

Annual and monthly fluctuations in humpback whale (*Megaptera novaeangliae*) presence in Skjálfandi Bay, Iceland, during the feeding season (April–October)

L. KLOTZ¹, R. FERNÁNDEZ² AND M.H. RASMUSSEN³

Contact e-mail: mhr@hi.is

ABSTRACT

Humpback whales are among the most common whale species occurring in Skjálfandi Bay, North Iceland. Since 2001, 309 photographed humpback whales have been identified and catalogued. The percentage of whales re-sighted from year to year has been always less than 27% and only 49 out of 309 identified individuals were sighted in the Bay in two or more years, indicating that the humpback whales occurring in Skjálfandi Bay have various feeding areas. Kernel Density Estimations indicated distribution changes within the bay and throughout the season. In early summer, humpback whale densities were higher in the southern and western part of Skjálfandi Bay, whereas as the season progressed whale concentration increased further north in the direction of the open sea.

Generalised Linear Models (GLMs) were used to analyse a 10 year time series of monthly humpback whale Sightings Per Unit of Effort (SPUE; sightings per minute) during the summer season (May–October). Whalewatching boats were used as research platforms. The total effort was 136,503 minutes. 1,401 sightings of humpback whales were recorded. GLMs show significantly higher SPUE in 2006 (0.0132), 2011 (0.0111) and 2012 (0.0246) when compared to the start of the time series. September showed a significantly lower SPUE (0.0024) when compared to the baseline month (May). An independent dataset derived from logbook data provided by commercial whalewatching operations was used to derive the percentage of humpback whale positive surveys (surveys where the species was seen) over a longer time series (1995–2012). These data were analysed using Generalised Additive Models (GAMs) and show an increase on the percentage of positive surveys in the period 2006–09, a slight decrease in 2010 and a new increase in 2011–2012. Annual trends in positive surveys for two additional species of locally abundant cetaceans, the harbour porpoise and the white-beaked dolphin, were explored for comparison purposes. No trend was found for porpoises while the percentage of positive surveys for white-beaked dolphins showed a general decrease after 2002.

Fluctuations in SPUE and percentage of positive surveys may be due to varying environmental conditions within the bay, with potential implications for whalewatching operations. Given the scientific value of these conclusions, this study also supports the value of integrating whalewatching vessels as opportunistic platforms for cetacean research.

KEYWORDS: HUMPBACK WHALE; PHOTO-ID; SIGHTINGS PER UNIT EFFORT; ICELAND; WHALEWATCHING; WHITE-BEAKED DOLPHIN; HARBOUR PORPOISE

INTRODUCTION

The humpback whale, *Megaptera novaeangliae* (Borowski, 1781), inhabits all oceans of the world except polar pack ice zones (Chittleborough, 1965) and is among the most common cetacean species occurring in Skjálfandi Bay, North Iceland. Between the winter (November–April) and the summer (May–October) seasons they migrate over long distances, switching between their warmer tropical breeding areas and their feeding grounds in higher latitudes (Norris, 1977; Pomilla and Rosenbaum, 2005). In the eastern part of the North Atlantic, the distribution of the species during their feeding season ranges from Iceland and Scotland to the Barents Sea (Stevick *et al.*, 2003a). There are two known breeding grounds in the North Atlantic, located in the tropical waters of Cape Verde (Baker *et al.*, 1990; Katona, 1986; Kellogg, 1929; Vigness-Raposa *et al.*, 2010; Wenzel *et al.*, 2009) and also in the Caribbean (Balcomb and Nichols, 1982; Whitehead, 1982).

Although the humpback whale is thought to be philopatric (Boye *et al.*, 2010; Mitchell, 1974; Palsbøll *et al.*, 1997; Whitehead, 1982), female humpback whales have been found 10,000km away from their natal breeding sites in the Southern Hemisphere (Stevick *et al.*, 2011). This was

considered an indication of behavioural flexibility in migration patterns of a typically philopatric species as the females were probably exploring new breeding grounds due to changeable environmental conditions.

The worldwide abundance of the species strongly decreased during the whaling periods in the 1800s and early 1900s (Tønnessen and Johnsen, 1982). The International Whaling Commission (IWC) protected humpback whales from commercial whaling in the North Atlantic in 1955 (Best, 1993). Since the cessation of humpback whaling, North Atlantic populations show signs of recovering (Stevick *et al.*, 2003b). Between 1986 and 2001, aerial surveys in coastal Icelandic waters revealed an increase in humpback whale numbers of about 12% and estimated up to 4,928 (CV 0.463) individuals (Pike *et al.*, 2009). Mark-recapture abundance estimates by Smith *et al.* (1999) and Stevick *et al.* (2003a) approximate a North Atlantic population size of 10,600 (95% CI 9,300–12,100) and 11,570 (95% CI 10,290–13,390) individuals, respectively, based on data collected during surveys during the mid–1990s. Multiple partial-area surveys from 1996 to 2001 estimated about 3,246 (CV 0.512) humpback whales in the eastern North Atlantic (Øien, 2009). Abundance has been constantly increasing in later years and

¹ Department of Limnology and Oceanography, University of Vienna, Althanstrasse 14, 1090 Austria.

² International Council for the Exploration of the Sea, HC Andersens Boulevard 44–46, 1553 Copenhagen, Denmark.

³ University of Iceland Research Center in Húsavík, Hafnarstétt 3, 640 Húsavík, Iceland.

the current IUCN (International Union for the Conservation of Nature) Red List category for the humpback whale is Least Concern, although some subpopulations, for example in the Arabian Sea, remain Endangered (Reilly *et al.*, 2008). During shipboard and aerial surveys around Iceland and the Faroe Islands, Paxton *et al.* (2009) estimated abundances of 10,521 (95% CI: 3,716–24,636) in 1995 and 14,662 (9,441–29,879) in 2001. This trend has been also observed by Víkingsson *et al.* (2015) where results from aerial and shipboard surveys between 1986 and 2009 indicated an increase in humpback whale numbers up to the year 2001 with a slight decrease thereafter. Studies conducted in 2007 by Pike *et al.* (2010) gave evidence for stagnating numbers in the North Atlantic. Conventional distance sampling analysis estimated 11,572 humpback whales (95% CI 4,502–23,807) which is similar to the number estimated in the mid 1990s by Stevick *et al.* (2003b).

Photo-identification is a popular method for studying cetacean movements and population size. This technique is particularly appropriate for the individual identification of humpback whales given that they show a unique black and white pattern on their flukes' ventral surface. Moreover, the shape of the dorsal fin, which is variable in size, as well as markings such as scars, can also be used for individual identification (Clapham and Mayo, 1987; Katona and Whitehead, 1981). Photo-identification matches have been registered between humpback whales that migrated between Iceland and the Caribbean (e.g. Martin *et al.*, 1984; Smith *et al.*, 1999; Stevick *et al.*, 2003), and one humpback whale that migrated between Iceland and the Cape Verde islands (Jann *et al.*, 2003). These show that the whales feeding in Icelandic waters possibly originate from two different breeding grounds.

Whalewatching started in Iceland in Skjálfandi Bay, Húsavík, in 1995 (Rasmussen, 2014). Since 2001, whalewatching boats have been used as research platforms and humpback whales observed in Skjálfandi Bay were photographed and catalogued by personnel from the Húsavík Whale Museum. In 2003 an additional and extended data

collection scheme started focusing on behavioural and habitat preferences of all the local cetacean species.

In this study photo-identification was used to investigate the number of new and re-sighted humpback whales in Skjálfandi Bay between 2001 and 2012 and seasonal patterns were examined in humpback whale distribution within the bay through Kernel Density Estimations. In addition, potential temporal trends were assessed in the Sightings Per Unit Effort (SPUE) and percentage of positive surveys (i.e. percentage of trips in which the species was seen) of humpback whales in the same area and similar time period (2003–12 and 1995–2012 respectively). Trends in the percentage of positive surveys of harbour porpoises (*Phocoena phocoena*) and white beaked dolphins (*Lagenorhynchus albirostris*) were also analysed (1995–2012).

METHODS

Data collection took place in Skjálfandi Bay, northern Iceland (see Fig. 1). Whalewatching boats 'Gardar', 'Bjössi Sör' and 'Náttfari', operated by North Sailing (www.northsailing.is), were used as research platforms. A dedicated data collection scheme was carried out over the whalewatching season (May–October) from 2003 to 2012. Additional data were provided from the Húsavík Whale Museum, in the form of a Humpback Whale Catalogue, which contains all humpback whale individuals photoidentified in Skjálfandi Bay since 2001. In 2001 and 2002 data collection was limited to photo-identification materials along with data on effort and environmental factors. These data were used to calculate sighting and resighting rates of individual humpback whales in Skjálfandi Bay.

Standard protocols for the collection of photo-identification data were followed as described in Bertulli *et al.* (2013). Between one and three trained observers worked on board and recorded effort and cetacean presence. Sighting data includes: the time and location of the sightings, the species and number of individuals and the animals' main behaviour. Effort data includes environmental conditions

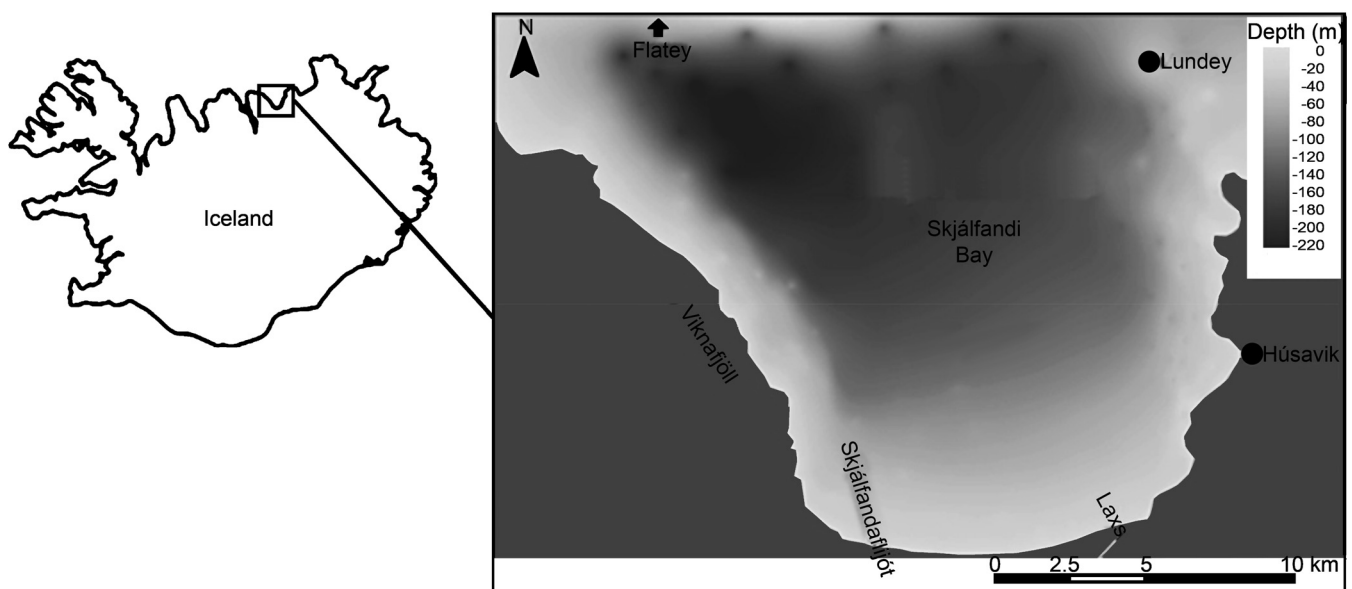


Fig. 1. Research area of Skjálfandi Bay.

such as cloud cover, sea state, precipitation, wind direction, glare, swell height and visibility. Time spent on effort started when leaving the harbour and continued until entering the port again. For every tour the route was tracked, with GPS-positions, determined every five minutes using GPSmap 60CSx GARMIN. Additional GPS coordinates were set when approaching a whale. Once humpback whales were sighted, photos were taken, using an EOS 60D CANON 28–135mm camera for individual identification (Clapham and Mayo, 1987; Katona and Whitehead, 1981). When several humpback whales were spotted at the same time they were considered a single sighting of several individuals. When a whale was first observed alone but more individuals approached the area, new sightings were recorded. Although the number of trips with observers increased over the years, the procedure of collecting data was standard over the years.

In addition the whalewatching company provided access to their logbooks, which contained the species and number of sighted cetaceans for each whalewatching tour from 1995 onwards. The logbook data were used solely to calculate the percentages of positive surveys of humpback whales, harbour porpoises and white-beaked dolphins in Skjálfandi Bay from 1995 to 2012.

To analyse the number of whales sighted in Skjálfandi Bay, cetacean sightings per unit effort (SPUE) were calculated using the formula:

$$\text{Sightings per Unit Effort} = \frac{\text{Number of Sightings}}{\text{Minutes Effort}}$$

$$\text{SPUE} = \frac{n}{LT}$$

Where n corresponds to the total number of sightings, LT is the total amount of time spent on surveys (total effort = minutes actively spent for searching).

To determine differences in the numbers of sightings and resightings per year, t-tests were performed using SigmaPlot 11.0.

To assess temporal trends in humpback whale SPUE, Gaussian Generalised Linear Models (GLMs) were used. SPUE was used as response variable and both year (2003–2012) and month (May–October) were used as explanatory variables (factors). The original SPUE data were Squared Root transformed to fulfil normal distribution requirements. Available data for 2003, 2004 and the month of October were limited, since humpback whales were recorded only one month during 2003 (August) and 2004 (July) and only two years during October (2010 and 2012), which compromised model validation. Subsequently 2003, 2004 and October were excluded from the temporal analyses. GLM models were optimised using a backwards selection, finally accepting the one with the lowest AIC (Akaike Information Criterion).

Trends in the percentage of positive surveys for three common cetacean species in the area (humpback whale, harbour porpoise and white-beaked dolphin) were investigated using Gaussian Generalised Additive Models (GAMs). The response variable was the yearly percentage of positive surveys (1995–2012) and year was introduced in the model as a continuous explanatory variable.

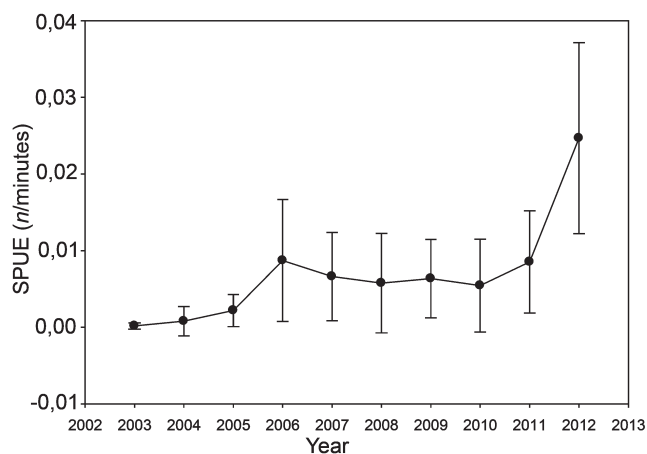


Fig. 2. Mean humpback whale SPUE and standard deviations from 2003 to 2012 (number of sightings/minute).

All models were validated by checking that no large ‘hat’ values (indicating influential data points) were detected, no over-dispersion was found, and serious patterns did not remain in the residuals. All models were performed in R.3.1.

To visualise humpback whale distribution patterns within the bay the most recent year in the data set 2012 was used as an example, GPS positions of the sightings were plotted using ArcGIS 10.1. Kernel Density Estimation, a method for estimating the probability distribution of a random variable (Silverman, 1986), was then performed to investigate the intensity of use of the study area across months. Kernel Density Estimation represents a uniformly consistent, continuous estimator of an unknown probability measure by a series of densities, often used in ecological analysis. Thus, the probability with which animals stay in a specified geographical area (i.e. ranging patterns) can be estimated (Rodgers and Kie, 2011).

RESULTS

The number of minutes spent on effort differed over the years, starting at a low level in 2003 (2,748 minutes) and continuing on a high, slightly increasing level from 2005 (11,522 minutes) onwards, peaking in 2012 (21,188 minutes). The monthly peak value was 7,711 minutes in July 2011 (Table 1). A total of 1,401 sightings of humpback whales was reported, of which 519 took place during 2012. In 2003 the SPUE was the lowest recorded (average: 0.0002), whereas 2006, 2011 and 2012 showed a higher SPUE (see Fig. 2).

GLM models identified both year ($p = 0.003$) and month ($p = 0.02$) as significant variables influencing SPUE (squared rooted). The deviance explained by the best model was 60.1% (Table 2). When looking at individual years and months, 2006 ($p = 0.04$), 2011 ($p = 0.02$) and 2012 ($p < 0.001$) showed significantly higher SPUE than the year used as baseline (2005) while the month of September had a significantly lower SPUE ($p = 0.008$) than the baseline month (May). Note that the years 2003 and 2004 and the months of April and October were not considered in the GLM due to lack of data (see Methods).

Results from GAMs highlighted a significant influence of year in the percentage of positive surveys of humpback whales ($p = 0.02$), showing an increase in the period 2006–

Table 1

Survey effort for 2003 to 2012 during summer research seasons. For each year, both monthly and total effort data, expressed in minutes, are reported.

| | May | June | July | August | September | October | Total effort |
|------|-------|-------|-------|--------|-----------|---------|--------------|
| 2003 | 245 | 184 | 1,373 | 946 | 0 | 0 | 2,748 |
| 2004 | 0 | 0 | 1,698 | 1,996 | 0 | 0 | 3,694 |
| 2005 | 0 | 3,046 | 4,201 | 3,497 | 778 | 0 | 11,522 |
| 2006 | 1,360 | 4,340 | 3,585 | 3,478 | 175 | 0 | 12,938 |
| 2007 | 2,164 | 4,488 | 4,449 | 3,279 | 470 | 0 | 14,850 |
| 2008 | 2,308 | 4,229 | 3,022 | 4,321 | 2,018 | 0 | 15,898 |
| 2009 | 4,277 | 4,441 | 3,673 | 2,848 | 526 | 0 | 15,765 |
| 2010 | 1,806 | 4,758 | 5,165 | 4,294 | 2435 | 624 | 19,082 |
| 2011 | 863 | 4,702 | 7,711 | 5,003 | 539 | 0 | 18,818 |
| 2012 | 4,677 | 4,408 | 4,620 | 2,886 | 2,486 | 2,111 | 21,188 |

Table 2

Comparison of the three GLM models considered in the present study where the response variable is humpback whale SPUE.

| GLM model | Explanatory variables | Deviance explained (%) | AIC |
|-----------|-----------------------|------------------------|-----------|
| GLM1 | Year | 41 | -138.4719 |
| GLM2 | Month | 19 | -131.702 |
| GLM3 | Year, month | 60 | -146.029 |

09, a slight decrease in 2010 and a new increase in 2011 and 2012 (Fig. 3). The percentage of positive surveys of white-beaked dolphins was borderline significantly influenced by year ($p = 0.047$) with a higher percentage in the period 1999–2003 and a later decline (Fig. 3). No yearly effect was observed in the percentage of positive surveys for the harbour porpoise ($p = 0.6$).

Regarding the ranging preferences within the bay from April to October in 2012, Kernel Density reached highest values in the western part of the bay, which represents the deepest area. Additional high densities were recorded in regions closer to the shore (Fig. 4).

The few sightings of humpback whales in April were spread over the whole bay, but mostly close to the shore. In

May and June the whales preferred the western and the southern part, but were also present in an area at approximately 8km distance from Húsavík harbour in the middle of the bay. Humpback whales occurred throughout Skjálfandi Bay in July, with the exception of the southernmost areas. In August, September and October the whales were mostly restricted to the northwestern part of the bay.

The total number of photo-identified humpback whales increased annually from 7 individuals (2001) to 39 individuals (2009). After a slight decrease in 2010 (33 individuals), 42 humpback whales were photo-identified in 2011. The peak value was reached in 2012 with 77 photo-identified individuals (Table 3). The rate of resightings always remained under 27%. The first resighting was recorded in 2004, the highest resighting rate (26%) was reached in 2007 and the two lowest (7% in both cases) in 2005 and 2006. The majority of the re-captures (77%) involved individuals that had been photographed in Skjálfandi Bay the year before their first resighting.

When the numbers of newly identified individuals are plotted against the total number of whale encounters per year (no data collection took place in 2003), the discovery curve increases without any signs of flattening (Fig. 5), which suggests that humpback whales in Skjálfandi Bay do not belong to a closed population.

DISCUSSION

Interannual occurrence of humpback whales in Skjálfandi Bay is prone to fluctuations. Our data show annual and seasonal variation; significantly higher SPUEs in 2006, 2011 and 2012 when compared to the baseline year (2005), increasing percentage of humpback whale positive surveys in the period 2006–09 and after 2010, and significantly lower SPUEs in September when compared to the baseline month (May). Furthermore, the discovery curve, representing the number of new identified humpback whales in relation to the total number of catalogued individuals, has not reached a plateau yet, indicating that the humpback whales observed in the bay do not form a closed population and that every year new individuals visit the bay.

The high SPUEs recorded in recent years are in agreement with previous studies in the North Atlantic. For example, based on aerial surveys, Pike *et al.* (2009) recorded an increase in humpback whale abundance of about 12% in northeastern and eastern Iceland (including Skjálfandi Bay)

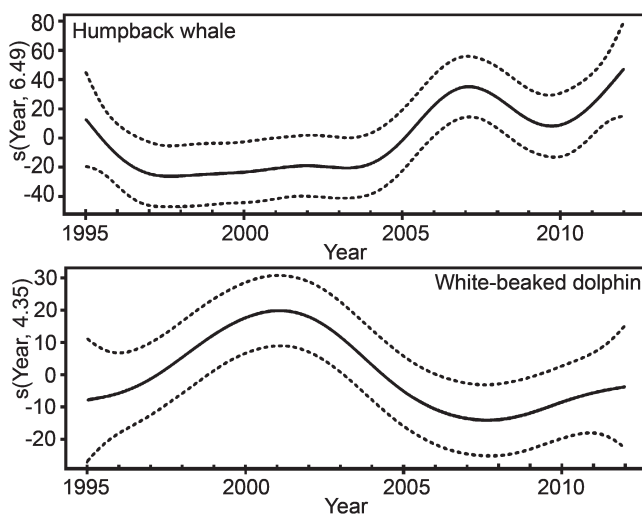


Fig. 3. Smoothed effect of year on percentage of positive surveys for humpback whale and white-beaked dolphin. The Y-axis represents the trend (positive or negative) in percentage of positive surveys in relation to year. Dotted lines are the approximate 95% confidence limits.

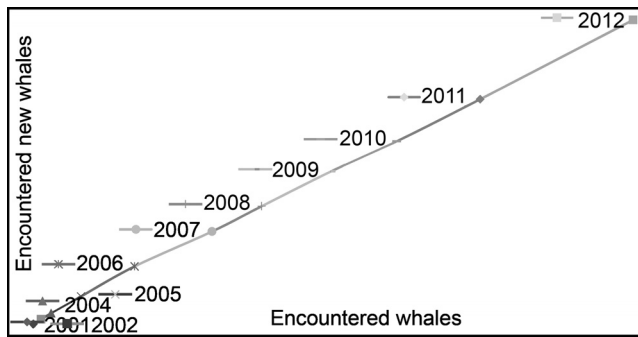


Fig. 5. Discovery curve of humpback whale individuals during the summer research season from 2001 to 2012. No data were available for 2003.

between 1986 and 2001. In West Greenland, the annual rate of increase in humpback whale sightings was 9.4% between 1984 and 2007 (Heide-Jørgensen *et al.*, 2012). These results have been related to the recovery of depleted populations previously subject to whaling. However, changes in humpback whale abundance trends within the northwest Atlantic could also be related to prey distribution shifts, comparable to what has been observed in the Gulf of Maine, where humpback whales have been shifting their distribution dependent on herring (*Clupea* sp.) and sandeel (*Ammodytes* sp.) occurrence (Stevick *et al.*, 2006).

A clear increasing trend in sightings of humpback whales in Icelandic waters was recorded from 1969 to 1988 by Sigurjónsson and Gunnlaugsson. It is possible that increasing numbers of whales might reflect changing feeding conditions, due to shifts in the distribution of small fish, or the immigration of whales from different North Atlantic stocks. However, recently published data indicate that the increase in numbers in Icelandic waters levels off after the year 2000, and no relationship was found with prey abundance (Vikingsson *et al.*, 2015).

For Skjálfandi Bay, the percentage of humpback whale positive surveys shows an increasing trend throughout the years. Since 2011, the humpback whale has been the most common cetacean species recorded in Skjálfandi Bay (Klotz, 2014). Our results indicate that the percentage of positive surveys remained constant during the research time period for the harbour porpoise and that it has decreased in recent years for white beaked dolphins. These patterns may be due to interspecific competition. For example, MacLeod *et al.* (2008) reported interspecific competition between white-beaked dolphins and common dolphins (*Delphinus delphis*). White-beaked dolphins dominated in waters less than 13°C, whereas common dolphins preferred temperatures above 14°C. Lynch and Whitehead (1984) recorded spatial segregation between different cetacean species in Newfoundland and Labrador in relation to capelin (*Mallotus villosus*) abundance and density.

In the present study whalewatching vessels were used as research platforms and the comparison between the percentages of positive surveys among different species could be biased. Whalewatching operators mostly focus on the most popular cetacean species, meaning that most of the time whale species such as humpback whales or blue whales (*Balaenoptera musculus*) are the target of their interest. Thus, a decreasing percentage of positive surveys for white beaked dolphin might be attributed to a higher focus on humpback

whales. However, the percentage of positive surveys of harbour porpoises did not change through time, suggesting that the registered increase of percentage of positive surveys of humpback whales is not due to bias. On the other hand, the number of tours per day varied throughout the season, and more trips with observers were carried out between June and August, which incorporates the main touristic season. Similarly, the number of research assistants was usually higher in mid-summer, when more volunteers worked for the Húsavík Whale Museum and the Húsavík Research Center. An increased number of tours per day in the peak season enabled a more intensive data collection as reflected in the fact that October (low season) had to be excluded from our GLM analyses due to lack of data.

The significantly lower SPUE recorded in September could be due to individual migration to southern latitudes, which starts in the autumn (Norris, 1977; Pomilla and Rosenbaum, 2005) and that could lead to decreasing encounter rates in Skjálfandi Bay.

Ranging patterns of humpback whales in 2012 as explored through Kernel densities varied temporally within Skjálfandi Bay. Higher densities have been estimated in the western part of Skjálfandi Bay close to the coast. These are the deepest areas (down to 220m), with steep slopes. In such areas different processes, particularly upwelling, lead to increased nutrient concentrations in surface waters, promoting primary production and plankton growth (Allen *et al.*, 2001; Olson and Backus, 1985; Woodley and Gaskin, 1996). Besides environmental variables such as Sea Surface Temperature, distance to shore and sea-floor topography, previous studies revealed that dynamic mesoscale oceanographic processes such as thermal fronts, eddies and upwellings, can influence prey distribution, growth of plankton and thus the abundance of planktivorous fish (Olson and Backus, 1985; Woodley and Gaskin, 1996). Interestingly, the distribution of humpback whales varied between months in 2012. In the beginning of the feeding season (April–May) the humpback whales need to restock their energy stores after a period of minimal feeding and the long migration. They therefore seek rich feeding grounds to gain as much energy as possible for the lowest amount of effort (Doniol-Valcroze *et al.*, 2007; MacArthur and Pianka, 1966). During April, May and June whale densities were higher closer to the shore, especially in the southern and western part of the bay, where nutrient input from rivers is highest. Freshwater nutrient input enhances plankton growth and thereby food availability for baleen whales (Gíslason, 2004). Densities changed during July when humpback whales occurred in every part of Skjálfandi Bay except for its southern-most area. July also represents the period when most of the humpback whales have reached their feeding grounds and individuals could spread out in the bay to avoid competition. In addition, in July most individuals have already restocked their energy stores and will expend energy in other activities such as breaching. Breaching events were more frequent during July and August independently of sighting location (Klotz, 2014). From August to October, high densities were limited to the north or northwestern part of the bay. This distribution may be due to the existence of food-exhausted areas within the southern bay and the start of the migration of some individuals.

Since 2001 only a small number of the humpback whales identified in the research area have been re-sighted. The Discovery curve (see Fig. 5) shows a linear increase of newly identified animals over the study period indicating that the humpback whale stock in Skjálfandi Bay is not a closed population that is returning to the bay every year, but part of a larger population in the North Atlantic with different or broader feeding areas.

Compared to other humpback whale feeding grounds, the resighting rate in Skjálfandi Bay is low (<27%). In contrast, in the Gulf of Maine for example, rates as high as 73.2% have been reported (Clapham *et al.*, 1993). Obtaining more information about humpback whale site fidelity and higher percentages of resightings in our research area would require covering a larger study area. However, Boye *et al.* (2010) and Weinrich (1998) found evidence for small-scale site fidelity for the majority of the whales within only a few squared kilometers in Godthaabsfjord, Greenland, and the Gulf of Maine, respectively. In different years, sightings of 16 individuals known from Skjálfandi Bay have been made in other coastal areas in Iceland such as Faxaflói, in southwest Iceland, or Eyjafjörður, further west of Skjálfandi Bay (Húsavík Humpback Whale Catalogue, unpublished). These resightings confirm that some individuals travel between different locations or move on to other regional feeding areas.

Fluctuations in SPUE and percentage of positive surveys may be due to varying environmental conditions within the bay, with potential implications for whalewatching operations. Given the scientific value of our conclusions, this study also supports the use of whalewatching vessels as opportunistic platforms for cetacean research.

Whalewatching operations in the bay are growing due to increasing cetacean sighting (of humpback whales, in particular) and of greatly increased tourism in general in Iceland. Although this business increases the public's awareness on whale conservation needs, strict guidelines for the vessels are needed to avoid disrupting the animals (Hoyt, 2001; Cunningham *et al.*, 2012). A recent study showed that whalewatching boats in Iceland can approach the whales at high speed and without keeping the suggested buffer distance of at least 50m (Martin, 2012). Our research, however, is an example of whalewatching best practice at sea and of a successful collaboration between the scientific community and the whalewatching industry.

ACKNOWLEDGEMENTS

Thanks to all the volunteers of the Húsavík Research Center for their help in collecting data. Furthermore, thanks to the staff of 'North Sailing' for allowing the use of their boats as research platforms. Thanks to volunteers from the Húsavík Whale Museum for their data collection in the past. Last but not least, a special thanks to Christian Schmidt, for his work in organising the Húsavík Humpback Whale Catalogue and providing many photographs to the catalogue.

REFERENCES

- Allen, S.E., Vindeirinho, C., Thomson, R.E. and Foreman, M.G.G. and Mackas, D.L. 2001. Physical and biological processes over a submarine canyon during an upwelling event. *Can. J. Fish. Aquat. Sci.* 50: 671–84.
- Baker, C.S., Palumbi, S.R., Lambertsen, R.H., Weinrich, M.T., Calambokidis, J. and O'Brien, S.J. 1990. Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. *Nature* 344(6,263): 238–40.
- Balcomb, K.C. and Nichols, G. 1982. Humpback whale censuses in the West Indies. *Rep. int. Whal. Commn* 32: 401–06.
- Bertulli, C.G., Rasmussen, M.H. and Tetley, M.J. 2013. Photo-identification rate and wide-scale movement of common minke whales (*Balaenoptera acutorostrata*) in the coastal waters of Faxaflói and Skjálfandi Bays, Iceland. *J. Cetacean Res. Manage* 13(1): 39–45.
- Best, P.B. 1993. Increase rates in severely depleted stocks of baleen whales. *ICES J. Mar. Sci.* 50(3): 169–86.
- Boye, T.K., Simon, M. and Madsen, P.T. 2010. Habitat use of humpback whales in Godthaabsfjord, West Greenland, with implications for commercial exploitation. *J. Mar. Biol. Assoc. UK.* 90(8): 1,529–38.
- Chittleborough, R.G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust. J. Mar. Fresh. Res.* 16(1): 33–128.
- Clapham, P.J., Baraff, L.S., Carlson, C.A., Christian, M.A., Mattila, D.K., Mayo, C.A., Murphy, M.A. and Pittman, S. 1993. Seasonal occurrence and annual return of humpback whales, (*Megaptera novaeangliae*), in the southern Gulf of Maine. *Can. J. Zool.* 71(2): 440–3.
- Clapham, P.J. and Mayo, C.A. 1987. Reproduction and recruitment of individually identified humpback whales, (*Megaptera novaeangliae*), observed in Massachusetts Bay, 1979–1985. *Can. J. Zool.* 65(12): 2,853–63.
- Cunningham, P.A., Huijbens, E.H. and Wearing, S.L. 2012. From whaling to whale watching: examining sustainability and cultural rhetoric. *J. Sustainable Tour.* 20(1): 143–61.
- Doniol-Valcroze, T., Berteaux, D., Larouche, P. and Sears, R. 2007. Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. *Mar. Ecol. Prog. Ser.* 335: 207–16.
- Gíslason, Á. 2004. Fish farming in Húsavík, Iceland. Arctic charr – Tilapia – Atlantic halibut – Turbot. Report of the Húsavík Academic Center, Iceland. 82pp.
- Heide-Jørgensen, M.P., Laidre, K., Hansen, R.G., Burt, M.L., Simon, M., Borchers, D.L., Hanssen, J., Harding, K., Rasmussen, M.H., Dietz, R. and Teilmann, J. 2012. Rate of increase and current abundance of humpback whales in West Greenland. *J. Cetacean Res. Manage* 12(1): 1–14.
- Hoyt, E. 2001. Whale watching 2001 – worldwide tourism, numbers, expenditures and expanding socioeconomic benefits. Report to IFAW, Crowborough, Sussex, UK. 158pp. [Available at: <http://www.ifaw.org>].
- International Whaling Commission. 2002. Report of the Scientific Committee. Annex H. Report of the Sub-Committee on the Comprehensive Assessment of North Atlantic Humpback Whales. *J. Cetacean Res. Manage. (Suppl.)* 4: 230–60.
- Jann, B., Allen, J., Carrillo, M., Hanquet, S., Katona, S.K., Martin, A.R., Reeves, R.R., Seton, R., Stevick, P.T. and Wenzel, F.W. 2003. Migration of a humpback whale (*Megaptera novaeangliae*) between the Cape Verde Islands and Iceland. *J. Cetacean Res. Manage.* 5(2): 125–29.
- Katona, S.K. 1986. Biogeography of the humpback whale, (*Megaptera novaeangliae*), in the North Atlantic. In: Pierott-Balts, A.C., Vander Spoel, S., Zahuanec, B.J. and Johnson, R.K. (eds). Pelagic Biogeography: Proceedings of an international conference, the Netherlands. 29 May – 5 June 1985. UNESCO Technical Paper in Marine Science 49. 295pp.
- Katona, S.K. and Whitehead, H.P. 1981. Identifying humpback whales using their natural markings. *Polar Rec.* 20: 439–44.
- Kellogg, R. 1929. What is known of the migration of some of the whalebone whales. Smithsonian Institution. Annual Report of the Board of Regents, 1928. pp.467–94+2pls.
- Klotz, L. 2014. Distribution of humpback whales in Skjálfandi Bay, Iceland. Annual and seasonal distribution patterns of *Megaptera novaeangliae* in Icelandic waters. Akademikerverlag, Reihe Realwissenschaften.
- Lynch, K. and Whitehead, H. 1984. Changes in the abundance of large whales off Newfoundland and Labrador, 1976–1983, with special reference to the finback whale. Paper SC/36/O2 presented to the IWC Scientific Committee, May 1984 (unpublished). 9pp. [Paper available from the Office of this Journal]
- MacLeod, C.D., Weir, C.R., Begona Santos, M. and Dunn, T.E. 2008. Temperature-based summer habitat partitioning between white-beaked and common dolphins around the United Kingdom and Republic of Ireland. *J. Mar. Biol. Assoc. UK.* 88: 1,193–98.
- Martin, A.R., Katona, S.K., Mattila, D., Hembree, D. and Waters, T.D. 1984. Migration of humpback whales between the Caribbean and Iceland. *J. Mammal.* 65(2): 330–3.
- Martin, S.M. 2012. Whale watching in Iceland: An assessment of whale watching activities on Skjálfandi Bay. Masters Thesis, University of Akureyri, Ísafjörður, Iceland. 96pp.

- McArthur, R.H. and Pianka, E.R. 1966. On optimal use of a patchy environment. *Am. Nat.* 100(916): 603–9.
- Mitchell, E. 1974. Trophic relationships and competition for food in northwest Atlantic whales. Paper number NA76/33 presented to the Working Group on North Atlantic Whales, Oslo, April 1976. 10pp. [Paper available from the Office of this Journal]
- Norris, K.S. (Ed.) 1977. *Whales, Dolphins and Porpoises*. Berkely, University of California Press. 789pp.
- Norris, K.S., Goodman, R.M., Villa-Ramirez, B. and Hobbs, L. 1977. Behavior of California gray whale, (*Eschrichtius robustus*), in southern Baja California, Mexico. *Fish. Bull.* 75(1): 159–72.
- Øien, N. 2009. Distribution and abundance of large whales in Norwegian and adjacent waters based on ship surveys 1995–2001. *NAMMCO Sci. Publ.* 7: 31–47.
- Olson, D.B. and Backus, R.H. 1985. The concentrating of organisms at fronts: A cold-water fish and a warm-core Gulf Stream ring. *J. Mar. Res.* 43(1): 113–37.
- Palsbøll, P.J., Allen, J., Bérubé, M., Clapham, P.J., Feddersen, T.P., Hammond, P.S., Hudson, R.R., Jørgensen, H., Katona, S., Larsen, A.H., Larsen, F., Lien, J., Mattila, D.K., Sigurjónsson, J., Sears, R., Smith, T., Spøner, R., Stevick, P. and Øien, N. 1997. Genetic tagging of humpback whales. *Nature* 388(6,644): 767–9.
- Paxton, C., Burt, M., Hedley, S., Víkingsson, G., Gunnlaugsson, T. and Desportes, G. 2009. Density surface fitting to estimate the abundance of humpback whales based on the NASS-95 and NASS-2001 aerial and shipboard surveys. *NAMMCO Sci. Publ.* 7:143–60.
- Pike, D.G., Paxton, C.G.M., Gunnlaugsson, T. and Víkingsson, G.A. 2009. Trends in the distribution and abundance of cetaceans from aerial surveys in Icelandic coastal waters, 1986–2001. *NAMMCO Sci. Publ.* 7: 117–42.
- Pomilla, C. and Rosenbaum, H.C. 2005. Against the current: an inter-oceanic whale migration event. *Biol. Lett.* 1: 476–9.
- Punt, A., Friday, N. and Smith, T. 2006. Reconciling data on the trends and abundance of North Atlantic humpback whales within a population modelling framework *J. Cetacean Res. Manage.* 8(2): 145–59.
- Rasmussen, M. 2014. The whaling versus whale-watching debate. pp.81–94. In: J. Higham, L. Bejder and R. Williams (Eds.) *Whale-watching: Sustainable Tourism and Ecological Management*. Cambridge University Press, Cambridge, UK. doi:10.1017/CBO9781139018166.009
- Reilly, S.B., Bannister, J.L., Best, P.B., Brown, M., Brownell Jr, R.L., Butterworth, D.S., Clapham, P.J., Cooke, J., Donovan, G.P., Urban, J. and Zerbini, A.N. 2008. *Megaptera novaengliae*. In: IUCN Red List of Threatened Species 2011.
- Rodgers, A.R. and Kie, J.G. 2011. HRT: Home Range Tools for ArcGIS®. User's Manual. 10. August 2011, S. 6ff. (accessed 5th November 2012).
- Sigurjónsson, J. and Gunnlaugsson, T. 1990. Recent trends in abundance of blue (*Balaenoptera musculus*) and humpback whales (*Megaptera novaengliae*) off west and southwest Iceland, with a note on occurrence of other cetacean species. *Rep. int. Whal. Commn* 40: 537–51.
- Silverman, B.W. 1986. *Density Estimation for Statistics and Data Analysis*. Chapman and Hall, London. 174pp.
- Smith, T.D., Allen, J., Clapham, P.J., Hammond, P.S., Katona, S., Larsen, F., Lien, J., Mattila, D., Palsbøll, P.J., Sigurjónsson, J., Stevick, P.T. and Øien, N. 1999. An ocean-basin-wide mark-recapture study of the North Atlantic humpback whale (*Megaptera novaengliae*). *Mar. Mam. Sci.* 15(1): 1–32.
- Stevick, P.T., Allen, J., Bérubé, M., Clapham, P.J., Katona, S.K., Larsen, F., Lien, J., Mattila, D.K., Palsbøll, P.J., Robbins, J., Sigurjónsson, J., Smith, T.D., Øien, N. and Hammond, P.S. 2003a. Segregation of migration by feeding ground origin in North Atlantic humpback whales (*Megaptera novaengliae*). *J. Zool. (London)* 259: 231–7.
- Stevick, P.T., Allen, J., Clapham, P.J., Friday, N., Katona, S.K., Larsen, F., Lien, J., Mattila, D.K., Palsbøll, P.J., Sigurjónsson, J., Smith, T.D., Øien, N. and Hammond, P.S. 2003b. North Atlantic humpback whale abundance four decades after protection from whaling. *Mar. Ecol. Prog. Ser.* 258: 263–73.
- Stevick, P.T., Allen, J., Clapham, P.J., Katona, S.K., Larsen, F., Lien, J., Mattila, D.K., Palsbøll, P.J., Sears, R., Sigurjónsson, J., Smith, T.D., Víkingsson, G., Øien, N. and Hammond, P.S. 2006. Population spatial structuring on the feeding grounds in North Atlantic humpback whales (*Megaptera novaengliae*). *J. Zool.* 270: 244–55.
- Stevick, P.T., Neves, M.C., Johansen, F., Engel, M.H., Allen, J., Marcondes, M.C.C. and Carlson, C. 2011. A quarter of a world away: female humpback whale moves 10,000 km between breeding areas. *Biol. Lett.* 7: 299–302.
- Tønnessen, J.N. and Johnsen, A.O. 1982. *The History of Modern Whaling*. C. Hurst and Co., London. i–xx+798pp.
- Vigness-Raposa, K.J., Kenney, R.D., Gonzalez, M.L. and August, P.V. 2010. Spatial patterns of humpback whale (*Megaptera novaengliae*) sightings and survey effort: Insight into North Atlantic population structure. *Mar. Mamm. Sci.* 26(1): 161–175.
- Víkingsson, G.A., Pike, D.G., Valdimarsson H., Schleimer, A., Gunnlaugsson, T., Silva, T., Elvarsson, B.Þ., Mikkelsen, B., Øien, N., Desportes, G., Bogason, V. and Hammond, P.S. 2015. Distribution, abundance, and feeding ecology of baleen whales in Icelandic waters: have recent environmental changes had an effect? *Front. Ecol. Evol.* 3:6pp. [Available at: <http://dx.doi.org/10.3389/fevo.2015.00006>].
- Weinrich, M. 1998. Early experience in habitat choice by humpback whales (*Megaptera novaengliae*). *J. Mammal.* 79(1): 163–70.
- Weinrich, M.T., Martin, M., Griffiths, R., Bove, J. and Schilling, M.R. 1997. A shift in distribution of humpback whales (*Megaptera novaengliae*) in response to prey in the southern Gulf of Maine. *Fish. Bull.* 95: 826–36.
- Wenzel, F.W., Allen, J., Berrow, S., Hazevoet, C.J., Jann, B., Seton, R.E., Steiner, L., Stevick, P., Lopez Suarez, P. and Whooley, P. 2009. Current knowledge on the distribution and relative abundance of humpback whales (*Megaptera novaengliae*) off the Cape Verde Islands, eastern North Atlantic. *Aquat. Mam.* 35(4): 502–10.
- Whitehead, H. 1982. Populations of humpback whales in the northwest Atlantic. *Rep. int. Whal. Commn* 32: 345–53.
- Whitehead, H. and Moore, M.J. 1982. Distribution and movements of West Indian humpback whales in winter. *Can. J. Zool. (Revue Canadienne de Zoologie)* 60: 2,203–11.
- Woodley, T.H. and Gaskin, D.E. 1996. Environmental characteristics of North Atlantic right and fin whale habitat in the lower Bay of Fundy, Canada. *Can. J. Zool.* 74:75–84.