dwyer *et al.*, 2014; McCordic *et al.*, 2014). These markings are used for photo-identification ('photo-id') techniques and capture-mark-recapture (CMR) models in order to estimate the population size and survival rates of cetacean species (e.g. Slooten *et al.*, 1992; Durban *et al.*, 2012; Nicholson *et al.*, 2012). Markings are also used to investigate social interactions (e.g. Slooten *et al.*, 1993; Gero *et al.*, 2005; Parra *et al.*, 2011), movement of individuals (e.g. O'Brien *et al.*, 2009; Bearzi *et al.*, 2010; Robinson *et al.*, 2012; Bertulli *et al.*, 2013), to describe individual, ontogenetic and geographic variations in colouration patterns (e.g. Mitchell, 1970; Tsutsui *et al.*, 2001; Arnold *et al.*, 2005; Rosso *et al.*, 2008; Keener *et al.*, 2011; Lodi & Borobia,

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2013) and to monitor the development of diseases in free-ranging whales and dolphins (e.g. Van Bressem *et al.*, 2003; Burdett Hart *et al.*, 2010; Maldini *et al.*, 2010). However, the use of natural marks to identify cetaceans has certain limitations (summarized in Hammond, 1986, 1990). Marks can change their appearance and vary in numbers as a result of both intra- and inter-specific interactions, or due to anthropogenic interactions (e.g. McCann, 1974; Hammond, 1986; Lockyer & Morris, 1990). As a result of their changeable nature it is essential to assess the stability over time of each mark used in photo-identification studies to avoid introducing a bias in any abundance estimate (Hammond, 1986, 1990).

Research on the suitability of natural marks used for photo-identification was solely conducted on a few species such as bottlenose dolphin *Tursiops truncatus* (Wilson *et al.*, 1999), sperm whale *Physeter macrocephalus* (Dufault & Whitehead, 2005), Northern bottlenose whale *Hyperoodon ampullatus* (Gowans & Whitehead, 2001), long finned pilot whale *Globicephala melas* (Auger-Méthé & Whitehead, 2007), Cuvier's beaked whale *Ziphius cavirostris* (Rosso *et al.*, 2011), pink river dolphin *Inia geoffrensis* (Gomez-Salazar *et al.*, 2011) and humpback whale *Megaptera novaeangliae* (Blackmer *et al.*, 2000). No such study has ever been conducted on

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Atlantic common minke whales (*Balaenoptera acutorostrata;* hereafter 'minke whales') and white-beaked dolphins (*Lagenorhynchus albirostris*). Since 1980 studies along the west coast of North America have shown that combining the use of natural markings such as notched fins, oval scars, body pigmentation with photo-identification techniques occurring on Pacific minke whales would enable researchers to discriminate between individual whales (Dorsey, 1983; Dorsey *et al.*, 1990; Joyce & Dorsey, 1990; Stern *et al.*, 1990). This method was used successfully to explore the site fidelity (Dorsey *et al.*, 1990; Gill *et al.*, 2000; Tscherter & Morris, 2005; Anderwald, 2009), the movements and minimum population size of minke whales (Bertulli *et al.*, 2013). Conversely, there is very limited knowledge regarding the abundance, distribution, movements and demographics of the white-beaked dolphin (summarized in Tetley & Dolman, 2013). This species has been identified using more permanent markings such as notches (Bertulli *et al.*, in press; Brereton *et al.*, 2013) associated with some temporary secondary features (e.g. depigmentation, skin lesions, scars and tooth-rakes in Brereton *et al.*, 2013). However, these studies never conducted an assessment of the stability of these skin marks.

Even though minke whales have a worldwide distribution, much of the information regarding the biology and ecology of the species remains depauperate (summarized in Robinson *et al.*, 2007), and similarly even less is known about the white-beaked dolphin (Tetley & Dolman, 2013). In Icelandic waters, information on photo-identification rate, small-scale distribution and movements are available on both free-ranging minke whales and white-beaked dolphins (Bertulli *et al.*, 2013; Bertulli *et al.*, in press). However, there is a current lack of knowledge regarding the basic demographic parameters of both species. In order to produce an unbiased estimation of both populations it is pivotal that the feasibility of individual identification by photo-identification is first ascertained. Therefore, the objectives of the present study are to describe and to assess the abundance and prevalence of natural markings visible in minke whales and white-beaked dolphins photographs. Moreover, the rates of mark gain and loss have been calculated in order to identify viable long-lasting marks.

MATERIALS AND METHODS

Field methods

Photographs of individual minke whales and white-beaked dolphins were collected from whale-watching boats based in Faxaflói Bay (64°24′N 23°00′W; SW coast), Reykjavik and Skjálfandi Bay, Húsavík (66°05′N 17°33′W; NE coast), Iceland, from 2002 to 2013. Digital cameras were mainly equipped with 70–300 mm lenses (AF-S VR Nikkor lens f/4.5–5.6 IF-ED), with photographers placed on the roof of the wheelhouse (5–8 m above sea level in Faxaflói Bay, 2.7–4.5 m in Skjálfandi Bay) of each boat. When possible the vessel would be manoeuvred parallel to the whale or dolphin group encountered, allowing researchers to photograph both sides of each individual, including fin, dorsum, flanks and peduncle (Agler *et al.*, 1990; Würsig & Jefferson, 1990).

Photographic analysis

Each photo-identification picture was assigned a quality rating (Q) from the lowest Q1 to the highest Q6, considering focus, exposure, angle and proportion of the frame occupied by the body of the animal. The Q-value of each image was independent of the marks visible on each individual. Only images rated $Q \geq 5$ were considered for the analysis (Gowans & Whitehead, 2001; Elwen *et al.*, 2009; Rosso *et al.*, 2011).

Mark prevalence and abundance

Photos in the databases were analysed chronologically in order to describe mark types. Mark prevalence and abundance were assessed using 200 randomly selected images per species similar to Gowans & Whitehead (2001) and Auger-Méthé & Whitehead (2007). The size of each mark was calculated using ImageJ software (http://rsb.info.nih.gov/ij; e.g. Fearnbach *et al.*, 2011) and available estimates of dorsal height (G. Vikingsson and S.D. Halldórsson, Marine Research Institute, Reykjavík, unpublished data) and their shape, location and colour were also defined.

A total of 28 mark types were identified and then classified into nine categories based on morphological features (Table 1):

(1) Fin outline: Marks occurring on the leading and trailing edge of the fin were included in this category. Notches, missing pieces of tissue (Würsig & Würsig, 1977) were defined as <1 cm in size. Those >1 cm and located on the trailing edge were defined as distinct notches (Dufault & Whitehead, 1993); if located on the leading edge they were defined as LE Distinct notches. Any protruding piece of tissue (Auger-Méthé & Whitehead, 2007) were also part of this category since they occurred along the outline of the fin.

(2) Body and fin pigmentation: This category included mottled pigmentation (Sears *et al.*, 1990), speckling (Arnold *et al.*, 2005; Krzyszczyk & Mann, 2012), hypo-pigmentation comprising highly pigmented patches typical of immature white-beaked dolphins, and patches of pigment on the fin. White patches resemble those described by Webber (1987) in his work on dusky dolphins (*Lagenorhynchus obscurus*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) and described as 'a zone of light coloration found on the dorsal fin of some *Lagenorhynchus*'. Grey patches only appeared on the fin and/or base of the fin although without histological and microbiological examination it was not possible to know if they were phenotypical features like the white patches or infections.

(3) Patches: White or black marks, either circular or irregular (Auger-Méthé & Whitehead, 2007; Gomez-Salazar *et al.*, 2011) occurred on all observed body parts and were included in this category.

(4) Bite marks: Bite marks from cookie-cutter sharks (*Isistius* spp.) and lamprey (*Petromyzon marinus*) (Dorsey *et al.*, 1990; Moore *et al.*, 2003; Nichols & Tscherter, 2011; Samarra *et al.*, 2012) were included in this category.

(5) Linear marks: This category included fine scrapes (<1 cm) or medium scrapes (>1 cm) (Rosso *et al.*, 2011). Scrape thickness was measured using ImageJ with a scale of reference determined previously in the study area for minke whales (28.8 cm fin height) and white-beaked dolphins (25.3 cm fin height; G. Vikingsson and S.D. Halldorsson, unpublished data). Tooth-rake produced by white-beaked dolphins (Ross & Wilson, 1996; Haelters & Everhaarts, 2011) and lamprey skidding bite marks (parallel light grey

Table 1. Mark types used to photo-identified minke whales and white-beaked dolphins.

Category	Mark type	Description	Colour	Body location	Estimates size
Fin outline	Notch	Semicircular, triangular, squared Indentation in shape	Skin	Trailing edge of the fin	≤1 cm
	Leading notch	Semicircular indentation in shape	Skin	Leading edge of the fin	≤1 cm
	Distinct notch	Indentation	Skin	Trailing edge of the fin	≥1 cm
	Leading Distinct	Indentation	Skin	Leading edge of the fin	≥1 cm
	Protruding Piece	Piece of tissue protruding	Skin	Trailing edge of the fin	<1 cm
Body and fin pigmentation	Mottling	Circular or small oval marks	Dark grey, black	Flank, peduncle	<5 cm wide
	Speckling	An ovoid mark usually of a contrasting colour as on the rest of the skin	Dark grey	Behind eye, flank, peduncle	<1 cm
	Hypo-pigmentation	Irregular hypo-pigmented patches	Off-white	Flank, peduncle	Vary in size
	Fin patches	Irregular patches	Grey, white or both	Fin	Vary in size
Patches	White mark	Small circular white marks or irregular patches	White	Flank, peduncle, below fin, dorsum	Punctiform to <1 cm
	Black mark	Irregular, small circular or punctiform marks	Black	Flank, peduncle, back	Punctiform to vary in size
Bite marks	Cookie-cutter bite	Oval shaped scars or crater-like wounds	Grey, light grey	Flank, peduncle, back	4.5 cm wide
	Lamprey bite	Circular scars with texture and raised borders	Grey, with/without dark outline	All body parts	≤3 cm
Linear marks	Skidding	Parallel, sinuous or linear sliding marks	Light grey	Flank, peduncle, dorsum, back	<3 m long
	Fine scrape	1 or 2 parallel linear marks	Off-white	All body parts	≤1 cm (thickness)
	Medium scrape	1 or 2 parallel linear marks	Off-white	Flank, peduncle, dorsum	≥1 cm (thickness)
	Tooth-rake	Multiple parallel lines made by conspecifics	Light or dark grey	All body parts	<1 cm (thickness)
Injuries	Wounds	Wounds of unknown origin	White to grey	Dorsum, flank, peduncle	Vary in size
	Antagonistic scars	Antagonistic marks e.g. orca tooth-rakes	Dark grey	Back, peduncle, flank	<3 cm (thickness)
	Anthropogenic scars	Anthropogenic scars e.g. rope, propeller scars and bullet scars	Grey to skin colour	Head, peduncle, flank, fin	1–2 cm (thickness)
	Back indentation	Semicircular Indentation	Skin	Dorsal ridge caudal to fin	<2 cm (thickness)
	Amputation	Significant losses of tissue/mutilation	Skin	Fin, snout	Vary in size
	Deformation	Change of normal shape and form of body tissue	Skin	Fin	Vary in size
Cutaneous elevations	Blisters	Skin elevations, single or numerous	Whitish to dark grey	All body parts (except for fin and ventrum)	Punctiform
Infectious lesions	Tattoo-like	Irregular hyper-pigmented marks with a dark outline, evoking a stippled pattern	Dark grey, grey	Dorsum, flank	Vary in size
	Herpes-like	Small black dot lesions	Black	Flank	Punctiform
	Wart-like	Hyperplasic lesions	Light grey	All body parts (no fin)	<7 cm wide
Miscellaneous	Miscellaneous	All other marks	Vary in colour	All body parts	Vary in size

marks; Pike, 1951; Bertulli *et al.*, 2012, figure 3c; Ólafsdóttir & Shinn, 2013, figure 3b) were also included in this category.

(6) Injuries: Large wounds from natural causes (e.g. predator attacks) and from anthropogenic causes (e.g. net entanglement and propeller but excluding notches on the leading edge of the fin) were included in this category following Bertulli *et al.* (2012). Measurements of tooth-rake mark interstices were within the range of 25 mm and 32 mm of killer whales (Craighead George *et al.*, 1994; Visser, 1999, figure 1b). This category also included major body indentations (Luksenburg, 2014, figure 3a), amputation and fin deformation (Van Waerebeek *et al.*, 2007, figure 6; Higdon & Snow, 2009; Mansur *et al.*, 2012, 'dorsal fin bend'; Luksenburg, 2014, figure 3k).

(7) Cutaneous elevation: Skin elevations including blisters and nodules of unknown origin, as described by Bertulli *et al.* (2012), were part of this category.

(8) Infectious lesions: Tattoo-like, wart-like and herpes-like lesions were included in this category based on their macroscopic appearance following Bertulli *et al.* (2012).

(9) Miscellaneous: This category was used to classify all other marks lacking diagnostic features of the previously described categories (Auger-Méthé & Whitehead, 2007; Auger-Méthé *et al.*, 2010).

For each mark type the following parameters were calculated: (1) the total number of occurrences for each mark n_i: i is the type of mark; (2) mark prevalence p_i: frequency of individuals with the i mark; (3) mark severity l_i: mean number of marks of i type only on individual with i occurrences; (4) relative portion r_i of each mark type to the total amount of marks R; and (5) mark abundance a_i: mean number of the i mark per

Table 2. Prevalence and abundance of marks: (a) minke whales (b) white-beaked dolphins. For each mark type the following parameters were calculated: (1) the total number of occurrences for each mark n_i: i is the type of mark; (2) mark prevalence p_i: frequency of individuals with the i mark; (3) the mark severity l_i: mean number of marks of i type only on individual with i occurrences; (4) relative portion r_i of each mark type to the total amount of marks R; (5) mark abundance a_i: mean number of the i mark per individual. Standard deviation are in parentheses.

Mark type	ni	pi	li	ri	ai	Ai range
(a) Common minke whales						
Notch	77	0.228	1.571 (0.77)	0.033	0.385 (0.748)	0−4
Leading notch	43	0.143	1.344 (0.67)	0.019	0.215 (0.548)	0−4
Distinct notch	44	0.185	1.100 (0)	0.019	0.220 (0.415)	0−1
Leading distinct	1	0.005	1	<0.001	0.005 (0.071)	0−1
Protruding piece	1	0.005	1	<0.001	0.005 (0.071)	0−1
Total fin outliners	166	0.460	1.644 (0.93)	0.072	0.830 (1.023)	0−4
Mottling	7	0.035	1 (0)	0.003	0.035 (0.196)	0−1
Speckling	0	–	–	–	–	–
Hypo-pigmentation	0	–	–	–	–	–
Fin patches	5	0.025	1 (0)	0.002	0.025 (0.140)	0−1
Total body and fin pigmentation	12	0.060	1 (0)	0.005	0.060 (0.238)	0−1
White mark	203	0.165	5.486 (5.56)	0.088	1.045 (3.230)	0−22
Black mark	84	0.029	12 (10.82)	0.036	0.420 (2.901)	0−30
Total patches	287	0.189	6.523 (7.14)	0.124	1.465 (4.323)	0−30
Cookie-cutter bite	199	0.262	3.262 (3.96)	0.086	0.995 (2.651)	0−21
Lamprey bite	294	0.211	6.125 (6.16)	0.127	1.470 (3.982)	0−28
Total bite marks	493	0.434	4.833 (5.48)	0.214	2.465 (4.596)	0−28
Skidding	52	0.139	1.625 (1.00)	0.022	0.260 (0.711)	0−5
Fine scrape	70	0.177	1.707 (1.37)	0.030	0.350 (0.923)	0−7
Medium scrape	4	0.005	4	0.002	0.020 (0.283)	0−4
Tooth-rake	0	–	–	–	–	–
Total linear marks	126	0.229	1.800 (1.36)	0.055	0.630 (1.175)	0−7
Wound	1	0.005	1 (0)	<0.001	0.005 (0.071)	0−1
Antagonistic scar	0	–	–	–	–	–
Anthropogenic scar	0	–	–	–	–	–
Back indentation	8	0.034	1 (0)	0.004	0.040 (0.196)	0−1
Amputation	10	0.042	1 (0)	0.004	0.050 (0.218)	0−1
Deformation	0	–	–	–	–	–
Total injury	19	0.084	1 (0)	0.008	0.100 (0.301)	0−1
Tattoo-like	0	–	–	–	–	–
Herpes-like	600	0.010	300.00 (0)	0.260	3.000 (29.924)	0−300
Wart-like	8	0.005	8.00	0.004	0.040 (0.566)	0−8
Total infectious lesions	608	0.013	202.67 (168.59)	0.264	3.040 (29.926)	0−300
Blister	558	0.010	1.21 (12.65)	0.242	2.790 (8.106)	0−80
Miscellaneous	37	0.010	2.06 (2.13)	0.016	0.185 (0.857)	0−37
Total marks	2306	0.842	13.70 (27.27)	1.000	11.53 (2.471)	0−300
(b) White-beaked dolphins						
Notch	195	0.531	1.726 (0.93)	0.126	0.975 (1.077)	0−7
Leading notch	17	0.040	2.125 (1.69)	0.011	0.085 (0.519)	0−6
Distinct notch	88	0.326	1.239 (0.40)	0.057	0.440 (0.631)	0−2
Leading distinct	0	–	–	–	–	–
Protruding piece	5	0.025	1 (0)	0.003	0.025 (0.156)	0−1
Total fin outliners	305	0.669	2.118 (1.29)	0.197	1.525 (1.326)	0−7
Mottling	0	–	–	–	–	–
Speckling	13	0.058	1 (0)	0.008	0.065 (0.247)	0−1
Hypo-pigmentation	15	0.067	1 (0)	0.010	0.075 (0.264)	0−1
Fin patches	88	0.440	9.778 (0)	0.057	0.440 (0.498)	0−1
Total body and fin pigmentation	116	0.442	1.196 (0.48)	0.075	0.580 (0.668)	0−1
White mark	20	0.018	5 (5.23)	0.013	0.10 (0.951)	0−12
Black mark	371	0.156	10.912 (20.38)	0.239	1.855 (9.343)	0−100
Total patches	391	0.174	10.289 (19.41)	0.252	1.955 (9.372)	0−100
Cookie-cutter bite	0	–	–	–	–	–
Lamprey bite	53	0.094	2.524 (1.94)	0.034	0.265 (0.990)	0−8
Total bite marks	53	0.094	2.524 (1.94)	0.034	0.265 (0.990)	0−8
Skidding	20	0.053	1.667 (0.98)	0.013	0.100 (0.459)	0−4
Fine scrape	223	0.397	2.593 (2.29)	0.144	1.115 (1.968)	0−13
Medium scrape	0	–	–	–	–	–
Tooth-rake	109	0.209	2.422 (2.02)	0.070	0.545 (1.385)	0−9
Total linear marks	352	0.464	3.451 (3.32)	0.227	1.760 (2.927)	0−13

Continued

Table 2. Continued

Mark type	ni	pi	li	ri	ai	Ai range
Wound	25	0.094	1.250 (0.40)	0.016	0.125 (0.387)	0 – 2
Antagonistic scar	39	0.022	7.800 (3.77)	0.025	0.195 (1.333)	0 – 14
Anthropogenic scar	2	0.010	1 (0)	0.017	0.010 (0.100)	0 – 1
Back indentation	3	0.015	1 (0)	0.002	0.015 (0.122)	0 – 1
Amputation	22	0.110	1.158 (0)	0.014	0.110 (0.314)	0 – 1
Deformation	1	0.005	1	<0.001	0.005 (0.071)	0 – 1
Total injury	92	0.228	1.957 (2.29)	0.059	0.460 (1.392)	0 – 14
Tattoo-like	52	0.022	13 (7.62)	0.033	0.260 (2.055)	0 – 23
Herpes-like	0	–	–	–	–	–
Wart-like	0	–	–	–	–	–
Total infectious lesions	52	0.022	13 (7.62)	0.033	0.260 (2.055)	0 – 23
Blister	20	0.005	20	0.013	0.005 (1.414)	0 – 20
Miscellaneous	170	0.165	4.857 (7.16)	0.110	0.850 (3.533)	0 – 40
Total marks	1551	0.892	8.72 (9.85)	1.000	7.755 (1.138)	0 – 100

individual. Standard deviations were calculated for mark severity and mark abundance.

Mark change – gain and loss rates

To assess changes in mark abundance and prevalence, all individuals in a photograph (same body side) in at least 2 consecutive years were selected. If numerous images were available for each year the highest quality frame was randomly chosen (Gowans & Whitehead, 2001). Photographs of sequential years were compared for presence or absence of each mark. Images containing marks below the water line and therefore not visible were not used in the analysis (Rosso *et al.*, 2011). Individuals photographed during gapped bins of consecutive years (e.g. 2008 – 2009, 2011 – 2013) were analysed separately and only for the consecutive year bins (Dufault & Whitehead, 1995). To avoid pseudoreplication when both left and right sides were photographed during consecutive years, only the side with the highest number of marks was included in the analysis. Formulas to estimate gain and loss rates, 'whale years' as well as 'whale years of available marks' (WYAM) were calculated following Auger-Méthé & Whitehead (2007). Marks showing no losses over the duration of the study were considered reliable marks for analysis (Gowans & Whitehead, 2001).

RESULTS

Our analysis contained 1670 $Q \geq 5$ photographs involving 784 minke whales and 886 individual white-beaked dolphins. A subsample of 200 photos were randomly chosen for each species and the mark abundance and prevalence were assessed (Table 2). The randomly selected images for mark type analysis contained 188 minke whales and 216 white-beaked dolphins. Applying our classification system, we identified 28 mark types (Table 1).

Mark abundance and prevalence

In minke whales a total of 24 mark types were distinguished and categorized into nine different mark categories (Figure 1). From the subsample of 200 minke whale images

21 mark types (Figure 1, Table 2) were considered. A total of 84.2% of the population showed at least one mark with a total of 2306 distinct marks identified. The most prevalent marks encountered were cookie-cutter bite ($p_i = 0.262$), notch ($p_i = 0.228$) and lamprey bite ($p_i = 0.211$) and the most abundant marks were herpes-like and blisters with a mean value of $a_i = 3$ and $a_i = 2.79$ marks per individual, respectively. Herpes-like lesions and black marks were the most severe mark types with a mean value of $l_i = 300$ marks per individual and $l_i = 12$ marks per individual, respectively.

In white-beaked dolphins a total of 22 mark types were distinguished and categorized into nine different mark categories (Figure 2). From the subsample of 200 white-beaked dolphins images, the same amount of mark types were considered (Figure 2, Table 2). A total of 89.2% of the photographed dolphins displayed at least one mark, with a total of 1551 distinct marks identified. The most prevalent marks were notch ($p_i = 0.531$), fin patches ($p_i = 0.440$) and fine scrape ($p_i = 0.397$) and the most abundant were black marks and fine scrapes, with a mean value of $a_i = 1.85$ and $a_i = 1.15$ marks per individual, respectively (Table 2). Blister lesions and tattoo-like were the most severe mark types with a mean value of $l_i = 20$ marks per individual and $l_i = 13$ marks per individual, respectively.

Gain and loss rates

Photographs of 47 individual minke whales observed in 66 whale years had 18 mark types of the 26 described earlier showing gain and/or loss rates (Table 3). Seven mark types demonstrated a total of 110 whale years of available marks: notch, leading notch, distinct notch, protruding piece of tissue, wound, back indentation and amputation. However, the marks with higher WYAM were notch (WYAM = 49), leading notch (WYAM = 24) and distinct notch (WYAM = 24). Ten mark types (38%, N = 26) showed gains with time.

Photographs of 59 individual white-beaked dolphins observed in 83 whale years had 20 mark types out of the 26 described earlier showing gain and/or loss rates (Table 3). Thirteen mark types demonstrated a loss rate of zero: notch, leading notch, distinct notch, protruding piece of tissue, hypopigmentation, white mark, lamprey bite, wound, antagonistic
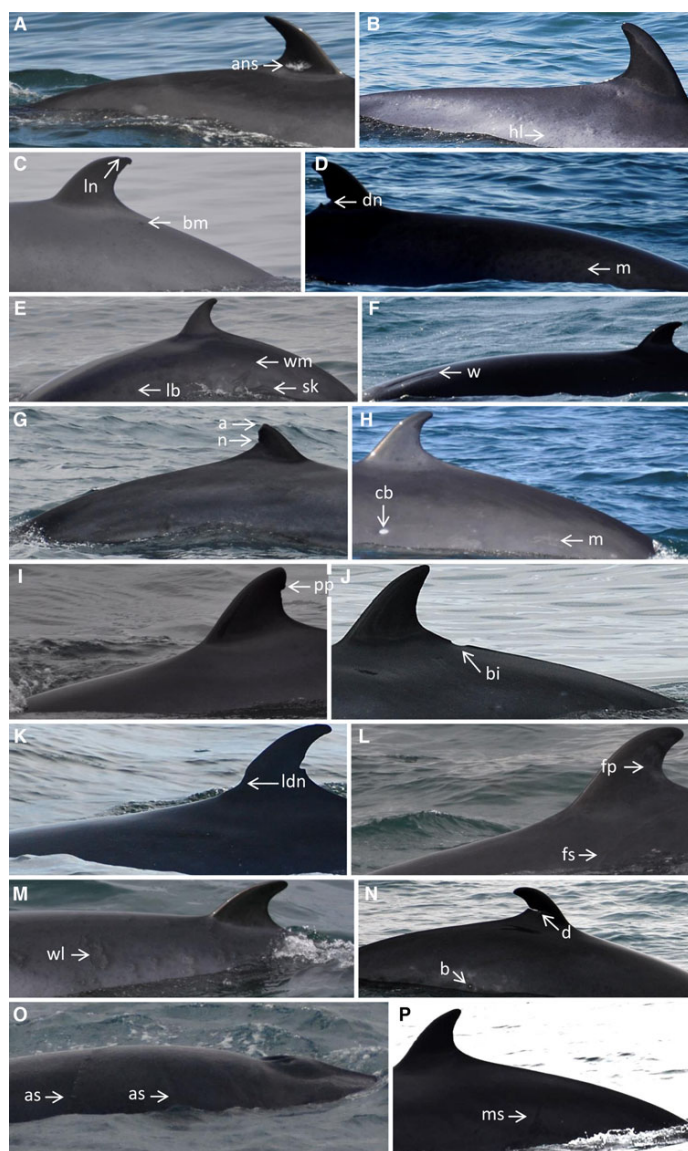
Fig. 1. The 24 mark types described in minke whales: (A) ans – antagonistic scars; (B) hl – herpes-like; (C) n – notch, ln – leading notch, bm – black marks; (D) dn – distinct notch, m – mottling; (E) wm – white marks, lb – lamprey bite; (F) w – wound; (G) a – amputation, sk – skidding; (H) cb – cookie-cutter bite, m – miscellaneous; (I) pp – protruding piece; (J) bi – back indentation; (K) ldn – leading distinct notch; (L) fp – fin patches, fs – fine scrape; (M) wl – wart-like; (N) d – deformation, b – blisters, (O) as – anthropogenic scars; (P) ms – medium scrape.

Fig. 2. The 22 mark types described in white-beaked dolphins: (A) n – notch, bi – back indentation; (B) a – amputation, fp – fin patches; (C) fs – fine scrape, tl – tattoo-like; tr – tooth-rake; (D) pp – protruding piece; (E) sk – skidding, bm – black mark; (F) d – deformation; (G) dn – distinct notch, ln – leading notch; (H) w – wound; (I) lb – lamprey bite-like; (J) b – blisters, ans – antagonistic scars; (K) wm – white mark; (L) m – miscellaneous; (M) as – anthropogenic scars; (N) hp – hypo-pigmentation, sp – speckling.

Table 3. Gain and loss rates: (a) minke whales. *Total whale year of 66 (b) white-beaked dolphins. **Total whale years of 72 for all marks excluding fin outliners, amputation, deformation and back indentation with a total of 83.

Mark type	Rate of loss		Whale years of available marks		Rate of gain	
	Ba	*La*	*Ba*	*La*	*Ba**	*La***
Notch	0	0	49	121	–	0.036
Leading notch	0	0	24	11	–	–
Distinct notch	0	0	24	40	–	–
Leading distinct	–	–	–	–	–	–
Protruding piece	0	0	2	6	–	0.012
Total fin outliners	0	0	99	178	–	0.048
Mottling	–	–	–	–	0.061	–
Speckling	–	–	–	–	–	–
Hypo-pigmentation	–	0	–	1	–	–
Fin patches	1.000	0.029	1	35	–	0.028
Total body and fin pigmentation	1.000	0.028	1	36	0.061	0.028
White mark	0.338	0	68	4	0.530	–
Black mark	1.000	0.391	11	110	–	0.042
Total patches	0.500	0.377	79	114	0.530	0.042
Cookie-cutter bite	0.125	–	48	–	0.182	–
Lamprey bite	0.200	0	70	3	0.697	0.056
Total bite marks	0.169	0	118	3	0.879	0.056
Skidding	1.000	–	10	–	0.015	0.014
Fine scrape	0.833	0.176	6	74	0.091	0.125
Medium scrape	–	–	–	–	–	0.014
Tooth-rake	–	0.333	–	18	–	0.097
Total linear marks	0.937	0.206	16	92	0.106	0.250
Wound	0	0	2	4	0.015	–
Antagonistic scar	1.000	0	1	4	0.015	–
Anthropogenic scar	–	0	–	1	–	–
Back indentation	0	0	2	1	–	–
Amputation	0	0	7	22	–	–
Deformation	–	–	–	–	–	–
Total injury	0.083	0	11	32	0.030	–
Tattoo-like	–	0	–	4	–	0.069
Herpes-like	–	–	–	–	–	–
Wart-like	–	–	–	–	–	–
Total infectious lesions	–	0	–	4	–	0.069
Blister	0.222	–	45	–	0.606	–
Miscellaneous	0.400	0.167	20	24	0.061	0.181

and anthropogenic marks, back indentation, amputation and tattoo-like lesion. Marks with the highest WYAM were notch (WYAM = 121), distinct notch (WYAM = 40) and amputation (WYAM = 22). Those individuals showed gains of notches over time (N = 11, 42%) (DEM54, DEM209 and DEM79), with one notch being acquired from one year to the next (Figure 3).

DISCUSSION

Fin outline and injuries

Marks on fin outlines and those associated with injuries are known to reliably assist with the identification of individual cetaceans from species including minke whales and white-beaked dolphins (Lockyer & Morris, 1990; Scott *et al.*, 1990; Wilson *et al.*, 1999; Auger-Méthé & Whitehead, 2007). Despite the low gain rate (<0.05 gains/individual per year) fin outline marks and injuries were generally very common (mainly notches, p_{iBa} = 0.228, p_{iLa} = 0.531) meaning that they are rarely acquired – that decreases the probability of

mark superimposition – but permanent in time, as already noted in other cetacean populations (Agler, 1992; Morris & Tscherter, 2005; Auger-Méthé & Whitehead, 2007). Moreover, large injury marks (e.g. wounds, antagonistic and anthropogenic scars, amputations) resembling the 'deeper and major wounds' as described by Lockyer & Morris (1990) were significantly more common in the white-beaked dolphins than minke whales (p_{iLa} = 0.228, p_{iBa} = 0.084; G = 18.29, df = 1, P < 0.001) indicating that dolphins are more prone to predation and anthropogenic interactions. Large injury marks were stable in time, with the only exception in a minke whale fin where killer whale tooth-rake marks resembling the description by Visser (1999, figure 2b) and Craighead George *et al.* (1994, figure 2f, left set) disappeared in 1 year. In Icelandic waters, killer whales seem to be natural predators to common minke whales and white-beaked dolphins, as shown by tooth-rake marks visible on their bodies (Bertulli *et al.*, 2012). We observed single events of killer whale predation on a minke whale (July 2008) in Skjálfandi Bay during the study period. However, a white-beaked dolphin (ID no. nDEM53, Figure 2J) was photographed with stable killer whale tooth-rake bites over 5 years and another
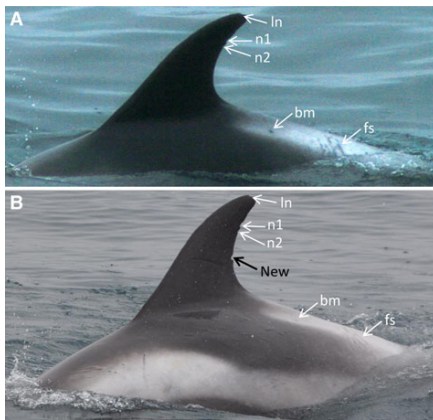
Fig. 3. White-beaked dolphin DEM79 photographed in 2009 and in 2010: (A) – (nl) nick on leading edge, (n1) (n2) nicks on trailing edge, (bm) black mark, (fs) fine scrapes; (B) – same marks visible with the addition of a new nick mid posterior on the trailing edge (New).

individual (ID no. nDEM68, Figure 2M) had a typical rope mark around the head over at least 4 years. Deformation was another injury mark analysed in this study which remained stable over the years which is similar to other dolphin species (Lockyer & Morris, 1990; Wilson et al., 1999). These results suggest that fin outline and injury marks are among the most accurate features to use to re-capture individuals among years even for these two cetacean species.

Body and fin pigmentation

Pigmentation patterns have been shown to be stable for many consecutive years in various cetaceans (Sears et al., 1990; Gowans & Whitehead, 2001; Gomez-Salazar et al., 2011). Our identification of pigmentation patterns in minke whales focused largely on mottling, which had zero rate of loss. As a colouration pattern component, mottling could vary with age and/or external conditions (e.g. stress, pollution; West & Packer, 2002; Marcoux, 2008; Wang et al., 2008) although no such information was collected during our study. The seasonal presence of diatomaceous algae films covering the skin of whales (Sears et al., 1990; Gerasimyuk & Zinchenko, 2012) could also be a confounding factor when identifying pigmentation patterns. As a result, mottling may not be a useful secondary photo-identification feature for this species. A grey fin patch was described for the first time in both minke whales and white-beaked dolphins (Figure 1L). Our images of grey fin patches resemble Pale Skin Patches (PSP) marks observed in Peale's (*Lagenorhynchus australis*) and Chilean dolphins (*Cephalorhynchus eutropia*) in translucent colour, shape, borders and even the location (Sanino et al., 2014). They can be classified as PSP-like until verifying other similarities as time-dynamics or the evolution of the patches overtime. The aetiology of this mark is currently unknown until further tests are conducted. Fin patches were common in white-beaked dolphins ($p_i = 0.440$) and they showed to be reliable secondary features, having a rate of loss <3% per individual per year.

Furthermore, the use of this mark in photo-identification studies for this species could increase the amount of identified individuals ~5% rate (in this study from $p_i = 0.732$ to $p_i = 0.772$).

A single adult white-beaked dolphin showed extensive hypo-pigmented areas, on flanks, peduncle and dorsum which differed from similar patches observed in immatures (e.g. juvenile and calf; Bertulli, unpublished data). These marks were found to be stable for 1 year indicating the possible use for photo-identification studies spanning at least this amount of time.

Patches and bite marks

Patches (i.e. white and black marks) had similar prevalence in both species. They were of unknown origin and generally carried high loss and gain rates, which was also found by Gomez-Salazar et al. (2011). Therefore, secondary features like white and black marks, which were present in low numbers, are not suitable to be used as photo-identification features for this species.

Cookie-cutter bites were not recorded in the white-beaked dolphin sample while they were the most frequent mark in minke whales. Cookie-cutter bites are generally found in species resident to tropical waters or in whales migrating to these areas during the breeding season (Lillie, 1915; Mackintosh & Wheeler, 1929; Mead et al., 1982) and they have been used previously as an identification feature for minke whales (Dorsey et al., 1990; Gill et al., 2000). In this study, cookie-cutter bites occurred with an average severity of $l_i = 3.26$ mark/whale and a low loss rate (0.125 mark per individual per year), resulting in a very small probability of all marks being lost over time ($P < 0.001$ per whale per year). Moreover, the use of this mark in minke whale photo-identification studies may increase the amount of identified individuals by ~28% (in this study, from $p_i = 0.502$ to $p_i = 0.641$). We would suggest that cookie-cutter bites should be considered as an important secondary photo-identification feature for this species. However, as Durban et al. (2012) suggested, particular attention needs to be spent with these marks as they cannot be so easily visible in low and flat light conditions.

Recently the presence of sea lampreys have been found in Icelandic coastal waters (Figure 1D, Ólafsdóttir & Shinn, 2013) and thought to be linked to the increasing sea temperatures in this area (Astþórsson & Pálsson, 2006). In Iceland *Petromyzon marinus* is the only species of lamprey observed, first found attached to fishes (Jónsson & Jóhannsson, 2008), then to killer whales (Samarra et al., 2012), minke whales (Bertulli et al., 2012; Ólafsdóttir & Shinn, 2013) and for the first time in Icelandic waters it was recorded on white-beaked dolphins in this study (Figure 2I). The absence of cookie-cutter marks on white-beaked dolphins could suggest that white-beaked dolphins may not undertake long-distance movements towards lower latitudes.

Linear body marks

Skidding marks show how lampreys change position on the body of their host by moving their mouth (i.e. oral disc) sideways creating parallel scars (Shetter, 1949; Pike, 1951, figure 6; Hardisty & Potter, 1971), likely searching for an area where the flow of water is not too strong but at the same time

favourable to obtain blood (Nichols & Tscherter, 2011). More recently, a study from eastern Canada (Nichols & Tscherter, 2011), documented their presence on minke whales and two other studies from Iceland (Bertulli *et al.*, 2012, figure 3b, c; Ólafsdóttir & Shinn, 2013, figure 3b) reported these linear marks associated with lamprey bites. Few other studies reported the presence of confirmed cases of lamprey marks on dolphin species (e.g. pygmy sperm whale *Kogia breviceps* in McAlpine, 2009).

Rakes produced by conspecifics were only visible on white-beaked dolphins and were found to have a similar loss rate as similar minor wounds found on bottlenose dolphins (Lockyer & Morris, 1990; Wilson *et al.*, 1999). Their occurrence was shown to depend largely on differences between males and females (Scott *et al.*, 2005; Marley *et al.*, 2013) although this could not be tested here since sex could not be determined for the majority of the identified dolphins. Scrape marks were previously described in Icelandic white-beaked dolphins but their origin could not be determined by visual assessment alone but would require a biopsy in order to diagnose. The rate of loss was lower compared with those of other dolphin species (e.g. single linear scrape, Long-finned pilot whale *Globicephala melas* in Auger-Méthé & Whitehead (2007); scrape, Pink river dolphin *Inia geoffrensis* in Gomez-Salazar *et al.*, 2011), but much faster than those of beaked whales (Cuvier's beaked whales, loss rate 0.010 mark per individual per year; Rosso *et al.*, 2011). Fine scrapes had an average severity of $l_i = 2.59$ mark per individuals and a loss rate of 0.176, therefore the probability of having all the fine scrape marks disappear on an individual is quite low ($P = 0.01$ per individual per year). The use of this mark in photo-identification studies – in addition to fin outliners, injuries and fin patches – may increase the number of identified white-beaked dolphins by a further 9% (in this study, from $p_i = 0.772$ to $p_i = 0.848$). However, since the loss rate is greater than 0.05, the fine scrape mark should be considered only for recaptures spanning not more than 5 years.

Other marks

Cutaneous elevations were previously described in minke whales and white-beaked dolphins in Icelandic waters (Bertulli *et al.*, 2012). In the present study, blisters were found to be among the most abundant in minke whales ($a_i = 2.790$). However, due to their high gain and loss rates they are not recommended as reliable features to identify our whale or dolphin species.

No new individual whales were found carrying wart and herpes-like marks compared with previous results (Bertulli *et al.*, 2012) but in this study four more white-beaked dolphin cases of tattoo-like lesions were reported. None of these three marks was prevalent ($p_i \leq 0.013$) although herpes-like lesions were among the most severe marks in minke whales.

In conclusion, as noted for other cetacean species the most stable and reliable natural marks were notches and injury marks. In this study, we also identified other mark types that should be used for future photo-identification projects on these species. Particularly, cookie-cutter shark bites and fin patches resulted as reliable marks for minke whales and white-beaked dolphin, respectively. Since these marks were amongst the most prevalent in these species, their addition will significantly increase the number of identifiable animals and subsequently allow for more accurate estimates of population analysis.

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Paper II

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Vertebral column deformities in white-beaked dolphins from the eastern

North Atlantic

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Authors contribution. Provided data: CGB, AG, CCK, MHR, RD, PJ, EJV, GJS, RS. Analysed the data: CGB, AG, RD, PJ, GKS, RCS, AW. Wrote the paper: CGB, AG, AW.

Vertebral column deformities in white-beaked dolphins from the eastern North Atlantic

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ABSTRACT: Five white-beaked dolphins *Lagenorhynchus albirostris* with outwardly vertebral kyphosis, kyphoscoliosis or lordosis were identified during a photo-identification survey of over 400 individuals (2002–2013) in Faxaflói and Skjálfandi Bays, Iceland. In addition, 3 stranding reports from Denmark, The Netherlands and the UK were analysed, providing both external observation and post mortem details of axial deviations of the vertebral column in this species. Two of the free-ranging cases and 2 of the stranded specimens appeared to have an acquired disease, either as a direct result of trauma, or indirectly from trauma/wound and subsequent infection and bony proliferation, although we were unable to specifically identify the causes. Our data represent a starting point to understand vertebral column deformations and their implications in white-beaked dolphins from the eastern North Atlantic. We recommend for future necropsy cases to conduct macro- and microscopic evaluation of muscle from both sides of the deformed region, in order to assess chronic or acute conditions related to the vertebral deformations and cause of death.

KEY WORDS: Vertebral column deformity · Kyphosis · Kyphoscoliosis · Lordosis · White-beaked dolphin · *Lagenorhynchus albirostris*

INTRODUCTION

Axial deviations of the vertebral column have been reported in several delphinid species (e.g. Nutman & Kirk 1988, Wilson et al. 1997, Berghan & Visser 2000, Watson et al. 2004, Berrow & O'Brien 2006, Van Bressem et al. 2006, Bearzi et al. 2009, DeLynn et al. 2011, Robinson 2014). They can be classified as deformities arising from congenital causes (e.g. bottlenose dolphin *Tursiops truncatus* with congenital

scoliosis, DeLynn et al. 2011) or that have been acquired following trauma (e.g. bottlenose dolphin with kyphosis due to conspecific aggression, Watson et al. 2004).

Such deformities are usually described within 3 categories (adapted from Noden & deLahunta 1985): (1) kyphosis — abnormal deviation of the vertebral column in a sagittal plane when vertebrae are fixed to produce a curvature of the vertebral column with concavity on the ventral side; (2) lordosis (opposite to

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kyphosis) — abnormal deviation of the vertebral column in a sagittal plane when vertebrae are fixed to produce a curvature of the vertebral column with concavity on the dorsal side; (3) scoliosis — abnormal deviation of the vertebral column in a dorsal plane so the vertebrae are fixed to produce a lateral curvature, possibilities of left- and/or right-sided curvatures. These deformities are often present in varying combinations.

Although cases of kyphosis have been reported in white-beaked dolphins *Lagenorhynchus albirostris* (Slijper 1936, van Assen 1975, Kompanje 1995), a review of vertebral column deformities in this species is not available. Here we review 8 cases of such deformities in white-beaked dolphins from Iceland, the UK, Denmark and The Netherlands.

MATERIALS AND METHODS

Data and photographs of free-ranging white-beaked dolphins in Iceland were collected during an 11 yr photo-identification study (2002–2013) in Faxaflói (64° 24′ N, 22° 00′ W, southwest coast, April to September in 2002–2011 and year-long in 2012–2013) and Skjálfandi Bays (66° 05′ N, 17° 33′ W, northeast coast, May to October in 2002–2013). The study was conducted in both bays from commercial whale-watching boats (20–25 m in length and providing multiple tours each day lasting approximately 3 h each) in sea states of 0 to 3 on the Beaufort scale. Several digital cameras equipped with different zoom lenses (55–200 to 70–300 mm for Faxafloi Bay, 28–135 to 40–150 mm for Skjalfandi Bay) were used in both study areas. Images were taken in both JPG (300 pixels inch^{-1}) and RAW formats. Further details on the classification of ID marks and quality rating system used during data analysis are available in Bertulli et al. (2015).

The white-beaked dolphins photographed were assigned to 1 of 4 age classes (adult, juvenile, calf and neonate) based on the estimated size of each individual compared to the average length of an adult, and by association with conspecifics. Adult white-beaked dolphins measure between 2.4 and 3.1 m, with males typically longer than females (Reeves et al. 1999, Kinze 2008, Galatius et al. 2013). Shorter animals (~$\frac{2}{3}$ of adult length), either seen swimming alone or in the company of an adult (excluding those in infant position) were classified as juveniles (Bearzi et al. 1997, Karczmarski 1999, Mann & Smuts 1999); individuals (<$\frac{1}{2}$

of adult length) always sighted swimming associated with an adult were considered calves. Neonates (<$\frac{1}{3}$ of adult length: Collet & Duguy 1981, Kinze 2008) were recognized by discolouration resulting from foetal folds (Karczmarski 1999). Additionally, cases were collected from outside Icelandic waters through the e-mailing list MARMAM (Marine Mammals Research and Conservation Discussion) in 2013. Images and post-mortem report information were shared by the UK Cetacean Strandings Investigation Programme at the Zoological Society of London (Case 6) and the Seal Rehabilitation and Research Centre in Pieterburen (Case 7), The Netherlands. A full necropsy was not conducted for Case 8, although the specimen was measured and examined at the Fisheries and Maritime Museum in Esbjerg, Denmark. The vertebrae from Case 6 were assembled by the Natural History Museum in London after being prepared by manual de-fleshing followed by non-chemical, cold-water maceration. Standard anatomical nomenclature and directional terminology was used based on the Nomina Anatomica Veterinaria (International Committee on Veterinary Gross Anatomical Nomenclature 2012).

RESULTS

Non-systematic photo-identification surveys conducted in Faxaflói and Skjálfandi Bays resulted in 426 photo-identified individuals (C. G. Bertulli unpubl. data). Among them, 5 dolphins (7 images) showed axial deviations suggestive of vertebral column deformities (Table 1), with an overall prevalence of 1.2%. Dolphins in Cases 1, 2, 4 and 5 were observed and photographed on only 1 occasion, whereas Case 3 was observed and photo-identified on 3 separate occasions.

Case 1 was a juvenile observed in July 2011 in a group of 20 dolphins, showing a marked dorsal convexity caudal to the fin, most likely involving the lumbar and caudal vertebrae and indicating kyphosis. On the left side was a deep, healing wound with granulation tissue along the dorsal ridge. There was evidence of lordosis in the region of the wound. Multiple scars were visible on the flank, peduncle and at the base of the fin (Fig. 1a; ID nDEM41; Skjálfandi Bay).

Case 2 was a juvenile observed in July 2011 with lordosis followed by kyphosis swimming within the same aggregation of 20 dolphins in which Case 5 was photographed. It had a deep wound on the left side

Table 1. Eight cases of free-ranging (Cases 1–5) and stranded (Cases 6–8) white-beaked dolphins *Lagenorhynchus albirostris* with axial deformations of their vertebral columns. N_{case}: number of images taken for each case; TBL: total body length; Ukn: unknown; A: adult; J: juvenile; M: male

Case no.	N_{case}	Side photographed	Date of sighting/ stranding (dd/mm/yy)	Sex	TBL (cm)	Age class	Weight (kg)	Type of malformation
1	1	Left	23/07/2012	Ukn	Ukn	J	Ukn	Kyphosis and lordosis
2	1	Left	23/07/2012	Ukn	Ukn	J	Ukn	Kyphosis and lordosis
3	3	Left	07/11/2012	Ukn	Ukn	J	Ukn	Kyphosis and lordosis
4	1	Left	30/07/2005	Ukn	Ukn	A	Ukn	Kyphosis
5	1	Left	04/04/2012	Ukn	Ukn	J	Ukn	Kyphosis and lordosis
6	6	Both	22/02/1995	M	173	J	82.5	Kyphoscoliosis
7	22	Both	06/01/1999	M	184	J	85	Kyphosis
8	4	Both	06/04/2003	M	187	J	100	Lordosis
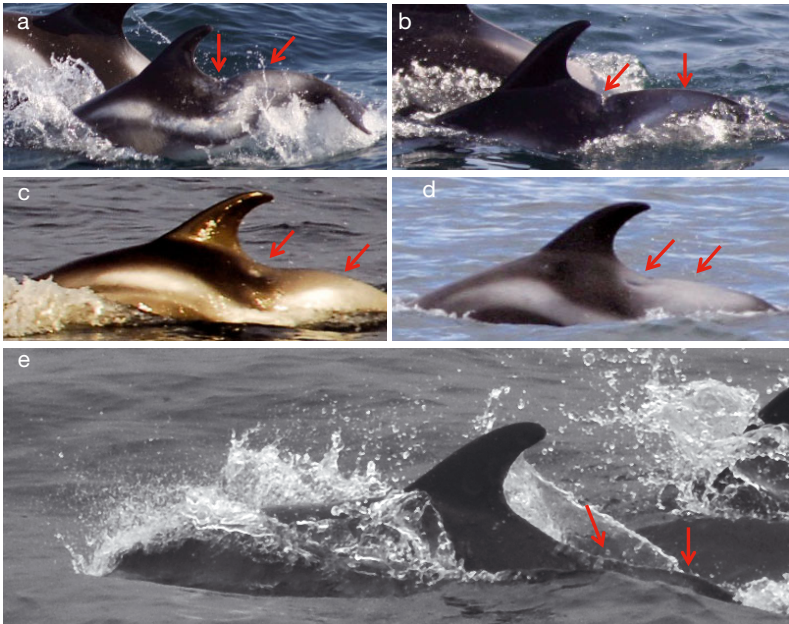
Fig. 1. Five cases of kyphosis and lordosis observed in white-beaked dolphins *Lagenorhynchus albirostris* in Icelandic waters. (a,b) Cases 1 and 2: juveniles with lordosis (left arrow) followed by kyphosis (right arrow) photographed in Skjálfandi Bay (photo credits: Zoe Burr, University of Iceland); (c) Case 3: juvenile with lordosis (left arrow) followed by kyphosis (right arrow) photographed in Faxaflói Bay (photo credit: Meggie Hudspith, University of Iceland); (d) Case 4: adult with kyphosis (right arrow) and a depressed oval wound (left arrow) photographed in Skjálfandi Bay (photo credit: Húsavík Whale Museum); (e) Case 5: juvenile with lordosis (left arrow) followed by kyphosis (right arrow) photographed in Faxaflói Bay (photo credit: Sarah Lawrence, University of Iceland)

transversely across the dorsal ridge, 10 cm caudal to the fin, caudal to which was the dorsal hump (Fig. 1b; ID nDEM42; Skjálfandi Bay).

Case 3 was a juvenile observed in November 2012 with lordosis and kyphosis. The dolphin was photo-graphically recaptured 9 mo later in Faxaflói Bay (August 2013), with the same deformity. There was an oval-shaped scar on the left flank caudal to the fin, which was only seen in November 2012 (Fig. 1c; ID nDEM85; Faxaflói Bay).

Case 4 was a juvenile observed in July 2005 with a dorsal convexity suggesting kyphosis. There was a depressed oval wound on the left flank caudal to the fin (Fig. 1d; ID nDEM84; Skjálfandi Bay).

Case 5 was a presumed juvenile photographed in April 2012 with a slight lordotic curvature of the vertebral column in the lumbo-caudal region followed by kyphosis (convex region in the peduncle) (Fig. 1e; not catalogued No. 2; Faxaflói Bay).

Three stranded white-beaked dolphin carcasses with vertebral deformities were reported from Europe: 1 from the UK, 1 from The Netherlands and 1 from Denmark (Table 1):

Case 6 was a juvenile male (total body length, TBL: 173 cm; 82.5 kg), stranded in a fresh condition (Code 2 sensu Rowles et al. 2001) in Bridlington, Humberside, England, on 22 February 1995. The dolphin was in a moderate nutritional condition (girth cranial to the fin of 112 cm; blubber thickness cranial to the fin, 11 mm mid-dorsal, 11 mm mid-lateral, 14 mm mid-ventral). The lateral extremities of the left and right flukes were cut off approximately 5 cm from the lateral tips, although the cut-off part of the right fluke was still attached to the rest of the fluke by a thin piece of epidermis. These wounds were consistent with mortality due to entrapment in fishing gear (e.g. Read & Murray 2000, Barco & Moore 2013). Midline to the caudal insertion of the fin and orientated at right angles to the long axis of the body was an older, deep, transverse chronic wound with underlying fibrosis of the blubber layer and surrounding epithelial nodular hyperplasia. The wound had a red base of granulation tissue surrounded by raised nodular epithelial tissue forming a deep cleft (Fig. 2a,b). The dorsal muscle mass was grossly normal. Skeletal preparation of the vertebral column revealed a marked kyphoscoliosis just caudal to the fin at the approximate level of the cutaneous wound. The transverse and spinous processes of the lumbar vertebrae were deformed, the transverse processes appearing progressively 'bent' dorsally and then ventrally, depending on the region of the vertebral column. Additionally, there was considerable periosteal reaction and new bone proliferation around the vertebral arches of the first few caudal vertebrae (Fig. 2c). There was no significant stenosis of the vertebral canal in the affected vertebrae. More caudally there was additional periosteal bone reaction on the ventral and ventrolateral aspects of the vertebral bodies of several caudal vertebrae, particularly Caudals 9, 10 and 11, without ankylosis, intervertebral disc compromise or erosion of the epiphyses (Fig. 2c). These changes were suggestive of severe osteomyelitis, perhaps originating from the dorsal wound.

Case 7 was a juvenile male (TBL 184 cm, 85 kg) with girth cranial to the fin of 105 cm. It stranded on the island of Terschelling, The Netherlands, on 6 January 1999 in a fresh condition (Code 2; Rowles et al. 2001). It had several skin marks and lacerations on the melon and lower jaw, possibly associated with fishery interactions (e.g. Read & Murray 2000, Barco & Moore 2013). The dolphin had a healed wound, approximately 2–3 cm deep caudal to the fin, immediately cranial to a prominent dorsal kyphotic hump (Fig. 3a,d). An unusual 'depression' was visible on the left flank ventrocaudal to the fin (Fig. 3c), and the vertebral anomalies extended from 17 cm caudal to the insertion of the fin to the level of the anus. The total length of the deformed region measured 72 cm.

Case 8 was a juvenile male (TBL 187 cm, 100 kg) stranded at Husby Klit, central west coast of Jutland, Denmark, on 6 April 2003. A full necropsy was not performed, and only the skull was recovered. Caudal to the fin there was a pronounced concavity indicative of lordosis (Fig. 4). Blubber thickness was only 14 mm, considerably less than the normal values for this time of year (25 mm, C. C. Kinze unpubl. data).

DISCUSSION

During this study, 8 white-beaked dolphins (5 free-ranging and 3 stranded) were observed with confirmed or probable kyphosis, lordosis or kyphoscoliosis. We were unable to specifically identify the cause in the 5 free-ranging dolphins from Iceland. However, 4 cases (free-ranging: Cases 1 and 2; stranded: Cases 6 and 7) showed indications of being caused by trauma, with linear (Figs. 1a,b & 2) or semi-circular (Fig. 3) shaped wounds caudal to the fin on the dorsal ridge. The remaining 3 free-ranging dolphins (Cases 3, 4 and 5) did not have any visible signs of previous trauma. In 2 stranded white-beaked dolphins from England (Case 6) and The Netherlands (Case 7), there was a clear association between trauma and kyphoscoliosis. These lesions may have led to osteomyelitis in Case 6.

The trauma that caused these deformities were most likely of anthropogenic origin. Deep oblique incision wounds across the dorsal lumbar region caudal to the fin in a free-ranging bottlenose dolphin (Fig. 1 in Dwyer et al. 2014) and killer whales (Fig. 1 in Visser 1999) have been suggested to be propeller strike wounds. Similar wounds in 8 Atlantic spotted dolphins *Stenella frontalis* (Fig. 3a in Luksenburg

Fig. 2. Juvenile male white-beaked dolphin *Lagenorhynchus albirostris* (total body length: 173 cm) with kyphoscoliosis stranded on the coast of England (Case 6). (a) Entire right lateral view, (b) detail of wound at caudal base of fin (arrow) and cut-off right fluke tip (arrowhead). (Photo credits: Zoological Society of London.) (c) Ventral view of the caudal vertebrae (2–12; cranial is to the right), showing periosteal bone reaction on the ventral and ventrolateral aspects of caudal vertebrae 9–11, which is suggestive of a severe osteomyelitis (arrow). (Photo credit: The Natural History Museum, London)
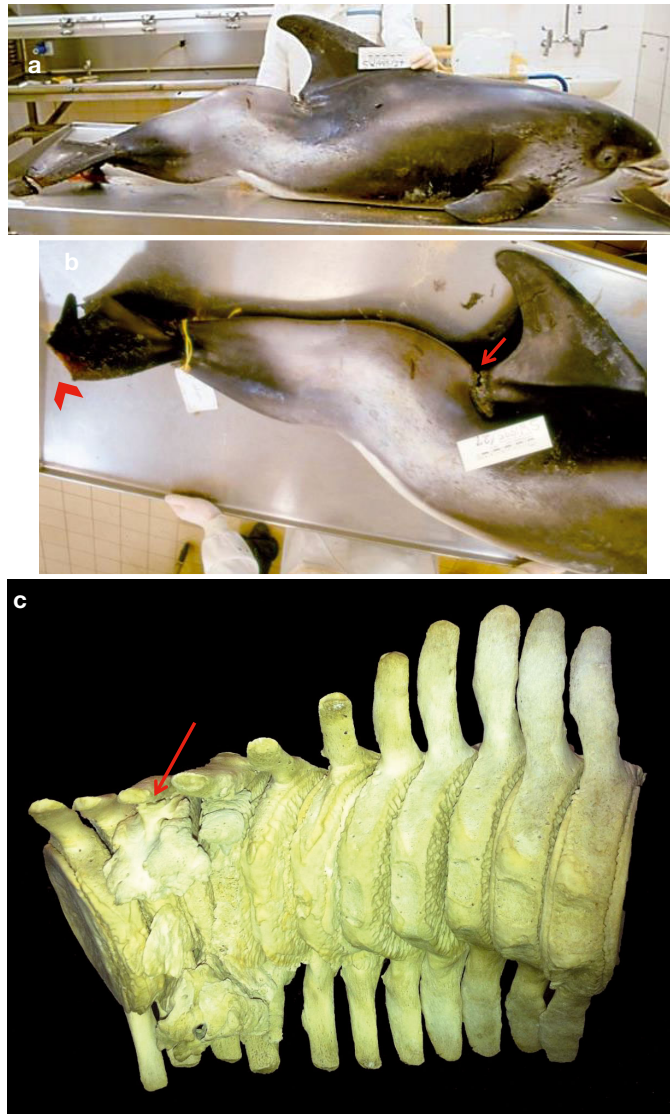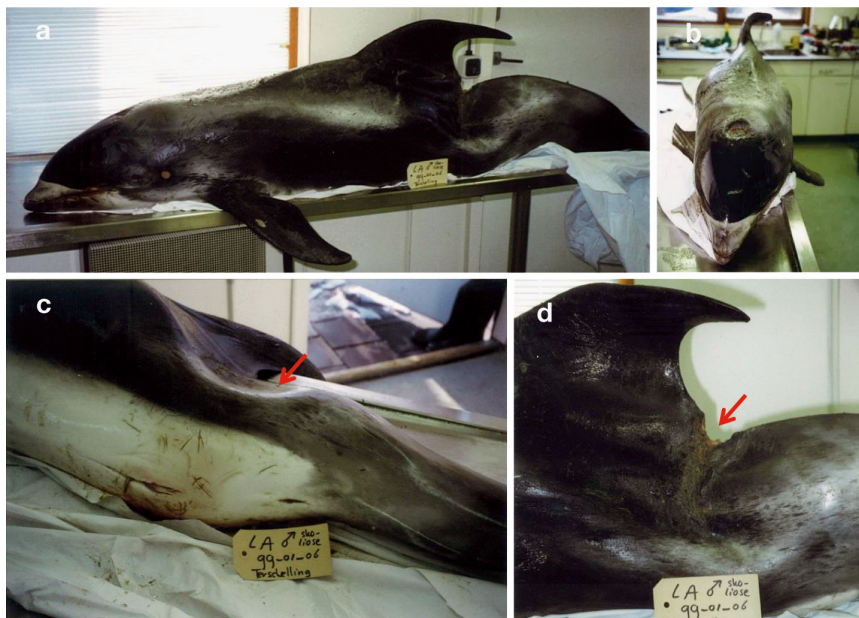
Fig. 3. Juvenile male white-beaked dolphin *Lagenorhynchus albirostris* (total body length 184 cm) with kyphosis stranded on the Dutch island of Terschelling (Case 7). (a) Entire left lateral view with wound caudal to the fin and visible kyphotic hump, (b) entire dorsal view with visibly deformed fin, (c) partial ventral view with visible 'depression' on left flank (arrow), (d) partial left lateral view with detail of wound at caudal base of fin (arrow). (Photo credits: Seal Rehabilitation and Research Centre, Pieterburen)

2014) and 4 Indo-Pacific bottlenose dolphins *Tursiops aduncus* (Fig. 4 in Kiszka et al. 2008) were reported to have anthropogenic origins (e.g. probably interaction with fishing gear). Additionally, propeller cut wounds were described on the dorsal ridge cranial to the fin in an Indo-Pacific humpback dolphin *Sousa chinensis* (Fig. 1 in Parsons & Jefferson 2000). With the exception of the wounds observed in the humpback dolphin, all lesions were located caudal to the fin and associated with deep incisions in the skin, as in our study. Furthermore, the wounds observed in our white-beaked dolphins were single, linear, approximately transverse marks similar to those reported in Atlantic spotted dolphins (Fig. 3a in Luksenburg 2014) and Indo-Pacific bottlenose dolphins (Fig. 4 in Kiszka et al. 2008), which is in contrast to the multiple roughly parallel curved, Z- or S-shaped or straight lacerations resulting from vessel interactions (Barco & Moore 2013). White-beaked dolphins are bycaught in gillnet and longline fisheries (Vík-

ingsson & Ólafsdóttir 2004, Pike et al. 2009) and in trawl nets (Kinze et al. 1997), but specific resultant wounds have not been reported. Whales, dolphins and porpoises swim by bending their vertebral column and moving the peduncle and flukes dorsoventrally (Fish & Hui 1991, Long et al. 1997, Pabst 2000). Thus, it is the interaction between muscles, tendons, vertebrae and ligaments which allows movement (Fish & Hui 1991, Long et al. 1997). As a result, severe consequences for the survival and movement of cetaceans may occur when a lesion compromises the elasticity or changes the normal arrangement of the vertebrae in the column (DeLynn et al. 2011).

In this study, 1 white-beaked dolphin (Case 6, Fig. 2) was affected by kyphoscoliosis. Although such a deformity is likely to impair normal locomotory functions, this dolphin had been able to catch food as indicated by the presence of fish bones in the oesophagus and remnants of partially digested fish in the fore-stomach compartment.

Fig. 4. Juvenile male white-beaked dolphin *Lagenorhynchus albirostris* (total body length 187 cm) with lordosis stranded on the coast of Denmark (Case 8). (a) Entire left lateral view with pronounced concavity in the dorsal lumbar area indicative of lordosis, (b) the pronounced S-shaped deformation of the vertebral column, (c) entire right lateral view with visible lordosis. A: anus; P: preputial opening. (Photo credits: C. C. Kinze)

Without more extensive data, it is difficult to assess the impact of these vertebral column abnormalities upon the survival of affected dolphins, although their longevity would probably be influenced by the extent of the abnormalities and the resulting complications (Berghan & Visser 2000, Haskins & Robinson 2007). There are some reported cases of individuals coping with a vertebral column deformity for several months, as in the case of a captive bottlenose dolphin surviving 12 mo with slight kyphoscoliosis (Watson et al. 2004) or a Risso's dolphin with abnormalities in the vertebral column estimated to have existed for several months but no longer than a year (Nutman & Kirk 1988). Berghan & Visser (2000) also reported a bottlenose dolphin (their Case 6 'Quasimodo') with 2 prominent kyphotic deformations which did not show any apparent changes for 8 consecutive years, while Haskins & Robinson (2007) identified a female bottlenose dolphin with slight lordosis which was photographically recaptured over 7 yr and gave birth

to calves twice during that time. A male common bottlenose dolphin with wounds on the fin caused by a boat propeller and scoliosis of the peduncle (acquired prior to the boat strike) was also reported to have survived at least 25 yr after the accident (Wells et al. 2008).

Our results indicate that vertebral column deformities occur in white-beaked dolphins and that some individuals may live with such anomalies for several months. With 426 identified white-beaked dolphins in Icelandic coastal waters (C. G. Bertulli unpubl. data), the overall prevalence of vertebral column deformities in this sample was 1.2%. However, an over- or under-identification of dolphins with deformities might have affected our results due to the lack of a formal stranding network in Iceland — a specimen with a deformity might not be regularly reported — and due to an increased observed elusive behaviour displayed by certain local individuals over the years (C. Bertulli pers. obs.). Prevalence of verte-

bral deformities varies among dolphin species and populations. Kyphosis and scoliokyphosis affected 0.18% (N = 545, 1990–1994) and 0.32% (N = 314, 1985–1989) of long-beaked common dolphins *Delphinus capensis* in Peru, respectively (Van Bressem et al. 2006), whereas axial conformational deformities in bottlenose dolphins from northeast Scotland was estimated at 4.9% (Fig. 2i in Wilson et al. 1997). A better understanding of the aetiology of these vertebral column deformities will be facilitated through appropriate necropsy examination of future cases, especially a microscopic evaluation of the musculature on either side of the deformed region(s).

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Paper III

Paper III

Color patterns in white-beaked dolphins (*Lagenorhynchus albirostris*)

from Iceland

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Color patterns in white-beaked dolphins (*Lagenorhynchus albirostris*) from Iceland

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ABSTRACT

The white-beaked dolphin (*Lagenorhynchus albirostris*) is a common species in temperate and sub-arctic North Atlantic waters. Yet, few studies have dealt with its natural complex pigmentation patterns, relying mainly on descriptions of dead specimens. Between 2002 and 2014, whale-watching trips in Iceland provided a platform of opportunity to collect a large body of photographs of free-ranging individuals from a single area of distribution for this species. Based on a total of 823 images, we analyzed pigmentation characteristics to describe 25 color pattern components and their ontogenetic variation, allowing us to discriminate between four age classes: adults, juveniles, calves and neonates. For the 25 components described, we used seven terms previously applied to white-beaked dolphins and 12 previously applied to other dolphin species. In addition, we proposed six new terms: mouth band, post-ocular crescent, semi-circular head blaze, peduncular ridge stripe, lateral patch and umbilical patch. We found the comparison of color pattern components to be useful in estimating maturity in white-beaked dolphins, a method that would benefit from the assessment of a geographically varied sample of freshly stranded specimens of known sex and age.

Key words: color pattern, pigmentation, speckling, ontogenetic variation, white-beaked dolphin, *Lagenorhynchus albirostris*, Iceland

Color patterns in mammals result from a combination of the availability, occurrence and distribution of pigmentation (*e.g.,* melanin) in the skin, hair and eyes (Fertl and Rosel 2002, Hofreiter and Schöneberg 2010). Cetaceans show a wide variety of color patterns, composed of separate components (Mitchell 1970), that change phenotypically from birth to adulthood (*e.g.,* Brodie 1989, Jefferson and Karczmarski 2001) and differ on an individual basis and with age, sex, maturity and stress (Perrin 2002, West and Packer 2002, Marcoux 2008, Wang *et al*. 2008). Their coloration may be useful in procuring food, defense (*e.g.,* camouflage) and communication, recognition of species, age, and sex (Yablokov 1963, Perrin 2002, Caro *et al*. 2011) and reproductive status (*e.g.,* speckling, as summarized in Krzyszczyk and Mann 2012). Coloration can be used in research to identify species (Perrin 2002, Caro 2005), estimate age class (*e.g.,* Myrick *et al*. 1986, Chivers and Myrick 1993, Kryszczyk and Mann 2012) and study geographical variation and population differentiation (*e.g.,* Evans *et al.* 1982, Baird and Stacey 1988).

White-beaked dolphins (*Lagenorhynchus albirostris*) are commonly sighted in Icelandic waters (Gunnlaugsson *et al.* 1988, Pike *et al.* 2009, Bertulli *et al.* in press), and have an abundance estimate of 31,653 animals (95% CI:17,679-56,672) based on North Atlantic Sightings Surveys

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(NASS) conducted from 1986–2001 (Pike *et al.* 2009). While the body coloration of white-beaked dolphins is known to be highly variable (Harmer 1927, Mercer 1973, Camphuysen 1991, Ree 1994), it has never been the topic of a formal study. Here, we use an extensive sample of photographs of free-ranging white-beaked dolphins collected in three areas around Iceland to describe the components that make up the color patterns and, where possible, ascribe them to ontogenetic variation.

<div align="center">MATERIAL AND METHODS</div>

Data collection

Surveys were conducted during boat-based whale-watching tours from June 2002 to March 2014 in Faxaflói Bay (4,440 km^2 in SW Iceland) and Skjálfandi Bay (1,100 km^2 in NE Iceland) (Bertulli *et al.* 2012), *ca*. 600 km apart. Images were also provided by colleagues conducting fieldwork in Breiðafjörður (W Iceland) (Fig. I). Observations were made during Beaufort 0-3 sea conditions, mainly during spring and summer months. Images were collected during each encounter with white-beaked dolphins, along with data on group size, composition and behavior. For photo-identification purposes, images of body pigmentation were acquired in addition to dorsal fin and skin marks to maximize the number of features available to distinguish individuals. Photographs were taken from 2-7 m above sea level using digital SLR cameras primarily equipped with 70-300 mm zoom lenses. To obtain useful images, the dolphins were photographed from </=100 m.

Data analysis

The white-beaked dolphins photographed were assigned to one of four age classes (adult, juvenile, calf and neonate, Fig. II) by estimating the relative body length of each individual, and by association with conspecifics. Adult: length ranges from 2.4-3.1 m (Dong *et al.* 2006, Kinze 2002, Galatius *et al.* 2013). Juvenile: about 2/3 to 3/4 of adult length, swimming independently or associated with an adult (Bearzi *et al.* 1997, Karczmaski 1999, Mann and Smuts 1999). In a sample of white-beaked dolphins from the North Sea, sexual maturity was attained at total lengths between 2.30- 2.55 m in males and 2.32- 2.38 m in females (Galatius *et al.* 2013), while Jansen *et al.* (2010, 2013) reported that immature individuals from Dutch waters measured between 1.70- 2.10 m. Calf: less than 2/3 of adult length and consistently escorted by an adult (Shane 1990, Karczmarski 1999, Karczmarski *et al.* 1999; Constantine 2001). Neonate: less than 1/2 of an adult length, usually with fetal folds or pale fetal lines resulting from the folds (Bearzi *et al.* 1997, Stockin *et al.* 2009), predominantly swimming in echelon position by an adult's mid-lateral flank, Gubbins *et al.* 1999); reported to be 1.1-1.2 m in length (Fraser 1974, Collet and Duguy 1981, Kinze 2009). It was difficult in the field to distinguish between neonates and very young calves without fetal lines, so the latter were lumped into the neonate age class.

Adult males are generally larger than females (Reeves *et al.* 1999, Kinze 2002, Galatius *et al.* 2013), however, their lengths overlap (*e.g.,* Galatius *et al.* (2013) reported total body lengths of 22 sexually mature males as 2.52-2.90 m, and 17 mature females as 2.42-2.65 m). Therefore, it was not possible to positively determine the sex of most dolphins photographed, and this study does not attempt to describe differences in coloration between males and females of any age class.

Images were rated for photographic quality based on proximity, sharpness and luminosity, using a quality rating system (Q) from the lowest, Q1, to the highest, Q6 (Elwen *et al.* 2009, Gowans and Whitehead 2001, Rosso *et al.* 2011). Two image datasets were analyzed for this study. The first consisted of 408 Q≥4 images used to evaluate color pattern components across all age classes, except for the dorsal fins of adults, which were evaluated from a second dataset of 415 ≥Q5

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images of dolphins individually photo-identified by dorsal fin edge marks (2002-2010 data in Bertulli *et al.* in press; Bertulli unpublished 2011-2013 data).

The probability of recapturing a previously photographed individual was relatively low due to the fact that the number of Icelandic coastal shelf white-beaked dolphins is very large in comparison to the survey datasets, and individuals are highly mobile, with potentially extensive home ranges (Rasmussen *et al.* 2013; Bertulli *et al.* in press). Supporting this, white-beaked dolphin photo-identification data collected from 2002 to 2010 show low annual re-sighting proportions of 21.4% in Faxaflói Bay and 1.7% in Skjálfandi Bay, and the rate of discovery curves continued to rise steadily (Bertulli *et al.* in press). To reduce sampling auto-correlation of non-identified individuals, only images taken during a single whale-watching tour per day were considered.

RESULTS

The 408 images in the first dataset captured 571 individual white-beaked dolphins that showed one or more color pattern components. We assigned them to the following age classes: 437 adults, 109 juveniles, 14 calves, and 11 neonates. Quantities presented below for the occurrence frequencies of the color pattern components are based on these 571 individuals, with the exception of the fin patch, for which we used the photo-identified second dataset of 415 marked dolphins. The majority of adults (62.7%, n=274) showed unique dorsal fin edge marks. We described 25 color pattern components, using seven terms previously applied to white-beaked dolphins and 13 previously applied to other dolphin species (Perrin 1970, Mitchell 1970, Perrin 1972, Mercer 1973, Webber 1987, Perrin 1997, Bertulli *et al.* 2015). In addition, we proposed five new terms (see Table 1 for a list of all components, Fig. III for components exhibited by adults).

1. Beak Blaze (BB)

Literature: Described in multiple other dolphin species as the coloration visible on the upper surface of the beak (Mitchell 1970, Fig. 2). The species name *'albirostris'* is Latin for 'white beak,' but not all individuals show a white beak. The beak blaze is variably white, and may appear light gray or gray, or include clusters of black spots giving it a mottled coloration (Fraser 1946, 1953, Jonsgård 1962, Mercer 1973, van Bree and Smeenk 1982, Fig. 3, Smeenk 1986, Fig. 3, 1989 Fig. 7, 1995 Fig. 1), but it is never all black (Kinze 2002).

This Study: Of the 56 adults for which the beak could be evaluated, 52% (*n*=29) had a dark gray beak with a white tip (Fig. 1A), 32% (*n*=18) had a beak with a pink tip and dark gray areas on a white background (Fig. 1B), 9% (*n*=5) had a beak with a white tip and dark gray areas on a white background (Fig. 1C). Only 7% of adults (*n*=4) had completely white beaks (Fig. 1D). In 32 juveniles, the beak was all light gray in 41% (*n*=13, Fig. 2A), gray with dark gray areas in 31% (*n*=10, Fig. 2B), or all dark gray in 28% (*n*=9, Fig. 2C-D). The beak was completely white in 4 of the 7 calves (Fig. 3A), gray in 2 (Fig. 3E), or gray with clusters of dark gray spots in one (Fig. 3B-C). The beak appeared to have a yellow wash in all neonates (*n*=6, Fig. 4A-B). In 52% of adults (*n*=29, Fig. 1A-B), 28% of juveniles (*n*=9, Fig. 2A-C) and 3 of 7 calves, a thin white band was visible immediately above the crease where the rostrum meets the forehead. This white streak appeared to be the beak blaze extending onto the forehead (Fig. 3C).

2. Lip Patch (LipP)

Literature: Described in multiple other dolphin species as two dark patches visible laterally and ventrally coloring the lower jaws (Mitchell 1970, Fig. 13, Smeenk 1986, Fig. 3, 1989, Fig. 7). Each patch covered an area from near the tip of the beak to just anterior to the gape, forming the anterior margin of the mouth band.

This Study: Lateral (Fig. 1A, Fig. 1C) and ventral views (Fig. 1L-M) of 62 adults showed that 94% (*n*=58) had dark gray coloration near the tip of the beak, and a lighter gray patch extending posteriorly and ventrally from near the midline of the lower jaw to near the end of the gape, where it ended at the mouth band. Only 6% (*n*=4) of adults did not show any lip patch (Fig. 1C). In 31 juveniles, 61% (*n*=19) had no lip patch visible, but showed a dark gray spot at the tip of the beak (Fig. 2A), and 39% (*n*=12) had dark gray lip patches similar to adults (Fig. 2C-D). Out of 7 calves, 4 had white lower jaws (without a visible lip patch, Fig. 3C, Fig. 3F), and the other 3 had light gray lip patches (Fig. 3A-B, 3E). No neonates (*n*=6) had lip patches; the area was white with a yellow wash, Fig. 4A-B.

3. Mouth Band (MB)

Literature: Images of this feature were found in the literature (Smeenk 1986, Fig. 3), but not described.

This Study: We propose the new term 'mouth band' for this component. It was a diagonal white band from the corner of the mouth, or gape, to the throat, blending into the white color of the throat. The mouth band is created by the lip patch and the dark gray area on the beak blaze forming the anterior edge of the band, and the flipper stripe (if present) or the gray of the sides below the eye forming the posterior edge of the band. Of the 53 adults for which the beak could be evaluated, 96% (*n*=51, Fig. 1A, Fig. 1D) had a visible mouth band. In juveniles, 9 of 11, which included all of those with the lip patch component, (Fig. 2C-D, 2I-J) showed a mouth band. Of 7 calves, only one (Fig. 3E), had a mouth band because it had lip patches. In the other 6 calves, all neonates (*n*=6, Fig. 4A-B), and 2 juveniles (Fig. 2A-B), the band was not visible because the light color of the beak and absence of lip patch caused this feature to blend into the white throat coloration.

4. Eye Patch (EP)

Literature: Frequently light gray, delimited by a narrow, off-white to paler gray circle around the perimeter (van Bree and Smeenk 1982, Fig. 3, Smeenk 1986, Fig. 3, Smeenk 1992, Fig. 4). Described in white-beaked dolphins, the term is used by Perrin (1970), Mitchell (1970) and most recently by Reeves *et al.* (1999), while Perrin (1997) uses the term 'eye spot' as a synonym of 'eye patch.'

This Study: A light gray circle surrounded the eye in all individuals of every age class: adults (*n*=74, Fig. 1B-D), juveniles (*n*=25, Fig. 2B-D), calves (*n*=7, Fig. 3A, Fig. 3E) and neonates (*n*=6, Fig. 4A).

5. Eye stripe (ES)

Literature: Described in white-beaked dolphins by Perrin (1997) as 'a dark-gray band of medium width extending forward from a large dark eye patch and disappearing into the white on the apex of the melon above the rostrum, and as a bordering lighter zone' (Fraser 1946, Jonsgård 1962, van Bree 1970, Mercer 1973, Leatherwood *et al*. 1976).

This Study: The eye stripe was visible in all individuals of every age class: adults (*n*=18, Fig. 1A), juveniles (*n*=26, Fig. 2D), calves (*n*=7), and neonates (*n*=6, Fig. 4A-B). When the beak was gray or dark gray, the white narrow remnant of beak blaze on the melon contrasted with the darker eye stripe immediately above it (Fig. 1F, Fig. 2D). In all calves, the eye stripe was visible as a dark gray narrow stripe extending from the eye patch and ending above the rostrum (Fig. 3A-C).

6. Post-ocular crescent (POC)

Literature: Visible in photographs (Mercer 1973, Fig. 1) and early illustrations (Cunningham 1876, Camphuysen *et al.* 2008, Fig. 11), this component was described by Mercer (1973), but not named.

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This Study: We propose the new term 'post-ocular crescent' for this component. In all adults (*n*=46), it was a crescent-shaped feature behind the eye with dorsal and ventral arms or chevrons pointing posteriorly (Fig. 1F, Fig. 1I). The dorsal arm variably merged into the anterior end of the dorsal flank blaze, and was located below the posterior extension of the blowhole chevron. The ventral arm of the post-ocular crescent extended posteriorly above the pectoral flipper and connected to the abdominal field of the lower flanks to form a near continuous gray feature in adults with gray abdominal fields. In all adults, the post-ocular crescent filled in with light gray color until the edges began to soften and lost shape. It was visible on all juveniles (*n*= 39, Fig. 2A-D) and calves (*n*=8, Fig. 3A, Fig. 3C). In all neonates (*n*=6), a faint version of the post-ocular crescent was visible (Fig. 4A, Fig. 4D), which increased and became more defined in calves and juveniles. In these latter two age classes, the post-ocular crescent extended posteriorly with dorsal and ventral tapering arms on the thoracic area, but did not connect to the lateral patch.

7. Flipper Stripe (FS)

Literature: Described in multiple other dolphin species, Mitchell (1970) uses the term 'flipper stripe,' while Perrin (1970) uses 'flipper band'. It is a line of light to dark gray color clearly visible from the corner of the mouth to the anterior insertion of the pectoral flipper (Fraser 1953, Fig. 1, Smeenk 1986, Fig. 2, Fig. 3, Mitchell 1970).

This Study: A dark gray stripe connected the corner of the mouth with the pectoral flipper. Of the 37 adults for which the flipper stripe could be evaluated, 51% (*n*=19, Fig. 1A, Fig. 1C, Fig. 1M) had a partially visible flipper stripe, and on 49% (*n*=18) it was fully visible where the dark gray of the upper part of the body formed a sharply-defined border with the white throat chevron (Fig. 1F). In all juveniles (*n*=30, Fig. 1A-E), calves (*n*=8, Fig. 3A-B, Fig. 3E) and neonates (*n*=5, Fig. 4A), the flipper stripe was a narrow dark gray band. In juveniles only, the flipper stripe cut through the pale color of the future throat chevron isolating a small white area above the flipper stripe (Fig. 2B-D).

8. Blowhole Chevron (BC)

Literature: Described in white-beaked dolphins (Mitchell 1970) as crescent-shaped off-white feature with an apex mostly posterior to the blowhole, at times encompassing it, with chevron blazes pointing posteriorly on each side, terminating without merging into the anterior end of the ventral flank blaze (Mitchell 1970, Fig. 13, Fig. 14, Smeenk 1986, Fig. 2, Smeenk 1992, Fig. 3).

This Study: All adults (*n*=68) had a nearly symmetrical white feature that extended as chevrons from the posterior edge of both sides of the blowhole towards the anterior end of the dorsal flank blazes, but not connected to them (Fig. 1F-I). The full blowhole chevron was not visible in juveniles (*n*=37, Fig. 2E) and calves (*n*=6, Fig. 3B). Instead, diffuse light gray pigment was present on the head in the area where it became the chevron arms on adults (Fig. 2A, Fig. 2C, Fig. 2E, Fig. 3B-C). Additionally, the semi-circular head blaze occupied some of the same area on juveniles (Fig. 2A, Fig. 2C, Fig. 2F), but not calves, and also appeared to be replaced by the blowhole chevron in adults. In 2 of the 6 calves (Fig. 3C) and all neonates (*n*=7, Fig. 4A-E), only a yellow-tinged helmet was visible on the head.

9. Semi-circular Head Blaze (SCHB)

Literature: Images of white-beaked dolphins showing this feature appear in Jefferson *et al.* (2008), but it is not described.

This Study: We propose the new term 'semi-circular head blaze' for this component. A thin semi-circular light gray blaze on each side of the blowhole curved laterally and ended just before making contact with the dorsal flank blaze in all juveniles (*n*=36, Fig. 2A, Fig. 2C, Fig. 2F, Fig.

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5D), but was absent on all adults (*n*=68), calves (*n*=6) and neonates (*n*=7). The semi-circular head blaze on juveniles appeared to be an augmentation of the light gray color that calves exhibited, and could be a precursor to the complete blowhole chevron on adults. Figure 3A shows light gray patches on the head of an individual in transition from calf to juvenile, which is likely a fading helmet, rather than a developing blowhole chevron. Note the yellow-tinged light gray helmet that would be consistent with this age class's coloration and the transition sequence of head color in white-beaked dolphins.

10. Helmet (H)

Literature: Described as a white 'helmet' in adult *Delphinus* species (Stockin and Visser 2005).

This Study: A yellow-tinged light gray helmet covered the left and right side of the blowhole in 3 of 6 calves (Fig. 3A) and all neonates (*n*=7, Fig. 4A-E), disappearing as they transitioned to the juvenile age class.

11. Fin Patch (FP)

Literature: Irregular off-white patch on the dorsal fin, frequently extending a short distance onto the back, located from the leading edge to about mid-fin, and not reaching the tip or posterior edge of the fin (Fraser 1953, Fig. 1, Mercer 1973, Fig. 1). Although not specifically mentioned, this feature is evident in Mitchell (1970, Fig. 1, Fig. 12). It was termed 'fin patch' in dusky dolphins (*Lagenorhynchus obscurus*) and Pacific white-sided dolphins (*L. obliquidens*) by Webber (1987), and described as 'a zone of light coloration found on the dorsal fin of some *Lagenorhynchus.'*

This Study: The fin patch was off-white, often with a hatched, sometimes spotted, appearance. Small dots (Fig. 1I), not to be confused with dark ovoid speckles (see speckling component below), appeared where the patch merges with the dark gray color of the fin. The patch was located near the leading edge to about mid-fin, reaching little more than half way to the tip, often extending onto the back below the base of the fin. Out of 415 photo-identified adults, 30% (*n* = 125) had a fin patch (Fig. 1I-K, Fig. 5C). Juveniles (*n*=70), calves (*n*=11) and neonates (*n*=9) did not have the fin patch.

12. Spinal Field (SF)

Literature: Described in multiple other dolphin species in Mitchell (1970), it is a dark gray field on the back and sides, from the end of the blowhole chevron behind the blowhole and between the chevron arms posterior to the dorsal fin, extending ventrally to the arcing diffuse edge of the dorsal flank blaze. The spinal field reaches its greatest ventral extension on the flank below the dorsal fin, and extends posteriorly a short distance as a rounded wedge to the location where the dorsal flank blaze and peduncular saddle connect. The spinal field usually includes a small dark area immediately behind the posterior insertion of the dorsal fin (Fraser 1946, Fig. 6, Mitchell 1970, Fig. 13, Mercer 1973).

This Study: The spinal field was very dark gray in all individuals of every age class: adults (*n*=171), juveniles (*n*=68), calves (*n*=11), and neonates (*n*=9). In adults, the spinal field had the same dark gray color as the dorsal fin (Fig. 1F-H, Fig. 1N). In some juveniles, when the peduncular saddle was darker gray but of a lighter gray tone than the spinal field and dorsal fin, the spinal field appeared to extend further back on the peduncle (Fig. 2G), as was the case for all calves and neonates (Fig. 3C-D, Fig. 4C, Fig. 4E).

13. Peduncular Saddle (PS)

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Literature: Applied to white-beaked dolphins in Mitchell (1970), it is a light gray pigmentation covering the area posterior to the dorsal fin, forming a saddle on the peduncle (Fraser 1953, Fig. 1, Mitchell 1970, Fig. 13, Reeves *et al.* 1999).

This Study: A light gray field posterior to the dorsal fin extended ventrally from near the peduncle ridge in a wide swath on the flanks to the flank patch. In all adults (n=133), the peduncular saddle was light gray (Fig. 1E-F, Fig. 1I, Fig. 1N), the same color as the flank patch and dorsal flank blaze. Of 64 juveniles, 95% (n=61) had a peduncular saddle that was darker gray than the adult coloration, but overall lighter than the dorsal fin and spinal field (Fig. 2G, Fig. 2K). The other 3 juveniles exhibited the light gray peduncular saddle coloration of adults (Fig. 2H). In all calves (n=9) and neonates (n=7), the peduncular saddle was not discernible because the entire area had the same dark coloration of the dorsal fin and spinal field (Fig. II, calf; Fig. 3D, Fig. 4C-E). In 5 of the neonates, yellow patches were also visible in the area posterior to the fin (Fig. 4C-E).

14. Peduncular Ridge Stripe (PRS)

Literature: Not described in the literature.

This Study: We propose the new term 'peduncular ridge stripe' for this component. This thin dark gray stripe along the dorsal midline from just posterior to the fin to the flukes was visible in all adults (n=12, Fig. 1E) and juveniles (n=4, Fig. 2K). This area was not captured in photographs of calves and neonates, so image analysis of this component was not possible for these age classes. The peduncular ridge stripe may result from the peduncular saddle patches on both sides not meeting at the ridge of the peduncle, leaving the dark pigmentation of the spinal field and fin visible as a thin line on the ridge.

15. Dorsal Flank Blaze (DFB)

Literature: Applied to white-beaked dolphins in Mitchell (1970), it is a light gray blaze originating from the flank patch extending dorso-anteriorly below the dorsal fin, bisecting the spinal field, becoming the dorsal margin of the dark thoracic field. It ends near, but without connection to, the posterior end of the blowhole chevron and blends with the top of the dorsal arm of the post-ocular crescent (Mitchell 1970, Fig. 13).

This Study: All adults (n=63) had a wide variable light gray blaze that connected to the flank patch posteriorly, approached the end of the blowhole chevron anteriorly but did not connect to it, and rose high on the spinal field, merging with the dorsal arm of the post-ocular crescent (Fig. 1F-I, Fig. 1M-N). In one anomalously dark-pigmented adult, the dorsal flank blaze was reduced and did not contrast with the dark gray body coloration above or below (Fig. 1O). The dark spinal and thoracic fields are in contact with each other, resulting in a continuously dark area on a portion of the sides of the chest to the top of the back. The dorsal flank blaze was not formed in juveniles (n=51, Fig. 2I) and calves (n=9, Fig. 3A), but in its place was a lateral patch. The dorsal flank blaze and lateral patch were absent in all neonates (n=7).

16. Thoracic Field (TF)

Literature: Described in multiple other dolphin species in Mitchell (1970), including dusky dolphins for which the term 'thoracic field' is used (Cipriano and Webber 2010). It is a dark gray area in all but neonates, comparable in color to the spinal field, encircled by light features: flank patch, dorsal flank blaze, post-ocular crescent and abdominal field. It is located in approximately the same area as the dark thoracic area on the hourglass dolphin (*Lagenorhynchus cruciger*) and the 'thoracic patch' in the short and long-beaked common dolphin (*Delphinus delphis* and *D. capensis*) (Mitchell 1970, Fig. 2, Fig. 13).

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This Study: A dark gray area that matched the spinal field and dorsal fin coloration was visible in all adults (n=51, Fig. 1F, Fig. 1L). In all juveniles (n=42) and calves (n=6), the lateral patches, precursors of the dorsal flank blaze, began to separate the thoracic field from the spinal field. In 3 neonates, a faint yellow-tinged area was visible as a precursor to the dark gray thoracic field of adults (Fig. 4D-E).

17. Lateral patch (LP)

Literature: Light gray patches on the flank and peduncle are visible in photographs (Mercer 1973, Fig. 1, Jefferson *et al*. 2008) and early illustrations (Cunningham 1876, Camphuysen *et al*. 2008, Fig. 11). Bertulli *et al*. (2015) refers to these as 'hypo-pigmented patches.'

This Study: We propose the new term 'lateral patch' for this component because it is more descriptive and less suggestive of an anomalous condition than 'hypo-pigmented patches.' Light gray patches infused with speckling (Fig. 2C, 2F, 2G-H, Fig. 5D) occurred on the flank, peduncle and thorax of all juveniles (n=81). Lateral patches were not present in adults (n=181) but they appeared on all calves (n= 9, Fig. 3A) and neonates (n= 7, Fig, 4C-E). In 4 of 7 neonates, a faint yellow-tinged area was visible as the precursor to the lateral patch of juveniles (Fig. 4C-E), which in turn was a precursor to the adult's dorsal flank blaze that replaced the juvenile's lateral patch.

18. Flank Patch (FP)

Literature: Described in multiple other dolphin species in Mitchell (1970), it is a variable light gray area on the side of the peduncle beneath the peduncular saddle, extending posteriorly towards the flukes. It is a low, wide feature on the peduncle and flank that rises high enough on the side to contact the ventral part of the light gray peduncular saddle, and continues anteriorly as the dorsal flank blaze (Mitchell 1970).

This Study: The flank patch appeared light gray in all adults (n=31, Fig. 1F). All juveniles (n=53) showed a speckled lateral patch in this area that enlarged to become the flank patch in adults (Fig. 2I). Of the 2 calves, none had a flank patch (Fig. 3D). This area was not captured in photographs of neonates, so image analysis was not possible for that age class.

19. Speckling (S)

Literature: Speckling has been reported in the pan-tropical spotted dolphin (*Stenella attenuata*), Atlantic spotted dolphin (*Stenella frontalis*), Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), and *Tursiops* spp. (*e.g.,* Ross and Cockcroft 1990, Smolker *et al*. 1992, Perrin *et al*. 1994; Perrin and Hohn 1994, Krzyszczyk and Mann 2012). Speckles are described in the literature (Fraser 1946, Fig. 6, Mercer 1973, Fig. 1), and visible in photographs and early illustrations (Cunningham 1876, Kinze 1993, Camphuysen *et al*. 2008, Fig. 11). The term 'speckling' was recently proposed as a component in a study of white-beaked dolphins (Bertulli *et al*. 2015).

This Study: Speckling appeared as dark ovoid spots behind the eye, sometimes higher than the eye, and extending down to the pectoral flipper. This feature was seen in all juveniles (n=81, Fig. 2C-D, Fig. 2I, Fig. 5D) and calves (n=10, Fig. 3A-B), but not detected in adults (n=140) and neonates (n=9). Speckling was also visible along the flank patch, lateral patch and dorsal flank blaze, as well as on the peduncular saddle, in animals that appeared to be transitioning from juvenile to adult, when these components were not yet fully developed. Speckles were dark gray, contrasting with areas of lighter coloration, including the ventral surface, lateral patches, and the light gray of the flank patch and peduncular saddle. All juveniles (Fig. 2G, Fig. 2I) and calves (Fig. 2A) showed lateral patches accompanied by speckling.

20. Throat Chevron (TC)

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Literature: Described in long-finned and short-finned pilot whales (*Globicephala melas* and *Globicephala macrorhynchus*) and false killer whales (*Pseudorca crassidens*) (Mitchell 1970, Fig. 9). In adults, it is visible as a broad chevron, including the throat and upper thorax between the pectoral flippers (van Bree and Smeenk 1982, Fig. 3, Smeenk 1986, Fig. 3, Kinze 2002). The throat chevron is analogous to the white feature located more posteriorly in Risso's dolphin (*Grampus griseus*) and northern right whale dolphin (*Lissodelphis borealis*) (Jefferson *et al*. 2008).

This Study: A white chevron covered the throat, extending posteriorly between the pectoral flippers when the abdominal field was a contrasting gray or dark gray. The throat chevron was seen in all adults (*n*=13, Fig. 1F, Fig. 1L-M), 4 of 7 juveniles (Fig. 2I) and 1 of 2 calves (Fig. 3E). This area was not captured in photographs of neonates, so image analysis was not possible for that age class.

21. Chin Blaze (CB)

Literature: Chin blaze is an anterior extension of the throat chevron, as described in pilot whales (*Globicephala*) and right whale dolphins (*Lissodelphis*) in Mitchell (1970). A photo of a white-beaked dolphin showing this feature appears in Jefferson *et al*. 2008.

This Study: It was visible when gray lip patches were present, and appeared as a forward extension of the white throat chevron. Out of 62 adults, 94% (*n*=58) had a visible chin blaze (Fig. 1L-M). Of 31 juveniles, only 39% (*n*=12, Fig. 2I-J) showed a chin blaze, as did 3 of 7 calves (Fig. 3E). It was located in approximately the same area as on long-beaked common dolphin, striped dolphin (*Stenella coeruleoalba*) (Jefferson *et al*. 2008) and common dolphin (Mitchell 1970, Fig. 1). This area was not captured in photographs of neonates, so image analysis was not possible for this age class.

22. Abdominal Field (AF)

Literature: Applied to white-beaked dolphins in Mitchell (1970), the term 'belly' is also used to describe this grayish color component (Kinze 2009). Normally, the entire abdominal area is white in younger individuals (Kinze 2002). Commonly, adults exhibit wide gray bands lateral to the narrow longitudinal white band on the medial abdomen. These bands become constricted as they continue above the pectoral flipper and connect to the ventral arm of the post-ocular crescent. The abdominal field on white-beaked dolphins is comparable to the abdominal field that rises dorsally from the belly onto the side and face of dusky dolphins (Cipriano and Webber 2010, Fig. 2, Fig. 2A). Alternately, the gray abdominal field can be viewed as a posterior and ventral extension of the ventral arm of the post-ocular crescent. In either interpretation, the gray bands form the ventral borders of each thoracic field, and establish the narrow midventral streak on the abdomen reported by Mitchell (1970) for long-finned pilot whale.

This Study: In all adults (*n*=13), the abdominal field was gray (Fig. 1L). In 4 of 7 juveniles, the abdominal field was pale gray (Fig. 2I), and in the other 3 individuals the area was white, indicating that no abdominal field was present (Fig. 2J). The abdominal field was pale gray on one of two available calves (Fig. 3E), and white (no abdominal field) with patches of yellow film on the other (Fig. 3F). This area was not captured in photographs of neonates, so analysis of this component was not possible for this age class. Figure 1N shows a pale gray abdominal field on an animal in transition between juvenile and adult age classes. This individual presents features of both adults (thoracic field, filled in post-ocular present, dorsal flank blaze) and immatures (flipper stripe, pale gray abdominal field and inconspicuous midventral streak with a pale whitish throat chevron color above the band).

23. Midventral Streak (MS)

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Literature: Described in long-finned and short-finned pilot whales, false killer whales, Risso's dolphins and northern right whale dolphins in Mitchell (1970). In adults, the throat chevron extends posteriorly as a narrow, white longitudinal band on the medial abdomen that widens slightly in the area of the umbilicus, and terminates at the light gray ventral extensions of the flank patches (van Bree and Smeenk 1982, Fig. 3, Smeenk 1986, Fig. 3, Kinze 2002).

This Study: A white medial linear band was seen on the belly of all adults (*n*=13, Fig. 1L-M). Out of 3 juveniles, it was visible in only one that had a pale gray abdominal field (Fig. 2I). Similarly, in a small sample of calves, it was seen in one of 2 individuals (Fig. 3E). This area was not captured in photographs of neonates, so image analysis was not possible for that age class.

24. Umbilical Patch (UP)

Literature: A widening of the midventral streak in the area of the umbilicus is seen in Mitchell (1970), and a photo of a white-beaked dolphin showing this component appears in Jefferson *et al*. (2008), but is not described.

This Study: We propose the new term 'umbilical patch' for this component. It was a white patch around the umbilical opening was seen on the belly of all adults (*n*=13, Fig. 1L-M). Out of 3 juveniles, it was visible in the only one that had a pale gray abdominal field (Fig. 2I). Similarly, it was seen in one of 2 calves (Fig. 3E). This area was not captured in photographs of neonates, so image analysis was not possible for that age class.

25. Genital patch (GP)

Literature: In adults, the genital patch is an enlargement of the narrow, white midventral streak in the area of the genital openings, and is described in Orcininae (*Feresa, Orcaella, Orcinus, Peponocephala, Pseudorca*, Mitchell 1970, Fig. 9; Perrin 2002, Fig. 6).

This Study: A white patch was seen on the belly of all adults (*n*=13) at the posterior end of the mid-ventral streak, which terminated posterior to the anal opening where the two flank patches met at the ventral midline on the peduncle (Fig. 1L). Out of 3 juveniles, it was visible in the only one that had a pale gray abdominal field (Fig. 2I). Similarly, it was seen in one of 2 calves (Fig. 3E). This area was not captured in photographs of neonates, so image analysis was not possible for that age class.

In addition to the 25 components described above, we found irregular light gray markings that may be evidence of a skin disorder in white-beaked dolphins (Fig. 5). They appear similar to the pale skin patches (PSP) described by Sanino *et al*. (2014, Fig. 11) in Peale's dolphins (*Lagenorhynchus australis)* and Chilean dolphins (*Cephalorhynchus eutropia*). In our Icelandic white-beaked dolphins, PSP-like marks were observed on the upper back near the fin, at the base of the fin, and on the fin. They consisted of irregularly shaped light gray blotches ranging in size from approximately 1 cm^2 to as large as covering the middle of the fin and the upper back (Fig. 1K-L). Of 415 photo-identified adults, 17% (*n* = 72) exhibited PSP-like marks, and 9% (*n*=39) bore both these irregularly shaped gray fin blotches and off-white fin patches (Fig. 5C). PSP-like marks were also seen in 6% (*n*=4) of juveniles (Fig. 2G), and were not present in calves (*n*=11) or neonates (*n*=9).

DISCUSSION

Variation in coloration

This study is the first to review the complex color patterns in the white-beaked dolphin, distinguish age classes (adults, juveniles, calves and neonates) by suites of color pattern components, and describe their ontogenetic variation. Previous works on this species display few adult specimens, illustrating mainly the color components and appearance of immature age classes

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(Mitchell 1970, Fig. 10, top image, Leatherwood and Reeves 1983, Kompanje 1999, Fig. 2, Wynne and Schwartz 1999, Kinze 2002, Wang *et al*. 2014). For the 25 components described, we used seven terms previously applied to white-beaked dolphins (eye patch, eye stripe, blowhole chevron, peduncular saddle, dorsal flank blaze, speckling and abdominal field), and 12 previously applied to other dolphin species (beak blaze, lip patch, flipper stripe, helmet, fin patch, spinal field, thoracic field, flank patch, throat chevron, chin blaze, midventral streak and genital patch). In addition, we proposed six new terms: mouth band, post-ocular crescent, semi-circular head blaze, peduncular ridge stripe, lateral patch and umbilical patch.

Historical review – The body coloration of white-beaked dolphins received scant attention in the early literature. Sundewall (1862) provides a sketch of a very young female, likely a neonate, measured as '4 Swedish feet' (1.19 m) that shows the contrast between the dark coloration of the upper body against the lateral patches in the thoracic area and peduncle. Cunningham (1876) described another young female, probably a calf, measuring 1.27 m. In his accompanying illustration (Plate LXIV, Fig. 1), the upper body is dark gray, except for a few areas behind the eye, and on the thorax, flank and peduncle, which appear off-white. The abdomen is white, and the beak has clusters of gray spots, and the flipper stripe creates a small white island with speckling above it. Speckling is also present on the flank and peduncle. This speckling is also seen in a drawing from 1888 of a 2.4 m male specimen caught near Frederikshavn, Denmark, reproduced in Kinze (1993). Finally, a stranding report notes 'a young female,' probably juvenile, 'mottled gray with black flecks behind the eye' (Fraser 1946, Fig. 6). One calf measuring 1.55 m caught near Tromsø, Norway, has the color components seen in neonates, along with faint elements of the flank patch, dorsal flank blaze and post-ocular crescent (Sparre-Schneider 1878). A light gray patch is visible on its head, resembling those patches seen in our images of calves. However, its beak blaze is white with a gray tip, and no lip patch or mouth band is visible. The features depicted in the historical illustrations above are consistent with the descriptions of immature (juvenile, calf and neonate) white-beaked dolphins in this study.

Brightwell (1846) reported an adult 'eight feet and two inches long' (2.49 m) female dolphin caught off Great Yarmouth, England, later recognized by Gray (1846a) as a white-beaked dolphin. Brightwell described the beak, lower jaw and belly as cream color 'varied in some parts by a chalky colored white', while the rest of the body, including fin and tail, is black. Brightwell's description, accompanied by a rather crude drawing (also reproduced in Gray (1846b), is the earliest information on the coloration of the white-beaked dolphin. Moore (1863) reported an adult (2.74 m) male white-beaked dolphin caught live in the River Dee (Wales, UK), describing the narrow gray flank blazes, gray peduncular saddle, white beak blaze with dark gray blotches where the white extended above the beak, and pure white color on the throat and belly. Turner (1891) reported an adult '8 feet and 6 inches long' (2.59 m) female with a white beak blaze with gray tint, falcate black dorsal fin, a gray peduncular saddle, gray dorsal flank blaze, white belly 'mottled with gray', and white throat chevron and a chin blaze. Another drawing of an adult (2.5 m) female caught in Denmark in 1860 provides lateral and ventral views with a visible lip patch and chin blaze (Kinze 1993; unpublished data, Natural History Museum of Denmark[1]).

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[1] C. Thornam, February 1860. Archive Natural History Museum of Denmark, University of Copenhagen, Østervoldgade 5-7, DK-1350 Copenhagen K

Ontogenetic variation – Our results showed that color pattern components may be used to distinguish four age classes of white-beaked dolphins: adults, juveniles, calves, and neonates (Table 1).

Adults were identified by any of several diagnostic features including fully-developed blowhole chevron, completely filled-in post-ocular crescent, continuous dorsal flank blaze, flank patch, peduncular saddle, dark gray abdominal field, beak blaze of dark gray color with white or pink tip, and flipper stripe as a demarcation line between the white throat chevron and the gray post-ocular crescent. One surprising result was that, despite its common name, only 7.1% of adult white-beaked dolphins had a pure white beak—a feature much more frequently seen in immature animals. Juveniles and calves were identified by the presence of any of three color components: speckling, semi-circular head blaze and lateral patch. Juveniles were unique in having the semi-circular head blaze and light gray beak blaze, while only calves showed a gray beak blaze and a yellow film on the abdominal field. Neonates were distinguished by yellow-tinging on the beak blaze, helmet, and on the small, dull-colored precursors of the thoracic field, lateral patch and post-ocular crescent, as well as by the usual presence of fetal folds.

Changes in coloration of the head across different stages of development are worth noting. The post-ocular crescent is a light colored patch behind the eye with tapering chevron-like arms both above and below the level of the eye, visible in calves and juveniles. In neonates this component was faint and poorly delineated, being the precursor of the more developed post-ocular crescent seen in juveniles and calves. In adults, this feature was enlarged and so strongly filled in with light gray color that it became diffuse, with details of the upper and lower arms often difficult to perceive. The yellow-tinged helmet of neonates transitioned to the light gray patches of calves that were augmented by pale semi-circular head blazes in juveniles, and finally replaced by the off-white blowhole chevrons in adults. The semi-circular head blaze, present only on juveniles, was a thin curved light gray band beginning on each side of the blowhole and extending posteriorly to the anterior end of the dorsal flank blaze, but not connected to it (Fig. 8F-G). Figure 3C shows a calf in transition to a juvenile with the first hint of this semi-circular head blaze. Jefferson *et al.* (2008) presents the only two photographs of white-beaked dolphins found in the literature that show the semi-circular head blaze. These individuals also show lateral speckling and lateral patches on the flank and peduncle, suggesting they are juveniles or calves.

In our study, lateral patches were present on the flanks and peduncles of juveniles, calves and neonates. In particular, these patches, visible in the spinal field of juveniles, were precursor elements to the dorsal flank blaze. Lateral patches were not observed in adults.

Dorsal flank blaze is a term first applied by Mitchell (1970) to the component that appears to originate from the flank patch and terminate near the head. Although flank blazes occur on all other species of *Lagenorhynchus* dolphins except the Atlantic white-sided dolphin, *L. acutus* (Mitchell 1970), the genus is acknowledged to be polyphyletic, with recent studies showing that the white-beaked dolphin is not closely related to most other species in the group (LeDuc *et al*. 1999, Harlin-Cognato and Honeycutt 2006, McGowen 2011). Some species have two flank blazes (Pacific white-sided and dusky dolphins) and others have one (white-beaked, hourglass, and Peale's dolphins). In those that have two, the dorsal blaze originates from the top of the flank patch or from a split in the anterior end of the flank patch. The upper blaze is described as a dorsal flank blaze, and the lower one as a ventral flank blaze. At the point of origin, the flank blaze on the white-beaked and hourglass dolphins resembles a ventral flank blaze that does not terminate abruptly, but continues anteriorly onto the back, sides or head. We note that the flank blaze on the white-beaked dolphin,

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relative to its point of origin, could be more correctly termed a ventral flank blaze rather than dorsal flank blaze as used by Mitchell (1970). However, we retain Mitchell's nomenclature for this component until a more in-depth review of color patterns across multiple species can be conducted.

The fin patch, applied here for the first time to white-beaked dolphins, is a patch of off-white coloration found on adult dorsal fins (Webber 1987) of several small odontocetes. Based on its coloration and location on the fin, the fin patch is described for: Pacific white-sided dolphin (light gray patch, covering 2/3 of the fin, central-posteriorly located), dusky dolphin (light gray patch, rarely covering more than 1/2 of the fin, central-posteriorly located), Peale's dolphin (light gray, covering less than 1/3 of the fin, posteriorly located), short-beaked common dolphin (off-white patch, covering less than 1/2 of the fin, low and usually nearer the back than the tip, central-anteriorly located), long-beaked common dolphin (light gray/yellow patch, covering less than 1/2 of the fin, also low and usually nearer the back than the tip, central-anteriorly located), Dall's porpoise (off-white patch, covering 1/2 of the fin, located on its upper part), Risso's dolphin (off-white patch, covering 2/3 of the fin, centrally-anteriorly located) (Leatherwood *et al.* 1982, Goodall 2002, Stockin and Visser 2005, Jefferson *et al.* 2008, Cipriano and Webber 2010; Tethys Research Institute, unpublished data[2]). Fin patches on white-beaked dolphins, only seen on adults in our study, were located low and anterior to middle of the fin, could extend from the fin onto the back, and often had a hatched appearance (not completely filled in with light pigment). When present, the fin patch of white-beaked dolphins is more similar to that seen in Risso's dolphins and both species of *Delphinus* than to those found in the three *Lagenorhynchus* species, which have crescent-shaped fin patches that are filled with off-white pigment, and located from the trailing edge of the fin towards its center.

Speckling was detected only in calves and juveniles, and could appear in multiple locations: behind the eye and occasionally above the eye, between the eye and pectoral flipper, on lateral and flank patches, and variably on the rest of the flanks. Interestingly, speckling decreased with age until it vanished when the dolphin became sexually mature, the opposite of most other dolphin species in which speckles appear as the animal matures (summarized in Krzyszczyk and Mann 2012). In delphinids, such as Atlantic spotted dolphins (Perrin 1970, Herzing 1997), Indo-Pacific bottlenose dolphins (Smolker *et al.* 1992, Krzyszczyk and Mann 2012) and Pan-tropical spotted dolphins (Hohn *et al.* 1985, Myrick *et al.* 1986), speckles are not present in neonates but appear later and increase with age. In narwhals (*Monodon monoceros*) mottling appears as the animal grows older (Jefferson *et al.* 2008, Heide-Jørgersen 2002). In contrast, subadult and young adult Indo-Pacific humpback dolphins (*Sousa chinensis)* are mostly covered by spots that are slowly and progressively lost as they age (Jefferson *et al.* 2012). Thus, the number of spots in spotted dolphins, Indo-Pacific bottlenose dolphins and narwhals increase throughout their lives, while the spots of Indo-Pacific humpback dolphins and white-beaked dolphins gradually fade during the transition from calf to adult.

Our results reveal that the white-beaked dolphin differs from its congeners by exhibiting speckling during part of its life, and by the shape, appearance and position of the fin patch. As noted above, the white-beaked dolphin is not closely related to most of the other species currently placed in the genus *Lagenorhynchus* (LeDuc *et al.* 1999, Harlin-Cognato and Honeycutt 2006, McGowen 2011). Indeed, the color pattern components unique to the white-beaked dolphin may support the contention that its nominal congeners be re-assigned to a different genus.

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[2] Sabina Airoldi, Tethys Research Institute, viale G.B. Gadio 2, 20121 Milano, Italy. April 2015

Anomalous pigmentation – An anomalously pigmented adult white-beaked dolphin with reduced light gray dorsal flank blazes was observed in Faxaflói Bay, on 22 August 2012 (Fig. 1O). This deviation from the typical adult pattern is not described in the literature, despite recent reviews of melanistic or darkly pigmented cetaceans (Visser *et al.* 2004, Stockin and Visser 2005), therefore we record its first occurrence for the species. An adult female caught in 1866 in Denmark (Lütken 1887) is noteworthy because it is similar to our dark phenotype individual from Iceland. The illustration of the Danish animal reveals many of the color pattern components seen in adults in our images, but the dorsal flank blaze, as well as the peduncular saddle, blowhole chevron and abdominal field are visibly diminished.

Skin anomalies

Blotchy skin marks co-occurred with fin patches, and appeared as irregular gray patches on the dorsal fin, the back at the base of the fin, or on both areas. They resemble in color, shape, borders and location, the pale skin patches observed as a syndrome in Peale's and Chilean dolphins by Sanino *et al.* 2014 (Figure 5). Their etiology is currently unknown, but the blotches we observed could be classified as PSP-like until verified. The study areas for the Peale's and Chilean dolphins and the Icelandic white-beaked dolphins share similar environments: relatively cold sea surface temperatures, influence of freshwater (Stefansson and Gudmusson 1978) and nearby land and sea-based salmon farms (IAA 2009). The relationship between salmon farms and the occurrence of PSP in Chile should prompt studies in Iceland to understand the consequences this industry may have on cetaceans.

Although not seen on the white-beaked dolphins in this study, other skin pathologies have the potential to confound the identification of underlying color patterns, including lacaziosis (Burdett Hart *et al.* 2010, Fig. 1), lobomycosis-like disease (Van Bressem *et al.* 2007, Fig. 4A), and infestations of epizoa (*e.g., Xenobalanus globicipitis*) (Toth-Brown & Hohn 2007, Fig. 1C). In a recent assessment of skin disorders in white-beaked dolphins, the only lesions of possible infectious origin were attributed to tattoo skin disease (Bertulli *et al.* 2012). These lesions occurred on 1.9% (9 of 461) of the dolphins in this study (see Fig. 1P, left, for an example) as medium to large, rounded, dark gray lesions with darker borders (Fig. 1O, right side).

The seasonal presence of diatomaceous algae films on the skin of whales and dolphins can also obscure, or even highlight, natural patterns (Sears *et al.*, 1990; Gerasymiuk and Zinchenko, 2012; Feinholz and Atkinson 2000; Durban and Pitman 2011). Yellow-tinged areas on the blowhole, helmet, flanks, peduncle, beak and yellow patches on the belly of all neonates and 3 calves (Fig. 1G, Fig. 2F, Fig. 4D, Fig. 6B, Fig. 8I, Fig. 10E-F, Fig. 12E) are reported here for the first time for white-beaked dolphins. These color patches resembled orange films seen in bottlenose dolphins (Wilson *et al.* 1997, Fig. 2G, Maldini *et al.* 2010, Fig. 1 II), Antarctic killer whales (*Orcinus orca)* (Durban and Pitman 2011, supplement 2, Fig. 1) and Dall's porpoise (Jefferson *et al.* 2008). A review of yellow coloration in dolphin calves suggests it might be a natural feature to distinguish calves among conspecifics, or caused by diatoms, physiological jaundice, or dietary carotenoids (Feinholz and Atkinson 2000). Sea surface temperatures (SST) ≤13°C are known to be favorable for the bloom of many diatom species (Nemoto *et al.* 1980). In Icelandic waters, diatoms have been observed on humpback whales (*Megaptera novaeangliae*) (McCormick 2013) and on the calves of killer whales (www.faxa-cetacean.org/Killer-Whale/). The average SST in our main study areas (Faxaflói and Skjálfandi Bays) during the 2001-2014 data collection was 6°C (derived from monthly composites of MODIS satellite data), with a range of 2°C in March to 12°C in August. Even in the warmest months, these conditions were favorable for the growth of diatoms on the skin

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of white-beaked dolphins. However, since the yellow film occurred only in neonates and calves, it could indicate slower skin regeneration, differences in skin surface temperature, or physiological maturity. A larger sample of individuals with this yellow skin coloration would need to be sampled and examined, possibly from stranded animals, to better understand this condition.

Conclusion

Adults could be identified by fully-formed color components; they also have two unique beak blaze coloration patterns: dark gray with a white or pink tip, and a pure white beak occurring at a low frequency. Juveniles and calves could be recognized by the presence of speckling, semi-circular head blazes, and lateral patches. Calves showed a yellow film on the abdominal fields, and some had gray beaks. Neonates were identified by yellow-tinged areas on the helmets, flanks and behind the eyes (post-ocular crescents). Future studies utilizing stranded specimens of known age and maturity would allow confirmation of these findings, and possibly reveal new age class-specific components, as well as sexually dimorphic differences not discussed in this study. Geographical variation could be investigated by comparing large image datasets and stranded animals from different parts of the North Atlantic.

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Figures

Figure I. Map of Iceland showing locations of the study sites: Faxaflói Bay, Breiðafjörður, and Skjálfandi Bay. Map courtesy of M.J. Tetley.

Figure II. Age classes: adult, juvenile, calf and neonate. Photo credits: C.G. Bertulli/University of Iceland (hereafter 'U.I.', A) and C. Schmidt/Húsavík Whale Museum (hereafter 'H.W.M.', B).

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Figure III. Adult white-beaked dolphin - location of color pattern components: beak blaze (BB), lip patch (LipP), mouth band (MB), eye patch (EP), eye stripe (ES), post-ocular crescent (POC), flipper stripe (FS), blowhole chevron (BC), fin patch (FinP), spinal field (SF), peduncular saddle (PS), peduncular ridge stripe (PRS), dorsal flank blaze (DFB), thoracic field (TF), flank patch (FP), throat chevron (TC), chin blaze (CB), abdominal field (AF), midventral streak (MS), umbilical patch (UP) and genital patch (GP). Drawings courtesy of J.B. Hlíðberg.

Figure 1. Adult white-beaked dolphin color components: beak blaze (BB); lip patch (LipP); mouth band (MB); eye patch (EP); eye stripe (ES); flipper stripe (FS); post-ocular crescent (POC); blowhole chevron (BC); fin patch (FinP); spinal field (SF); peduncular saddle (PS); peduncular ridge stripe (PRS); dorsal flank blaze (DFB); thoracic field (TF); flank patch (FP); throat chevron (TC); chin blaze (CB); abdominal field (AF); umbilical patch (UP); genital patch (GP). Photo credits: F. Christiansen/U.I. (A), S. Martin/U.I. (B), J.J. Puebla Colin/U.I. (C), S. Harlow/MRI, University of St. Andrews (hereafter 'U. of St. A.', D), N. Goddard/U.I. (E), J. Bridda/Marine Research Institute (hereafter 'M.R.I.'), U. of St. A. (F), O. Graillot/U.I. (G), K. McCormick/U.I. (H), H.W.M. (K), K. Matthews/U.I. (I), D. Saffroy/U.I. (J), M. Gelippi/U.I. (K, L), M.H. Rasmussen/U.I. (M), T. Klesse/U.I. (O left), N. Goddard/U.I. (O right).

Figure 2. Juvenile white-beaked dolphin color components: beak blaze (BB) lip patch (LipP); mouth band (MB); eye patch (EP); eye stripe (ES); post-ocular crescent (POC); flipper stripe (FS); blowhole chevron incomplete (BC); semi-circular head blaze (SCHB); spinal field (SF); peduncular saddle (PS); peduncular ridge stripe (PRS); thoracic field (TF); lateral patch (LP); flank patch (FP); speckling (S); throat chevron (TC); chin blaze (CB); (19) abdominal field (AF); midventral streak (MS); umbilical patch (UP); genital patch (GP). Photo credits: A. Suzuki/U.I. (A,J), J.J. Puebla Colin/U.I. (B), O. Filatova/M.R.I., U. of St. A. (C,G-H), N. Brennan/U.I. (D), M.T. Mrusczok/U.I. (E,K), K. Matthews/U.I. (F), M.H. Rasmussen/U.I. (I).

Figure 3. Calf white-beaked dolphin color components: beak blaze (BB); lip patch (LipP); mouth band (MP); eye patch (EP); eye stripe (ES); post-ocular crescent (POC); flipper stripe (FS); blowhole chevron incomplete (BC); spinal field (SF); thoracic field (TF); lateral patch (LP); speckling (S); throat chevron (TC); chin blaze (CB); abdominal field (AF); midventral streak (MS); umbilical patch (UP); genital patch (GP). Photo credits: J.J. J. Bridda/ M.R.I., U. of St. A. (A,F), J.J. Puebla Colin/U.I. (B-C), A. Fromant/U.I. (D) and L. Guéry/U.I. (E).

Figure 4. Neonate white-beaked dolphin color components: beak blaze (BB); eye patch (EP); eye stripe (ES); post-ocular crescent incomplete (POC); flipper stripe (FS); helmet (H); spinal field (SF); thoracic field incomplete (TF); lateral patch incomplete (LP). Photo credits: J.J. Puebla Colin/U.I. (A-B, D-E) and H.W.M. (C).

Figure 5. Skin anomalies associated with color components: Adults (A-C), Juveniles (D). Fin patch (FinP); Pale Skin Patch-like (PSP-like). Photo credits: H.W.M. (A), N. Goddard/U.I. (B), C.G. Bertulli/U.I. (C); N. Brennan/U.I. (D).

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Figure I

Figure II

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Figure III

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Figure 1

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Figure 2

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Figure 3

Figure 4

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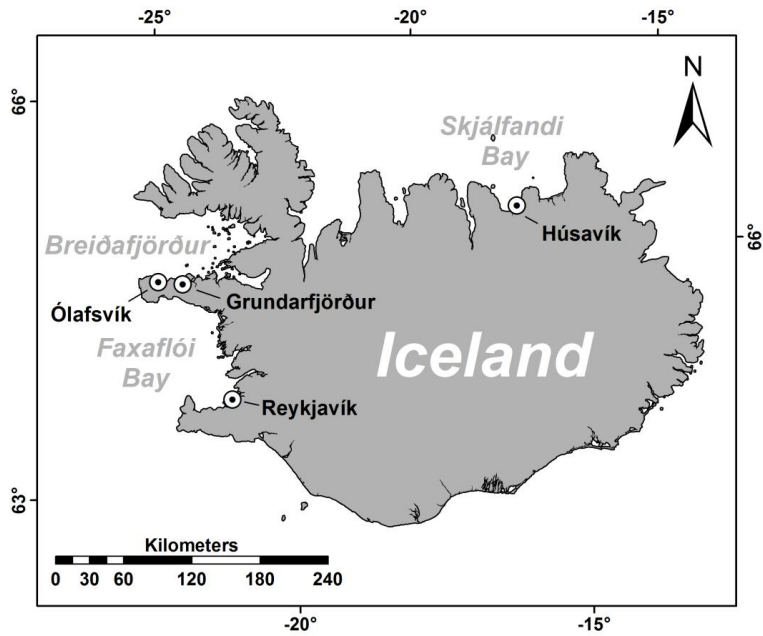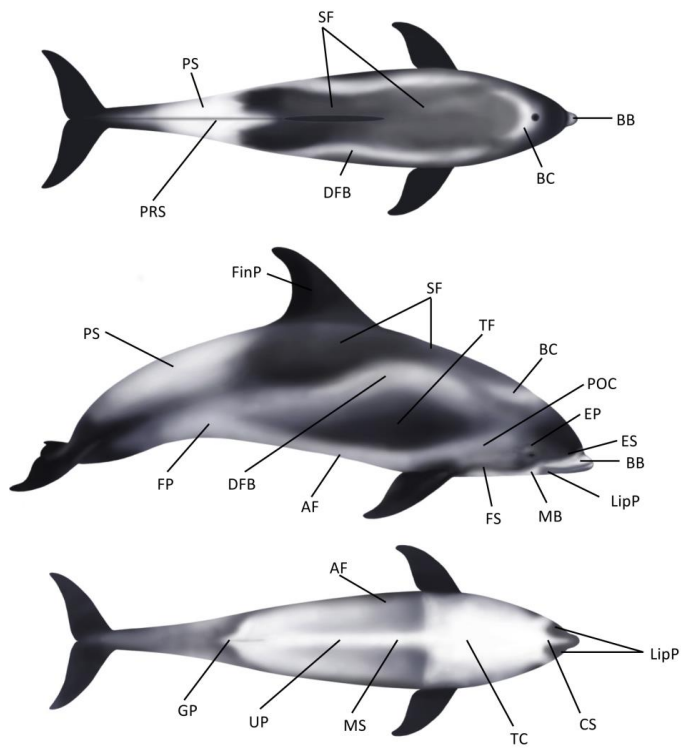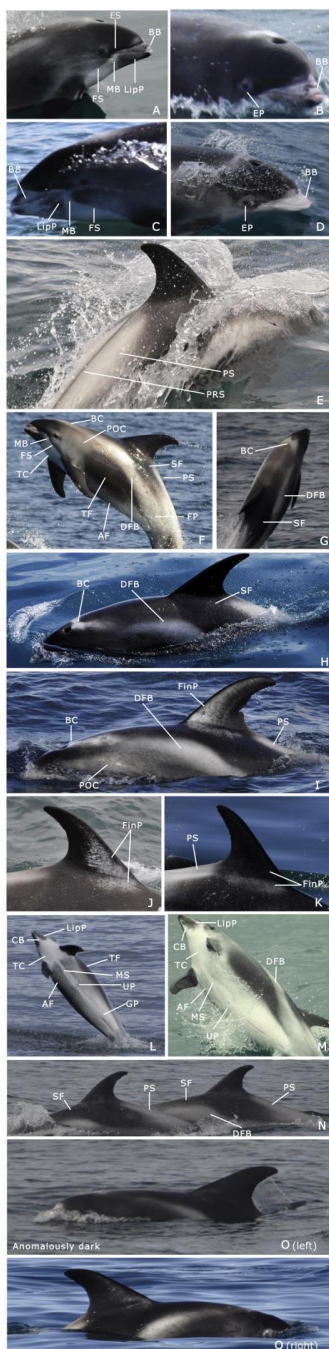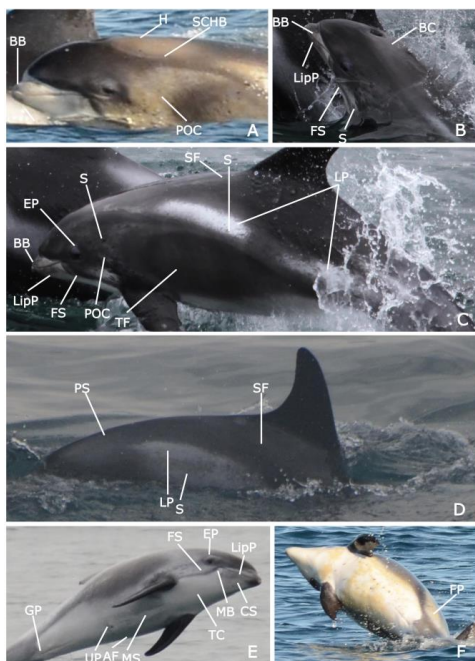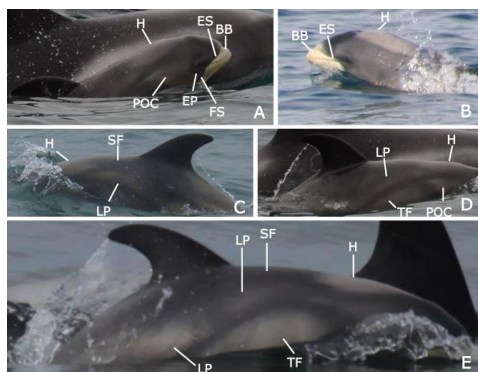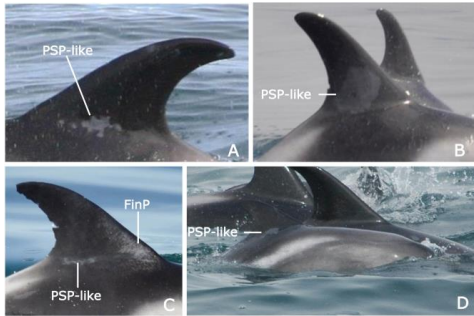
Figure 5

Tables

Table 1. Color components for each age class. ++ = present; - = absent; +/- = present on some animals; + = component not fully developed or incomplete; 0 = datum not available. n = number of individuals analyzed for each color component per age class. A = adult, J = juvenile, C = calf and N = neonate.

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Table 1. Color components for each age class. ++ = present; - = absent; +/- = present on some animals; + = component not fully developed or incomplete; 0 = datum not available. n = number of individuals analyzed for each color component per age class. A = adult, J = juvenile, C = calf and N = neonate.

| No.	Color component	Abbreviation	A	J	C	N	n_A	n_J	n_C	n_N	First reference
1	Beak blaze	BB	+/-	++	+/-	++	56	32	7	6	Mitchell 1970
2	Lip patch	LipP	+/-	+/-	+/-	-	62	31	7	6	Mitchell 1970
3	Mouth band	MB	+/-	+/-	+/-	-	53	11	7	6	This paper
4	Eye patch	EP	++	++	++	++	74	25	7	6	Perrin 1970
5	Eye stripe	ES	++	++	++	++	18	26	7	6	Mitchell 1970
6	Post-ocular crescent	POC	++	++	++	+	46	39	8	6	This paper
7	Flipper stripe	FS	+/-	++	++	++	37	30	8	5	Perrin 1970
8	Blowhole chevron	BC	++	+	+	-	68	37	6	7	Mitchell 1970
9	Semi-circular head blaze	SCHB	-	++	-	-	68	36	6	7	This paper
10	Helmet	H	-	-	+/-	++	68	36	6	7	Stockin & Visser 2005
11	Fin patch	FinP	++	-	++	-	415	70	11	9	Webber 1987
12	Spinal field	SF	++	++	++	++	171	68	11	9	Mitchell 1970
13	Peduncular saddle	PS	++	+/-	-	-	133	64	9	7	Mitchell 1970
14	Peduncular ridge stripe	PRS	++	++	0	0	12	4	0	0	This paper
15	Dorsal flank blaze	DFB	++	-	-	-	63	51	9	7	Mitchell 1970
16	Thoracic field	TF	++	++	++	+	51	42	6	3	Mitchell 1970
17	Lateral patch	LP	-	++	++	+	131	81	9	7	This paper
18	Flank patch	FP	++	++	-	0	31	53	9	7	Mitchell 1970
19	Speckling	S	-	++	++	-	140	81	10	9	Bertulli *et al.* 2015
20	Throat chevron	TC	++	+/-	+/-	0	13	7	2	0	Mitchell 1970
21	Chin blaze	CB	++	+/-	+/-	0	62	31	7	0	Mitchell 1970
22	Abdominal field	AF	++	+/-	+/-	0	13	7	2	0	Mitchell 1970
23	Midventral streak	MS	++	+/-	+/-	0	13	3	2	0	Mitchell 1970
24	Umbilical patch	UP	++	+/-	+/-	0	13	3	2	0	This paper
25	Genital patch	GP	++	+/-	+/-	0	13	3	2	0	Mitchell 1970

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Paper IV

Paper IV

Association patters of white-beaked dolphins *Lagenorhynchus albirostris*

in Iceland: insights into social organization

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Association patters of white-beaked dolphins (*Lagenorhynchus albirostris*) in Iceland: insights into social organization

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ABSTRACT

Given the variability in social structures exhibited among delphinids, it is important to document lesser known species, in extreme habitats, in order to contrast and compare mechanisms driving sociality. Here, we describe the social structure of white-beaked dolphins (*Lagenorhynchus albirostris*) using an 11 year dataset (2002-2013) of photo-identifications collected from whale-watching vessels on the southwest (Faxaflói Bay) and northeast coasts (Skjálfandi Bay) of Iceland. We identified a total of 489 white-beaked dolphins, but restricted the analytical dataset to 35 adults which were sighted on ≥ 5 different days. Social differentiation in this community was high (S=1.830, se=0.369) indicating diverse social relationships (mean HWI= 0.39, SD=0.21) which differed from random based on permutation tests (random=1.876, observed=2.569, p=1.000). Modularity (Q=0.36639) divided an average linkage hierarchical clustering dendrogram into seven different clusters (mean$\pm$SD=5.0$\pm$2.38 individuals, range=2-9). Temporal associations best fit the model of 'casual acquaintances' against the standardized lagged association rates (SLAR), which showed a rapid decrease after 10 days, a final drop at around 450 steadily declining and falling below the null association rate on two occasions. This study expands the latitudinal range for which social structure has been described for oceanic dolphin species and specifically one for which very little has been published.

Key words: association patterns, white-beaked dolphin, *Lagenorhynchus albirostris*, Iceland

To understand the biology of marine mammal species and their role in the environment it is important to study their social structure (Whitehead and Van Parijs 2010), knowledge of this can then be used for important decisions related to management and conservation (Sutherland 1998, Whitehead *et al*. 2004, Lusseau 2005, Parra *et al*. 2011). Social structure varies dynamically across different taxa and it influences population biology, behaviour, conservation, genetics, fitness, physiology, ecology, transmission of diseases (Wilson 1975, Sutherland 1998, Altizer *et al*. 2003, Krützen *et al*. 2003, Whitehead *et al*. 2004, Silk 2007, Archie *et al*. 2008).

Although studying cetacean social organization contains logistical and methodological challenges - whales and dolphins spend most of their time underwater (Mann 1999) compared to terrestrial animals - such information has been collected from populations of killer whales with stable and long-lasting social bonds (Bigg 1982, Heimlich-Boran and Heimlich-Boran 1990, Bigg *et al*. 1990) to bottlenose dolphins with more temporary and changing associations within societies which vary regularly in composition (Würsig and Würsig 1977, Wells *et al*. 1987, Smolker *et al*. 1992, Connor *et al*. 2000). The differences in social structure among these two species are based on the presence or absence of preferred partners (Wells *et al*. 1987, Smolker *et al*. 1992) and they are

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affected by environmental parameters such as availability of food resources, predation risk (Wrangham and Rubenstein 1986) and by movement patterns (Bräger *et al.* 2004).

Due to the great variability in social structures among cetaceans, it is important to study lesser known species to examine the depth of this variation. The white-beaked dolphin (*Lagenorhynchus albirostris)* is a common species in temperate and sub-arctic North Atlantic waters (Kinze *et al.* 1997, Northridge *et al.* 1997, Reeves *et al.* 1999). In Icelandic coastal waters (≤600m depth contour), they can be found year-round (Magnúsdóttir 2007) with aerial surveys suggesting higher occurrences on the SW-coast, on the NE-coast and on the SE coast (Gunnlaugsson *et al.* 1988, Pike *et al.* 2009). White-beaked dolphins are the second most commonly sighted species in the southwest (Bertulli 2010) and the third most commonly sighted species in the northeast (Cecchetti 2006, Cooper 2007) from commercial whale watching tours. Previous studies conducted on white-beaked dolphins estimated a population of 31,653 animals (95% CI:17,679–56,672, Pike *et al.* 2009) in Icelandic waters and indicated site fidelity to some coastal areas, with certain individuals undertaking movements 300 km or greater between the south-west and the north-east coasts of Iceland (Tetley 2006, Rasmussen *et al.* 2013, Bertulli *et al.* 2015b).

In the present work, we use a photo-identification dataset collected over a 11-year study to describe the social organization and patterns of association of white-beaked dolphins for the first time. Specifically, we address the following two questions: 1) Do white-beaked dolphins form a diversity of type's social relationships and do these patterns differ from random? 2) How do association patterns change over time. This study extends the latitudinal range of our understanding of delphinid social structure to include a difficult to study arctic species for which little has been previously published on any topic.

MATERIAL AND METHODS

Data collection

Photo-identification was conducted from onboard whale-watching boats in Faxaflói Bay (hereafter 'Faxaflói'), Reykjavík (April-September in 2002–2011 and year-long in 2012-2013) and in Skjálfandi Bay (hereafter 'Skjálfandi'), Húsavík, Iceland (May-October in 2002–2013). The study area covered approximately 4,440 km^2 in FB and 1,100 km^2 in SB (Fig. 1). Data were collected when conditions were below sea state three only. Further details about boat size, tour frequency and duration, data forms and photographic gear used during data collection are available in Bertulli *et al.* 2013 and Bertulli *et al.* 2015. Due to the nature of data collection from whale-watching vessels, our methods were limited in two ways which are common to all studies based on platforms of opportunity: 1) we were only able to approach animals to within 50-100m which increased the difficulty in completely identifying the individuals in the groups. 2) The duration of each encounter with a dolphin group was determined based on the time limitations of the tours (*e.g.*, Coscarella *et al.* 2011, Bertulli *et al.* 2013).

Defining associations

Individuals were considered as part of the same group if they were no more than 100m away from each other and coordinating their movement and behavior (Wells *et al.* 1987, Shane 1990). When larger groups were encountered their size was estimated by counting each group separately (Bearzi *et al.* 1997). Best estimates of group size were estimated *in situ* by an observer during each sighting and when groups were large and animals were actively moving around the vessel, it was estimated

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by at least two people located in different places on board, and the obtained mean of the best estimate was recorded (*e.g.*, Chilvers and Corkeron 2002).

Data analysis

Photo-identification

Photo-id images were quality rated (Q) using a scale 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 (Elwen *et al*. 2009, Gowans and Whitehead 2001, Rosso *et al*. 2011). Only images rated Q≥4 were considered good enough for the analysis. As the Q-value attributed to each image was not dependent of the marks visible on each individual, we also assessed the distinctiveness of each fin based on a grading system from 0-4 (1-*very distinctive*, 2-*distinctive*, 3-*slightly distinctive*, 4-*not distinctive*) and only *distinctive* and *very distinctive* fins were incorporated in the analysis (Zaeschmar *et al*. 2014).

In addition to traditional dorsal fin photoidentification (Würsig and Würsig 1977), white-beaked dolphins were also identified using supplementary injury marks (*e.g.*, wounds, antagonistic and anthropogenic scars, back indentation, amputation, deformation, see Bertulli *et al*. 2015a). Proportions of identifiable individuals per groups were calculated to estimate coverage.

Group size

Individuals were classified into one of four age classes based on the estimated size of each individual compared to the average length of an adult, and by association with conspecifics. *Adult*: body length ranging between 2.4 and 3.1 m (Dong *et al.* 2006, Kinze 2002, Galatius *et al.* 2013). *Juvenile*: about two-thirds to three quarters of adult length, swimming independently or associated with an adult (Bearzi *et al*., 1997, Karczmaski 1999, Mann and Smuts 1999). *Calf*: less than two-thirds of adult length and were consistently escorted by an adult (Shane 1990, Karczmarski *et al.* 1999, Degrati *et al*. 2008). *Neonate*: less than one-half of an adult length and with fetal folds or pale color bands associated with their former location (Bearzi *et al*. 1997, Karczmarski *et al*. 1999, Stockin *et al.* 2009); reported to be 1.1 to 1.2 m in length (Tomilin 1967, Fraser 1974, Collet and Duguy 1981, Kinze 2009). Calves and neonates were excluded from the analysis. In addition, the vast majority of juveniles (98%) did not carry any distinguishing marks on their dorsal fins and were therefore omitted from analysis based on distinctiveness.

Association patterns

Dolphins were considered associated when identified within the same group with a sampling interval of 1 day in order to account for potential demographic effects (Whitehead 2008a). Only dolphins that were sampled ≥5 times were including in analyses. All analyses were performed using SOCPROG 2.5 (Whitehead 2009).

The half-weight-index (HWI; Cairns and Schwager 1987, Ginsberg and Young 1992) was used to quantify the proportion of time a pair of dolphins spends associating (Whitehead 2008). It was chosen as Cairns and Schwager (1987) suggested it accounts for bias when a pair is more likely to be observed separate than when together, as is often the case in photoidentification studies. However, considering that estimated relationship measures might contain an error because in real life the time a pair spends together might be different (Whitehead 2008b), we wanted to test how accurate it was to use these estimated measure to build up models and social representations. Thus, the correlation coefficient (r) and social differentiation (S) were calculated using formulas and

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Poisson and likelihood approximation methods proposed by Whitehead (2008a, b). r indicates the accuracy of association measures used to construct social structures with models and S indicates the variability of a social system, from homogenous to very well differentiated (Whitehead 2008a).

Testing for non-random associations
The null hypothesis stated that there were no preferred associates or avoidances given the number of groups in which each animal was seen during each sampling period (Chilvers and Corkeron 2002, Whitehead 2008). This hypothesis was tested using Whitehead's (2009) variation of the permutation test by Bejder *et al*. (1998). Association data were permuted 25000 times until *p* value stabilized.

Hierarchical cluster analysis: average linkage method
The cophenetic correlation coefficient (CCC) was estimated, with values ≥ 0.8, generally indicating there are clustering in the population and that the created dendrograms accurately represented the complexity of the white-beaked dolphin social structure (Whitehead 2008a). Modularity was assessed with values ≥0.3 suggesting the population is well divided (Newman 2004). Coefficients of associations were classified according to Quintana-Rizzo & Wells (2001) as low 0.01–0.20, medium–low 0.21–0.40, medium 0.41–0.60, medium–high 0.61–0.80 and high 0.81–1.

Lagged association rates
In order to study how a dyadic association changes over time, lagged association rates (LAR) were estimated (Whitehead 1995) using individuals associating ≥2 times. Additionally, to interpret them null association rates were used, representing the expected LAR values if animals associated randomly (*e.g*., no preferred associates) (Whitehead 2008a, 2009). Lagged and null association rates were standardized (SLAR, Whitehead 1995) since during this study it was not possible to properly photo-identified all individuals in each encountered group (Gowans *et al*. 2001, Karczmarski *et al*. 2005). Precision of the estimated lagged association rates was performed using the temporal jackknife procedure (Sokal and Rohlf 1995) implemented in SOCPROG 2.5 and standard errors were created (Efron and Gong 1983) similarly to previous studies on cetaceans (e.g. Gowans *et al*. 2001, Karczmarski *et al*. 2005, Wiszniewski *et al*. 2009). We fit models to the observed SLARs (Whitehead 1995, Whitehead 2008a) using maximum likelihood technique including 1) constant companions, who are permanently together, (2) casual acquaintances, who associate for some time, disassociate, and possibly re-associate later, (3) constant companions and casual acquaintances and (4) two levels of casual acquaintances who associate and disassociate at two different time scales. The best model fit model was selected by the lowest quasi Akaike Information Criterion (QAIC) value (Burnh am and Anderson 1998; Whitehead 2007). The difference in QAIC values (ΔQAIC) between the best-fit model and the others indicate the level of support: strong support (0-2), some support (4-7) and no support (>10) (Burnham and Andersen 2002).

<div align="center">RESULTS</div>

Photo-identification
Over a total of 223 h of survey effort (143 h in Faxaflói, 80 h in Skjálfandi), a total of 489 white-beaked dolphins were photo-identified, 292 solely photographed in Faxaflói, 173 in Skjálfandi. There were also 24 'core users' (*i.e.*, frequent users, Tezanos-Pinto 2009), individuals photographed in both bays, moving between them during the study period. A total of 1119 dolphin groups (n=610

<div align="center">4</div>

in Faxaflói, n=509 in Skjálfandi) were encountered. Photo-id images quality rated Q4 or higher were taken for 26% (n=297) of these groups. A total of 22% (n=64) of these groups had 50% or more individuals identified within each group.

Group size

Group size estimates varied between one and 300 individuals in Faxaflói with an overall mean group size of 7.9 (SD=16.23, n=610) and with the majority (87%) of the groups observed consisted of ≤10 dolphins (Fig. 2). In Skjálfandi, estimates varied between one and 150 individuals with an overall mean group size of 10.0 (SD=16.43, n=509) and with groups of ≤10 dolphins observed most frequently (79%) (Fig. 2). With regard to group composition, all groups included adults and only 12% included immatures in Faxaflói and 28% in Skjálfandi.

Association patters

A total of 35 adult white-beaked dolphins were sighted five or more times and they were used to analyze the association patterns. The estimate of social differentiation, CV of true association indices, (S±SE=1.830±0.369) close to one indicated that the associations were very varied. The estimate of correlation between true and estimated association indices using Poisson approximation was equal to 0.692 (SE=0.033, SE's from bootstrap with 1000 replications). With the likelihood method a value of 0.3 was obtained. Data on associations were randomly permuted 25000 times when p-values stabilized and the resulting SD (observed mean=0.1, random mean=0.07, p=1.000) values of the real data were significantly higher compared to the random proving associations among individuals are not random but preferred and/or avoided during the 11 years of study. Additionally, the SDs of non-zero association indices were higher in the observed data (SD_o=0.13503) compared to the random data (SD_r=0.05158), indicating companionships that persist across sampling periods. The proportion of non-zero association indices was higher for random data (0.24474) indicating the presence of avoidance among some individuals (Table 1).

Hierarchical cluster analysis: average linkage method

The cophenetic correlation coefficient (CCC) of the average-linkage clustering dendrogram was estimated to be 0.846 indicating that it represents well the association data of white-beaked dolphins in the present study. Maximum modularity (type 1; when controlling for gregariousness, Q=0.36639) with an association index of 0.061 generated seven different clusters (mean±SD=5.0±2.38 individuals, range=2-9) (Fig. 3). Additionally, the overall association index resulting from HWI had a mean of 0.39 (SD=0.21) and the coefficients of associations (COA) were for the majority low (37%, n=13), followed by moderate-low and moderate (each 23%, n=8) and moderate-high (17%, n=6). There was one dyad with the highest COA (=0.8) made of 'core-users' DEM199-DEM154.

Lagged association rates

The best model which represented the association patterns of our data were of 'casual acquaintances' (Table 2, Fig. 4). The lagged association rate showed a rapid decrease after 10 days, a final drop at around 450 days steadily declining and falling below the null association rate on two occasions, the first one at around 1120 days (~ 3 years). The error bar dropped below the null association rate at around 1000 days. The association rate persisted above the null rate for at least 1200 days (~ 3 years) as shown by the standardized lagged association rate (SLAR, Fig. 4). 'Two

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level of casual acquaintances' (SLAR4, Table 2) shows a very similar curve (red line, Figure 4) and a ΔQAIC of 2.62 suggesting some support (Table 2).

<div align="center">DISCUSSION</div>

Group size

The observed mean group size of white-beaked dolphins recorded during this study were similar to those found in other coastal white-beaked dolphin populations (Weir and Stockin 2001, Canning *et al*. 2008, Weir *et al*. 2008, Weir *et al*. 2009, Fall and Mette-Skern-Mauritzen 2014). The estimates recorded in Faxaflói (mean±SD; mean=7.9 ± 16.23) were comparable with mean group sizes in Scotland (mean=7.7; Weir and Stockin 2001, Weir *et al*. 2008, Weir *et al*. 2009) and the Barents Sea (mean=8.0; Fall and Mette-Skern-Mauritzen 2014), while the Skjálfandi estimates (mean=10.0 ± 16.43) were similar to those recorded in the Gulf of St. Lawrence and Halifax (mean=8.6, Kinglsey and Reeves 1998, mean=9.1, Simard *et al*. 2006) but larger than the others. Overall, in this study larger group sizes were recorded compared to those collected in Iceland in previous years (*e.g.*, mean group size 6.3 95% CI 5.6-7.1, Pike *et al*. 2009) and compared to strandings data from the UK and Ireland (mean=4.2, SD=2.77; Canning *et al*. 2008). Previous studies suggested that cetacean group size varies according to predation pressure, ocean climate variation, food availability, interspecific competition and habitat type (*e.g.,* Connor *et al*. 1998, Lusseau *et al*. 2004, Gowans *et al*. 2007, Parra *et al*. 2011, Ersts and Rosembaum 2003). In Iceland small (7.9 in Faxaflói) to moderate group sizes (10 in Skjálfandi, Acevedo-Gutiérrez 2002) could be a reflection of a low predation risk and patchy food resources. In Icelandic waters, predators to white-beaked dolphins are killer whales which are sighted few times every year crossing the whale-watching grounds in Faxaflói and Skjálfandi. Killer whale tooth-rake marks on white-beaked dolphins were only photographed on 5 individuals (Bertulli *et al*., 2012, 2015a). The distribution and abundance of many fish species was altered after 1995 by changes in temperature and salinity in the Icelandic marine ecosystem, on the south, west and north coasts (Vikingsson *et al*. 2015). Some of these fish species (*e.g.*, Vilhjálmsson 1997, summarized in Björnsson and Pálsson 2004, Guðmundsdóttir and Sigurðsson 2004, Astthórsson *et al*. 2007) are known to be part of the white-beaked dolphins' diet (van Bree and Nijssen, 1964, Víkingsson and Ólafsdóttir 2004, Canning *et al*. 2008). Similarly to white-beaked dolphins, dusky dolphins (*Lagenorhynchus obscurus*) in Admiralty Bay, New Zealand, have similar mean group size (7.9±6.0, Pearson 2009) to the Faxaflói individuals and low occurrence of predators. It was suggested prey availability and female estrous are the main factors influencing grouping for this species.

Association patters

Results indicated white-beaked dolphins in Icelandic coastal waters live in a differentiated society associating non-randomly with one another like other dolphin species (*e.g.*, Parra *et al*. 2011, Augusto *et al*. 2012, Louis *et al*. 2015). Similarly to oceanic delphinids (*e.g.*, dusky dolphins, Commerson's dolphins, spinner dolphins, common dolphins *Delphinus* sp., Atlantic bottlenose dolphins) they live in fission-fusion societies, have few preferred associations and have mainly weak bonds with one another (Bruno *et al*. 2004, Markowitz 2004, Karczmarski *et al*. 2005, Viricel *et al*. 2007, Pearson 2008, Coscarella *et al*. 2011, Augusto *et al*. 2012, Elliser and Herzing 2014, Martinho *et al*. 2014, Stockin *et al*. 2014).

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In this study, avoidance among some individuals was detected. With information on sex, maturity and genetic structure of the identified individuals, it might be possible to further understand this finding.

Hierarchical cluster analysis: average linkage method
In this study, white-beaked dolphins in Icelandic waters showed coefficient of associations which were highly fluid and with few long-term bonds (weak associations) similarly to other dolphin communities (Rogan *et al*. 2000, Quintana-Rizzo and Wells 2001, Chilvers and Corkeron 2002, Keith *et al*. 2002, Mourão 2006, Coscarella *et al*. 2011, Louis *et al*. 2015). Coefficients of association can be influenced by population size, with the smaller the population the larger the coefficient, but also by grouping patterns (Whitehead 2008a). In Icelandic coastal waters white-beaked dolphin are part of a large population (>30,000 individuals, Pike *et al*. 2009) and they are forming small to moderate sized groups, so the type of associations they establish are the results of both population and group size.

Lagged association rates
The association patters of white-beaked dolphins inhabiting the coastal waters of Faxaflói and Skjálfandi Bays are best described as 'casual acquaintances', which is similar to the bottlenose population in the Sado Estuary (Augusto *et al*. 2012) and Sétubal Bay (Martinho *et al*. 2014), Portugal. Casual acquaintances is also the best fit model for associations in humpback dolphins in Cleveland Bay, Australia (Parra *et al*. 2011) and Pacific humpback-dolphins in the coastal waters surrounding Hong Kong, China (Dungan *et al*. 2012). The SLAR associate rate showed a first drastic decline after approximately 10 days, then the lagged association rate goes up again around 450 days (roughly 1 year) to then decline once again. A fall in the SLAR might suggest that individuals after associating for a certain period of time (*e.g.*, 10 days) separated, possibly due to death or movement of the individuals outside of the identified population (*e.g.*, 'emigration', Whitehead 2008a). Declines in the SLAR could also be a reflection of the effort spent collecting data, where interruptions in the data collection *e.g.*, winter months from 2002-2011 in Faxaflói, and all years in Skjálfandi are when the curve falls; photo-id data not collected in the year 2005 in Faxaflói. After the first fall, the curve ascended again at around 450 days (roughly 1 year; between 2002-2003, Fig. 4) to fall around those days drastically a second time, suggesting the majority of associations between individuals did not seem to last longer than a year. This second fall could be due to emigration and re-immigration, in a population of identified individuals where some reside in our study areas while others are occasionally transiting out. In a previous study (Bertulli *et al*. 2015b) a movement of white-beaked dolphins between both our study sites (*i.e.*, Faxaflói and Skjálfandi) was detected. This movement suggested individual dolphins to be highly mobile and transient, inhabiting large-scale coastal range of the Icelandic coast, possibly due to scarce and patchy resources or to its large population size (Bertulli *et al*. 2015b). Photo-identification data (2002-2013) collected on this species also showed a low 'inter-annual re-sighting proportion' (18.3%) and 'intra-annual re-sighting proportion' (19.2%), and a 'rate of discovery' curve that continued to rise steadily (Bertulli *et al.* 2015b). At around 1000 (around 3 years; after 2004) and 1600 days (4 years; year 2006) the error bars dropped below the null association rate with a thirst drop of the SLAR. It is likely that this fall reflected a stop in data collection during the year 2005. The error bar crossing the null association rate which was observed in this study was recorded in

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other studies (Ottensmeyer and Whitehead 2003, Beck *et al.* 2012). A similar scenario appears in Argentina with Commerson's dolphins where 13 marked individuals associated for 15 days before disassociating (Coscarella *et al.* 2011).

Conclusion

White-beaked dolphins inhabiting Icelandic coastal waters live in a fission-fusion society defined by a majority of moderate-low associations but showing preferred associations throughout the whole study period. The data collected in Iceland form a good start to understand the social structure of white-beaked dolphins and can be used as a guideline for further research. It is recommended to collect data from other sites around the Icelandic coastline covering the west and east areas in order to test the results presented here.

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Table 1. Results of permutation tests for preferred/avoided companions (n=35 dolphins sighted ≥5 times). The permute associations within samples test was used. *P* values stabilized at 25,000 permutations (1,000 flips per permutation). Significant variation were tested using a two-tailed test (α=0.05). Sampling period was set to a day.

	SD of Mean AI	SD of Non-zero AI	Proportion of non-zero AI
Real Data	0.09940	0.13503	0.18824
Random Data	0.07331	0.05158	0.24474
p value	1.00000	1.00000	1.00000

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Table 2. Standardized lagged association rate (SLAR) for all marked white-beaked dolphins sighted together ≥ 2 times. The best fitted models to the standardized lagged association rate (SLAR).

Model	Explanation	Best Fit	QAIC	ΔQAIC	Model support
SLAR1	Constant companions	g'= 0.036865	965.1812	10.57	No support
SLAR2	Casual acquaintances	g'= 0.049148*exp (-0.00064064*td)	954.6144	0	Best
SLAR3	Constant companions + casual acquaintances	g'= 0.032994+0.082262*exp (-0.10386*td)	959.4630	4.85	Considerably less support
SLAR4	Two levels of casual acquaintances	0.27846*exp (-1.7792*td)+0.047791*exp (-0.00061118*td)	957.2390	2.62	Some support

Figures headings

Figure 1. (a) Map of the study area in Iceland, with boat surveys conducted within gray-hatched areas in Faxaflói and Skjálfandi, Iceland. (b) Faxaflói with effort tracks, (c) Skjálfandi with effort tracks when searching for white-beaked dolphins.

Figure 2. Estimated group sizes of white-beaked dolphins in Faxaflói (gray bars) and Skjálfandi (black bars), Iceland. Gray dashed line shows the mean group size in Faxaflói and the black line in Skjálfandi.

Figure 3. Dendrogram of the hierarchical cluster analysis using average linkage for 35 photo-identified individual white-beaked dolphins off Iceland. The star symbol indicates the strongest association. CCC=0.85. The dashed line indicates cluster division occurs at AI = 0.39 (modularity = 0.366).

Figure 4. SLARs for white-beaked dolphins sighted off Iceland with a moving average of 400 associations. Vertical bars indicate approximate standard errors calculating using the temporal jackknife method. The best fitting models were 'casual acquaintances' (green line) and 'two levels of casual acquaintances' (red line). Light blue line is The null association rate (violet line) is the lagged association rate expected if individuals were associating at random. Red arrows indicate: (I) first drop ~10 days, (II) peak ~450 days, (III) error bar drops below null ~1000 days and (IV) data drop below null ~1200 days.

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a)

b) c)

Figure 1.

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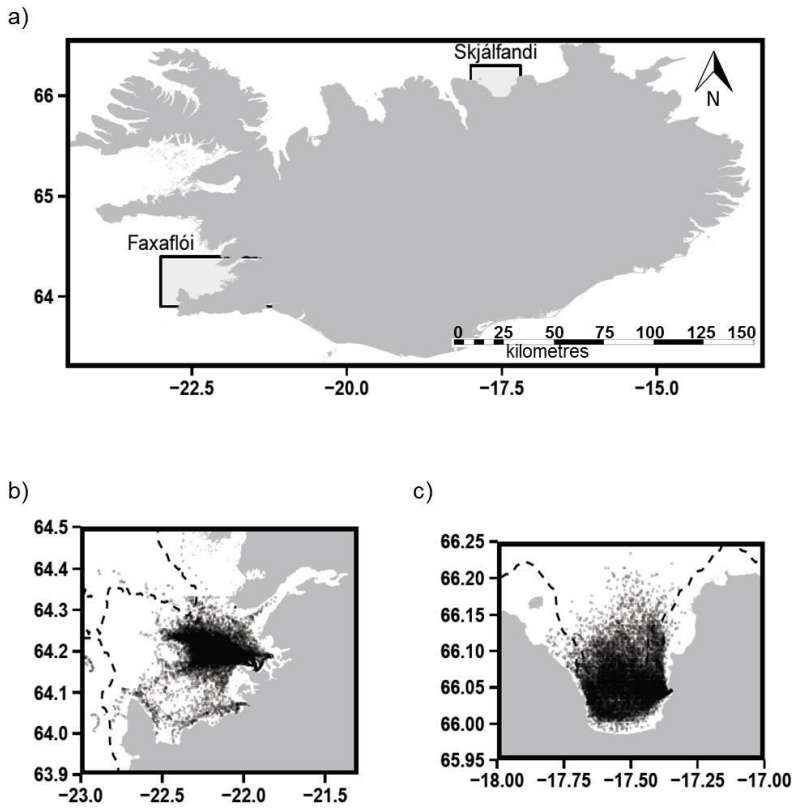
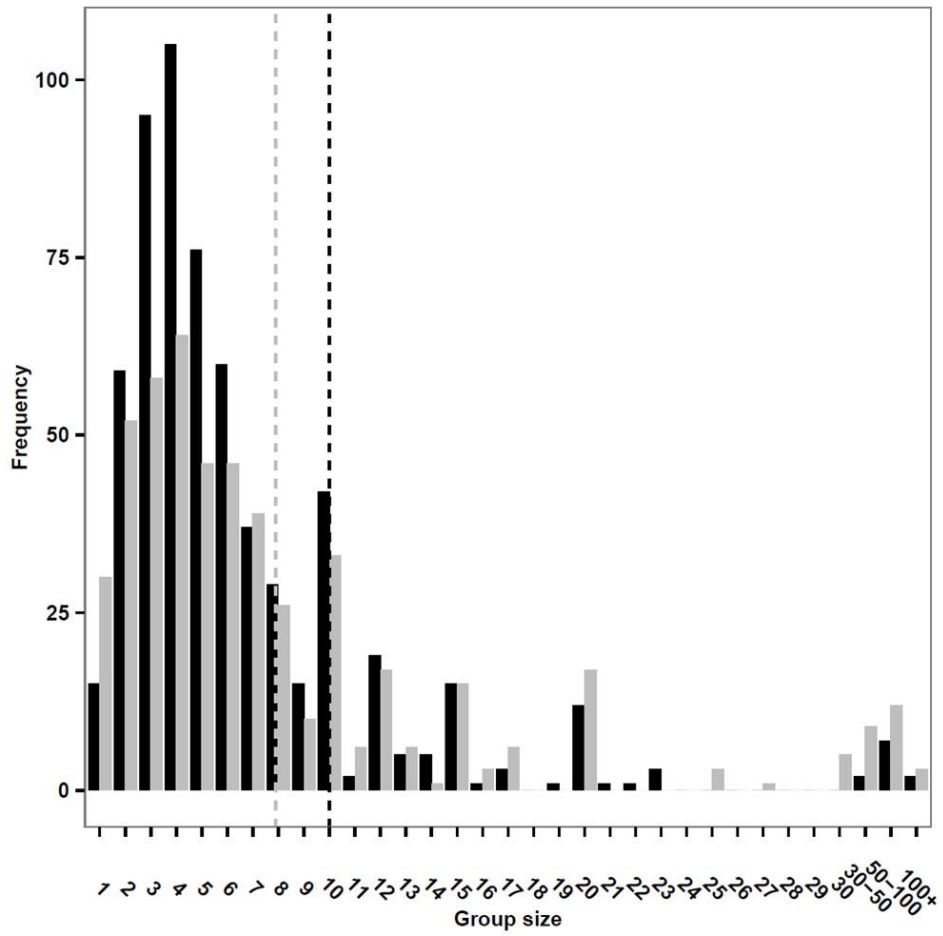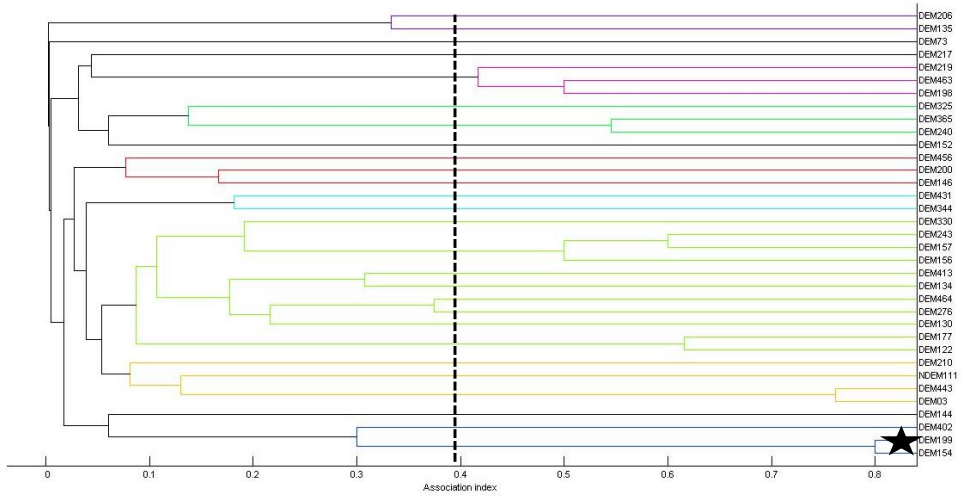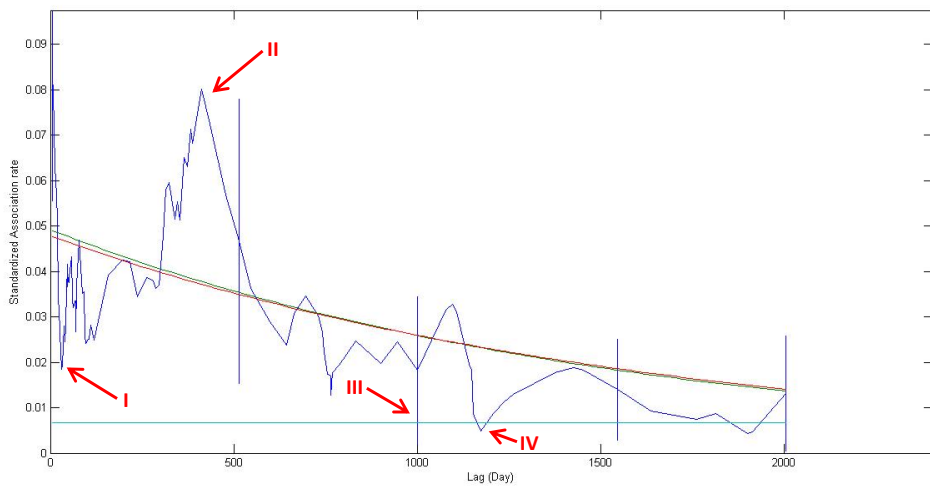*Figure 2.*

Figure 3.

Figure 4.

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Paper V

Paper V

Abundance and survival estimations of photographically identified humpback whales, white-beaked dolphins and common minke whales, in Icelandic coastal waters using capture recapture methods

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Abundance and survival of photographically identified humpback whales, white-beaked dolphins and common minke whales, in Icelandic coastal waters using capture-recapture methods

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ABSTRACT

Identification photographs of common minke whales, white-beaked dolphins and humpback whales were collected for 12 years (2001–2013) from on-board commercial whale watching vessels in the coastal waters of Faxaflói (SW coast, ~4,400 km^2) and Skjálfandi Bays (NE coast, ~1,100 km^2), Iceland. We fitted open capture-recapture (CR) models to these data to estimate abundance and survival while accounting for imperfect detection. A transient effect was accounted for whenever required to estimate the population of resident individuals. We estimated an average abundance of 81 humpback whales (Mn; 95% confidence interval: 53–125) in Skjálfandi Bay; 226 white-beaked dolphins (La; [169–301]) in Faxaflói Bay; and 70 minke whales (Ba; [53–93]) in Faxaflói Bay and 18 (12–27) in Skjálfandi Bay. We also found that apparent survival was constant for all three species (Mn: 0.50 [0.40–0.60], La: 0.75 [0.67–0.82], Ba-Faxaflói: 0.86 [0.76–0.93], Ba-Skjálfandi: 0.97 [0.71–1.00]). These first CR-based estimates of abundance and survival of humpback whales, white-beaked dolphins and minke whales occurring in Icelandic coastal-shelf waters will be used to inform and develop future sustainable conservation management practices in Iceland for these species.

Key words: abundance, survival, capture-recapture, humpback whale, *Megaptera novaeangliae*, white-beaked dolphin, *Lagenorhynchus albirostris*, common minke whale, *Balaenoptera acutorostrata*, Iceland.

For management and conservation purposes, it is essential to gather information about abundance, survival, movement and distribution of free-ranging populations of cetaceans (Thompson and Mayer 1996, Wilson *et al.* 1997, Whitehead and Wimmer 2005, Silva *et al.* 2009, Dick *et al.* 2011). To monitor wild whales and dolphins, animals are usually photographed and the pictures are processed to get individual resightings using natural markings (*e.g.*, notches on the dorsal fin or pigmentation pattern on the flukes) (Hammond *et al.* 1990). These data are then analyzed using standard capture-recapture (CR) methods to estimate abundance and demographic parameters (*e.g.*, Calambokidis and Barlow 2004, Elwen *et al.* 2009, Ansmann *et al.* 2013, Alves *et al.* 2014). However, when mortality occurs and open-population models are used, particular attention is required because of phenomena that some whales and dolphins species exhibit, such as 'transience'

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(Silva *et al.* 2009, Conn *et al.* 2011, Madon *et al.* 2012, Orgeret *et al.* 2014). 'Transience' occurs when whales are passing through an area only once with no further chances to be encountered or sighted again (Pradel *et al.* 1997). Transience can introduce bias in abundance estimates especially for migratory species such as baleen whales that are known to undertake migrations (Madon *et al.* 2012). Two recent studies on marine mammals showed that abundance could be highly overestimated if transience was not properly accounted for in CR models (Madon *et al.* 2012, Conn *et al.* 2011). Additionally, not considering transience can generate a negative bias on survival caused by the unfeasibility to differentiate between emigration and death (Pradel *et al.* 1997).

Common minke whales (herein as 'minke whales'), white-beaked dolphins and humpback whales are commonly sighted in Icelandic waters (Pike *et al.* 2009), with white-beaked dolphins occurring all year long (Magnúsdóttir 2007). Minke and humpback whales are mainly observed from March to November (Bertulli 2010, Magnúsdóttir *et al.* 2014), although occasional presence in the winter has also been reported (Víkingsson 2004, Magnúsdóttir *et al.* 2014). Using aerial surveys covering Icelandic coastal waters (≤600m depth contour) (Gunnlaugsson *et al.* 1988, Pike *et al.* 2009), the abundance of minke whales was estimated via line transect methods to be 43,633 (95% confidence interval [CI]: 30,148–63,149) in 2001, 18,262 (7,381–24,919) in 2007, and 9,588 (5,274–14,420) in 2009 (Borchers *et al.* 2009, Pike *et al.* 2009, 2011). The only available abundance estimate for white-beaked dolphins in Icelandic waters dates back to 2001 (North Atlantic Sighting Surveys conducted from 1986–2001), resulting in an estimated 31,653 animals (17,679–56,672) (Pike *et al.* 2009) though a minority of other dolphins species were combined into this dolphin category during the analysis. In the same survey 4,928 (1,926–12,611) humpback whales were estimated (Pike *et al.* 2009), with 586 individuals recorded in the coastal waters of the northeast shelf that includes Skjálfandi Bay (Block 4, 175 – 1,956).

In all three species site fidelity was detected on the southwest coast (Faxaflói Bay off Reykjavik) and the northeast coast (Skjálfandi Bay off Húsavík), although the majority of individuals were sighted only once and then never seen again (Bertulli *et al.* 2013, Bertulli *et al.* 2015b, Klotz 2013). They are also subject to various pressures related to whale-watching (Christiansen *et al.* 2013) and fishery activities (Víkingsson and Ólafsdóttir 2004, Pike *et al.* 2009, Bertulli *et al.* 2011, Basran 2014), changes in the marine coastal environment (Víkingsson *et al.* 2014) and predatory attacks (Bertulli *et al.* 2012, McCordic *et al.* 2014, Bertulli *et al.* 2015a).

The main objective of this study was to produce the first assessment of population abundance and survival for humpback whales, white-beaked dolphins and minke whales occurring in Icelandic coastal waters using CR methods. To do so, we resorted to individual-based monitoring that could be conducted from whale-watching boats operating in shoreline waters, selecting two bays with a known high occurrence of humpback and minke whales, and of white-beaked dolphins near shore.

MATERIAL AND METHODS

Data collection

From 2001 to 2013 non-systematic and opportunistic surveys were conducted from on board whale-watching boats in order to obtain photo-identification images of minke whales, white-beaked dolphins and humpback whales in Icelandic shelf waters. The covered area included the coastal waters of Faxaflói Bay (64°24'N, 22°00'W; Stefánsson and Guðmundsson 1978, Stefánsson *et al.* 1987) and Skjálfandi Bay (66°05'N, 17°33'W; Gíslason 2004), two relatively wide bays approximately 600 km apart from each other and located respectively in the southwest and northeast

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of Iceland (Fig. 1). The study area was around 1,100 km² in Skjálfandi Bay and 4,440 km² in Faxaflói Bay (Bertulli *et al*. 2012). These areas were chosen because of the predictable seasonal high occurrence of whales and dolphins close to shore and the presence of well-established whale-watching operations offering multiple daily tours. Boat surveys were conducted in sea state of zero to three on the Beaufort scale. Further details about boat size, tour frequency and duration, data forms and photographic gear used during data collection, as well as the number of observers, are available in Bertulli *et al*. 2013 and Bertulli *et al*. 2015b.

When possible, vessels would run parallel to whales and dolphin groups, allowing researchers to systematically shoot the entire surfacing pattern of each encountered individual. When study species were encountered within groups of more than one individual, no preference was given to marked animals over unmarked animals (Williams *et al*. 1993, Currey *et al*. 2008). A range of digital cameras were used in both study areas, with zoom lenses ranging from 55–200mm to 70–300 mm for Faxaflói Bay and 28–135 mm to 40–150 mm for Skjálfandi Bay. Images were taken in both JPG (300 pixel/inch) and RAW formats.

Photo-identification

Photographs of adults only were rated into six grades (Q1 to Q6) according to focus, angle, luminosity, sharpness and proportion of the frame occupied by the body of the animal. Only images rated $Q \geq 5$ were considered good enough for the analysis (Elwen *et al*. 2009, Gowans and Whitehead 2001, Rosso *et al*. 2011). Dorsal fins were then rated into four grades based on distinctiveness (1 to 4: 1-*very distinctive*, 2-*distinctive*, 3-*slightly distinctive*, 4-*not-distinctive*). Only *distinctive* and *very distinctive* fins were incorporated in the analysis (Zaeschmar *et al*. 2014). Regarding minke whales and white-beaked dolphins, dorsal fin outline marks (*e.g.,* notches on trailing and leading edges, protruding tissues) and injury marks (*e.g.*, wounds, anthropogenic and antagonistic scars, back indentation, amputation and deformation) were used as primary features to identify all animals (Wilson *et al*. 1999, Augé-Méthé and Whitehead 2007, Bertulli *et al*. 2015a). Linear marks for white-beaked dolphins (*e.g.*, fin scrapes) and bite marks for minke whales (*e.g.*, cookie-cutter shark bites) were found to be reliable marks, but only for recaptures spanning 5 and 8 years respectively (Bertulli *et al*. 2015a). Thus, these marks were only used as secondary features, solely in addition to primary marks. Humpback whales were identified using pigmentation patterns on the ventral side of their flukes and/or the presence of notches in the fluke edge. Photos of marked dorsal fins were used as a secondary features. Photo-id images were matched in chronological order of collection to detect any change of outline and body marks over time. Additionally, during the matching process, a single qualified person was responsible for quality-grading each photo-identification image, which was also systematically evaluated by up to two people throughout each field season (Sears *et al*. 1990, Davies *et al*. 2001).

Data analysis

We used the year as a time unit (*e.g.*, Silva *et al*. 2009), whereby each year was made of 3 to 12 months (see Table 1). A standard Cormack-Jolly-Seber (CJS) open-population model (*e.g.*, Lebreton *et al*. 1992) was used with two different parameters, namely the recapture (p) and survival (ϕ) probabilities. We considered constant or time effects on these parameters, which resulted in four different models: (1) both ϕ and p were constant over time; (2) ϕ was constant and p was time-dependent; (3) ϕ was time-dependent and p was constant; and (4) both parameters were time-dependent. RMark (Laake 2013) was used to fit these CR models and estimate survival whilst

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accounting for detectability of less than one. Program U-CARE (Choquet *et al*. 2009) was used to assess the quality of fit of CJS models to the photo-id CR data (Pradel *et al*. 2005). We detected a transient effect for both populations of minke whales (see Results section). Therefore a transient effect was incorporated in the models following Pradel *et al.* (1997). Specifically, we used a two-age class on survival and considered the age in CR analysis as the time passed since the animal was first sighted. Individuals that were sighted only once were part of the first age-class while all the others were part of the second (*e.g.*, Ramp *et al*. 2006, Madon *et al*. 2012). The proportion of transients was estimated and the abundance estimate amended accordingly (Madon *et al*. 2012). To determine the most parsimonious model, the model with the lowest AICc score (Akaike Information Criterion corrected for small sample sizes; *e.g.,* Burnham and Anderson 2002) was selected. The selected model was then used in a bootstrap procedure (with 500 iterations) to calculate 95% confidence interval for population size (*e.g.*, Cubaynes *et al*. 2010). To assess trends in abundance, we performed weighted linear regressions of the estimated parameters over time, using the inverse of the squared bootstrapped standard deviation as the model weights.

The minke whale data from both Faxaflói and Skjálfandi Bay were used; each bay was considered separately to calculate abundance. Two individual whales (DEM72 and DEM217) were identified in both bays but due to the low number of exchanges (DEM72 sighted four times; DEM217 sighted seven times), they could not be used to estimate movement probabilities in multisite CR models (*e.g.*, Lebreton *et al*. 2009). These two individuals were sighted more often in the Faxaflói Bay area, and were thus considered as part of the Faxaflói Bay population. The white-beaked dolphins data from only Faxaflói Bay were used, since only three individual dolphins were resighted in Skjálfandi Bay between years. Similarly, the humpback whale data from only Skjálfandi Bay were used, since only five individuals were resighted in Faxaflói Bay between years.

RESULTS

Humpback whales

From May 2001 to September 2013, a total of 510 days (1570 sightings, Table 1) were spent using whale-watching boats to collect photo-identification images in the coastal waters of Skjálfandi Bay, northeast Iceland. A total of 210 individual adult humpback whales were photo-identified during these surveys, with 88% (n = 185) of individuals photographed more than once and 28% (n = 59) photographed across multiple years. Table 2a provides information about the number of marked, newly detected and total number of resighted humpback whales per year, showing that the cumulative number of identified individuals ('in catalogue' in Table 2a) of humpback whales did not decrease with time in the study area. In Skjálfandi Bay, the test of transience was not significant (TEST 3.SR, χ^2 = 7.8, df = 8, P = 0.46), and we found an appropriate fit of the CJS model to the data (χ^2=16.2, df = 20, P = 0.71). The best model retained constant survival and time-dependent recapture probability (Table 3), though there was some uncertainty in whether time dependence should be included or not, as the AICc of the two best models (with/without time-dependence on the detection probability) differed by less than 2 units. In theory, a model-averaging approach should be used for inference, at the cost of making the bootstrap procedure for calculating abundance confidence interval much more tedious. Therefore, we checked that the estimated detection probability in the constant model was close to the average of the time-varying estimated detection probabilities in the best model; inference was based on the model with time-varying detection probability. The estimated constant survival was 0.50 (0.40–0.60). The highest detection probability was recorded in 2013 (0.89, SE = 0.17) and the lowest in 2008 (0.16,

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SE =0.11), with an overall estimate of 0.51 (SE = 0.06, Fig. 2a). On average, we estimated a total abundance of 81 humpback whales in Skjálfandi Bay (53–125). The annual abundance varied from 37 whales in 2007 (95% CI: 20–80, SD = 7.87) to 116 in 2012 (95% CI: 70–185, SD = 28.91, Fig. 2b). We found a significant positive trend over time in the abundance estimates (adjusted r^2 = 0.641, P = 0.019). Due to very low recapture rates, reliable abundance estimates could not be obtained for the first five years (2001-2006).

White-beaked dolphins

From May 2002 to September 2013, a total of 856 days (651 sightings, Table 1) were spent using whale-watching boats to collect photo-identification images in the coastal waters of Faxaflói Bay, southwest Iceland. A total of 283 individual adult white-beaked dolphins were photo-identified during these surveys, with 36% (n = 103) of individuals photographed more than once and 24% (n = 67) photographed across multiple years. Table 2b provides information about the number of marked, newly sighted and total number of resighted humpback whales per year. In Faxaflói Bay, the test of transience was not significant (TEST 3.SR, χ^2 = 5.8, df = 6, P = 0.45), and we found that the CJS model fitted the data well (χ^2 = 25, df = 21, P = 0.25). The best CJS model retained constant survival and time-dependent recapture probability (Table 3). The estimated constant survival was 0.75 (0.67–0.82). The highest detection probability was recorded in 2008 (0.41, SE = 0.10) and the lowest in 2010 (0.17, SE = 0.05), with an overall estimate of 0.25 (SE = 0.03, Fig. 3a). On average, we estimated a total abundance of 226 white-beaked dolphins in Faxaflói Bay (169–301). The annual abundance varied from 134 whales in 2008 (82–223) to 280 in 2010 (172–489, Fig. 3b). We did not find a linear effect of time in abundance estimates (adjusted r^2 = -0.123, P = 0.539). Due to low recapture rates, reliable abundance estimates could not be obtained for the first five years (2002-2007).

Minke whales
Faxaflói Bay

From May 2007 to December 2013, a total of 667 days (2417 sightings, Table 1) were spent using whale-watching boats to collect photo-identification images in the coastal waters of Faxaflói Bay, southwest Iceland. A total of 206 individual adult minke whales were photo-identified during these surveys, with 46% (n = 95) of individuals photographed more than once and 33% (n = 68) photographed across multiple years. Table 2c provides information about the number of marked, newly detected and total number of resighted minke whales per year in Faxaflói Bay, showing that the cumulative number of identified individuals ('in catalogue' in Table 2c) of minke whales did not decrease with time in the study area. In Faxaflói Bay, the test of transience was significant (TEST 3.SR, χ^2 = 25, df = 5, P<0.001). Once a transient effect was accounted for, the CJS model fit the data well (χ^2 = 6.3, df = 11, P = 0.85). The best model retained a transient effect on survival and constant recapture probability (Table 3). The average proportion of transients in the photo-identified minke whales was 46% (32%-58%). The estimated survival was estimated at 0.86 (0.76–0.93) for resident individuals. A constant recapture probability was estimated at 0.48 (0.39–0.57). On average, we estimated a total abundance of 71 minke whales in Faxaflói Bay (53–93). The annual abundances varied from a low 28 whales in 2007 (14–47) to a high 94 in 2010 (66–135, Fig. 4a). We detected a significant positive time trend in abundance estimates (adjusted r^2 = 0.627, P = 0.021).

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Skjálfandi Bay

From May 2001 to September 2013, a total of 656 days (1442 sightings, Table 1) were spent using whale-watching boats to collect photo-identification images in the coastal waters of Skjálfandi Bay, northeast Iceland. A total of 44 individual adult humpback whales were photo-identified during these surveys, with 52% ($n = 23$) of individuals photographed more than once and 48% ($n = 21$) photographed across multiple years. Table 2c provides information about the number of marked, newly captured and total number of recaptured humpback whales per year, showing that the cumulative number of identified individuals ('in catalogue' in Table 2c) of humpback whales did not decrease with time in the study area. In Skjálfandi Bay, the test of transience was significant (TEST 3.SR, $\chi^2 = 15.2$, df = 6, $P = 0.02$). Once a transient effect was incorporated, the CJS model fit the data well ($\chi^2 = 15.4$, df = 18, $P = 0.63$). The best CJS model retained a transient effect on survival and constant recapture probability (Table 3). The average proportion of transients in the photo-identified minke whales was estimated 24% (0.1%-46%), with substantial uncertainty due to the low number of individuals in the dataset and imprecise survival estimates. The estimated survival for resident individuals was 0.97 (0.71–1.00). A constant recapture probability was estimated equal to 0.49 (0.37–0.61). On average, we estimated a total abundance of 18 minke whales in Skjálfandi Bay (12–27). The annual abundance varied from 15 whales in 2008 (5–29) to 35 in 2012 (21–50, Fig. 4b). We detected a significant positive time trend in the abundance estimates (adjusted $r^2 = 0.830$, $P = 0.007$). Due to low detection rates, reliable abundance estimates could not be obtained for the first six years (2001-2007).

DISCUSSION

This study presents the first abundance and survival estimates using CR for humpback whales, white-beaked dolphins and minke whales inhabiting the Icelandic coastal waters of Faxaflói and Skjálfandi Bays.

Abundance

The results in this study showed the presence of transience for minke whales in both Faxaflói and Skjálfandi bays. Generally, transience introduces heterogeneity in a population with some animals being capturable (*i.e.*, the 'residents') and other with a null probability of being recaptured (*i.e.*, the 'transients'). By correcting our population size estimates by the proportion of transients, the abundance estimate obtained did not carry biases (*i.e.*, overestimation). The transient effect detected in this study could not be interpreted as an effect of true age (*e.g.*, a difference in survival between young and adults) since only adults were used in this study. It has been suggested that transience could be a result of heterogeneity in the sampling effort (Silva *et al*. 2009, Madon *et al*. 2012). Table 1 shows lower sampling effort in the year 2008 for minke whales in Faxaflói and in 2003-2004 for the same species in Skjálfandi. It is unlikely though that the observed transience was caused by so few years out of 7 of data collected for minke. The transient effect could be also sex-specific. A recent study demonstrated female humpback whales in New Caledonia are more prone to be transient than males during the breeding season (Madon *et al*. 2012), which was attributed to females' relatively more elusive behavior (Smith *et al*. 1999, Garrigue *et al*. 2004, Madon 2010) and shorter residency times (Palsbøll *et al*. 1997, Craig *et al*. 2001). Assessing the sex-ratio in minke whales could inform us about the transiency we found in this species and possibly help in providing more accurate demographic estimates for Iceland. Previous studies conducted in Iceland reported a minke whale (DEM217) migrating (*ca*. 600 km) between the Faxaflói and Skjálfandi

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bays (Bertulli *et al*. 2013), and we found another case in this study (see *Data analysis* in the Material and Methods section). We therefore believe that the transient effect we detected was due to individuals moving from one area to the other. We acknowledge, however, that a larger sample size and a monitoring on more geographical areas are needed before drawing firm conclusions about residency vs. transience patterns in Icelandic waters.

A significant positive trend in abundance was detected for two species: humpback and minke whales. For minke whales, this datum could suggest possible partial recovery of this species on the southwest coast (Faxaflói Bay), where it was reported to be declining since 2007 in southern and western waters (Borchers *et al*. 2009, Pike *et al*. 2009, 2011, Víkingsson *et al*. 2015). The abundance of humpback whales showed an increase from 1986 to 2001 before reaching a plateau in 2000 (Pike *et al*. 2009, Víkingsson *et al*. 2015). Therefore, the positive trend in abundance we found could be mirroring this existing trend.

A number of caveats should be mentioned with respect to the methods employed for this study. There might have been some temporary emigration and with individuals who are therefore not available for capture (Nicholson *et al*. 2012). Temporary emigration might have also occurred due to uneven sampling of the study areas (*e.g.*, data collection was dependent on whale-watching tours or due to non-dedicated efforts) or due to some individuals with home ranges within each bay that extended beyond areas of survey effort. As a consequence, our abundance estimates could have been biased towards lower range estimates (*e.g.*, Read *et al*. 2003). Usually, in such situations, a robust design approach is adopted to account for temporary emigration (*e.g.*, Nicholson *et al*. 2012, Daura-Jorge *et al*. 2013, Smith *et al*. 2013). The Pollock's closed robust design (Pollock 1982, Kendall *et al*. 1997) could be used in the future pending some modifications to the sampling protocol. In particular, future research could be conducted in other bays on the west and east coasts of Iceland that would provide further knowledge on patterns of distribution and movement of whales and dolphins. This would be very helpful in redesigning how to distribute future photographic effort using CR techniques.

Survival

The estimated overall survival rate for humpback whales (0.50, [0.40–0.60]) in this study was similar to estimates of resident Southeastern Pacific humpback whales from Ecuador (0.45, [0.32–0.58], Felix *et al*. 2011). In general, however, humpback whale apparent survival estimates are much higher (*e.g.*, Barlow and Clapham 1997, Calambokidis and Barlow 2004, Felix *et al*. 2011). White-beaked dolphin survival rates in this study (0.75 [0.67–0.82]) were similar to Hector's dolphins in New Zealand (0.77, Slooten *et al*. 1992, 0.72, Gormley *et al*. 2005) but overall lower than most of values reported in other dolphin studies (*e.g.*, Lockyer *et al*. 1988, Currey *et al*. 2009, Mansur *et al*. 2011, Fearnbach *et al*. 2012, Nicholson *et al*. 2012, Pusineri *et al*. 2014, Tyne *et al*. 2014). The ecological features of each study site could have influenced differences between these values (Currey *et al*. 2009). Survival estimates for resident minke whales in both bays (Faxaflói Bay: 0.86 [0.76–0.93]; Skjálfandi Bay: 0.97 [0.71–1.00]) are similar to other reported whale survival estimates (*e.g.*, Barlow and Clapham 1997, Calambokidis and Barlow 2004, Felix *et al*. 2011). Ryan *et al*. (2014) suggested that lower estimates could reflect an outward migration (*e.g.*, temporary or permanent migration). Here, we estimated 'apparent' survival, *i.e.*, the product of true survival and the study area site fidelity (Lebreton *et al*. 1992). 'Apparent' survival is underestimated, than when compared to the true survival, unless permanent emigration equals zero. Additionally, if the study area is contained within a wider area, this can induce bias in survival

estimates (Gilroy *et al*. 2012). Future analyses could resort to recently developed methods to infer true survival, such as kernel models (Gilroy *et al*. 2012) or spatially-explicit CR models (Schaub and Royle 2013). Alternatively, Felix *et al*. (2011) argued that lower survival estimates might be caused by a 'transient effect'. In our case, failing to detect transience for humpback whales could be due to a lack of statistical power. The lower survival rates for humpback whales and white-beaked dolphin could also be the result of the overlap of our study areas with fishing activities. Whale-watching activities do not appear to affect adult minke whale survival in Faxaflói Bay (Christiansen *et al*. 2015). However, Christiansen *et al*. (2015) also proposed to investigate into the overall exposure of whales to whale-watching, which might show a significant effect on whales. Whaling of minke whales was conducted in the Iceland continental shelf area between 1975 and 1985, and resumed in 2003 until the present time (Marine Research Institute 2014). From 2008 to 2013, a total of 324 individuals were caught (Marine Research Institute 2014) in different bays around Iceland, with the majority of catches in Faxaflói Bay. In the future, we recommend the use of CR models allowing the incorporation of cause-specific death (*e.g*., Koons *et al*. 2014) – *i.e.*, taking whaling into account – to disentangle natural mortality from human-induced mortality. Lastly, according to findings in other locations outside of Iceland (Kasuya and March 1984, Ramp *et al*. 2010), survival rates in whales and dolphins are sex-dependent; regrettably, sex could not be reliably determined for all minke whales, humpback whales and white-beaked dolphins used in the analyses for this study. Future studies assessing sex among whales and dolphins occurring in Icelandic coastal waters could clarify if these differences explain the low survival values obtained in this study.

Recapture probability

In this study, the time-varying recapture probability estimates of humpback whales and white-beaked dolphins could be a result of differences in sampling effort, type of vessels used, survey equipment used, variations in individual patterns of residency (*e.g*., site fidelity: Silva *et al*. 2009, Straley *et al*. 2009, Cantor *et al*. 2012, Alves *et al*. 2014), or environmental conditions. The low recapture probability for white-beaked dolphins suggests low site fidelity, with a high proportion of non-resident individuals and migration of dolphins between Faxaflói Bay and outside areas (Bertulli *et al*. 2015b). All humpback whales did not perform the fluking-out behavior observed in this species before a deep-dive during sightings, which could explain the differences in recapture probabilities obtained for humpback whales, as observed in other populations (*e.g.*, Straley *et al*. 2009).

Other sources of bias

Other sources of bias that can be introduced into abundance and survival estimates include 'trap dependence' effects. 'Trap dependence' *lato sensu* occurs when the detection of individuals is different depending on whether or not it was detected before (Pradel 1993). We did not detect trap-dependence for any of our populations (TEST 2.CT for humpback whales: $\chi^2 = 3$, df = 4, $P = 0.56$; white-beaked dolphins $\chi^2 = 7$, df = 5, $P = 0.19$; minke whales-Faxaflói: $\chi^2 = 3$, df = 4, $P = 0.58$; minke whales-Skjálfandi $\chi^2 = 9$, df = 7, $P = 0.26$). The trap-dependence effect can have several explanations in the photo-identification study context. For example, observer effects or species site fidelity (see review in Pradel and Sanz-Aguilar 2012). To the authors' knowledge, the impact of trap-dependence on the estimation of abundance in an open-population has only been investigated once in a study that showed to what extend abundance could be underestimated when detection events were correlated (Lenoël *et al.* submitted).

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In conclusion, we estimated abundance and survival for three cetacean species occurring in Icelandic coastal-shelf waters using CR methods to account for imperfect detection and a transient effect. This was the first instance that capture-recapture methods were used to estimate the abundance and survival for all three species in Icelandic waters. In the future, we recommend enlarging the sampling area and collecting data from multiple sites to increase our knowledge on whales and dolphins' habitat use, residency patterns and movements.

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Figures headings

Figure 1. Map of the study area showing Faxaflói Bay and Skjálfandi Bay, Iceland. Surveys were conducted within shaded areas.

Figure 2. (a) Estimates of recapture probability for adult humpback whales in Skjálfandi Bay, with 95% confidence intervals (vertical bars); (b) Estimates of abundance for adult humpback whales in Skjálfandi Bay, with 95% confidence intervals (vertical bars). The gray fitted straight line represents the linear trend in abundance.

Figure 3. (a) Estimates of recapture probability for adult white-beaked dolphins in Faxaflói Bay, with 95% confidence intervals (vertical bars); (b) Estimates of abundance for adult white-beaked dolphins in Faxaflói Bay, with 95% confidence intervals (vertical bars).

Figure 4. (a) Estimates of abundance for adult minke whales in Faxaflói Bay, with 95% confidence intervals (vertical bars)*;* (b) Estimates of abundance for adult minke whales in Skjálfandi Bay, with 95% confidence intervals (vertical bars). The gray fitted straight line represents the linear trend in abundance.

Tables

Table 1. Annual effort spent for each species (MW = minke whale, WBD = white-beaked dolphin, HW = humpback whale) in each site (FB = Faxaflói Bay, SB = Skjálfandi Bay) from 2001 to 2013.

Table 2.
Summary of number of marked adult (a) humpback whales from Skjálfandi Bay, (b) white-beaked dolphins from Faxaflói Bay and (c) minke whales from both bays, in each year (2001-2013).

Table 3.
AICc scores for the four models (1-4) for each species. HW = humpback whale, MF = minke whale, Faxaflói Bay, MS = minke whale, Skjálfandi Bay, WBD = white-beaked dolphin. The best model for each species is in bold font.
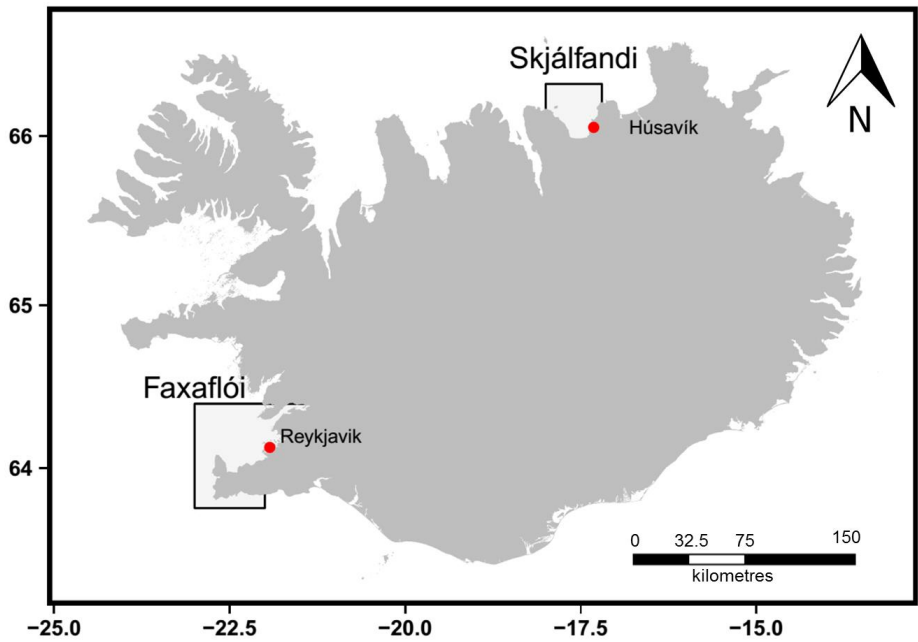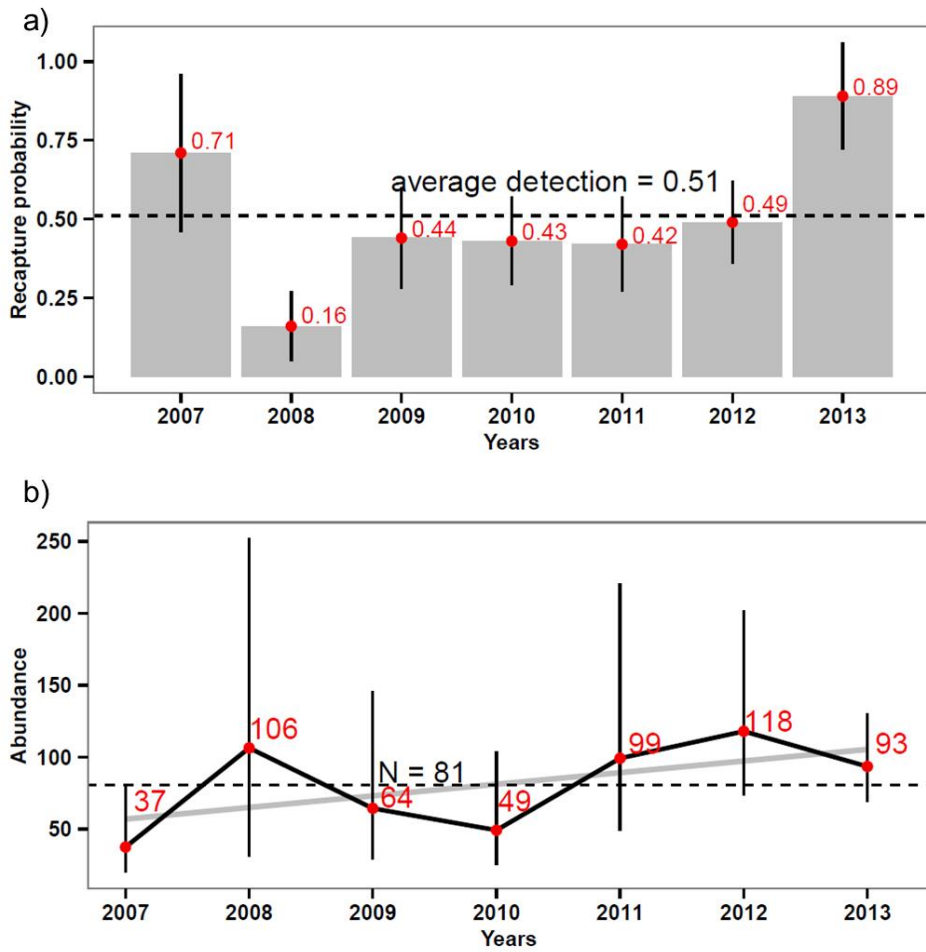
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Figure 1.
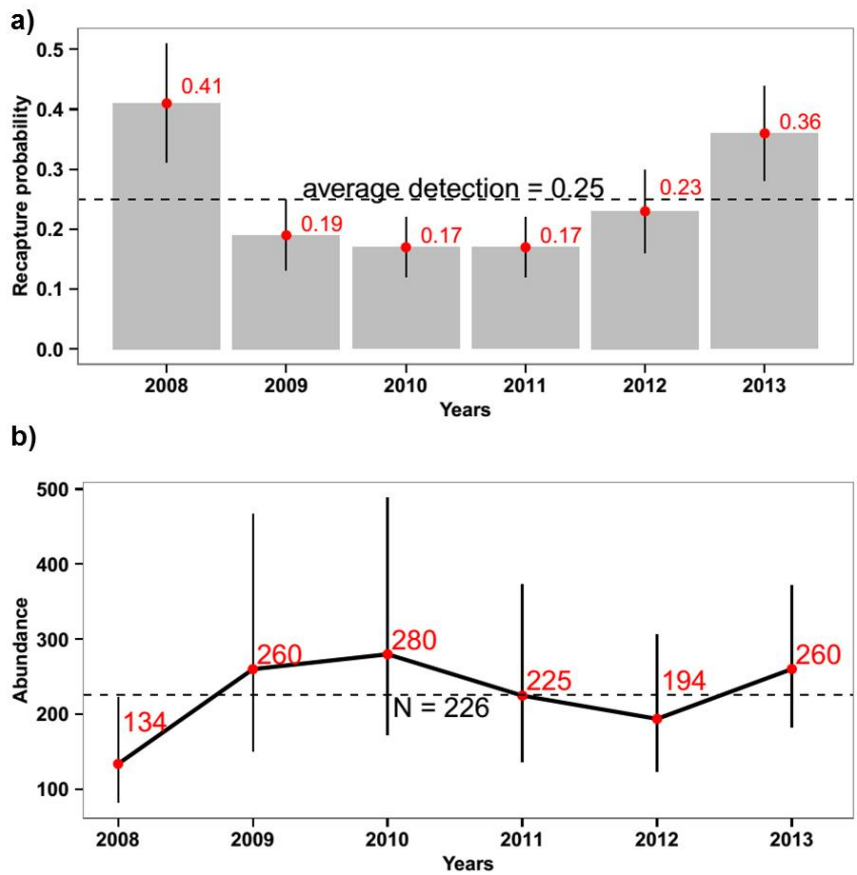
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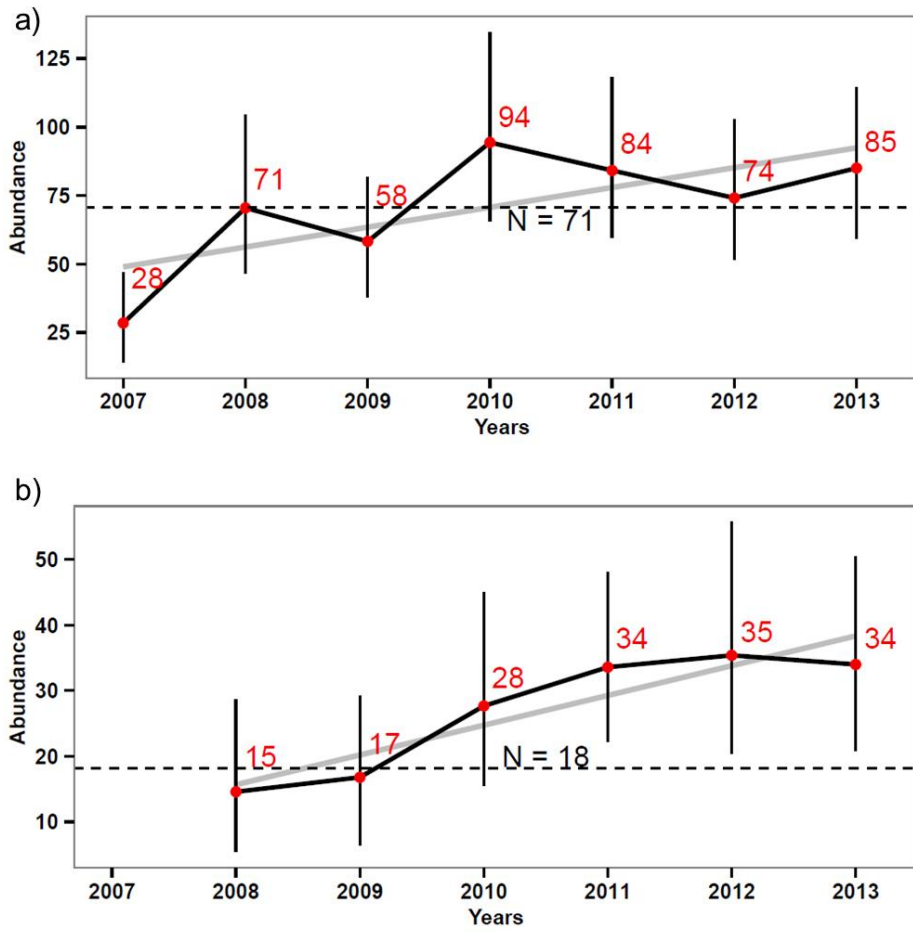
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Figure 2.

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Figure 3.

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Figure 4.

Table 1. Annual effort spent for each species (MW = minke whale, WBD = white-beaked dolphin, HW = humpback whale) in each site (FB = Faxaflói Bay, SB = Skjálfandi Bay) from 2001 to 2013.

Species-Site	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	Total
HW-SB														
Capture occasion	NA	NA	27 Mag - 24 Aug	10 Jul - 25 Aug	7 Jul – 16 Sept	11 Mag - 3 Sept	2 Mag - 19 Sept	12 Mag - 15 Sept	2 Mag - 20 Sept	17 Mag - 14 Oct	6 Mag – 6 Sept	13 Apr - 30 Sept	16 Apr - 29 Sept	
Days	NA	NA	1	5	3	38	77	54	56	29	82	103	119	567
Trips	NA	NA	1	5	3	38	77	57	65	32	99	135	211	723
Sightings	NA	NA	1	8	6	127	112	96	117	46	197	382	631	1723
Obs. time	NA	NA	NA	1.08	15.44	58.11	56.46	40.59	47.16	20.41	75.11	99.08	165.21	578
WBD-FB														
Capture occasion	-	20 Apr - 29 Sept	9 Apr - 19 Oct	14 Apr - 7 Oct	25 Mar - 27 Nov	12 May - 22 Oct	15 May - 9 Sept	21 Apr - 25 Aug	14 Apr - 19 Aug	7 Apr - 11 Sept	25 Mar - 22 Sept	1 Apr - 18 Dec	10 Jan - 22 Dec	
Days	-	94	94	99	98	53	42	65	46	43	41	66	115	856
Trips	-	112	119	130	127	75	62	96	61	55	55	76	120	1088
Sightings	-	NA	NA	NA	NA	NA	NA	124	80	57	74	107	209	651
Obs. time	-	NA	NA	NA	NA	NA	NA	24.20	19.40	12.58	16.22	30.22	60.01	163
MW-FB														
Capture occasion	-	-	-	-	-	-	15 Mag - 9 Sept	21 Apr - 25 Aug	14 Apr - 19 Aug	7 Apr - 11 Sept	25 Mar - 22 Sept	1 Apr - 18 Dec	10 Jan - 22 Dec	
Days	-	-	-	-	-	-	73	72	82	83	83	143	131	667
Trips	-	-	-	-	-	-	145	144	157	147	172	233	196	1194
Sightings	-	-	-	-	-	-	NA	302	411	295	426	569	414	2417
Obs. time	-	-	-	-	-	-	NA	69.43	96.00	95.37	149.20	163.28	124.13	697
MW-SB														
Capture occasion	NA	NA	27 Mag - 24 Aug	10 Jul - 25 Aug	7 Jul - 16 Sept	11 Mag - 3 Sept	2 Mag - 19 Sept	12 Mag - 15 Sept	2 Mag - 20 Sept	17 Mag - 14 Oct	6 Mag – 6 Sept	13 Apr - 30 Sept	16 Apr - 29 Sept	
Days	NA	NA	45	25	47	53	59	55	61	105	60	66	80	656
Trips	NA	NA	48	25	49	55	59	59	80	141	63	85	121	785
Sightings	NA	NA	122	66	86	103	91	90	145	266	120	130	223	1442
Obs. time	NA	NA	NA	14.40	27.50	22.04	23.41	31.42	34.10	62.58	21.11	50.17	72.58	359

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Table 2.
Summary of number of marked adult (a) humpback whales from Skjálfandi Bay, (b) white-beaked dolphins from Faxaflói Bay and (c) minke whales from both bays, in each year (2001-2013).

Humpback whale – Skjálfandi Bay

Year	Marked	New	In catalog
2001	3	3	3
2002	2	2	5
2004	1	1	6
2005	4	3	9
2006	19	17	26
2007	23	17	43
2008	15	13	56
2009	25	19	75
2010	19	12	87
2011	37	31	118
2012	54	43	161
2013	78	49	210

(a) White-beaked dolphins – Faxaflói Bay

Year	Marked	New	In catalog
2002	1	1	1
2003	22	22	23
2004	13	12	35
2006	6	6	41
2007	22	22	63
2008	51	39	102
2009	45	36	136
2010	44	32	168
2011	38	25	193
2012	43	25	218
2013	92	65	283

(b) Minke whale – Faxaflói Bay

Year	Marked	New	In catalog
2007	24	24	24
2008	57	51	75
2009	39	23	98
2010	62	37	135
2011	55	33	168
2012	45	19	187
2013	50	19	206

Minke whale – Skjálfandi Bay

Year	Marked	New	In catalog

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2001	1	1	1
2002	1	1	2
2004	1	1	3
2005	1	1	4
2006	3	2	6
2007	3	2	8
2008	7	4	12
2009	8	4	16
2010	15	10	26
2011	18	9	35
2012	19	7	42
2013	16	2	44

Table 3.

AICc scores for the four models (1-4) for each species. HW = humpback whale, MF = minke whale, Faxaflói Bay, MS = minke whale, Skjálfandi Bay, WBD = white-beaked dolphin. The best model for each species is in bold font.

Model	Survival probability	Recapture probability	AIC$_c$
1$_{HW}$	Constant	Constant	347.76
2$_{HW}$	**Constant**	**Time**	**347.11**
3$_{HW}$	Time	Constant	352.80
4$_{HW}$	Time	Time	369.37
1$_{MWF}$	**Transience**	**Constant**	**574.58**
2$_{MWF}$	Transience	Time	593.48
3$_{MWF}$	Transience + Time	Constant	584.58
4$_{MWF}$	Transience + Time	Time	605.86
1$_{MWS}$	**Transience**	**Constant**	**193.19**
2$_{MWS}$	Transience	Time	213.98
3$_{MWS}$	Transience + Time	Constant	204.28
4$_{MWS}$	Transience + Time	Time	235.00
1$_{WBD}$	Constant	Constant	582.68
2$_{WBD}$	**Constant**	**Time**	**563.66**
3$_{WBD}$	Time	Constant	579.15
4$_{WBD}$	Time	Time	582.45

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