The singing behaviour of humpback whales (*Megaptera novaeangliae*) in subarctic waters

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Dissertation submitted in partial fulfilment of a
Philosophiae Doctor Degree in Biology

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Abstract

The cyclically-repeated song of the male humpback whale (*Megaptera novaeangliae*) is an important social display on their breeding grounds, functioning in male-male interactions and/or as a reproductive display to attract females. The songs are gradually synchronized into a predominant pattern shared by the majority of the singers. Transmission of songs within an ocean basin is evidently important for vocal convergence within a population and for sharing song components with other breeding populations. Songs of humpback whales have traditionally been associated with tropical or subtropical breeding grounds, however, a growing body of literature shows that songs are also sung on high-latitude feeding grounds and during migration. The purpose of the high-latitude singing is, however, not clear.

This study provides detailed analyses of humpback whale songs recorded in the subarctic waters of Iceland using passive acoustic recorders collected in 2008–2009, 2009–2010, and 2011 during which singing was detected in all years. Peak song occurrence was detected during the months of January and February in all years, this timing overlaps with the timing of the peak breeding season of humpback whales in the Northern hemisphere. Songs were only detected during the winter months whereas other non-song sounds were detected throughout the year. The songs observed in Iceland were decomposed to the unit and phrase level and compared to songs recorded on traditional humpback breeding grounds in the North Atlantic, i.e. the Cape Verde in 2011–2012 and the West Indies in 2012. The aim was to investigate the purpose of singing in the subarctic and find if these songs could have a role in the cultural transmission of humpback whale songs in the North Atlantic. Markov matrices were utilised to observe the cyclical pattern and consistency of the songs in the subarctic and subtropics whereas similarity analysis (Levenshtein Distance, Levenshtein Similarity Index and Dice’s Similarity Index) were used to measure the song progression in Iceland and the level of song sharing between Iceland and the subtropical breeding grounds.

The results showed that continual singing of consistent songs with a typical progression pattern occur during the breeding season in the subarctic. Furthermore, the findings clearly suggest that songs are transmitted between individuals on the joint Icelandic subarctic feeding ground. This indicates the importance of subarctic waters as a winter habitat, resulting in cultural transmission of songs and as a potential mating ground for overwintering humpback whales.

Útdráttur

Á æxlunartíma hnúfubaksins (*Megaptera novaeangliae*) syngja tarfarnir flókna og langa söngva sem samanstanda af endurteknum og fjölbreyttum söngerindum. Á hverjum tíma og stað syngja tarfarnir sömu söngvana. Söngvarnir virðast einna helst mikilvægir í samskiptum tarfanna þegar þeir eru á æxlunarstöðvunum en líklega eru þeir jafnframt mikilvægir í tilhugalífi dýranna. Nýlegar rannsóknir hafa staðfest að hnúfubakstarfar eru einnig iðnir við söng utan æxlunarstöðva, t.d. á farleiðum og á fæðuslóðum á og við heimskautasvæðin. Tilgangur sönghegðunarinnar á fæðuslóðum er enn að miklu leyti á huldu.

Rannsóknir fóru fram á hljóðmyndun hnúfubaka við norðausturströnd Íslands á heilsársgrundvelli með áherslu á sönghegðun að vetri. Hljóðgögnum var safnað yfir þriggja ára tímabil. Upptökurnar leiddu í ljós að hnúfubakar syngja á fæðustöðvum sínum norðaustur af landinu á veturna og voru söngvarnir í mestum mæli á æxlunartíma þeirra. Jafnframt mynduðu þeir margvísleg samskiptahljóð allt árið sem flokkast ekki sem söngvar. Upptökur af söngvum fengust einnig frá þekktum æxlunarstöðvum hnúfubaka í Norður Atlantshafi, þ.e. frá Grænahöfðaeyjum úti fyrir norðvesturströnd Afríku og frá Karíbahafi. Markmiðið var að bera íslensku söngvana saman við söngva frá þessum æxlunarstöðvum.

Ef líkindi finnast milli söngva og þess hvernig þeir þróast á fjarlægum búsvæðum bendir það til þess að hvalir frá þeim svæðum eigi í samskiptum og tilheyri líklega sama æxlunarstofni. Fyrsta stigs Markov-líkan var notað til að meta samræmi og festu í myndun söngrunanna innan tímabila en samanburðargreiningar voru svo nýttar til að kanna líkindi milli söngvanna frá þessum ólíku svæðum og tíma. Ásamt því hversu miklum tíma hvalirnir vörðu í söng sýndu niðurstöðurnar fram á að söngvarnir frá Íslandi voru í samræmi við það söngform sem þekkist á hefðbundnum æxlunarstöðvum í hitabeltinu. Því er ólíklega um tilviljunarkennda söngva að ræða, öllu heldur eru líkur á að söngvarnir á Íslandi eigi þátt í tilhugalífi hvalanna. Söngvar með svipaða uppröðun erinda voru sungnir við Ísland og á æxlunarsvæðunum. Það bendir til þess að hvalirnir skiptist á hljóðum á Íslandsmiðum og/eða á farleiðum og flytji þau svo með sér suður á æxlunarstöðvarnar.

Þar sem söngvar heyrðust fram í mars er ljóst að einhverjir hnúfubakar halda til við Ísland yfir veturinn. Þannig geta íslensk hafsvæði nýst hvölunum á veturna og fram á vor til bæði fæðuöflunar, söngiðkunar og mögulega til mökunar. Niðurstöðurnar varpa þannig nýju ljósi á mikilvægi íslenskra fæðustöðva fyrir hnúfubaka að vetri til.

Dedication

To Martin for all your support and for being there for me since you came along

To Aðalsteinn Logi for your cheerfulness, for your support, the special kind only a child can give, for your love of animals and for becoming the whale expert you are

To Arnar Magnús for being such a joy and a reminder of staying in the present

To my family for supporting me the whole way and for making this possible

List of Original Papers

This thesis is based on the following papers which are referred to throughout the text by Roman numerals assigned to each paper. These papers are included at the end of this thesis.

Paper I: **Magnúsdóttir, E. E.,** Rasmussen, M. H., Lammers, M. O., & Svavarsson, J. 2014. Humpback whale songs during winter in subarctic waters. *Polar Biol*, *37*(3), 427–433.

Paper II: **Magnúsdóttir, E. E.**, Miller P. J., Lim R., Rasmussen M. H., Lammers M. O., Svavarsson J. 2015. Humpback whale (*Megaptera novaeangliae*) song unit and phrase repertoire progression on a subarctic feeding ground. *J Acoust Soc Am,*138:3362–3374

Paper III: **Magnúsdóttir E. E.** and Lim, R. Why sing in the sub-arctic? Humpback whale (*Megaptera novaeangliae*) song structure and progression from an Icelandic feeding ground during winter. Manuscript.

Paper VI: **Magnúsdóttir, E. E.**, Garland, E. C., Miller P. J., Conor, R., Gero, S. T., Rasmussen M. H, Svavarsson J. The importance of a subarctic feeding ground for humpback whale song transmission to subtropical breeding grounds in the North Atlantic Ocean. Manuscript.

Other papers published during the course of this study

Dudzinski, K. M., Brown, S. J., Lammers, M. O., Lucke, K., Mann, D. A., Simard, P., Wall, C. C., Rasmussen, M. H., **Magnúsdóttir, E. E.**, Tougaard, J. & Eriksen, N. 2011. Trouble shooting deployment and recovery options for various stationary passive acoustic monitoring devices in both shallow-and deep-water applications. *J Acoust Soc Am*, 129, 436–448.

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

Other publications during the course of this study

Magnúsdóttir, E. E., Rasmussen, M. H., Torfason, O. P. and Óskarsson, T. 2013. The Icelandic Humpback Whale: The Songs and Sounds [CD]. Arctic Sounds

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Abbreviations

ANOVA	Analysis of Variance
BIC	Bayesian Information Criterion
CAR	Acoustic recording dataset from the Island of Dominica in the Caribbean Sea
CVI	Acoustic recording dataset from the Cape Verde Islands
DF	Discriminant Functions
DFT	Discrete Fourier Transform
DPCA	Discriminant Analysis of the Principal Components
DSI	Dice’s Similarity Index
Dur	Duration (s)
EAR	Ecological Acoustic Recorder
F25	Frequency at ¼ of signal duration (Hz)
F50	Frequency at ½ of signal duration (Hz)
F75	Frequency at ¾ of signal duration (Hz)
FEnd	End frequency of signal duration (Hz)
FFT	Fast Fourier Transform
FMax	Maximum frequency (Hz)
FMin	Minimum frequency (Hz)
FMod	Frequency modulation ratio
Frange	Frequency range ratio

FStart	Start frequency of signal duration (Hz)
FTrend	Frequency trend ratio
HSD	Honest Significant Difference
ICE	Acoustic recording dataset from Iceland
KM	Kohonen Set Median
LD	Levenshtein Distance Analysis
LSI	Levenshtein Similarity Index
OR	Odds Ratio
PC	Principal Component
PCA	Principal Component Analysis
PeakF	Peak frequency (Hz)
PMax	Percentage to maximum frequency (%)
SD	Standard Deviation
SE	Standard Error
SM	Set Median

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1 Introduction

1.1 Cetacea

Roaming this world's oceans are behemoths which possess song cultures unparalleled with any non-human animal. Their strange, sometimes haunting and yet enchanting presence has likely been an incentive for tales of sea monsters and other oceanic mythical creatures in the past. These descendants of extinct terrestrial tetrapods have adapted remarkably well both physically and behaviourally to the acoustic properties of water. Acute hearing (measured in odontocetes) and the ability to produce a diverse repertoires of sounds allows them to communicate over long distances underwater, gather prey and drive off unwanted rivals or predators, a trait that has drawn the attention of scientists for decades.

Diversification occurred within the infraorder of the Artiodactyla order Cetacea (Brisson, 1762) around 35–30 million years ago into two extant parvorders Mysticeti and Odontoceti (Sasaki *et al.* 2005). Odontocetes are toothed whales such as dolphins and sperm whales. Mysticetes, on the other hand, are baleen whales; filter feeding cetaceans which lost their teeth throughout the course of evolution and replaced them with filtering keratinous baleen plates (Fitzgerald 2006). This specialized filtering gear allows the owner to forage on small, yet nutritious school forming prey which is filtered out of the water. For efficient foraging on small prey items, the mysticetes have evolved buccal cavity of great volume or as large as 1/3^{d} of the whales' body length (Werth 2004). Unlike other baleen whales, such as the large headed bowhead whale (*Balaena mysticetus* Linnaeus, 1758) and the right whales (*Eubalaena* spp. Gray, 1864) of the Balaenidae family, the Balaenopteridae family, or rorquals, have uniquely adapted to energy conservative swimming with more hydrodynamic bodies without having to sacrifice the large volume of their buccal cavity (Goldbogen *et al.* 2010). This physical adaptation allows rorquals to travel long distances between suitable feeding and breeding locations without having to consume too much energy (Fish 1994; Lafortuna *et al.* 2003). The majority of rorqual species migrate seasonally between optimal high-latitude feeding grounds and low-latitude breeding grounds. A few deviations from that behaviour do exist such as for the Brydes whale (*B. brydei* Olsen, 1913), which is found to be mostly tropical (Jonsgard 1966).

1.2 The humpback whale

With a unique physique, the humpback whale (*Megaptera novaeangliae* Borowski, 1781) sports anatomical proportions which show little resemblance to the sleek and streamlined bodies of its cousins in the Balaenopteridae family, like the fin (*Balaenoptera physalus*

Linnaeus, 1758), blue (*B. musculus* Linnaeus, 1758) and minke whales (*B. acutorostrata* Lacepède, 1804 and *B. bonaerensis* Gray, 1874). The humpback whale's trunk is stocky, the caudal fin is proportionally large and their characteristic long pectoral fins are likely the longest appendices found on any extant species in the animal kingdom. Thus, before the currently applied genetic analysis (Sasaki *et al.* 2005), the humpback whale was placed in its own subfamily Megapterinae, a sister clade to the subfamily Balaenopterinae which together comprised the family Balaenotperidae (Rice 1998). More recent and robust mtDNA methods, have shown a sister relationship of humpback and fin whales which now comprise a joint linage within the Balaenopteridae family (Sasaki *et al.* 2005) despite little physical or behavioural similarity (Clapham & Mead 1999). These two species separated approximately 15 million years ago (Sasaki *et al.* 2005). A recent study by Jackson *et al.* (2014) provides genetic evidence which support a taxonomic revision of *M. novaeangliae* into three subspecies; the North Pacific humpback whale (*M. n. kuzira*), the North Atlantic humpback whale (*M. n. novaeangliae*) and the Southern Hemisphere humpback whale (*M. n. australis*). These potential subspecies appear to be on an independent evolutionary trajectory (Jackson *et al.* 2014).

1.2.1 Migration in humpback whales

The benefits of migration

The migration of baleen whales generally involves persistent movement between two destinations. Each destination needs to provide essential resources for the proliferation of the species. As a result, the migration of baleen whales includes the longest known annual movement of any mammal (Stone *et al.* 1990). For most migrating baleen whales the summers are spent at productive high-latitude feeding grounds while the winters are spent on warmer and less productive low-latitude breeding grounds (Clapham 2000).

What drives baleen whales to migrate is not clear but probable hypothesis have been made which focus on the direct benefit to the calf, such as easier thermoregulation in warmer waters (Horwood 1988; Clapham 1996; Dingle 2014) and calmer waters for nursing (Whitehead & Moore 1982). The thermoregulation hypothesis is not particularly strong since smaller cetaceans, such as killer whales (*Orcinus orca* Linneus, 1758), white-beaked dolphins (*Lagenorhynchus albirostris* Gray, 1846) and harbour porpoises (*Phocoena phocoena* Linnaeus, 1758) are residents in cold temperate waters and do not require such warm waters for thermoregulation of their calves. However, these resident cold water species most commonly give birth during spring and summer (Read 1990; Galatius *et al.* 2013) apart from the killer whales which can become pregnant and give birth throughout the year (Robeck *et al.* 1993). Corkeron and Connor (1999) argued that newly born baleen whale calves would be considerably threatened by killer whale predation in high latitude waters. Therefore, they proposed that it would be a major advantage to a pregnant female baleen whale to actually reduce the risk of killer whale predation on their new-born calf by avoiding high latitude areas the first few months after giving birth.

The abundance of killer whales is substantially greater on higher latitudes than that in tropical and subtropical waters (Hammond 1984; Wade & Gerrodette 1993; Forney & Wade 2007). Specialized marine mammal eating killer whales are found in the North Pacific and the Southern Oceans (Ford & Ellis 1999; Pitman & Ensor 2003) whereas killer whales in the North Atlantic appear to be either specific fish eaters or generalists which occasionally feed on small baleen whales or calves (Foote *et al.* 2009). Young calves are nonetheless threatened by shark attacks (Long & Jones 1996) on low-latitude breeding grounds but the opposing threat by sharks is possibly insubstantial compared to coordinated hunting groups of killer whales. Suggestions have been made that if calving occurred in polar waters, killer whales would preferentially feed on young baleen whale calves as they would represent a large individual nutritional source that is relatively easy to hunt (Corkeron & Connor 1999). Smaller cetaceans, which are also subject to killer whale attacks, generally find safety in numbers which likely reduces the risk of a successful attack. Baleen whales are generally solitaire animals and cannot rely on assistance when threatened. Humpback whales are, however, often seen in groups when migrating (Valsecchi *et al.* 2002) which inter alia can function as a temporary protection for killer whale attacks. Humpback whales have shown mobbing behaviour and intra- and interspecific altruism towards marine mammals in distress, such behaviour has primarily been witnessed during killer whale attacks (Pitman *et al.* 2017). This behaviour has not been well studied in humpback whales and the current knowledge is mostly based on sightings from opportunistic vessels. Mobbing behaviour and altruism appears to exist in this species nonetheless and might be sufficient in low-latitude breeding aggregations where sharks and sometimes false killer whales appear to be the main threats to neonates (Long & Jones 1996). Due to the generally unstable nature of humpback whale group formations (Weinrich 1991; Clapham 1996) they might not serve as a reliable protection on high latitude feeding grounds where killer whales are abundant and humpback whales are possibly more dispersed than in breeding aggregations. These hypotheses focus, however, less on the males and females without calves. Since, females sometimes ovulate post-partum (Lockyer 1984; Herman et al. 2011), they become oestrous soon after giving birth and, thus, attract males (Tyack & Whitehead 1983). Since non-pregnant females without calves are also found on these breeding grounds (Craig & Herman 1997; Craig *et al.* 2002) they should benefit from such aggregations where males are concentrated.

When is the best time to migrate?

Many baleen whales migrate long distances and reproduce on a finite store of energy where budgeting the use of limited energy reserve is important to ensure survival during migration and breeding and to maximize reproductive investment (Braithwaite *et al.* 2015). The breeding period of humpback whales in the northern hemisphere has been estimated to extend from approximately January to April (Nishiwaki 1966). Therefore, humpback whales should be capable of optimising their energy consumption until late winter on feeding grounds before migrating to their low latitude breeding grounds. Few evidence exist for humpback whales feeding during migration or in low-latitude areas (Dawbin 1966; Stockin & Burgess 2005; Stamation *et al.* 2007; Findlay *et al.* 2017).

Previous findings have shown that the location of the feeding ground affects the migration timing of individual humpback whales on breeding grounds along with age, sex and reproductive status (Dawbin 1966; Brown *et al.* 1995; Stevick *et al.* 2003a; Noad & Cato 2007). Overwintering on feeding grounds has been reported several times for mysticete species. For decades humpback whales and fin whales (*Balaenoptera physalus*) have been observed at high latitude feeding grounds of the Arctic as well as in the Antarctic during winter (Ingebrigtsen 1929; Mattila *et al.* 1987; Straley 1990; Christensen *et al.* 1992; Simon *et al.* 2010; Van Opzeeland *et al.* 2013). For example, humpback whales are regularly seen on Icelandic feeding grounds during winter following the capelin (*Mallotus villosus* O. F. Müller, 1776) migration (Víkingsson 2004; Magnúsdóttir 2007). Additionally, satellite tagged humpback whales stayed within a northeast Icelandic feeding area during November 2014–January 2015 when during mid-January one of the tagged whales migrated to Silver Bank and Navidad Bank off the coast of the Dominican Republic[1]. During the time of tagging in Eyjafjörður, NE-Iceland, the whales were found in a large group of 7–13 individuals (Gísli Víkingsson personal communication). These evidences suggest that the feeding period of humpback whales on mid- to high-latitude coastal waters extends into the winter. Furthermore, some female humpback whales (Brown *et al.* 1995; Craig & Herman 1997; Herman *et al.* 2011) and juvenile humpback whales of unknown sex (Straley 1990; Clapham *et al.* 1993) do not necessarily undertake a complete migration to low latitudes annually. Also, humpback whales are present year round in the tropical waters of the Arabian Sea in the north-western Indian Ocean (Whitehead 1985; Mikhalev 1997) and feeding super-groups have been reported in the low latitudes of the Benguela Upwelling System (Findlay *et al.* 2017). This accumulation of evidences shows that the typical annual long-range migration of humpbacks between high-latitude summer grounds and low-latitude winter grounds is not an obligatory condition for the species. Studies on gender ratio in breeding grounds have shown that females are usually underrepresented (Brown *et al.* 1995; Palsbøll *et al.* 1997; Smith *et al.* 1999; Herman *et al.* 2011) while the gender ratio on feeding grounds has shown to be even (Clapham *et al.* 1995). This supports the evidence of incomplete or lack of migration among some females and suggests that mating opportunities can be found out of the known traditional low latitude breeding grounds. Therefore, the decision to migrate and the migration timing appears to vary by individuals and is evidently affected by multiple ecological factors.

1.2.2 Feeding in arctic and subarctic waters during winter

The feeding ecology of humpback whales on high-latitude feeding grounds in the North Atlantic has not been well documented. However, humpback whales have been reported feeding on both krill, i.e. euphausiids, and small pelagic schooling fish such as capelin and

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[1] Marine Research Institute (Hafrannsóknastofnun): http://www.hafro.is/hvalamerki/hnu1R.html?a=5

herring (*Clupea harrengus* Linnaeus, 1758) (Clapham 2009). North Atlantic feeding grounds off Norway and Iceland can provide whales with various pelagic species, these are primarily capelin, herring, Atlantic mackerel (*Scomber scombrus* Linnaeus, 1758), Atlantic blue whiting (*Micromesistius poutassou* A. Risso, 1827), krill (e.g. *Meganyctiphanes norvegica* M. Sars, 1857 and *Thysanoessa inermis* Krøyer, 1846), copepods (*Calanus* spp. Leach, 1819) and squids (*Gonatus fabricii* Lichtenstein, 1818) (Nøttestad *et al.* 2014a).

The pelagic fauna of the Icelandic Sea primarily consists of juvenile and adult capelin as well as adult blue whiting and herring, mostly the Norwegian spring spawning herring, 0-group cod (*Gadus morhua* Linnaeus, 1758), haddock (*Melanogrammus aeglefinus* Linnaeus, 1758) and a number of species on larval stages (Pálsson *et al.* 2012). During the winter capelin is mainly distributed off the northeast coast of Iceland and migrates clockwise around the country where it is usually found off the southwest coast in March (Magnússon *et al.* 2005; Anon. 2012a). Humpback whales have regularly been seen feeding while following the capelin migration around Iceland (Víkingsson 2004; Magnúsdóttir 2007). In some years the capelin has been found in large numbers just outside of Skjálfandi Bay, NE-Iceland during winter (Anon. 2012a) where the studies of this thesis were conducted. The majority of the Icelandic summer spawning herring catch in Icelandic waters has been in Breiðafjörður during winter (Anon. 2012b). The Marine Research Institute reported a track of a satellite tagged humpback whale off the SSW-coast of Iceland in December 2009 which was reportedly feeding on herring in the area[2].

Findings by Nøttestad *et al.* (2014b) from 2006 to 2007 show an increase in sighting number and a more northward distribution of humpback whales in the Norwegian Sea during summer associated with the Norwegian Spring Spawning herring. Late fall and winter sightings of humpback whales have been reported from Tromsø (Balsfjord), North Norway, feeding off herring since at least the year 2010[3]. Two herring species have been identified in Balsfjord during the summer, i.e. the Atlantic herring and the Pacific herring (*C. pallasii* Valenciennes, 1847) (Jørstad *et al.* 1991; Laakkonen *et al.* 2013). Two populations of the Atlantic herring are mixed within the Balsfjord system, i.e. the local Balsfjord herring and the Norwegian spring spawning herring (Jørstad *et al.* 1994; Libungan *et al.* 2015). The Norwegian spring spawning herring is known for entering the northern fiords of Norway during the fall and early winter before migrating to the main spawning site off the west coast of Norway in January (Foote *et al.* 1996; Varpe *et al.* 2004). Thus, it is likely that the humpback whales wintering in Norway are benefiting from the occurrence of the local Balsfjord herring, the migrating Norwegian spring spawning herring and the Pacific herring. In Iceland, the humpback whales appear to have access to primarily capelin and the Icelandic summer spawning herring in the winter. The availability of krill during winter has not yet been estimated for Icelandic and Norwegian coastal waters.

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[2] Marine Research Institute (Hafrannsóknastofnun): http://www.hafro.is/undir.php?ID=210&REF=2

[3] Forskning.no: http://forskning.no/2014/11/hjelp-forskerne-i-hvaljakten

1.2.3 Humpback whale distribution and abundance in the North Atlantic

The humpback whale world population is currently divided into 14 distinct population segments (DSP) (Figure 1) according to the proposed revision of species-wide listing by the National Oceanic and Atmospheric Administration Fisheries (NOAA) (Anon. 2016). Discrete regional populations are found ocean wide based on the breeding ground assemblies (Jackson *et al.* 2014). Humpback whale stocks were depleted world-wide by whaling operations in the 19th and 20th century (Reeves *et al.* 2001; Reeves *et al.* 2004) but received total protection in 1955 when the species had been hunted down to very low levels. The first estimated absolute abundance of humpback whales in Icelandic waters was obtained from the North Atlantic Sighting Surveys (NASS) conducted in 1987 and resulted in an estimate of around 2000 individuals (Gunnlaugsson & Sigurjónsson 1990). Since then and until 2001 there was an estimated 12% increase per year in abundance within the Icelandic shelf area (Pike *et al.* 2009) but that rate slowed down after 2001 and appeared to reach a plateau (Pike *et al.* 2010). Current total estimates for humpback whales in the North Atlantic range between approximately 11,000–15,000 animals (Paxton *et al.* 2009; Pike *et al.* 2010; Víkingsson *et al.* 2015) and the latest estimate for Icelandic coastal waters during the summer is around 11,000 individuals (Víkingsson *et al.* 2015).

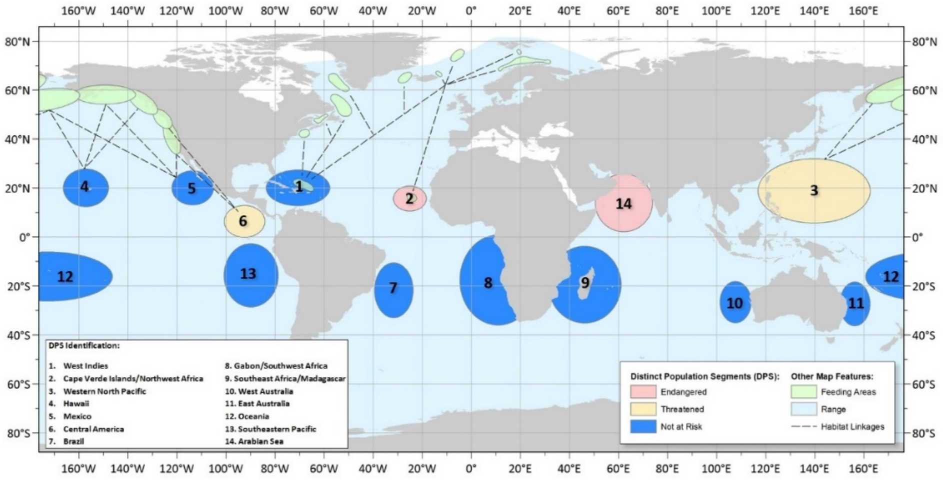

Figure 1 The current distinct humpback whale worldwide population segments. Each distinctive breeding ground is labelled from 1–14 where breeding populations labelled 1–6 belong to the Northern Hemisphere and 7–14 belong to the Southern Hemisphere. Despite of being located north of the equator within the Indian Ocean, population 14 is a residential population but has a Southern Hemisphere ancestry. © National Oceanic and Atmospheric Administration (NOAA) Fisheries

Traditional feeding grounds in the North Atlantic stretch northwards from the east coast of North America from the Gulf of Maine and towards West Greenland. Central North Atlantic feeding grounds are found off Iceland and Jan Mayen while eastern feeding grounds stretch from the north coast of Norway towards the Barent Sea (Stevick *et al.* 2006). Most of these feeding grounds are characterized by high maternally directed site fidelity where little interchange has been observed between aggregations (Clapham *et al.* 1993; Stevick *et al.* 2003a; Stevick *et al.* 2006). The feeding grounds off Iceland are considered important for North Atlantic humpback whales. Results from sighting surveys have shown that approximately 80% of the recorded whales have been found in Icelandic waters (Reilly 2008; Smith & Pike 2009).

Humpback whale sighting records from high latitude areas show that the abundance on feeding grounds increases substantially during the summer with lowering numbers in the winter months (Christensen *et al.* 1992; Clapham *et al.* 1993; Sigurjónsson & Víkingsson 1997). Variation in the occurrence of individuals on feeding grounds appears to be related to the abundance of prey but also possibly to regional preferences (Ingebrigtsen 1929; Clapham *et al.* 1993). A significant number of animals have been found in mid- and high-latitude areas during winter (Ingebrigtsen 1929; Clapham *et al.* 1993; Swingle *et al.* 1993), indicating that migration to low latitude breeding grounds is ongoing until winter or as previously suggested, some humpback whales might not always migrate.

The North Atlantic humpback whales are known to aggregate on breeding grounds off the Caribbean Islands in the West Indies and around the Cape Verde Islands, NW-Africa, during winter (Charif *et al.* 2001) (Figure 1). According to the DSP segments there are two distinct breeding populations assigned to the North Atlantic, one in the Caribbean and the other in the Cape Verde region. It is, however, not clear if these distant breeding grounds represent distinct populations or stocks. The Cape Verde breeding population is currently very small, with a recent estimation of approximately 260 individuals (Ryan *et al.* 2014) while the estimates for the West Indies breeding population is in excess of 11,000 individuals (Stevick *et al.* 2003b). The largest breeding aggregations in the West Indies occur on Silver Bank and Navidad Bank near the Dominican Republic while fewer whales have been found aggregated further east off Puerto Rico, the Virgin Islands and the Lesser Antilles (eastern Antilles) (Stevick *et al.* 2003b; Reilly 2008).

Humpback whales from central and eastern feeding grounds, such as Iceland and Norway, appear to be underrepresented in these large western Caribbean breeding aggregations, e.g. the Dominican Republic area, whereas humpback whales from western feeding grounds are more abundant in that area (Stevick et al. 2003a). Guadeloupe is a specific breeding aggregation within the eastern island clusters of the Caribbean and belongs to the Lesser Antilles. Despite of being less than 1000 km away from the Dominican Republic breeding ground there seems to be a very small interchange between these two West Indies breeding aggregations (Stevick *et al.* 2016). Recent studies have identified few individuals that have been sighted in both Guadeloupe and the Cape Verde, though none was sighted in both locations during the same winter season (Stevick et al. 2016). These individuals originated from eastern feeding grounds. Additionally, two satellite-tagged humpback whales have been tracked migrating from Guadeloupe towards central and eastern North Atlantic feeding grounds (Kennedy *et al.* 2013). Similarly, humpback whales that have been identified in the Cape Verde have either been from the central or eastern North Atlantic feeding grounds, such as Iceland and Norway, but not western feeding grounds (Jann *et al.* 2003; Stevick *et al.* 2003a).

The arrival of humpback whales in the Cape Verde and Guadeloupe before March is very rare. The mean sighting date in the Cape Verde is 11th of April and 3rd of April in Guadeloupe while the mean sighting date off the coast of the Dominican Republic is in February (Stevick *et al.* 2016). Thus, both the mean sighting dates in Guadeloupe and the Cape Verde, coupled with the tag results, the photo-identification studies and abundance estimates suggests a migratory affinity of individuals from central and eastern North Atlantic feeding grounds to the Cape Verde and Guadeloupe (the Lesser Antilles) breeding grounds. Smith and Pike (2009) estimated that 40% of the Icelandic and 87% of the Norwegian feeding populations breed outside of the western breeding area, presumably in the eastern grounds. Supporting this suggestion is the asymmetrical annual increase on north eastern feeding grounds, primarily in Iceland, and the western breeding grounds, i.e. the West Indies. The rate of population growth in the Caribbean was 3.1% per year between 1979–1993 (Stevick *et al.* 2003b) while the growth rate was 6.5% per year in the Gulf of Maine during 1979–1991 (Barlow & Clapham 1997), a 9.4% rate of increase per year off West Greenland between 1984–2007 (Heide-Jørgensen *et al.* 2012) and, as previously mentioned, around 12% growth per year in Iceland between 1970–2001 (Sigurjonsson & Gunnlaugsson 1990; Pike *et al.* 2009). This increase in Iceland and other North Atlantic feeding grounds would have also likely been reflected in the West Indies if this area is the main breeding ground of the North Atlantic humpback whales. Hence, suggesting that another unidentified breeding ground exists for humpback whales from central- and eastern feeding grounds in the North Atlantic.

1.3 Sound production and sound communication in baleen whales

With sound speed being four to five times faster in water than in air and with only limited propagation of light in water, vision is not nearly as reliable underwater as the auditory system. Accordingly, aquatic animals have many adapted senses to these acoustical properties of water. Whales are no exception, and on the contrary, their adaptation to underwater sound perception and production marks an important evolutionary advancement in this group of mammals (Nummela *et al.* 2004). The re-introduction of the ancestors of whales into the ocean required a dramatic shift in not only locomotion for swimming but also in the sensory system to utilise the new sensory environment (Tyack & Clark 2000). As a result, cetaceans have adapted to perceiving and producing a variety of sounds used for either navigation, orientation, finding prey, hunting, signalling out different messages and detecting and decoding the calls of conspecifics.

Sound by terrestrial mammals is produced when air from the lungs passes perpendicularly across the vocal folds ("vocal cords") which are located in the larynx and into the oral cavity. Changes in the shape and tension of the vocal folds along with changes in the buccal cavity (tongue and lips) are responsible for various types of sound production (Reidenberg & Laitman 2005). Until quite recently, vocal folds were thought to be absent in whales. However, studies on baleen whale anatomy indicate that they possess a laryngeal vocal fold called the U-fold which is their sound source (Mercado 1998; Reidenberg & Laitman 2007). The adduction/abduction and elevation/depression of the U-fold is thought to control parallel airflow where the vibration of its edges generate sounds. Additionally, baleen whales have a laryngeal air sac which can expand and contract, functioning as a resonant space which has the ability to propagate vibrations (Reidenberg & Laitman 2007) (Figure 2). The laryngeal sac is also used for air capturing and recycling, by pumping air between the sac and the lungs, this allows the same volume of air to be reused repeatedly with multiple vocalizations produced while submerged (Reidenberg & Laitman 2008). Consequently, the baleen whale vocal production system is more complex than those of terrestrial mammal species (Adam *et al.* 2013).

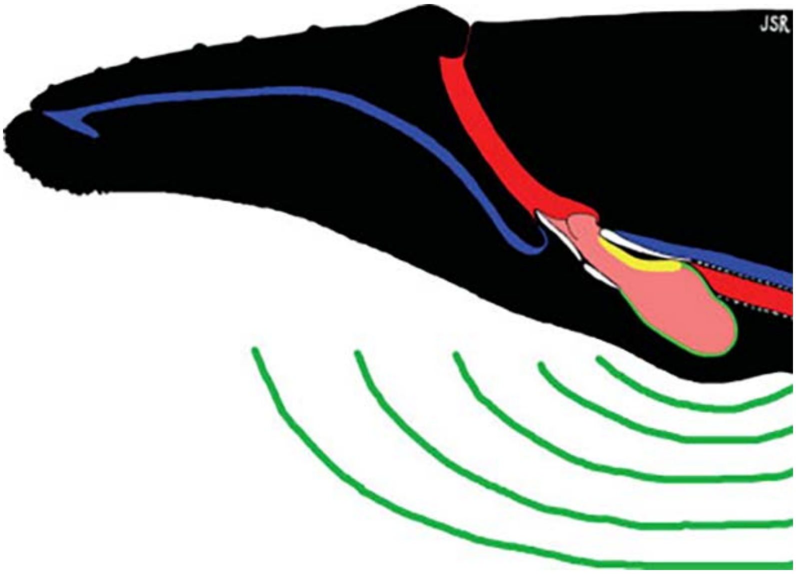

Figure 2 This schematic diagram shows the suggested mechanism of sound production and transference to water. Red: respiratory tract; blue: digestive tract; pink: laryngeal lumen; white: midline cartilages; yellow: U-fold; green: inflated borders of laryngeal sac and resulting sound pressure waves radiating from the ventral aspect of whale's throat. Adduction of the U-fold vocal process extensions (yellow) and dorsal elevation against the cricoid cartilage causes restriction of airflow from the trachea (red) into the laryngeal sac (pink lumen outlined with thin green line). U-fold edges may vibrate with airflow, causing pulses. Laryngeal sac walls may also vibrate with pulsed inflations, causing distention of ventral throat grooves. Throat distention may transfer pulses to water as sound pressure waves (green arcs) (from Reidenberg and Laitman (2007)).

1.3.1 Underwater communication

The communication of cetaceans is influenced by their marine environment (Janik 2009a). Cetaceans living in stable societies and sometimes closely knit family groups have in some cases developed a complex sound repertoire which is used for intraspecific communication and group cohesion (Janik & Slater 2000). Toothed whales are capable of producing clicks and tonal sounds for communication and echolocation (Au 1993). The best studied examples of toothed whales are bottlenose dolphins (*Tursiops* sp. Gervais, 1855), killer whales and sperm whales (*Physeter macrocaphalus* Linnaeus, 1758), where bottlenose dolphins and killer whales are a typical representatives of delphinids. The complex social systems of delphinids have influenced how these animals use communication signals based on complex cognitive skills (Janik 2009a). Sperm whales use repetitive patterns of clicks called codas when socializing at the surface (Watkins & Schevill 1977), which seem to be used primarily to maintain group cohesion (Weilgart & Whitehead 1993). Different coda dialects have been identified amongst different groups (Weilgart & Whitehead 1997) and it is suggested that these signals are maternally transmitted through generations (Whitehead *et al.* 1998).

Sound communication is very conspicuous in baleen whales spanning a large frequency range from the infrasonic moans of the blue whale song (McDonald *et al.* 2001) to the 10,000 Hz (Cerchio *et al.* 2001) wails or chirps of the humpback whale. However, most commonly observed sounds in baleen whales are low frequency vocalizations with most energy below 1000 Hz (Tyack & Clark 2000). These sounds primarily have a communicative function though it has been proposed that potential targets of baleen whales, such as the swim bladder of fish, lungs of marine mammals and larger targets such as the sea floor, sea surface, sea ice presence and sea ice thickness could be detected with these sounds (George *et al.* 1989; Frazer & Mercado 2000; Tyack & Clark 2000; Mercado & Frazer 2001).

Studies on the social structure of baleen whales are rare. Long-term association in baleen whales have not been frequently reported, except for the mother-calf bond, a short term association lasting few hours is most commonly observed (Tyack 1986; Weinrich 1991; Dunlop *et al.* 2008). Though still regarded as rare exceptions stable associations have been reported for humpback whales (Ramp *et al.* 2010). Such associations are often linked with foraging activities (Wiley *et al.* 2011; Parks *et al.* 2014) and are primarily seen between non-lactating females and males which lasted up to two weeks and even longer as the breeding season approached. Another type of association, also identified in this same study, was between non-lactating females which lasted up to six years. These females also had the highest reproductive output. Feeding cooperation seemed to be the most plausible explanation for these long term bonds since, to date, such grouping has only been observed on feeding grounds.

Though stable associations seem rare, baleen whales rely heavily on sound in conspecific communication. Contact calls are produced by animals that are joining into groups, such as in southern right whales (*Eubalena australis* Desmoulins, 1822) (Clark 1983) and humpback whales (Dunlop *et al.* 2008). Bowhead whales also use contact calls when members of a dispersed group or herd coordinate their swimming patterns (Clark 1991; Würsig & Clark 1993). Humpback whales use particular sound signals in competitive groups on breeding grounds (Silber 1986; Dunlop *et al.* 2008). Right whales produce high-intensity, low frequency sounds during agonistic situations while females produce sequences of screams when engaged in sexually active groups (Kraus & Hatch 2001). Blue whales produce audible down sweep calls during social interaction (Berchok *et al.* 2006) and on feeding grounds while feeding (Akamatsu *et al.* 2014), however, the context of these calls have not been described.

1.3.2 The act of singing

Several species of baleen whales sing for reproductive advertisement display. The songs are produced with repetitive acoustic patterns that are highly predictable and are often produced for long periods of time by single individuals but all identified baleen whale singers have been males (Janik 2009b; Herman *et al.* 2013). The humpback whale song has been described as the longest, most complex and sophisticated of any other animal (Payne & Webb 1971). Other conspicuous baleen whale singers belong to the Balaenopteridae family, i.e. blue whales (McDonald *et al.* 2006), fin whales (Croll *et al.* 2002; Delarue *et al.* 2009b; Morano *et al.* 2012) and possibly minke whales (Risch *et al.* 2014). The bowhead whale is the only whale outside of that family known to sing. The bowhead whale sings fairly complex songs (Stafford *et al.* 2008; Delarue *et al.* 2009a; Johnson *et al.* 2015) which are more similar to humpback whale songs than any other reported baleen whale song.

For singing animals it is predicted that such communication should enhance the Darwinian fitness of the signaller. The energetic cost of singing varies with the characteristics of the signal, including duration, intensity and acoustic frequency and presumably with body size (Eberhardt 1994; Chappell *et al.* 1995; Gil & Gahr 2002; Thomas 2002; Adam *et al.* 2013). Another cost could also be when an unwanted receiver opportunistically exploits the signal as has been shown with many song bird species (Verrell 1991; Bradbury & Vehrencamp 1998). For baleen whales, an unwanted receiver could be a potential predator, e.g. killer whales. Therefore, if a baleen whale species could be exposed to killer whale attacks such songs would most likely occur outside of high density areas of these predators or in aggregations where there may be safety in numbers. Both have been shown for humpback whales and could also apply to other baleen whale species. Baleen whale songs are usually composed of low-frequency, non-directional sound elements which are capable of spreading far distances (Payne & Webb 1971; Stafford *et al.* 1998; Mellinger *et al.* 2007). According to avian literature (Boncoraglio & Saino 2007) such sound production is beneficial if the signal is used in sexual context and could be perceived by diverse receivers at the same time. Boncoraglio and Saino (2007) suggested that fitness advantages of efficient communication should have selected for songs that do not deteriorate as they travel long distances in order to reach unaltered many designed receivers. They also point out that selection for the avoidance of the costs of eavesdropping should have led to the evolution of songs whose singer is not easily localized by possibly threatening receivers. The low-frequency non-directional sounds of baleen whale songs would fit well into that criteria. Additionally, Boncoraglio and Saino (2007) suggest that the habitat structure is a main factor shaping the evolution of bird song acoustics. That hypothesis could also fit in baleen whale singing tactics. For example, some coastal baleen whale species, e.g. humpback whales, bowhead whales, right whales and minke whales, tend to produce a variety of signals which could account for topographic variation of coastal habitats. Off shore species, however, such as blue and fin whales (Pike & MacAskie 1969; Gunnlaugsson & Sigurjónsson 1990; Víkingsson *et al.* 2009) possess simpler repertoire of low-frequency and even infrasonic moans which have low attenuation characteristics and can travel long distances in open offshore waters, primarily via the deep sound channel, but is not as efficient in coastal waters (Urick 1983; Spiesberger & Fristrup 1990; Jensen *et al.* 1997; Stafford *et al.* 1998; Mercado & Frazer 1999).

The deep sound channel or the Sound Fixing and Ranging channel (SOFAR) is a horizontal layer of water in the ocean centred on the depth where the cumulative effect of temperature, water pressure and salinity combine to create a space of minimum sound speed (Munk 1974). As a result, the sound waves are bent upwards and downwards and become entrapped inside the channel, thus, the sound loses less energy and can transmit over hundreds of kilometres. As an example, songs of the blue whales have been detected from at least 200 km distance from the sound source (Miller *et al.* 2013).

1.3.3 The song of the humpback whale

Male humpback whales sing complex and patterned cyclical songs during the breeding season while at their low latitude breeding grounds. Humpback whale songs are characterized by high intensity vocal signals forming a hierarchical song. The song is further characterized by the ordering of the shortest, most basic element in the song called a ‘unit’, ranging approximately from 8 to 10,000 Hz (Cerchio *et al.* 2001; Mercado *et al.* 2010; Stimpert *et al.* 2011). The units combine to form ‘sub-phrases’ and ‘phrases’ which are repeated in succession to form ‘themes’ that, when sung continuously, form a ‘song session’ (Payne & McVay 1971).

Males sing actively during the breeding season where they conform to the same song. The songs are gradually synchronized into a predominant pattern shared by the majority of the singers though the chorus is usually asynchronous (Payne & McVay 1971). The songs develop during the course of the breeding season and often change quite dramatically between years (Payne & Payne 1985; Noad *et al.* 2000; Eriksen *et al.* 2005). It has been suggested that the continual song development is a result of this species ability to copy song elements from other singers (Mercado *et al.* 2005) and the ability to innovate (Noad *et al.* 2000; Cerchio *et al.* 2001).

Females have rarely been observed approaching male singers, whereas several studies have confirmed that the majority of individuals approaching singers are males (Smith *et al.* 2008;

Darling *et al.* 2012; Herman *et al.* 2013). Behavioural studies from low-latitude breeding grounds have also shown that some males form cooperative alliances while others display agonistic behaviour towards one another (Tyack 1981; Clapham *et al.* 1992; Darling *et al.* 2006) which has led to suggestions that songs support male organizations on the breeding grounds. When a male escorts a female on the breeding ground he often sings and even continues to do so if the escort duo is joined by other males (Smith *et al.* 2008). Smith *et al.* (2008) suggested that males approach other singers as a low-cost strategy to locate females, however, singers escorting females continue to sing since the song is an important reproductive display during courtship. Furthermore, it has been proposed that the lower frequency components of the songs could indicate the size, robust health and sexual maturity of the singer (Adam *et al.* 2013). Frankel (1996) compared the production of the same unit types within the same song by various singers and found significant differences between individual singers, suggesting that the whales could identify the difference. Supportive of these findings and assumptions is that immature males, which are differentiated by being smaller than mature males, also sing (Herman *et al.* 2013). Larger males are more likely to be successful during agonistic encounters when competing for access to a female and usually get better access to females as principal escorts (Spitz *et al.* 2002). However, female choice could be a result of the physical competition between the competing escorts, rather than from the acoustic display. Even though a female attraction has, to date, not been detected by observers, this behaviour cannot be ruled out. If humpback whales, and other baleen whales, can assess the size of singers from the lowest song components the songs could also serve to advertise for one’s size meant for rival males to avoid physical contact or as previously suggested meant to signal the physical quality to females. Further hypothesis have been proposed for song function, such as that the songs promote synchrony of oestrous in females (Baker & Herman 1984), and that they have means of navigation or orientation, as a migratory beacon (Clapham & Mattila 1990), as a male spacing mechanism (Frankel *et al.* 1995) or as a type of sonar to locate females (Frazer & Mercado 2000) but, to date, have not been verified with further examination.

Herman *et al.* (2013) suggested that the broad participation of males in singing on breeding grounds is a lekking aggregation. Leks have been defined as male display aggregations that females attend primarily for the purpose of mating (Jiguet *et al.* 2000). The participation of many singers yields a heightened signal level (Au *et al.* 2000) that could attract more females into the area. Herman *et al.* (2013) suggested that the asynchronous singing chorus in the lek could be an instance of by-product mutualism. The songs advertise the sex of the singers and possibly a readiness to mate and engage in male-male interaction (Tyack 1981). Furthermore, a recognizable song pattern could guide the whales into a hotspot breeding area occupied by animals of their own species and possibly of their own population. A recent playback study (Darling *et al.* 2012) showed that singers on a Hawaiian breeding ground usually approached playbacks where songs similar to their own were played but avoided playbacks of very different songs. If this is a general response in humpback whales, it would further support the male-male social connection facilitated with singing on breeding grounds.

It should, however, be noted that humpback whales may interpret very different and foreign songs by conspecifics as a sound produced by another species. That could also explain the lack of interest or avoidance in relation to these foreign sounds. A replication of this study would be needed to verify if such response is general for this species. Darling *et al.* (2006) suggested that both the songs and the male relationships ranging from cooperative to agonistic behaviour are the key elements of male behaviour during the breeding season. Furthermore, they hypothesized that the continuous change in songs and the adoption of these changes by all nearby singers is a real time measure of association between individuals which could provide a means of reciprocity for mutual assistance in mating. If so, it is evident that song exchange between male singers, consequently leading to a mutual song each breeding season, is important for mating success in this species.

The reason for the striking complexity of the humpback whale song, with few analogues in the animal kingdom, still remains unexplained. It has been shown from empirical and theoretical data that when whales sing in shallow water environments, the lowest frequencies they produce will not propagate as far as the higher frequencies they produce (Urick 1983; Jensen *et al.* 1997; Mercado & Frazer 1999). Since humpback whale breeding grounds are generally characterized by shallow coastal waters, Mercado and Frazer (1999) pointed out that no single frequency would optimally propagate to all positions within the coastal water column. They suggested that humpback whales increase the range of frequencies produced within the song to increase the number of positions within a shallow water environment from which the pattern can be detected. Since the same song can be sung on different breeding grounds within the same ocean basin, it is unlikely that songs are customized to each coastal breeding aggregation. Rather, the whales choose various unit types from low to high frequency, with varying frequency and amplitude modulation to account for varying coastal topography.

The wide vocal range of the humpback whale is not only demonstrated by the male breeding songs but are also found in the non-patterned sounds produced by both males and females. These sounds are often called “non-song sounds” to discriminate them from the songs, but are sometimes called “social sounds” since they are often produced in a social context both on feeding and breeding grounds (Dunlop *et al.* 2007; Dunlop *et al.* 2008; Stimpert *et al.* 2011; Björnsson 2014). Therefore, both sexes can produce various sounds, often in non-sexual context (Dunlop *et al.* 2008). Therefore, the ability to produce and maintain complex sound repertoire might not be only due to sexual selection. However, the ability to innovate and remember complex sequences could be a sexually selected trait. Possibly, the acoustic environment in coastal waters along with frequent conspecific social interactions, compared to other Balaenopterids, may have influenced the evolution of the humpback whale’s vocal trait.

1.3.4 Cultural transmission of songs

Cultural transmission is the social learning and sharing of information or behaviours between conspecifics within a population or subpopulation and has been observed among humpback whales (Rendell & Whitehead 2001; Garland *et al.* 2011). Cultural traits can change the way in which individuals interact with their environment within and over generations, directly and indirectly affecting feeding success, survival rates, and fitness (Marcoux *et al.* 2007). Songs of some bird species change or evolve progressively over time due to accumulating song errors which are copied by other conspecifics over periods of decades (Slater 1986) while in some cases, rapid and continuous song learning and matching by conspecifics occur (Payne 1985; Trainer 1989). Evidences of cultural transmission have been found in a number of other groups of animals, such as odontocetes (Deecke *et al.* 2000; Yurk *et al.* 2002; Rendell & Whitehead 2003) and primates (Whiten *et al.* 1999; Horner *et al.* 2006).

Different modes of cultural transmission exist within the humpback whale species and can include both vertical (parent-offspring) and horizontal transmission. One of the most apparent vertical cultural traits exhibited by humpback whales occurs when young offspring follow their mothers on initial migrations between breeding and feeding grounds, later repeating these migrations independently while continuing to show strong site fidelity (Rendell & Whitehead 2001). Another example is a feeding behaviour called ´lobtail feeding‘ (Weinrich *et al.* 1992), which spread between generations of humpback whales in and around the Gulf of Maine for three decades (Allen *et al.* 2013). Humpback whale songs are constantly changing within a population over time, and these changes are recognized as cultural evolution and if the changes are complete they are referred to as cultural revolution. Such behaviour is learned through horizontal cultural transmission across unrelated individuals. A population will therefore conform to singing similar dialects or song types within a shared ocean basin. Differences begin to appear and increase with distance of proximity between populations (Helweg *et al.* 1998; Darling *et al.* 2014) but are distinctly different between geographically isolated populations (Winn *et al.* 1981).

Cultural transmission of songs between different breeding populations in the western and central South Pacific Ocean has been reported showing changes and radiation of songs consistently and unidirectional from the west to the east in a series of cultural waves (Garland *et al.* 2011). The occurrence of song revolution in humpback whales has been reported from the Australian east coast in the Pacific Ocean (Noad *et al.* 2000). The humpback whale song from that area was replaced completely by the song of humpbacks from the Indian Ocean population at the Australian west coast. The authors suggested that novelty could stimulate change in the humpback whale songs. Song similarity has been observed between populations within the same ocean basin suggesting that song exchange occurs before the whales reach their low-latitude breeding destination, i.e. on feeding grounds or during migration where individuals from different breeding populations meet (Payne & Guinee 1983; Helweg *et al.* 1998; Garland *et al.* 2011).

The synchronization of songs within the habitual range of humpback whale stocks have been proposed as a way to define stock or coherent population units based on the assumption that singers singing the same or similar song must associate (Winn *et al.* 1981; Payne & Guinee 1983; Noad *et al.* 2000; Cerchio *et al.* 2001; Darling & Sousa-Lima 2005; Murray *et al.* 2012; Garland *et al.* 2013b; Darling *et al.* 2014). It has been demonstrated that humpback whale songs can be useful for investigating the grouping of individuals into dialect regions, describing the directionality in movement of individuals as well as the level of contact between populations within an ocean basin (Garland *et al.* 2013a; Garland *et al.* 2013b).

1.3.5 Singing on feeding grounds and migration routes

The synchronization of songs appears to start during migration (Payne & Guinee 1983) and possibly when the whales are still on their feeding ground where individuals from different populations meet (Payne & Guinee 1983; Helweg *et al.* 1998; Garland *et al.* 2011). Accumulations of singing humpback whales have been recorded at mid-to high-latitude feeding grounds (Baker *et al.* 1985; Mattila *et al.* 1987; McSweeney *et al.* 1989; Clark & Clapham 2004; Vu *et al.* 2012; Stanistreet *et al.* 2013), primarily during spring and fall. Intermittent recordings of songs in the North Atlantic were discovered by Mattila *et al.* (1987) from March through November, in the Stellwagen Bank National Marine Sanctuary (mid-latitude feeding ground). One full song was recorded in south-eastern Alaska by McSweeney *et al.* (1989) on one day in August 1979 and in one day of September 1981. Findings from both studies indicated that singing usually occurred during late autumn months on feeding grounds prior to the start of migration. Clark and Clapham (2004) employed the first long-term continuous acoustic monitoring program for humpback whales feeding in the Stellwagen Bank National Marine Sanctuary and found a daily occurrence of song during the spring months, May to June. One of the most recent acoustic studies, from the North Atlantic, was reported by Vu *et al.* (2012) who described continuous year-long singing from a mid-latitude feeding ground. Vu *et al.* (2012) found songs in almost every month of the year, with increased singing detected during shoulder seasons of spring, from April to May and late fall from October to December (2006 to 2008). In the high latitude feeding grounds of Antarctica humpback whales were recorded singing into late austral fall, between May and June, i.e. during a shoulder season (Stimpert *et al.* 2011). The majority of these publications have reported feeding ground singing during shoulder seasons and could indicate that the breeding behaviour continues just before and during migration and also shortly after arriving back to the feeding grounds, particularly if females are still in oestrous. This singing activity out of low-latitude breeding grounds also shows that direct transmission and sharing can take place through mixing and communication between individuals sharing feeding grounds and during migration (Payne & Guinee 1983; Payne & Payne 1985; Garland *et al.* 2013a).

A study by Garland *et al.* (2013a) supported one of the song sharing mechanism previously proposed by Payne and Guinee (1983) that singing on feeding grounds could aid the cultural transmission process of humpback whale songs. Garland *et al.* (2013a) reported on how songs were transmitted between a Southern Ocean feeding ground and breeding grounds in the western and central South Pacific. Additionally, findings from the North Pacific have shown how songs from different breeding grounds within the same ocean basin displayed strong similarity despite of being separated by more than 2000 km (Cerchio *et al.* 2001; Darling *et al.* 2014).Therefore, the potential interaction and song exchange at high latitude feeding grounds could also be important for cultural transmission and song exchange between the North Atlantic humpback whale populations. Winn *et al.* (1981) previously described humpback whale song similarity from the West Indies and the Cape Verde Islands, suggesting that song exchange could occur on central and eastern feeding grounds, e.g. Iceland and North Norway, before the whales would reach their two separate breeding grounds. However, to date, this comparison has not yet been validated with other studies.

2 Objectives

The aim of this study was to investigate the singing activity and song culture of humpback whales on a subarctic feeding ground in the North Atlantic by applying quantitative statistics on measured song components. Additionally the aim was to investigate the importance of an Icelandic subarctic feeding ground for the evolution and transmission of songs with a comparison of the subarctic songs with songs from traditional breeding grounds in the North Atlantic (i.e. the Cape Verde and the Caribbean). Finally, the aim was to provide insight into the importance of Iceland’s coastal waters as an alternative mating ground for overwintering whales in the central and eastern North Atlantic waters.

In Paper I recordings collected from Skjálfandi Bay during 2008–2009 were used to investigate the occurrence of humpback whale songs throughout a single year and to test if the extreme light conditions of the subarctic could affect the singing behaviour of humpback whales. Humpback whale song recordings from these same winter seasons in addition to recordings from the next two winter seasons in Iceland, i.e. 2009–2011 are presented in Paper II. The aim of Paper II was to further examine the persistence in singing in the feeding ground during winter and to verify if singing by humpback whales on a subarctic feeding ground is comparable to singing on breeding grounds in terms of consistent song production across years and the song dynamics over time. Also, the aim was to measure and classify song unit characteristics with statistical methods to examine the variation of song units within and between years. By further expanding the findings in Paper II the study in Paper III uses the 2011 recordings from Skjálfandi Bay, which included longer recordings, to seek evidences of whether the songs detected during the breeding season in Iceland could serve as mating displays and be used as a mode of cultural transmission for humpback whale songs in the North Atlantic. Quantitative analyses were applied on delineated songs to uncover the song type vocalized in this high latitude feeding ground and to investigate temporal development of the songs. The data used in Paper IV were from the 2011 winter recordings in Iceland, previously used in Paper II and III, and recordings obtained from collaborators in the Cape Verde Islands during spring 2011 and 2012 and in Dominica in the Caribbean in 2008 and 2012. The aims of Paper IV were to quantitatively compare the previously described song structure from Iceland, presented in Paper III, with songs from these breeding grounds and consequently find if subarctic feeding grounds could be important for cultural transmission of humpback whale songs in the North Atlantic.

3 Methods

3.1 Passive acoustic monitoring

This study was primarily based on long-term acoustic data collection applying passive acoustic monitoring (PAM). Using underwater recordings to study cetaceans is a highly effective way to gather information about the acoustic behaviour, movement and occurrence of all cetaceans within the detectible range of the hydrophones. Depending on the recording setup sound data can be collected on a long term basis using fixed acoustic recording devices while short term focal studies are usually conducted using hand held hydrophones or recording tags which are attached to the whales. The latter two methods allow for mixed studies of visual and acoustic focal observations though only during short sessions whereas fixed passive acoustic deployments are useful for long-term monitoring within an area. The short term focal studies where visual conformation is made parallel to the acoustic recordings provide important background information for interpretation of the biological signals detected by the PAM units without visual confirmation. Passive acoustic monitoring methods have become increasingly widespread for cetacean observations (Moore *et al.* 2006; Mellinger *et al.* 2007). The first ocean scale monitoring of the acoustic activity of different baleen whale species were conducted in the north Pacific and North Atlantic, including the off-shore waters off Iceland, using the Navy’s SOSUS network, (Watkins *et al.* 2000; Charif *et al.* 2001). Prior to the study of this thesis, the application of PAM in Icelandic coastal waters to collect and study biological sounds during several months at a time had not been conducted before. Traditional visual survey methods have been used in Icelandic coastal waters since 1987 (Sigurjónsson *et al.* 1989) which provide valuable data for the estimation of the absolute or relative abundance of cetacean species within a short time frame. In addition to the more costly visual observations, the cost effective passive acoustic sampling provides means to monitor cetacean occurrence and behaviour within sampling areas over months at a time.

3.2 Recordings of humpback whale songs

3.2.1 Study sites

Acoustic recordings were collected from Skjálfandi Bay (Figure 3), NE-Iceland during three consecutive winters: September 2008–February 2009, November 2009–April 2010 and January–March 2011. Skjálfandi Bay is located in the subarctic part of the North Atlantic 66°07‘N, 17°32‘W (Figure 3). During the winter darkness prevails (average ~3 h of daylight) and the water temperature is near freezing (~+2°C) in contrast to the summer months where the days are long (average ~18 h of daylight) and the water temperature rises up to ~+8°C (Jónsson 2004). During summer, the bay is populated by many cetacean species, primarily humpback whales, minke whales, blue whales, white-beaked dolphins and harbour porpoises (Cecchetti 2006; Vallejo 2013; Akamatsu *et al.* 2014). Other species occasionally sighted in the bay include killer whales, northern bottlenose whales (*Hyperoodon ampullatus* Forster, 1770), sei whales (*Balaenoptera borealis* Lesson, 1828) and sperm whales (pers. obs.). Whale watching operation has grown rapidly in NE-Iceland since 1995 since this area provides one of the best whale watching locations in Europe due to the frequent sightings of these many cetacean species (Parsons & Rawles 2003; O’Connor *et al.* 2009). Consequently, and due to favourable logistics, Skjálfandi Bay was chosen as a prominent location to conduct long-term monitoring of cetaceans in Iceland using bottom moored passive acoustic methods.

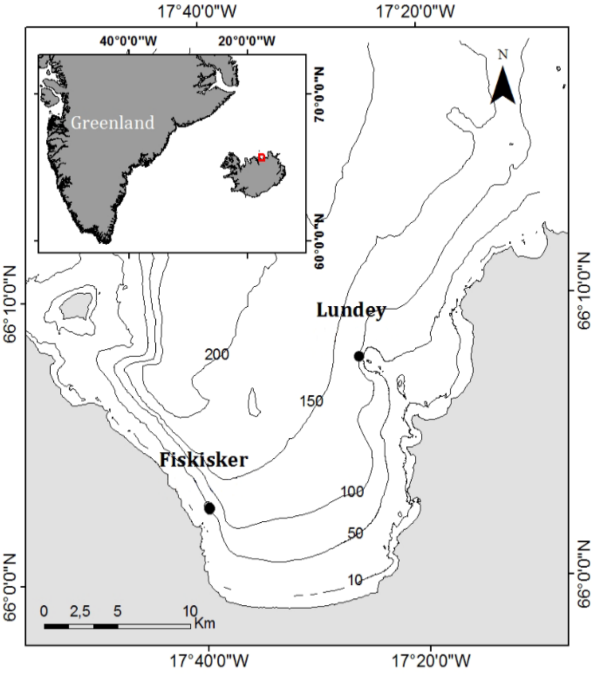

Figure 3 EAR recording locations in Skjálfandi Bay, NE-Iceland. Source: 1) Hydrographic Department of the Icelandic Coast Guard, 2012, 2) National Land Survey of Iceland, 2012.

The recordings were made using two bottom-moored PAM units of the type Ecological Acoustic Recorders (EARs) (Figure 4). Details of the deployment, recovery and troubleshooting of the first two years of this survey can be found in Dudzinski *et al.* (2011). The EAR is a microprocessor-based autonomous recorder (Lammers *et al.* 2008). One of the EAR recording units did not record during the 2009–2010 and 2011 recording periods due to an unknown malfunction, and thus data from only one recording unit, deployed at Fiskisker (Figure 3), was used during all the recording periods. During the first two winter seasons, whale acoustic data was collected over approximately 5 month period at a time using a duty-cycled recording schedule of 1 minute 'on' every 15 minutes at a sampling rate of 64 kHz to collect a broad range of sounds from as many cetacean species as possible. When humpback whale songs were found in these recordings during the winter, additional recordings were made during the 2011 winter season using a recording duty cycle of 10 minute recordings 'on' every 15 minutes at a sampling rate of 16 kHz to obtain longer song samples. The detection range of the EARs for humpback whale signals below 1 kHz, based on the minimum (171 dB) and maximum (189 dB) source levels, are 12 and 28 km, respectively, assuming spherical spreading.

Figure 4 An EAR unit ready for deployment in Skjálfandi Bay by Edda E. Magnúsdóttir, NE-Iceland. Left: a) sandbag weights (~45 kg) were connected to the EAR unit by a 1 m long and 3mm wide rust-free wire, b) the EAR unit. Right: 1) The hydrophone, 2) an aluminium housing, 3) a syntactic foam float and 4) two acoustic release units. Left © Yann Kolbeinsson, right © Edda Elísabet Magnúsdóttir

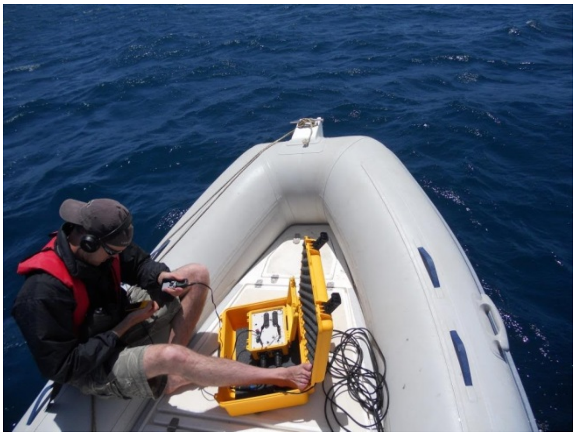

Figure 5 Dr. Ryan Conor collects acoustic recordings from Boa Vista, Eastern Cape Verde Islands, using a MAGREC HP30 hand held hydrophone. © Pedro Lopez-Suarez

Recordings were obtained from two distinct breeding grounds in the North Atlantic, i.e. the Cape Verde Islands in the southeastern North Atlantic and the Caribbean Islands in the southwestern North Atlantic (Figure 6). The recordings from the Cape Verde were collected by Dr. Conor Ryan (Figure 5) from the Galway-Mayo Institute of Technology

Galway, Ireland and the Irish Whale and Dolphin Group, Merchant's Quay, Kilrush, Co. Clare, Ireland. The Caribbean recordings were obtained from Dr. Shane Gero at the Zoophysiology, Institute for Bioscience, Aarhus University, Aarhus, Denmark. The recording sites were located 1) west off the island Boa Vista (16°5‘N, 23°5‘W) in the Cape Verde archipelago located off the NW-coast of Africa and 2) off the island Dominica (15°23’N, 61°30’W) among the Windward Islands in the eastern Antilles archipelago, i.e. the Lesser Antilles, in the Caribbean Sea (Figure 6). Dominica lies south of the island Guadeloupe and north of the island Martinique.

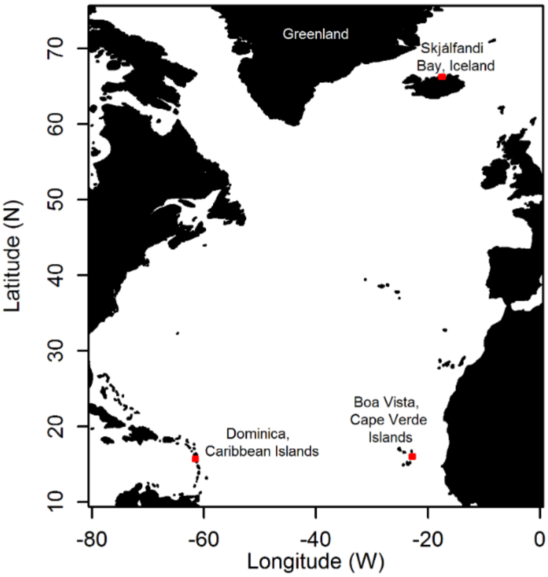

Figure 6 The recording sites are labelled with red squares, i.e. Skjálfandi Bay, NE-Iceland (66°’N, 17°30’W), Boa Vista (16°5‘N, 23°5‘W) in the eastern Cape Verde archipelago and the Island of Dominica in the Lesser Antilles archipelago (Caribbean Islands) (15°22’N, 61°1’W).

The recordings in the Cape Verde were collected during dedicated humpback whale sighting and biopsy surveys in the continental shelf waters to the west of Boa Vista during two consecutive breeding seasons (April 2nd and May 11th 2011 and again in 2012 between April 17th and May 15th). The study area, comprising 206 km^2 of inshore waters (up to 8 km from shore) off western Boa Vista, was chosen based on high sightings rates of humpback whales from previous expeditions (Wenzel *et al.* 2009). The recordings where collected from a stationary 5 m vessel using a dipping hydrophone at a 32 kHz sampling rate using a MAGREC HP30 with a flat response between 200 Hz and 20 kHz. The hydrophone signal was amplified through a MAGREC HP-26 SB amplifier box with high-pass filter at 1kHz. The recordings from the Caribbean were obtained from near the island of Dominica in the Lesser Antilles during research conducted by the Dominican Sperm Whale Project during two separate years, i.e. in 2008 and 2012. The recordings from 2008 were collected during March 2nd, March 28th and April 4th and a single recording was collected in May 9th in 2012. The recordings were collected using a custom built towed hydrophone array based on two Benthos AQ-4 elements with a frequency response between 100 Hz and 30 kHz. A filter box with high-pass filters up to 1 kHz was used resulting in a recording chain with a flat frequency response across a minimum of 2–20 kHz (Gero *et al.* 2016) deployed from a 12 m sailboat. The recording was made on a laptop PC using a Fireface 400 sound card and PAMGuard software (Gillespie *et al.* 2008) with a sampling rate of 96 kHz. All recordings covered the frequency range of the humpback whale song.

3.3 Analysis of the humpback whale song

3.3.1 Automatic detection of signals from long-term recordings: *Papers I–III*

Automatic detectors for animal vocalization is widely used for analysing large recorded data sets (Mellinger 2004; Mellinger *et al.* 2011). Humpback whale vocalization recorded during the long term recordings in Iceland during 2008–2011 were detected using the software packages Ishmael 2.0 (Mellinger 2002; Mellinger *et al.* 2011) and Osprey (Mellinger 2000). A frequency contour algorithm was employed to detect tonal signals ranging in frequency from 100–1000 Hz (Fast Fourier Transform (FFT) 0.2048 sec., 75% overlap, Hamming). The algorithm works by tracking spectral peaks over time, grouping together peaks in successive time slices in a spectrogram if the peaks are sufficiently near in frequency and form a smooth contour over time (Mellinger *et al.* 2011). Such detectors are useful for detecting humpback whale song units which contain significant energy in the selected detection frequency band and have long enough duration, i.e. duration in the order of seconds (Mellinger *et al.* 2011). Despite spanning only a part of the humpback whale tonal frequency range, the detector primarily detected humpback whale signals with minimal false positive detections. To reduce the background noise in the recordings, one second of spectrogram equalization was applied (Mellinger 2002; Mellinger *et al.* 2011). Each detected signal was inspected visually and aurally to verify detections. The detected humpback whale signals were categorized manually as 1) song units and 2) non-song signals. Song units were defined as signals found in rhythmic context (i.e. phrases). Non-song signals were defined as randomly occurring signals with no rhythmic context and not considered a part of a song (Dunlop *et al.* 2007; Dunlop *et al.* 2008).

3.3.2 Song unit analysis: *Papers I & II*

Humpback whale song analyses have traditionally focused on the song structure and patterns where the cyclical repetitions of themes or phrases are investigated (Payne & McVay 1971). Measurements of variation both on the overall pattern level, as well as on the level of individual song units, are important for understanding the characteristics of humpback whale song progression over time (Cholewiak *et al.* 2013).

In Paper I the main goal was to describe the time of occurrence of singing on a subarctic feeding ground throughout the year including basic measurement to describe the observed song units. In Paper II the song unit repertoires in this same subarctic location as reported in Paper I were examined further and now across three consecutive winter seasons. The aim of Paper II was to measure and classify song unit characteristics with statistical methods to examine the variation of song units within and between years. Such analysis can reveal the variation and pattern of song structure and the rate of changes within the songs in terms of modification and replacement of units. Units are sometimes made up from even smaller components called sub-units which are usually only visualized with appropriate number of points in a Fast Fourier Transform (FFT). Sub-units refer primarily to the discontinuities or inflection points in units and are useful for automatic classification (Pace *et al.* 2010). Sub-units were not considered essential, thus disregarded in this study when classifying units and delineating the songs.

Commonly, subjective human aural classification has been used to group humpback whale signals (Au *et al.* 2006; Dunlop *et al.* 2007; Garland *et al.* 2011). However, quantitative, statistical studies or automatic classifications on large datasets of humpback whale sounds have become increasingly common (Stimpert *et al.* 2011; Ou *et al.* 2013). Automatically categorizing the song unit dataset using statistical methods likely result in fewer distinct groups compared to completely subjective categorizations with aural and visual methods. The aural perception of frequency and changes in frequency, as well as the ability to visually categorize signals from spectrograms, can vary between observers. That can often result in individually specific and sometimes too detailed classification of similar signals that cannot be perfectly replicated. Therefore it is important to include automatic classifications for large datasets, primarily to expedite the clustering process and to promote consistency between observers. Nonetheless, the variables used to objectively categorize sounds are selected subjectively because they are believed to be important for human observers and may not necessarily be of importance to the whales (Dunlop *et al.* 2007). Notably, such bias could not be avoided in this study. Although there is currently no way to determine how a whale would categorize song units (Mercado *et al.* 2010), it is important to include statistical methods for categorization to minimize sorting errors and increase the reliability of the sorting results. This allows for a more effective comparison between studies conducted by different observers.

Measuring song unit characteristics

The sound files including humpback whale songs in Iceland were graded and categorized as very poor, poor, medium, good, and excellent. Files where all signal details were distinctly visible with high amplitude units and harmonics (i.e. good signal to noise ratio with a minimum of 10 dB above the background noise) were marked as good to excellent quality and used in further sound unit measurements. The peak frequency at every 0.05 second throughout the song units' duration was measured from a spectrogram with the software Raven Pro 1.4[4] called pitch tracking (Figure 7).

The program measures the maximum power within a selection window as dB relative to 1 dimensionless sample unit (re 1 su). The peak frequency of the fundamental frequency (f0) was measured when distinguishable. In cases where harmonics were much clearer than the f0

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[4] Cornell Lab of Ornithology, Ithaca, NY, U.S.A., http://www.birds.cornell.edu/brp/raven/ravenoverview.html

or when the f0 was not visible (Figure 8), then the peak frequencies of the clearest harmonic were measured, including the harmonic interval to assess the frequency of the f0. For lower frequency signals (< 100 Hz) where the f0 was not visible and/or the signals included discrete pulses, the pulse rate was measured from the spacing of spectral bands (Watkins 1968).

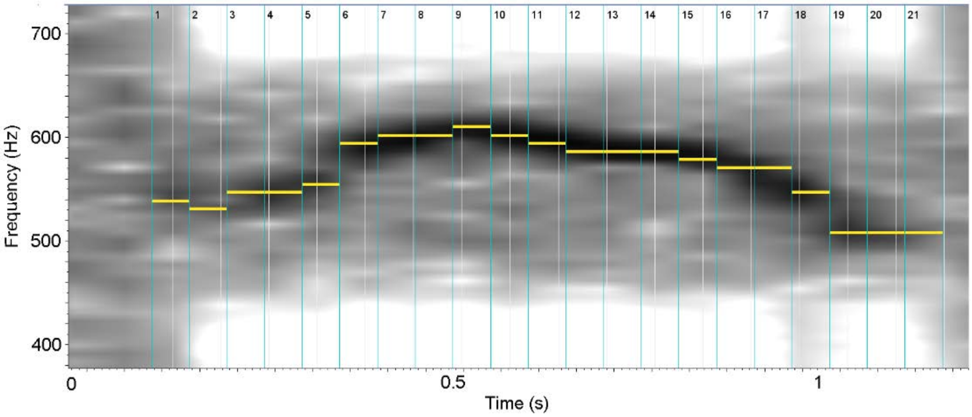

Figure 7 Pitch tracking of the fundamental frequency (f0) of a song unit. The spectrogram from the beginning and to the end of the signal is divided into parallel windows of the size 0.05 s (numbered grey vertical lines). Raven Pro measured and highlighted the signals' dominant frequency over time by detecting the strongest amplitude within each window slice (horizontal lines). Other sound signals or higher frequencies would sometimes be erased from the recording to ensure a continual tracking of the fundamental frequency only and eliminate any distortion of the tracking curve due to overlapping singers or background noise from the recording.

From the frequency measurements of the pitch tracking, the peak frequency at ¼ of duration, at ½ of duration and at ¾ of duration of the signals were extracted in order to compare the contours of the song units. Other song unit measurements included the duration, the start and end frequency, the peak frequency, the maximum and minimum frequency, the ratio of start to end frequency (frequency trend), the ratio of maximum to minimum frequency (frequency range), the frequency modulation (standard deviation of signal frequency/mean signal frequency) and the percentage of duration to the maximum frequency of the signal (PMax) (Table 1). Ratios of frequencies were measured since they better match a mammal's perception of pitch rather than differences of frequencies (Todd *et al.* 1996). A low value for frequency trend (< 1) indicated an upsweep angle and a high value for frequency trend (>1) indicated a down-sweep angle, while a frequency trend equalling 1 indicated no or small difference between start and end frequency. Low values of frequency modulation (close to 0) indicated less frequency variation in the signals whereas high values (close to 1) indicated more frequency variation in the signals. Similar measurements were made by Maeda *et al.* (2000) and Dunlop *et al.* (2007).

Table 1 Measurements including description of measurements made on each song unit.

Measurement	Abbr.	Description
Duration (s)	Dur	Duration of sound signal
Minimum frequency (Hz)	FMin	Minimum fundamental frequency of sound signal
Maximum frequency (Hz)	FMax	Maximum fundamental frequency of sound signal
Start frequency (Hz)	FStart	Initial fundamental frequency of sound signal
Frequency at ¼ (Hz)	F25	Peak fundamental frequency at 25% of the signal duration
Frequency at ½ (Hz)	F50	Peak fundamental frequency at 50% of the signal duration
Frequency at ¾ (Hz)	F75	Peak fundamental frequency at 75% of the signal duration
End frequency (Hz)	FEnd	Terminal fundamental frequency of sound signal
Peak frequency (Hz)	PeakF	Frequency of the maximum amplitude in the signal
Percentage to maximum frequency (%)	PMax	Percentage of duration to the maximum fundamental frequency within the signal
Frequency trend ratio	FTrend	StartF/EndF
Frequency range ratio	FRange	MaxF/MinF
Frequency modulation ratio	FMod	Standard deviation of fundamental frequency parameters (StartF, F25, F50, F75, EndF) divided by the mean of the frequency parameters

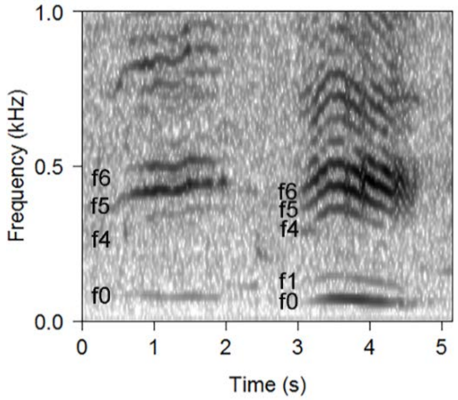

Figure 8 Spectrographic representation of two low frequency signals of the type Li1 (Paper II), generated using fast Fourier transformation (FFT) size 512 Hanning window and 95% overlap. The harmonics in these signals, primarily the 5th– 6th harmonics (f5– f6) ranging between 350–500 Hz, are stronger than the fundamental frequency (f0) at around 80–100 Hz. The 2nd and 3rd harmonics, ranging between approximately 160–350 Hz are attenuated and hardly visible on the spectrogram.

Clustering song units based on measured characteristics

The principal components of the measured signal variables, which primarily discriminated between the song units, were found using Principal Component Analysis (PCA). The measured frequency parameters were converted to a logarithmic scale prior to the PCA as this better matches a mammalian perception of pitch (Deecke & Janik 2006). Other parameters were log-transformed to increase the normality of their distribution when needed. The dataset was clustered based on the measured variables using a k-means algorithm to assign each song unit into a group. The k-mean clustering algorithm finds a given number (k) of groups maximizing the variation between groups. To identify the optimal number of clusters (groups), k-means is run sequentially with increasing values of k, and different clustering solutions are compared using Bayesian Information Criterion (BIC) (Jombart *et al.* 2010). The optimal clustering solution should ideally correspond to the lowest BIC. Since the fundamental frequency of humpback whale signals can vary greatly, from approximately 8 to 10 000 Hz (Cerchio *et al.* 2001; Mercado *et al.* 2010) the dataset was primarily separated into the lowest optimal number of clusters. Each of the major clusters was then separated with more detail into sub-clusters using k-mean.

A discriminant analysis of the principal components (DAPC) as described by Jombart *et al.* (2010) was applied using the program R (version 3.1.2) and the R-based *adegenet* package (version 1.4-2) to verify the optimal number of song unit clusters in the dataset originally performed by the k-means clustering. The discriminant functions (DFs) are constructed as linear combinations of the original measured parameters that have the largest between-group variance and the smallest within-group variance. Discriminant analysis provided membership probabilities of each song unit for the different subgroups based upon the retained discriminant functions. The subgroups providing the best membership fit were chosen for the dataset.

3.3.3 Delineation of humpback whale songs: *Papers III & IV*

Phrases were identified based on previously defined methods by Cholewiak *et al.* (2013). Phrases are composed of subphrases which are sequences of one or more units that are sometimes repeated in a series (Payne *et al.* 1983) (Figure 9). Since themes are made of the repetition of the same or similar phrases, a transitional phrase is often found between two types of subsequent themes. Transitional phrases combine units from two different phrase types which belong to different themes (Payne & Payne 1985). The unit groups defined in Paper II were used when identifying and categorizing phrase types.

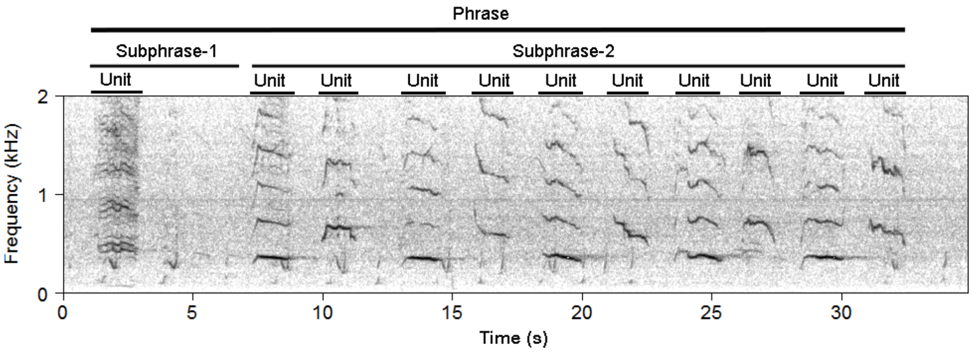

Figure 9 A spectrographic view of an example of a phrase from the Icelandic recordings. The labels indicate the components of the phrase which is composed of sub-phrases. The sub-phrases are made from one or more different types of units, the smallest component of a song (apart from sub-units which can occur occasionally).

The delineation of phrases can be difficult and ambiguous since the structure is subjective as the observer must choose where within a sequence of units one will start a phrase and where a new phrase starts. Variations in song unit production and repetitions of units within phrases can be found within the same song of the same singer (Noad *et al.* 2000; Arraut & Vielliard 2004). Such variations should be accounted for without categorizing the variations as a new phrase type. A completely different phrase type was defined when the pattern, composition or number of units in a phrase differed dramatically and was maintained within the sequence (Cholewiak *et al.* 2013). Where multiple singers were recorded singing simultaneously, the phrases from each singer were tracked manually if transitions between phrases were clearly visible on the spectrogram (Figure 10). The minimum number of singers per recording was estimated by investigating overlapping phrases that could not have been produced by the same animal. This assumption has previously been applied as a referent in studies on humpback whale songs (Payne & Payne 1985; Murray *et al.* 2012). Delineation was terminated when there was too much overlap of similar phrases sung by different whales.

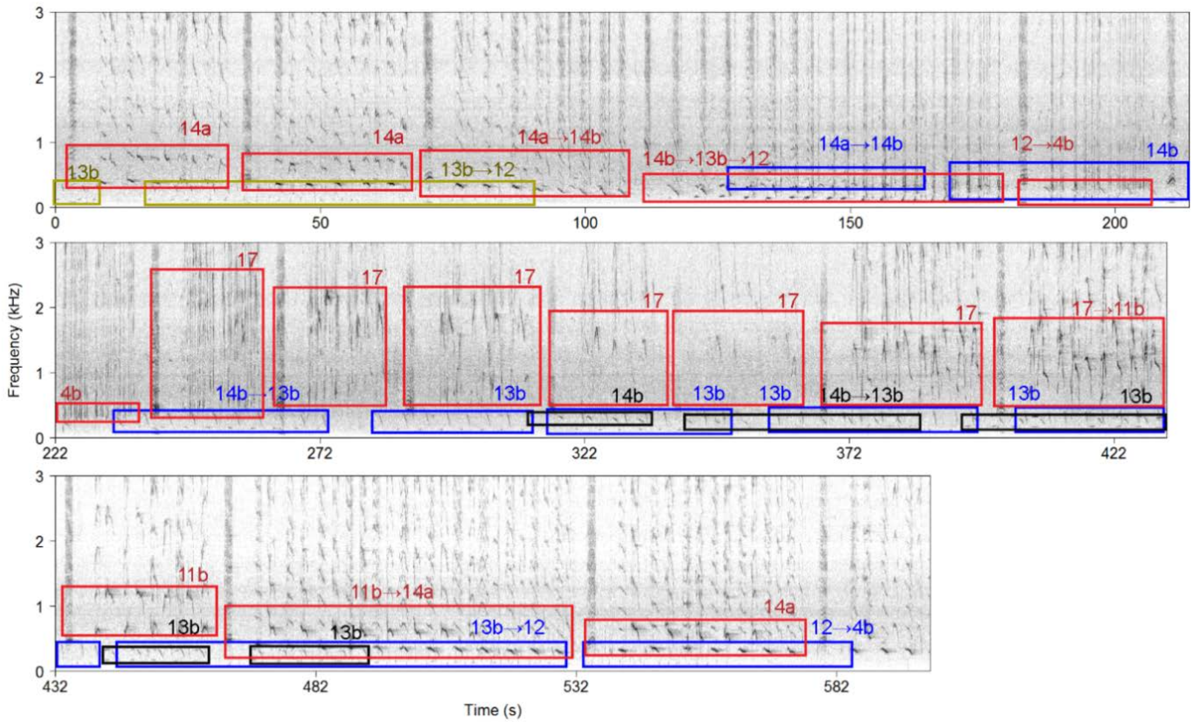

Figure 10 A spectrographic view of a 10 minute long recording where phrase sequences from at least 3 different singers were delineated. Each singer has an assigned colour, with a single phrase identified using both a coloured box and a corresponding coloured phrase label (singer A = red, singer B = green, singer C = blue, singer D = black). Arrows between phrase labels indicate a transitional phrase. Singer B's signal attenuates at the beginning of the recording and because it is not certain if singer D is the same singer, a new label is assigned. At least 3 songs overlapped at time periods within the recording, indicating that a minimum of 3 singers were singing within the detection range of the EARs during this recording. A full song sequence captured from singer A, measured from phrase-14a to phrase-14a, lasted approximately 8 minutes and 50 seconds

Due to the long-term application and data storing limitations of the EAR recordings in Iceland, the dataset was not continuous, i.e., each 10 minute recording was followed by a 5 minute break and each 1 minute recording was followed by a 14 minute break before the start of the next recording. The datasets from 2009 and 2010 included a large sample of 1 minute long sound files which allowed for phrase inspection but did not capture phrase sequences and was thus only used to compare the phrase repertoire to other sets in Paper II and IV. The dataset from Iceland in 2011 usually did not contain many complete songs within the 10 minute sound files and never contained a full song cycle within a single recording, so complete songs could not always be extracted directly from the recordings. To create a dataset for a group of singers which would be used for song sequence analysis, four to six adjacent sound files of excellent quality were acquired from 16 different days throughout the course of the recording period. These 16 different days were divided into four distinct periods of four days each. By subsetting the dataset into even sets (periods) we could avoid biasing the results towards groups of singers for which we had a higher number of song sequences. This allowed for comparison of songs between the quarters to search for temporal changes in the songs in Paper III. Division into fewer periods could result in too low resolution of the data and, thus, higher risk of averaging out possible changes while greater number of periods would include too small dataset each. To provide a consistent comparison between the four periods, the same number of days were required for each period.

In Paper IV, recordings from the Cape Verde Islands (CVI), in the eastern North Atlantic, and the Caribbean Islands (CAR) in the western North Atlantic, were compared to the songs from Iceland (ICE) from 2008–2011. However, only the songs analysed from Iceland in 2011 (Paper III) were used for song sequence comparison in Paper IV (described in section 3.3.5) since that dataset included recordings with several phrase transitions unlike the datasets from previous years in Iceland. The CVI and CAR datasets were composed of opportunistic recordings of varying lengths. Few longer recordings contained full songs while shorter recordings did not always contain a full song. The CVI recordings were collected at the end of the breeding season in 2011, which followed the Icelandic data directly in time, CVI recordings were repeated a year later in 2012 and a single song from the CAR recorded in 2012 was also delineated for comparison. The CAR songs from 2008 were not delineated for song sequence analysis since they were too distant in time from the Icelandic recordings in 2011 and were, thus, not useful for assessing the level of song sequence sharing. The CAR songs from 2008 were, however, useful for phrase repertoire comparison.

3.3.4 Testing song consistency: *Papers III & IV*

To account for the fractioned recordings where complete songs were not captured, a Markov transition analysis was applied to each of the four periods in Iceland in Paper III (from 2011) and additionally to the CVI (2011–2012) and the CAR (2012) recordings in Paper IV to estimate the most likely sequence of phrases belonging to a full song cycle during each time and location. The Markov matrices calculate probabilities for each occurring transition, providing results that can be used to determine whether or not the phrase belongs to the same sequence. This is a common method used to interpret bird song organization and predict dependent behavioural states (Lemon & Chatfield 1971; 1973; Dobson & Lemon 1979; Katahira *et al.* 2011).

In Paper III a Fishers Exact test was used to estimate the consistency of phrase transitions between periods to investigate the progression of songs in Iceland throughout the recording season. That was an important strategy to find if there is evidence of song progression in the subarctic as has been shown to occur on traditional low latitude breeding grounds. To do so, a contingency table was created for each phrase type, with table rows representing the periods and columns representing each phrase from which the phrase of interest was transitioning to. A P-value was calculated for each contingency table and assessed. If $P > 0.05$ then the null hypothesis was rejected and it could be stated that the phrase of interest transitioned consistently to the same phrase or phrases, i.e. the transitions were non-random between periods. However, if $P < 0.05$ then the null hypothesis was accepted and it could be stated that the phrase of interest did not transition consistently to the same phrase or phrases between the four periods, i.e. transitions occurred randomly between periods.

3.3.5 Testing song similarity: *Papers III & IV*

When delineating humpback whale songs the start and end of a song sequence is not always clear and must be determined visually by the observer/-s. Furthermore, if the same phrase reoccurred within a sequence, the sequence was considered terminated, with the subsequent phrase beginning a new sequence. For example:

[**15**-14a-13b-12-4b-**15**-14a] → [**15**-14a-13b-12-4b], [**15**-14a]

where each character (number or number and letter) represents a single phrase type and the hyphen indicates the transitioning event between the phrases. Sequences are shown within the brackets. Since ‘15’ occurs twice within the first sequence, this sequence is terminated at the phrase ‘4b’ which is the phrase directly preceding the second incidence of ‘15’. This results in two shorter sequences. Since the dataset from Iceland was large and contained many song sequence samples the Markov analysis could reveal the most likely start phrases (i.e. phrase 17 and 15) and end phrases (i.e. phrases 4a and 4b), referred to as the “start label” and “end label”. Due to the smaller sample sizes of the CVI and CAR datasets presented in Paper IV the likely start and end label had to be subjectively assessed. Phrases in the CVI and the CAR-12 dataset similar to the start label phrases in the Icelandic dataset were anchored as the “start labels” in the CVI and CAR-12 sequences. Phrases that commonly occurred before the start labels in the CVI and the CAR-12 datasets were assigned an “end label”.

A quantitative method based on the Levensthein distance (LD) technique (Garland *et al.* 2012; Garland *et al.* 2013b) was used in Paper III and IV to evaluate the similarity of the observed sequences between sets. Only sequences with a minimum number of four transition phrases extracted directly from the recordings were used in this analysis to exclude small sequence fragments which are unlikely representatives of song sequences.

The LD calculates the minimum number of changes, i.e. insertions, deletions and substitutions, needed to transform one string of phrases into another (Kohonen 1985; Garland *et al.* 2012; Garland *et al.* 2013b). A representative string, called the *Set median* (SM), was found for each of the four periods (sets) in Iceland and for the two periods, i.e. 2011 and 2012, in the CVI and used to compare sequence similarity between these sets (Kohonen 1985; Helweg *et al.* 1998; Tougaard & Eriksen 2006; Garland *et al.* 2013b). Each string of phrases within a given period (set) was compared to all other strings within that period. The SM was the string of phrases with the smallest summed LD compared to all other strings in the set. To ensure that the SM was the best representation of each period, a set of hypothetical medians, called *Kohonen medians* (KM) (Kohonen 1985; Garland *et al.* 2012; Garland *et al.* 2013b), were created to find if a smaller summed LD score could be obtained. The KM is created by systematically substituting each phrase in the sequence with all possible phrases found within the set. If the KM had a smaller summed LD than the SM, the KM was used instead of the SM as a representative sequence for that set. To investigate the similarity between the representative strings (SM or KM) for each set a Levenshtein distance similarity index (LSI) was used. The LSI normalizes the LD score against the longest string (Helweg *et al.* 1998; Petroni & Serva 2010; Garland *et al.* 2012; Garland *et al.* 2013b). The incorporation of the string length into the analysis allows the LD scores to be standardized so that the length of strings being compared does not increase the difference between the two strings. This enabled the difference in phrase types and phrase order to be the primary determinant of string differences. The LSI produced a proportion of similarity that ranged from 0 (0%) for no similarity to 1 (100%) for complete similarity between a pair of strings. The resulting LSI scores formed a matrix of LSI similarity which was converted to dissimilarity by subtracting each score from 1. Since only one song sequence from a single singer was obtained from the CAR 2012 data it was not possible to find an SM for that dataset, therefore, the single sequence was used instead in the comparison analysis.

The representative sequences (SM/KM) for each set were hierarchically clustered using the dissimilarity matrix and the statistical program R (version 3.1.2). The single-linkage clustering (nearest neighbour clustering) method was employed to place the most similar sequences together. These sequences were then successively linked to other sequences/clusters of sequences (Garland *et al.* 2013b). This method analysed how similar the representative sequences were between periods, allowing for evaluation of song sequence progression.

The presence and sharing of phrases in the songs from all years and locations within and between sets was inspected using Dice’s similarity index (Garland *et al.* 2015). Note that this analysis does not consider the sequential characteristics of the songs. Dice’s coincidence index was originally designed as a measure of the amount of association between two species (Dice 1945). Here, the index is used as a measure of phrase sharing (a method that was previously used by Garland *et al.* (2015)) between the sets, i.e.

$$\mathrm{SI} = 2A/(B + C)$$

where SI is the song phrase similarity between population pairs, A is the number of shared phrases, B is the total number of phrases present in population-1 (e.g. period-1), and C is the total number of phrases present in population-2 (e.g. period-2). In Paper IV, the observed phrase repertoire from all the datasets, i.e. CAR 2008 and 2012, ICE 2008–2011 and CVI 2011 and 2012, were used in this similarity analysis.

4 Results and Discussions

4.1 The discovery of humpback whale songs in the subarctic: *Papers I & II*

The long-term recordings from the subarctic feeding ground in Iceland, Skjálfandi Bay, revealed active singing during the breeding months of winter. During the first year of recording presented in Paper I, both EARs collected sounds from the bay during an entire year, i.e. September 2008–February 2009 and April–September 2009 (Figure 11) with a gap in the recordings in March. These recordings included songs during the breeding months of winter with occasional songs being heard in October and November and only non-song sounds during the summer. Non-song sound activity was much greater during the winter. Previous studies from traditional low-latitude breeding grounds have shown active non-song signal communication between both males and females (Dunlop *et al.* 2007; Dunlop *et al.* 2008) during the breeding season.

The detections of humpback whale songs and non-song signals presented in Paper I showed no diel trends throughout the winter (Cochrane–Orcutt autocorrelation test: song: $F_{3,1628} = 0.25$, $P = 0.86$; non-songs: $F_{2,1077} = 0.27$, $P = 0.77$). Additionally, there was no significant difference in the levels of song (ANOVA: $F_{2,1629} = 0.33$, $P = 0.72$) and non-song (ANOVA: $F_{2,1077} = 0.66$, $P = 0.52$) detections between the light regimes during the winter. However, compared with the detection of non-song signals, the relative proportion of songs was significantly higher during dark hours than daylight hours (Fishers exact test: $P = 0.02$, OR = 1.65). In comparison, diel patterns were observed for non-song sounds during the summer (Cochrane–Orcutt autocorrelation test: non-song: $F_{1,1054} = 4.62$, $P = 0.004$) and a statistically significant difference in the mean level of detections between dark and light hours (TukeyHSD: $P = 0.002$). Despite of no clear diel trend in singing during the winter on this subarctic feeding ground, the results suggested that humpback whales did spend a higher proportion of their time singing during dark hours than during the few daylight hours of the winter. Similarly, fin whales detected in the Arctic during winter usually sang intensively during the dark period of the day while they were assumed to use the short daylight hours for feeding (Simon *et al.* 2010).

It was confirmed with Paper II, with continual deployments the next year during November 2009–April 2010 and additionally during January–March 2011, that consistent singing during the winter on this subarctic feeding ground occurs between approximately December and March with the greatest singing activity and increased variability in song units in the months of January–February in all years (Figure 11). This is in contrast with a study from a mid-latitude feeding ground in the North Atlantic (Vu *et al.* 2012), where singing activity generally decreased or was non-existent during the time of increased singing in Iceland. The increased singing activity in Iceland coincides with the peak breeding season of humpback whales in the northern hemisphere (February), although the period extends at least from January to April (Nishiwaki 1966). Singing on low latitude breeding grounds in the Northern hemisphere has also been documented to be most active during this period (Winn & Winn 1978a; Au *et al.* 2000; Herman *et al.* 2013).

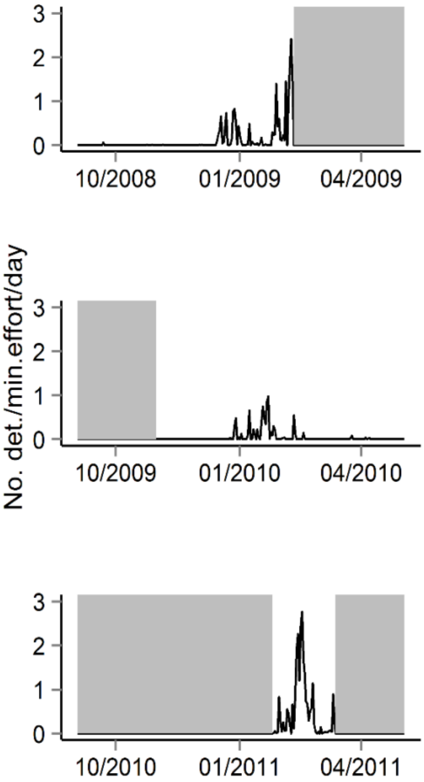

Figure 11 The black line represents the number of automatically detected sounds per minute of recording effort for each recording season. The shaded areas represent periods of no recordings

The average automatic detection rate during January–February decreased between 2008–2009 and 2009–2010, from 0.176 (±0.26 SD) detections/min of effort per month to 0.04 (±0.07) detections/min of effort per month, respectively, but increased intensely in 2011 to 3.75 (±2.72) detections/min of effort per month. The received signal level (dB re 1 su) was similar during 2008–2009 and 2009–2010 (Tukey differences of means = 0.2 dB, P = 0.77), but statistically significantly higher in 2011 (Tukey differences of means = 14 dB, P<0.001). During the 46 day recording period in 2011 songs were detected in 42 days (91.3%) with only 4 days of no confirmed singing within the detection range of the EARs. High rates of detections were captured every day from February 9th to February 26th 2011. Such commitment and investment of time in singing is noteworthy and could indicate a seasonal formation of a humpback whale lekking ground in the subarctic. The lower detection rate and received signal level during the first two years of recording indicate that the singing aggregation was located further outside of the bay than compared to the singing in 2011 which occurred more actively within closer proximity to the EARs.

4.2 Song characteristics: *Papers II & III*

4.2.1 Song unit repertoire

To study the song development between the three winter seasons of recording the analysis were primarily focused on the fundamental components of the songs, i.e. the song units. The long-term recordings from the first two winters were designed to collect long term samples from the bay with 1 min. recording every 15 minutes on a 64 kHz sampling rate to capture sound from as many cetacean species as possible and were, thus, not suitable to analyse phrase sequences.

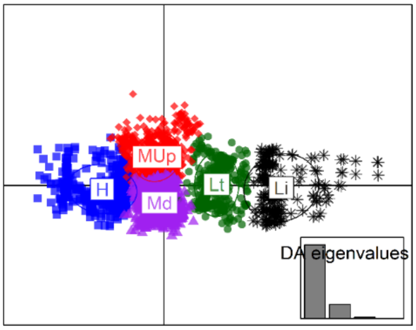

Figure 12 Discrimination of the whole song unit dataset into the five main sets by the discriminant analysis of principal components (DAPC) using two discriminant functions (DFs). The groups were created using k-mean analysis prior to the DAPC. Song units above the horizontal line have more upward slope but more downward slope below the horisontal line. Song units to the left of the vertical line have higher fundamental frequency whereas the frequency becomes lowere in the right direction

The measured song units presented in Paper II from 2008–2011, were grouped according to statistical results into five main sets of sounds that were primarily based on the fundamental frequency and the sweep of the signals, i.e., upward or downward contour (Figure 12). These major groups were further divided into subgroups resulting in 14 different song unit groups. The types of parameters contributing substantially to the variance within each of the major groups often differed widely. This could be explained by the wide variety of signal characteristics found within the humpback whale songs and that the variety could be simplified with broader category groupings. The duration and frequency range of the units were 0.1–4.6 s and from ~15 to 2200 Hz, respectively. The duration of the signals resembled measurements of units from distant breeding grounds in the Pacific (Maeda *et al.* 2000; Au *et al.* 2006; Mercado *et al.* 2010). The minimum frequency was similar to what has been observed in other locations; however, the maximum frequency was somewhat lower when compared to studies applying short range recordings (Mercado *et al.* 2010; Stimpert *et al.* 2011). In studies where the recordings are made from stationary recorders, some signal types such as high frequency signals and low amplitude signals, might be lost due to attenuation since the sound source is generally further away from the recording unit. Humpback whale songs usually consist of a variety of song units with different acoustic characteristics. Commonly observed song units are tonal, harmonic sounds (e.g., chirps, cries, moans, and wails), broadband, impulsive signals with often no or weak harmonics and where the peak amplitude is distributed over a large spectrum (e.g., gulp, whop, yup, purrs, trills, snores, ratchets) or a mixture of both, i.e., amplitude modulated sounds with harmonics (complex sounds: e.g., barks, bellows, creaks, screeches) (Winn & Winn 1978a; Au *et al.* 2006; Dunlop *et al.* 2007; Mercado *et al.* 2010). Song units from these previously described categories were found in the humpback whale songs in Iceland. The song units observed from this study period were primarily harmonic, tonal sounds (H-, Md-, MUp-, and Lt-groups) and also complex sounds (Li1 subgroup), whereas broadband impulsive sounds (Li2 subgroup) were infrequent within the songs (Paper II).

4.2.2 Phrase repertoire and progression between years in Iceland

A total of 25 different phrases were identified from the three winter seasons in Iceland. The sequences of units of each phrase type were delineated using the assigned song unit groups when subjectively categorizing phrases (Figure 13). Of these, 9 different phrases were found in the 2008–2009 songs, 10 different phrases in the 2009–2010 songs, and 15 different phrases in the 2011 songs. In Paper II a total of 14 phrases were presented, however, during the analysis of phrases for Paper III, two additional and rare phrases (phrase-1a and phrase-6) were identified and the high frequency phrases 16 and 17 were pooled together since the contour of high frequency signals is sometimes less consistent between and within individuals compared to mid- to low frequency signals and explains why these phrases were originally split. As a result, the phrase analysis from 2011 resulted in 15 different phrases from that winter period. Considerable sharing of phrases was found between the years of study. Five phrases were carried between the winters of 2008–2009 and 2009–2010, and three phrases were shared between the 2009–2010 season and the 2011 season, two of which were shared between all years in Iceland, i.e., phrases 4a and 8. The larger variety of phrases observed in 2011 compared to the previous two winter seasons of this study could be partially explained by humpback whales singing closer to the recording units for a longer continual time, thus, providing a better chance of collecting larger proportions of the songs. However, because the majority of the phrases in 2011 were not observed in the two previous years and substantial changes in the song unit repertoire were observed that year, it is possible that the songs from this season represented an increased level of song exchange.

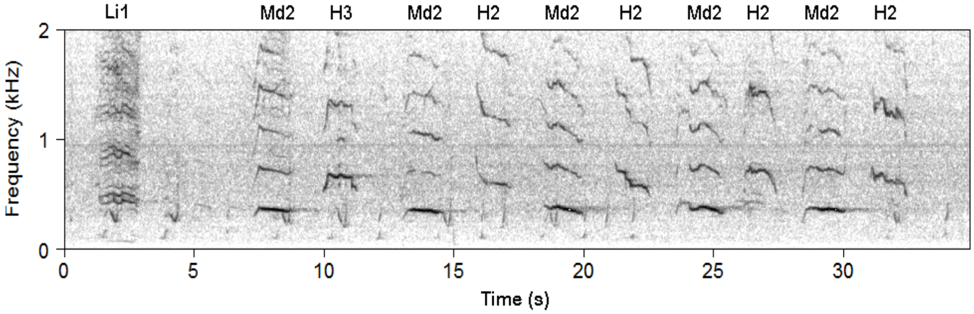

Figure 13 Spectrographic view of phrase-14a recorded in Skjálfandi Bay during the winter in 2011. The labels on top of the spectrogram show the subgroup name of each unit within the phrase, the song units were assigned to subgroups in Paper II.

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The progression of song changes was evident between years in the study area based on the changes in song unit repertoire and change or replacement of phrases. A few of the phrase types were possibly modified versions from previous years, therefore, these were assigned the same number but separated with letters as different phrase types, i.e., phrase 3a, 3b and 3c, phrases 5a and 5b, and phrases 11a and 11b.

4.2.3 Song characteristics from the winter in the subarctic

The delineated songs from this subarctic feeding region displayed a sophisticated, hierarchical structure and a fundamental theme order shared by almost all of the observed singers in 2011 (Paper III). Additionally, these subarctic winter songs represented a characteristic song type for this region with indications of gradual progression during the 2011 winter season.

Themes were generally sung in the same order by all the singers but not in synchrony which is usually typical for humpback whale singers on breeding grounds (Payne & McVay 1971; Payne 2000). The consistency of these songs was tested by applying Fisher‘s Exact test on the Markov matrices. The Fishers Exact test showed very small variations in transition occurrences per phrase between the four periods, with most phrases transitioning rather consistently to certain phrase types throughout the course of the recording period. A fundamental sequence of static phrases, and consequently static themes, i.e. [13b-12-4b], occurred at the end of the majority of extracted sequences and was also the most common sequence according to the Markov matrices (Paper III). Phrase sequences occurring before this fundamental sequence varied within the songs between periods. Of these, four phrase types (phrase-17, -13c, -14a, and -3c) transitioned more inconsistently to various phrases, thus, contributing substantially to the song variance. Payne *et al.* (1983) showed that unstable themes which are not part of the vast majority of the songs are either increasing or decreasing in the songs. Phrase-17 increased and 3c decreased during the single winter season in Iceland in 2011 while the occurrence of phrases-13c fluctuated and -14a remained stable.

The analysed song sequences ranged up to 22 phrases within the 10 minute sound files. When only including sequences with a minimum of four phrases, the average length of the captured phrase sequences was 8.9 phrases (± 4.6) per observed sequence. The average number of different phrase types in these full songs, when only including a minimum of 4 different phrases, were 5.6 (SD = ±0.6), ranging between 5–7 different phrase types. The total length of the observed phrase sequences increased from period-1 to period-4 (Tukey's differences of mean = 4.3 increase in no. phrases, $F_{3,163} = 8.7$, $P<0.001$) within the 10 minute sound files. Since the recordings were not continuous, it was not possible to measure the length of each song and confirm a gradual lengthening of the songs. Song length can change dramatically through the course of a single breeding season which is the result of lengthening of themes due to greater repetition of phrases within the themes. This evidence of song lengthening found in the subarctic songs are commonly seen on traditional breeding grounds as well as the opposite, i.e. gradual shortening of the songs (Payne *et al.* 1983). Both types of development indicate a song progression.

The set median sequences for all the four periods in Iceland displayed at least 80% similarity between each other according to the LSI and 85–97% of the phrases were shared between all periods according to the DSI. These results suggest that the songs analysed from these four periods in Iceland represented a single song type since a minimum of 40% LSI similarity between songs has been required to group songs together as the same song type (Garland *et al.* 2013b). The entropy, i.e. the lack of predictability, of the songs appeared to increase close to and around the middle of this recording season, which coincides with the increasing number of song detections during that time, but returned again to a more homogenous cluster of songs close to the end of the recording period (Figure 14) indicating a synchronization progress among the singers. Evidences of song evolution, primarily recognized in the change of the use of phrases as the period progressed, was identified during the course of the recording period.

In Paper II the repertoire of song units analysed from this study area noticeably evolved during the course of three winter seasons while new phrases were being formed and adopted every year with modification and changes of song units. Particular phrases from previous years were found to be carried over to the next year while other phrases were completely omitted after one season (Figure 15). These conformed changes over time indicate that humpback whale singers feeding in the subarctic waters of Iceland share a repertoire of sounds. Such cultural development within and between years is continually shown on many traditional breeding grounds (e.g. Winn & Winn 1978b; Payne & Payne 1985; Noad *et al.* 2000; Eriksen *et al.* 2005; Mercado *et al.* 2005) and evidently occurs in this subarctic feeding ground. As a result, the song characteristics observed in Paper III closely resemble reported songs quantified from low latitude, traditional breeding grounds.

4.3 Cultural transmission of humpback whale songs in the North Atlantic: *Paper IV*

Direct transmission and sharing of song components can take place through mixing and communication between humpback whales sharing feeding grounds or during migration (Payne & Guinee 1983; Garland *et al.* 2013a). The importance of a subarctic feeding ground for cultural transmission of humpback whale songs in the North Atlantic was investigated and presented in Paper IV. A comparison of song structure was made between the Icelandic songs described in Paper III and songs from the only known North Atlantic breeding grounds, i.e. the Cape Verde Islands (CVI) to the east and the Caribbean Islands (CAR) to the west. As previously reported in Paper II a total of 9 different phrases were identified in Iceland in 2009, 10 in 2010 and 14 different phrases were identified in the songs from Iceland in 2011. A total of 12 different phrases were identified in the Cape Verde songs from 2011 and nine in the Cape Verde songs from 2012, finally eight different phrases were identified in the Caribbean song from 2008 and six from 2012.

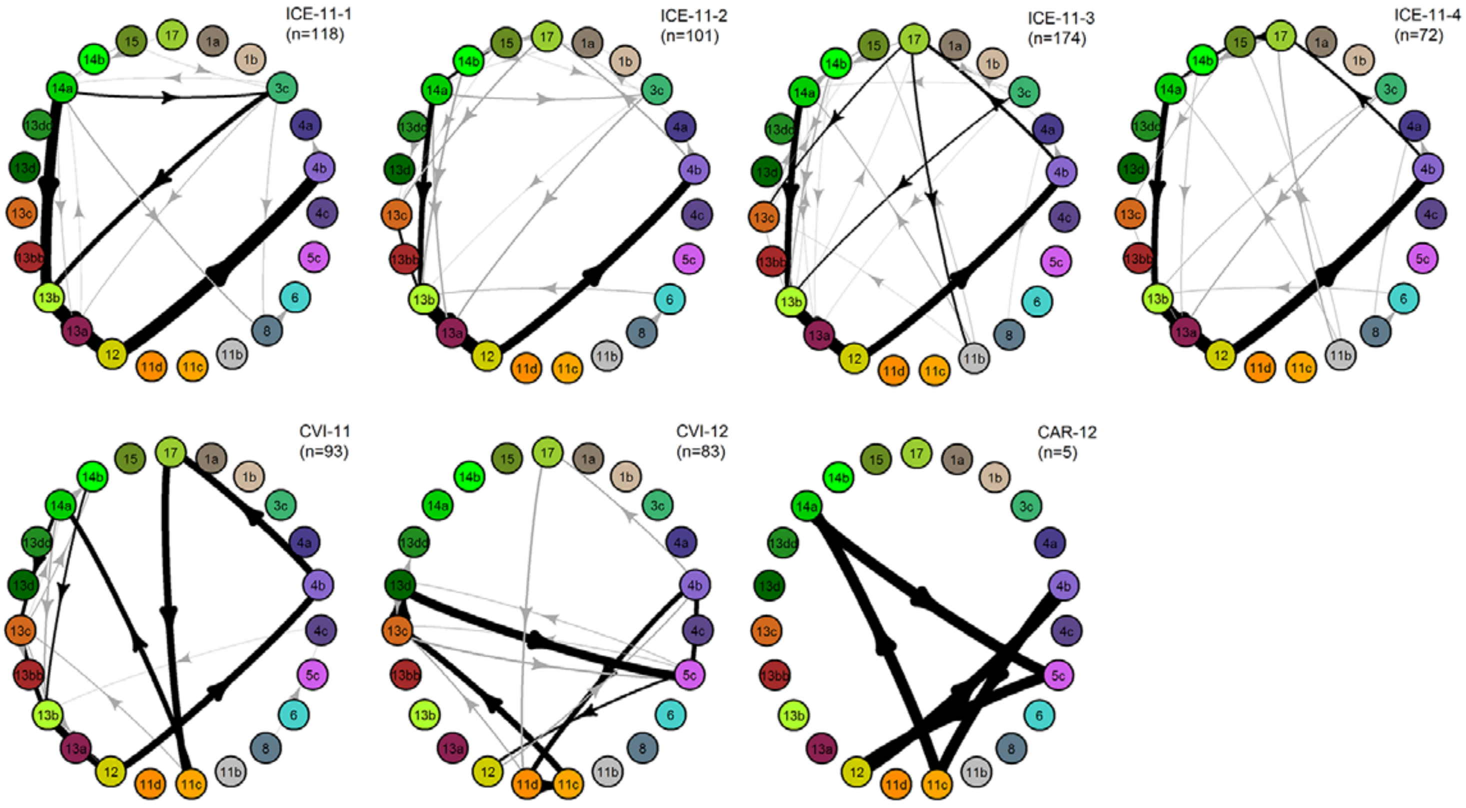

Figure 14 Transition diagrams from each period and location (set) based on Markov transition matrices. The data points (n) represent the number of analysed transitions observed during each period. Each diagram contains all the observed phrases from songs in Iceland, the Cape Verde and one song cycle from the Caribbean. The grey lines represent transitions occurring less than 5% of the time and black lines occurred more than 5% of the time. The line thickness indicates the percentage likelihood of a transition to occur with wider line corresponding to greater percentage.

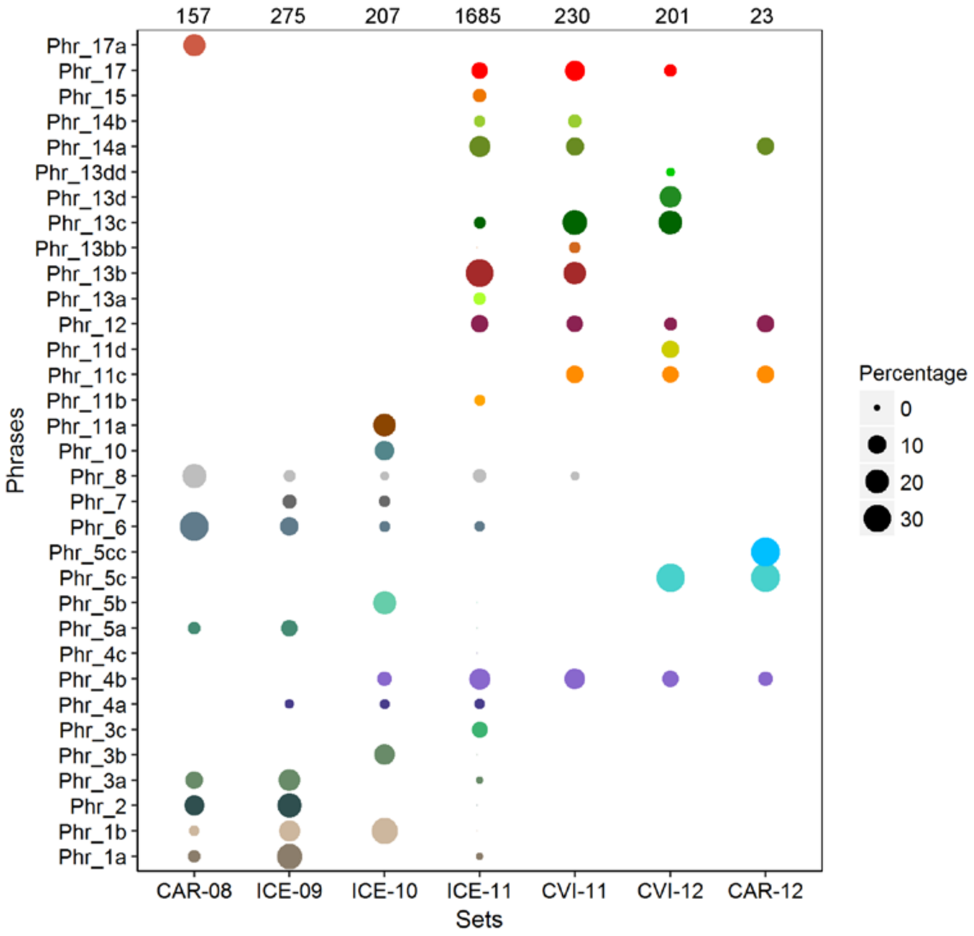

Figure 15 The percentage of occurrence of each observed phrase (consequently a theme) during each location and period (i.e. within set). The sizes of the dots indicate the percentage of occurrence of each phrase within a set i.e. Iceland in 2009–2011 (ICE-09–ICE-11), Cape Verde in 2011–2012 (CVI-11 and CVI-12) and Dominica in 2012 (CAR-12). The values above each set show the sample size (n), i.e. the number of phrases included in the analysis during each location and year. The sizes of the dots indicate the percentage of occurrence of each phrase within a set (location and year).

As a result, a total of 33 unique phrases (Figure 15), including phrase variants, were observed during the entire study period from 2008 in the Cape Verde and until 2012 in Cape Verde and the Caribbean.

With a combination of Markov matrices (Figure 14) and similarity analysis (Levenshtein Distance, Levenshtein Similarity Index and Dice’s Similarity Index) it was possible to investigate which song components were transmitted between the subarctic and the subtropical habitats. The phrase sequences comprising the songs from the winter in Iceland were very similar to the sequences recorded in the Cape Verde Islands during the following spring of 2011. As a result, all the set medians from that breeding season were grouped into a single cluster called ICE-CVI 2011 according to LSI analysis and hierarchical clustering (Figure 16).

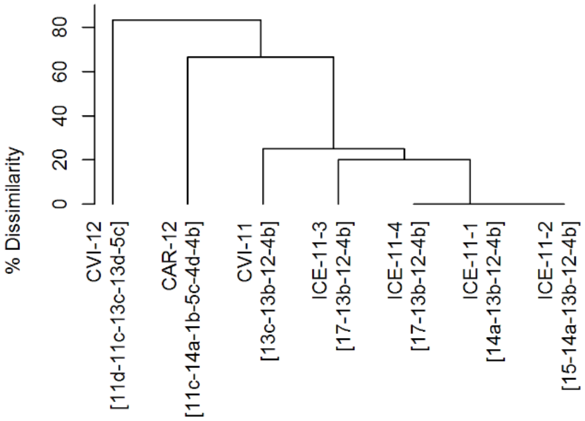

Figure 16 A nearest neighbour clustering of representative sequences based on the LSI values. The set median sequences from Iceland in 2011 (ICE-11) and the Cape Verde in 2011 (CVI-11) formed a single cluster named ICE-CVI 2011. The set median for the songs from the Cape Verde in 2012 (CVI-12) and the sequence from the Caribbean in 2012 (CAR-12) form two other separate clusters**.**

The total song structure between the three song groups was somewhat similar in terms of unit types being sung from the beginning to the end of the songs. More precisely, high frequency units (e.g. 17, 11b-d, 13c) were followed by themes made from mid- and low-frequency units (e.g. 14a, 14b, 13b, 13d) and these were often followed by themes made from short repeated up-call units (12, 4b, 4d) which then transitioned back to high frequency units. The songs from ICE-11 and CVI-11 shared 52–67% of the phrases according to the DSI analysis. The development of the songs from the winter in Iceland and until late spring in the CVI in 2011 was primarily a result of insertion, deletion and modification of themes. Modification of themes occurred as spectral parameters of at least one unit type changed or new units were inserted into older phrases. Analysis and comparisons of songs recorded a year later in the same subtropical breeding ground of the Cape Verde (CVI-12) demonstrated more pronounced substitution and re-ordering of themes. Innovative examples were found within the song sequences of a few singers, primarily as spectral modifications of signals, or with addition or deletion of units into the phrases. The single song recording from Dominica in the Caribbean during spring in 2012 (CAR-12) revealed a similarity with the set median sequence from the Cape Verde during that same spring, or a 27% similarity according to the LSI (Figure 16). However, the total songs from these two breeding grounds in 2012 shared 53% of the phrases according to the Dice’s Similarity Index (DSI) analysis. It must be noted, however, that when interpreting these results the small sample size from the CAR-12 data is likely to overlook the variations of songs occurring during that period in Dominica (CAR). With a collection of more song sequences from many different singers would have likely resulted in a greater theme variation in the Caribbean dataset. Nonetheless, the results support previous findings by Winn *et al.* (1981) that songs from these different breeding grounds share thematic similarities. The level of phrase sharing between adjacent sets (location and year) ranged from 34–82% DSI where the strongest phrase repertoire similarity between different locations was found between the Caribbean in 2008 and Iceland in 2009 (82% DSI). The Dice’s Similarity Index (DSI) revealed a general trend of gradual decrease in DSI phrase repertoire similarity from each period and to the period furthest away in time (Paper IV).

Some of the new phrases observed in 2012 in both the CVI and CAR appeared to be modified phrases from the ICE-CVI 2011 songs, e.g. 11d and 11c seemed to have developed from 11b. Phrase 5c from the Cape Verde and the Caribbean in 2012 was very similar to phrases 1a and 5a recorded in Iceland during the winter in 2009 and published in Paper II. Modification of phrases occurred as spectral parameters of at least one unit type changed or new units were inserted into older phrases (see Paper IV). The phrase-4b and -12 were the most consistent phrases throughout the study since they first occurred in Iceland in 2010 and until the 2012 season in the subtropics. The phrase-4b is primarily composed of repeated wop sounds (MUp3; Paper II), a sound type commonly described in humpback whale songs as well as within non-song repertoires from different geographical regions (Dunlop *et al.* 2007; Pace *et al.* 2010; Stimpert *et al.* 2011; Garland *et al.* 2013a). Another resilient phrase, i.e. phrase-8, which is composed of low frequency impulsive song units (Li2; Paper II), was first found during the 2008–2009 season and continued to appear until the 2011 breeding season despite of only representing a small part of the phrase repertoire in each year. This sharing of phrases and song sequences between the subarctic and subtropics provides evidence of a high level of transmission of song culture between these locations in the Atlantic Ocean.

Paper IV notably demonstrates clear evidence of song transmission of humpback whale breeding songs between Icelandic subarctic feeding grounds and the subtropical breeding grounds in the Cape Verde archipelago and the Lesser Antilles archipelago (eastern Antilles) in the Caribbean Sea. As a result, these singers in Iceland either migrate to or are at least associated with humpback whales breeding in the Cape Verde and the Lesser Antilles. These two unique breeding locations are currently the only ones recognized for humpback whales in the North Atlantic. The Cape Verde Islands and the Caribbean Islands share similar latitudes, or approximately 15–16°N, but are separated by an ocean basin of at least 4000 km. Due to different geographical locations of these subtropical breeding grounds and a converse angle from Iceland it is unlikely that the migration routes to these destinations would greatly overlap. Additionally, since movements between breeding grounds within-season have only rarely been observed, the sharing of song components in the North Atlantic would be expected to be most active prior to migration on a joint feeding ground. That would explain the similarity observed in the songs from these distant breeding grounds. A continual song sharing between migrating individuals heading for the same breeding assembly would lead to further evolution of the songs, resulting in slightly different songs for these two breeding grounds. The active singing in Iceland until mid-March 2011 and a clear similarity with the songs from the Cape Verde in 2011 strongly suggest that vocal convergence for North Atlantic humpback whales occurs in this subarctic feeding ground. The potential interaction and song exchange at the high latitude feeding grounds of Iceland could be a key driving force behind continued cultural transmission and song exchange between the North Atlantic populations of humpback whales.

5 Concluding remarks

Due to changing global climate and trends in sea ice reduction, especially in the northern hemisphere, it is suspected that seasonally migrant cetaceans will range farther north and possibly spend a larger proportion of the year in high latitudes (Moore & Huntington 2008). The fundamental reason appears to be a predicted increase in forage fish stocks as a result of the boost to pelagic community production which would accompany reductions in sea ice (Hunt *et al.* 2002; Bluhm & Gradinger 2008). The decreased sea ice will also result in the opening of the northern waters (Hovelsrud *et al.* 2008) for cargo transport, tourism, military activity, seismic surveys and commercial fisheries. Such activities may pose increased physical risk to marine mammals due to boat strikes, fisheries interactions and entanglement, acoustic injuries and noise pollution in addition to altering their physical and acoustic habitat. Over the past century, the propulsion noise of motorized shipping has profoundly changed the acoustic environment of the world's oceans, elevating average deep-sea ambient noise by 10 to 100 times in the 20 to 500 Hz region (Urick 1983). The level of background noise is expected to continue to rise in these subarctic and Arctic waters in the coming years which decreases the communication distance of baleen whales with sound masking in addition to producing a more stressful environment (Burek *et al.* 2008; Moore *et al.* 2012). The future of humpback whales and other marine mammals in these changing subarctic and Arctic conditions is ambiguous. There is a growing demand for continual and enhanced research on wildlife in the subarctic and Arctic waters to provide means to counteract the adverse development of human activity in these areas.

The findings of this study have provided further insight into and broadened the perspective of the known migration and breeding behaviour of humpback whales. Furthermore, the findings carry implications with respect to the importance of northern Icelandic waters as a stopover for humpback whales during or before migration, for the evolution and transmission of songs, and the possibility that this subarctic region could serve as an alternative mating ground for non-migrating whales feeding in central and eastern North Atlantic waters. The time of singing in Iceland during winter extends far into the breeding period and tallies with the average time of arrival in the Cape Verde Islands and the eastern Caribbean Islands. As a result, there appears to be an opportunity for these whales to start their southbound migration later, allowing them to extend the time of feeding without necessarily delaying mating or at least mating displays. Evidence showing that females sometimes do not finish migration or even overwinter in high latitude regions exist (e.g. Ingebrigtsen 1929; Brown *et al.* 1995), thus, indicating that there could be a tangible mating opportunity for singers in the subarctic during the breeding season. It is therefore possible that the breeding habitat of humpback whales in the North Atlantic is not only limited to the low latitude areas but extends into their subarctic feeding grounds. Future studies on the social structure, gender ratio and reproductive status of humpback whales wintering in subarctic feeding grounds and more extensive song comparison between feeding and breeding grounds in the North Atlantic would enable confirmation of critical habitats and timings for this species in the North Atlantic. Such knowledge would be essential for addressing management considerations for this species with the better understanding of possible segregation into stocks and units within the North Atlantic.

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Paper I

Paper I

Humpback whale songs during winter in subarctic waters

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Authors' contribution
Designed the study: EEM MHR MOL.
Prepared recording units for data collection: EEM.
Deployed and retrieved recording units: EEM MHR.
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SHORT NOTE

Humpback whale songs during winter in subarctic waters

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Abstract The songs of the male humpback whales (*Megaptera novaeangliae*) have traditionally been associated with mating at tropical and subtropical mating grounds during winter. However, songs also occur out of mating season, both on feeding grounds in spring, late summer and fall. This study provides the first report of humpback whale singing behaviour in the subarctic waters of Northeast Iceland (Skjálfandi Bay) using long-term bottom-moored acoustic recorders during September 2008–February 2009 and from April to September 2009. Singing started in late November and peaked in February, within the breeding season. No songs were detected from spring to fall, despite visual detections of humpback whales. Non-song sound signals from humpback whales were detected during all recording months. Songs were partly composed of fundamental units common with other known mating grounds, and partly of song units likely unique to the study area. The variety of song unit types in the songs increased at the end of the winter recordings, indicating a gradual change in the songs throughout the winter season; as has been shown on traditional mating grounds. The relative proportion of songs compared with non-song signals was higher during dark hours than daylight hours. The short light periods of the winter, and where food is available, likely influence the daily occurrence of humpback whales' songs in the subarctic.

Keywords Humpback whale · *Megaptera novaeangliae* · Songs · Non-songs · Subarctic waters

Introduction

North Atlantic humpback whales (*Megaptera novaeangliae*) forage in various temperate to Arctic coastal waters from spring to fall (Stevick et al. 2003). Many undertake seasonal migrations where the winters are spent in the less productive tropical breeding grounds of the West Indies (Martin et al. 1984; Katona and Beard 1990; Stevick et al. 1998), or of the northwest coast of Africa (Charif et al. 2001). However, humpback whales and other migrating baleen whale species do sometimes stay until winter, or even overwinter, in the polar regions (Thiele et al. 2004; Moore et al. 2006; Stafford et al. 2007; Simon et al. 2010; Acevedo et al. 2011). It is not known if portions of these populations have always overwintered on high-latitude feeding grounds. Nonetheless, humpback whales are regularly seen on Icelandic feeding grounds during winter following the capelin (*Mallotus villosus*) migration (Víkingsson 2004; Magnúsdóttir 2007), and they have been sighted during winter on northern feeding grounds for decades (Ingebrigtsen 1929; Christensen et al. 1992). At present, limited information exists about the abundance, behaviour and movement of humpback whales wintering in a subarctic region.

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On lower latitude breeding grounds, wintering male humpback whales produce long and complex songs, comprising ascending hierarchical series of units, phrases and themes (Payne and McVay 1971; Mattila et al. 1987; Cerchio et al. 2001; Mercado et al. 2003). Within each breeding ground, all males sing the same or very similar songs at any given time (Winn and Winn 1978) but songs tend to change gradually throughout the mating season (Payne et al. 1983; Payne and Guinee 1983; Payne and Payne 1985; Cerchio et al. 2001); only male humpback whales have to date been detected singing (Smith et al. 2008; Herman et al. 2013).

Humpback whale songs have been detected at higher latitudes, outside of the breeding grounds and reproductive periods, both on migratory routes during early and late autumn (Clapham and Mattila 1990; Norris et al. 1999; Charif et al. 2001), and in spring and mid-winter on the southernmost feeding grounds of the North Atlantic (Clark and Clapham 2004; Vu et al. 2012). The function of songs outside of traditional breeding areas is not well understood, but they may serve as an opportunistic mating strategy or intra-sexual display (Clark and Clapham 2004; Smith et al. 2008; Wright and Walsh 2010).

Male singing is believed to have a role in reproduction (Tyack 1981; Mobley et al. 1988; Smith et al. 2008) and has so far only been associated with mating strategies (Darling and Bérubé 2001; Darling and Sousa-Lima 2005). Ovarian and testis data obtained from humpback whales caught on breeding grounds in the Northern Hemisphere (Ryukuan waters) showed that females ovulated and testis weight in mature males increased from January to April (Nishiwaki 1959, 1960, 1962). Thus, singing for mating purposes could also be expected by overwintering mature whales in the Arctic region.

This study describes an effort to investigate singing occurrence in the subarctic on a year-round basis. The aim was to evaluate the structure and development of the songs, changes in the incidences and properties of the song components as the mating period progressed (as has been shown on traditional mating grounds), if songs in the subarctic could also have a reproductive purpose, and if the extreme light conditions of the subarctic could affect the singing behaviour.

Materials and methods

Two bottom-moored microprocessor-based autonomous ecological acoustic recorders (EARs; Lammers et al. 2008) were deployed in Skjálfandi Bay from September 2008 to February 2009 and from April 2009 to September 2009. Skjálfandi Bay is located on the northeast coast of Iceland (at 66°07′N, 17°32′W) (Fig. 1). During the winter darkness prevails (average ~3 h of daylight) and the water temperature is near freezing (~+2 °C) in contrast to the summer months where the days are long (average ~18 h of daylight) and the water temperature rises up to ~+8 °C (Jónsson 2004). EAR-1 "Lundey" was placed on an outcrop at about depths of 65 m named Lundey (66°08′N, 17°26′W), and EAR-2 "Fiskisker" was placed approximately 12.5 km away on a slope named Fiskisker (66°03′N, 17°40′W) at about 62 m depth. EAR-1 "Lundey" was retrieved on 28 February 2009, and EAR-2 "Fiskisker" was retrieved on 23 March 2009. Both EARs were redeployed to their same exact locations on 3 April 2009 and retrieved on 9 September 2009.

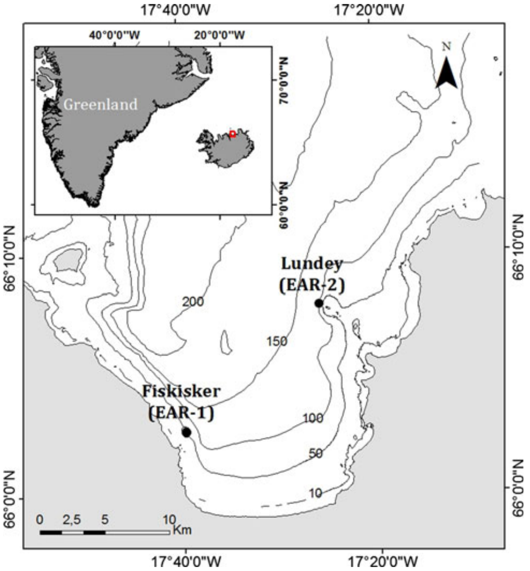

Fig. 1 The study area in Skjálfandi bay, NE Iceland. The *two black circles* represent the location of each EAR recording unit. Depth contours are in metres. *Source* (1) Hydrographic Department of the Icelandic Coast Guard, 2012, (2) National Land Survey of Iceland, 2012 and (3) Esri, DeLorme Publishing Company, Inc. The map was created using ArcGIS® software (version 10.1) by Esri

The EARs were programmed to record for 1 min every 15 min at a sampling rate of 64 kHz to collect a broad range of sounds from as many cetacean species as possible, over a long period, approximately 5 months per deployment. The detection range of the EARs for humpback whale signals below 1 kHz, based on the minimum (171 dB) and maximum (189 dB) source levels, are 12 and 28 km, respectively, assuming spherical spreading.

Acoustic data were analysed using the software packages Ishmael 2.0 (Mellinger 2002; Mellinger et al. 2011) and Osprey (Mellinger 2000). A frequency contour algorithm was employed to detect tonal signals ranging in frequency from 100 to 1,000 Hz (FFT 0.2048 s., 75 %

overlap, Hamming). To reduce the background noise in the recordings, one second of spectrogram equalization was applied (Mellinger 2002; Mellinger et al. 2011). Each detected signal was inspected visually and aurally to verify detections.

The humpback whale signals evaluated in this study were categorized as: (1) song units and (2) non-song signals. Song units were defined as signals found in rhythmic context (i.e. phrases). Non-song signals were defined as randomly occurring signals with no rhythmic context and not considered a part of a song (Dunlop et al. 2008). Due to the nature of the data sampling scheme (i.e. 1-min sound files recorded every 15 min), it was not always possible to obtain whole phrases and never whole themes. Therefore, the focus was placed on describing these smaller units. For each sound, the start and end times, the high and low frequencies and the frequency change were measured. Types were categorized visually by their shape and frequency range, and aurally. The units were named alphabetically as they occurred during inspection. Only sound files with clear signals where frequency parameters could be easily measured were used for measuring the frequency and duration of song units. These sound files were all obtained from Lundey (EAR-1) during 13 December 2008–12 February 2009. That period was divided into 12 5-day sub-periods to search for evidence of changes in song structure and song variability as the mating season progressed. The R-based *pastecs* package (version 1.3-11) was used to obtain descriptive statistics for the occurrence of units per sub-period. The number of sound files from each EAR containing song units was counted for and a paired *t* test was used to look for statistical differences in the number of detected sound files on each EAR.

All detections of humpback whale song units and non-song units, from both recording periods, were used to examine the effect of light conditions on the occurrence and combinations of song and non-song units. The null hypothesis was that the levels of calling are the same for all light regimes and that the relative proportions of song detections were independent of non-song detections during different light regimes. Three light regimes, light, dusk and dark hours, were defined by the altitude of the sun as described in Stafford et al. (2005). The timing of each light regime was determined by measurements of the United States Naval Observatory Astronomical Applications Department website (http://aa.usno.navy.mil) for the location 66°07′N, 17°32′W for each hour of data analysed. Since there was a substantial variance in the number of detected humpback whale signals between days, the mean number of sound signals each day was subtracted from the number of sound signals per hour for each day (Hjellvik et al. 2001; Stafford et al. 2005).

Diel trends in acoustic detections were analysed using Cochrane–Orcutt autocorrelation in the R-based *orcutt* package (version 1.1). The difference in the adjusted average number of calls per light period was tested using a one-way ANOVA and Tukey's HSD (honestly significant difference) test. Finally, Fishers exact test was used to investigate the relative proportions of song detections and non-song detections during different light regimes.

Results

Occurrence of songs and non-songs

The EAR-1 "Lundey" recorded for 162 days, and the EAR-2 "Fiskisker" recorded for 146 days during the winter (first deployment). The first humpback whale song units were detected at Lundey in September 2008, and at Fiskisker in December 2008; "Fiskisker" stopped recording earlier than expected. A total of 1,129, 1-min sound files containing humpback whale signals were detected during the winter (first deployment) of which 86 % included components of a song, and 14 % included non-song sounds. During the summer (second deployment), both EARs recorded for 165 days, resulting with just 79, 1-min sound files containing humpback whale signals, of which none were songs or traces of song units. Humpback whales were, however, visually observed in the area from June to September 2009 (pers. obs. by E.E. Magnúsdóttir, unpublished data).

The first occurrence of measureable song units was during mid-December 2008; the number of different song

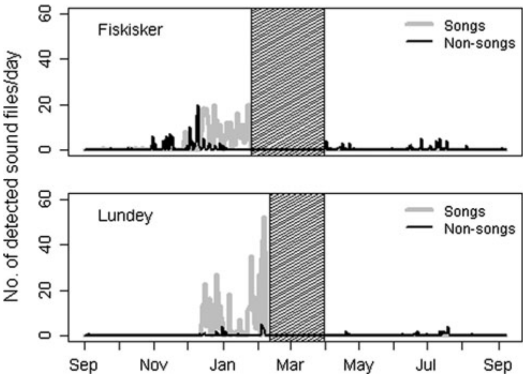

Fig. 2 Number of sound files per day containing humpback whale song units (*grey*) and non-song signals (*black*) from both locations during the two deployments, i.e. fall 2008 through spring 2009 and spring through fall 2009. The *shaded column* represents periods of no recording

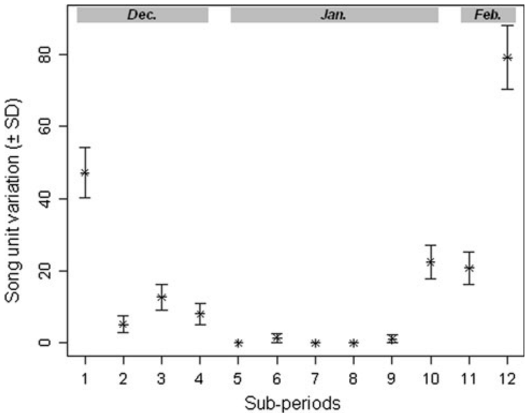

Fig. 3 Song unit variation within each of the 12 5-day sub-periods, during 13 December 2008–12 February 2009

units produced varied throughout the singing period. The occurrence of humpback whale song units increased extensively in mid-December, and the greatest number of detections occurred in February despite only 12 days of recording that month (Fig. 2). Detections of non-song sounds started in September at both locations, whereas the number of detections increased considerably between November and December at Fiskisker and decreased again as the occurrence of songs increased. There was no significant difference in the number of song file detections per day between the two recording locations ($t = 1.08$, $df = 371$, $P = 0.28$). However, the detections of non-song sounds per day were significantly higher at Fiskisker ($t = 3.83$, $df = 371$, $P < 0.001$). The largest variety in song unit production, in terms of the number of occurrences per unit type, was observed during the last sub-period, (6–12 February), and the lowest during the mid-season corresponding to less song detection during those sub-periods (Fig. 3).

Song components

A total of 550 song units were measured, of which 23 different song units were identified (see Online Resource 1). The average duration of a single humpback whale song unit was 0.96 s (SE = ±0.02), average low frequency was 281.09 Hz (SE = ±4.48), average high frequency was 527.97 Hz (SE = ±8.47) and average frequency range was 246.9 Hz (SE = ±7.54). A special type of unit with down-swept harmonics not found in the literature was categorized as song unit I (Fig. 4). This unusual type of unit was almost exclusively observed in a pattern with other known song units and accordingly recognized as a humpback whale song unit.

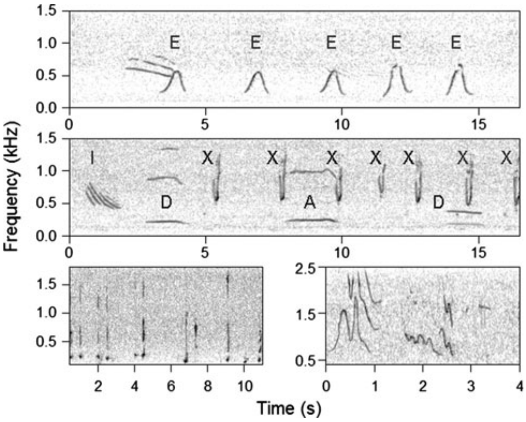

Fig. 4 Examples of some of the most commonly detected song units (*A*, *D*, *E* and *I*) embedded in phrases and song units from the end of the winter period (*X*). The *first two spectrograms* include song phrases, whereas the *two bottom spectrograms* display two recordings of different non-song signals, i.e. short up calls (*left*) and high-pitched screams (*right*). The top spectrogram includes a version of the I unit which is not produced by the same individual as of the *E* units. The second spectrogram includes one whole phrase (*I-X-X-X-X-X-X*) produced by one individual and a part of another phrase (*D-A-D*) produced by another individual

The most commonly detected song unit was C followed by E, I, D and A (Fig. 4; see Online Resource 1) which all were detected throughout the entire period of singing activity. Unit C had the highest mean number of occurrences per sub-period. Other song units mostly occurred during specific sub-periods and peaked either during early or late winter (see Online Resource 2).

Diel trends in song and non-song signals

The detections of humpback whale songs and non-song signals showed no diel trends throughout the winter (Cochrane–Orcutt autocorrelation test: *songs*: $F_{3,1628} = 0.25$, $P = 0.86$; *non-songs*: $F_{2,1077} = 0.27$, $P = 0.77$). Additionally, there was no significant difference in the levels of song (ANOVA: $F_{2,1629} = 0.33$, $P = 0.72$) and non-song (ANOVA: $F_{2,1077} = 0.66$, $P = 0.52$) detections between the light regimes during the winter. However, compared with the detection of non-song signals, the relative proportion of songs was significantly higher during dark hours than daylight hours (Fishers exact test: $P = 0.02$, OR = 1.65), but was the same during dark and dusk hours (Fishers exact test: $P = 1$, OR = 0.98) and not considered significantly different between dusk and daylight hours (Fishers exact test: $P = 0.06$, OR = 1.68). In comparison, diel patterns were observed for non-song sounds during the summer (Cochrane–Orcutt autocorrelation test: $F_{1,1054} = 4.62$, $P = 0.004$) and a statistically significant difference in the mean level of detections between dark and light hours (TukeyHSD: $P = 0.002$) and dark and dusk hours (TukeyHSD: $P = 0.035$) but not between light and dusk hours (TukeyHSD: $P = 0.49$).

Discussion

This study investigated the occurrence of songs in subarctic waters on a year-round basis, whether there are evidences of changes in the song structure based on changes in song unit types as the winter progresses, and whether the limited daylight conditions of the subarctic winter could affect the occurrence of singing as has been shown for other baleen whale species. While it was not possible to address the structure of whole songs for comparison to those of humpback whales in other regions, due to the nature of the data sampling (1-min sound files recorded every 15 min), analysis of the occurrence and variability of different song units and changes in unit types produced per time during the mating season showed variability of phrases in song and that properties of song in this region change throughout the season. This study shows that humpback whales sing in subarctic waters during winter and that the types of song units used within an area can be useful for comparison to other feeding and breeding grounds.

While non-song signals were found in the same recordings as song units, this was not used as criterion for non-song signal classification and behaviours associated with the non-song signals were not analysed in this study. Non-song signals can be used by humpback whales for various purposes and be related to various group combinations, both during social interaction and feeding (Dunlop et al. 2008). Specific study on non-song sounds in Skjálfandi bay is being conducted that will investigate such behavioural correlates more thoroughly.

The songs found in this study were fundamentally characterized by five regularly occurring song units (A, C, D, E, and I), and the other units were added more sporadically to the songs. The occurrence of different song units changed gradually throughout the season. Of the 23 measured song units, only six were concentrated to the end of the period, indicating gradual changes in song construction throughout the winter as has been seen in other breeding areas (Payne et al. 1983; Payne and Guinee 1983; Payne and Payne 1985; Cerchio et al. 2001). Also, the variety of units in the songs increased at the end of the season suggesting greater effort in inter- or intra-sexual display when reaching the peak of the reproductive season, despite geographical location.

At least three of the fundamental song units (A, D and E) could be matched with song units described in the West Indies (Mattila et al. 1987) and on a western North Atlantic feeding ground (Clark and Clapham 2004). We are not aware of any other published studies that contain more extensive song descriptions for humpback whales in the North Atlantic for further comparison.

The song unit “I” differed from other reported stereotypical humpback whale song units. The structure of units can vary between areas, since they can change differently within each mating ground due to cultural innovation (Cerchio et al. 2001). It seems that a part of the units recorded in Skjálfandi Bay belongs to fundamental song components shared by other remote areas while a part of the song units could be special for this subarctic region.

The timing of increased singing activity in Iceland corresponds to the timing of songs for other distant breeding populations, such as in Hawaii (Herman et al. 1980; Au et al. 2000), but in contrast with studies from northern feeding grounds which have shown high singing activity before and after the peak mating season (Clark and Clapham 2004; Vu et al. 2012). Likely causes for these singing events are individuals that prolong their feeding season into the mating season or do not migrate at all. It has been shown that mature humpback whales often appear later on feeding (Gregr et al. 2000) and breeding grounds and also leave their breeding grounds later (Nishiwaki 1959, 1960, 1962). Therefore, mature males may start singing while still on their feeding grounds to gain access to more females. Humpback whale females, which commonly have two year reproductive cycle (Chittleborough 1958; Glockner-Ferrari and Ferrari 1984; Baker et al. 1987; Steiger and Calambokidis 2000), sometimes overwinter at high latitudes (Brown et al. 1995; Craig and Herman 1997; Smith et al. 1999). It could be a trade-off strategy for both sexes to overwinter in the subarctic or migrate late and attempt at mating while still having access to an abundance of food. Similar evidence has been found for fin whales (*Balaenoptera physalus*) during winter in the Davis Strait (Simon et al. 2010).

Studies from tropical mating grounds have shown diel variation in singing intensity (Au et al. 2000) and the observed behaviour of male humpback whales (Helweg and Herman 1994). However, this study showed no obvious diel trends in acoustic activity during the winter in relation to light conditions, only for non-song sounds during the summer. On the other hand, the results suggest that humpback whales spend a higher proportion of their time on singing during dark hours than during the few daylight hours of the winter. Fin whales detected in the Arctic during winter usually sing intensively during the dark period of the day while they are assumed to use the short daylight for feeding (Simon et al. 2010). The short light periods, and where food is available, likely influence the daily occurrence of humpback whales’ songs in the subarctic.

Further studies are required with longer recording sessions to capture larger proportion of the songs in this area. Additionally, more intense visual observations along with skin sample or biopsy collection would be needed for a better understanding of the humpback whales sex ratio and behaviour during the winter in this part of the world.

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Paper II

Paper II

Humpback whale (*Megaptera novaeangliae*) song unit and phrase repertoire progression on a subarctic feeding ground

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Authors' contribution
Prepared recording units for data collection: EEM.
Deployed and retrieved recording units: EEM MHR.
Analysed the data: EEM.
Wrote the paper: EEM
Reviewed the manuscript: EEM PJOM MHR MOL JS.

Humpback whale (*Megaptera novaeangliae*) song unit and phrase repertoire progression on a subarctic feeding ground

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The songs of the male humpback whales have traditionally been associated with breeding activities at low latitude breeding grounds during winter. This study provides the first detailed analysis of humpback whale songs recorded in the subarctic waters of Iceland using passive acoustic recorders. Recordings were collected during three winter seasons: 2008–2009, 2009–2010, and 2011 during which singing was detected in all seasons. Peak song occurrence was during January–February in all years; this coincides with the timing of the peak breeding season of humpback whales in the Northern hemisphere. A total of 2810 song units from all years were measured and statistically divided into 14 groups, which constructed 25 phrases. The song unit repertoires included stable song unit types that occurred frequently in songs during all years while the occurrence of other song unit types varied more between years. Around 60% of the phrases were conserved between the first two study seasons, while the majority of phrases found during the last study season had not been observed before. This study indicates the importance of a subarctic feeding ground for song progression and song exchange and possibly as an opportunistic mating ground for migrating or overwintering humpback whales. © *2015 Acoustical Society of America*.

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I. INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) generally migrate from high latitude summer feeding grounds to low latitude winter breeding grounds every year (Dawbin, 1966). In the North Atlantic, humpback whales aggregate on breeding grounds in the West Indies (Martin *et al.*, 1984; Stevick *et al.*, 2003) or off the coast of Cape Verde, NW-Africa (Charif *et al.*, 2001) during winter. Traditional feeding grounds in the western North Atlantic coast stretch northwards from the Gulf of Maine and towards West Greenland. Central North Atlantic feeding grounds are found off Iceland and Jan Mayen while eastern feeding grounds stretch from the north coast of Norway towards the Barent Sea (Stevick *et al.*, 2006). Most of these feeding grounds are characterized by high maternally directed site fidelity where little interchange has been observed between aggregations (Clapham *et al.*, 1993; Stevick *et al.*, 2003; Stevick *et al.*, 2006).

Humpback whales feeding in Icelandic waters have been found migrating to breeding grounds both in the West-Indies and off the Cape Verde Islands (Jann *et al.*, 2003; Stevick *et al.*, 2003; Kennedy *et al.*, 2013). Humpback whales from Iceland and Norway have, however, been underrepresented on Silver Bank, a common breeding ground in the West Indies (Stevick *et al.*, 2003), and only few sightings of humpback whales feeding in Icelandic waters have been reported in the Cape Verde Islands (Jann *et al.*, 2003). Therefore, there is still a considerable lack of information regarding the breeding ground destinations of humpback whales feeding in Icelandic and Norwegian waters.

A notable behavior associated with these assemblies is the male humpback whales' singing behavior, which is believed to have an important role in reproduction and possibly male-male social organization (Smith *et al.*, 2008; Darling *et al.*, 2012). To date, only males have been identified as singers (Herman *et al.*, 2013). These songs are usually long, complex, and structured in a hierarchical order in which acoustically distinct units are produced in a characteristic sequence to form a phrase, which consequently are

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repeated to form a theme. Different themes joined in a predictable sequence forms the final song (Payne and McVay, 1971). Singing in humpback whales is a socially learned behavior and is passed between unrelated individuals (horizontally), rather than from a parent to offspring (vertically) (Rendell and Whitehead, 2001; Garland *et al.*, 2011). Humpback whales modify the song units and song patterns they produce throughout their lives; this results in progressive changes in songs within a population within and between seasons (Payne and Guinee, 1983). Because new song types are transmitted horizontally, male humpback whales within the same breeding ground conform to a similar version of the song and modify the song through the course of the breeding season quite synchronously (Cerchio *et al.*, 2001). Additionally, songs can be similar amongst populations within the same ocean basin (Garland *et al.*, 2011; Darling *et al.*, 2014) likely due to the fact that the migration routes of different breeding populations often overlap. Furthermore, it has been speculated that males could move between breeding areas and also that songs could be transmitted over long distances in the open ocean (Noad *et al.*, 2000; Cerchio *et al.*, 2001; Garland *et al.*, 2011). However, humpback whales from geographically isolated oceans or populations that do not mix generally sing different songs during the same breeding season (Payne and Guinee, 1983; Darling *et al.*, 2014). Song similarity decreases with increasing time (Payne and Guinee, 1983). However, the rate of song change varies with sometimes a complete turnover to a new song in five winter seasons or more (Payne and Payne, 1985) or even only in two winter seasons (Noad *et al.*, 2000). The evolution of songs is usually characterized by changes in the acoustic structure of song elements (units, phrases, and themes), as well as the adoption of new sounds and/or reordering of song units which lead to changes in phrases, themes, and the overall songs (Payne and Payne, 1985; Cholewiak *et al.*, 2013). The process of continual song evolution could be due to individual modifications or innovation (Noad *et al.*, 2000), song copying as a result of interactions between different breeding populations, differences in individual ability to produce or perceive a particular sound (Arraut and Vielliard, 2004), the ability to remember sounds, or due to distortion of song features after a long-range transmission.

Songs have been detected outside of the mating season at mid-latitude (42°N) feeding grounds in the North Atlantic during spring, late summer, autumn, and winter (Mattila *et al.*, 1987; Clark and Clapham, 2004; Vu *et al.*, 2012) and on migratory routes during early and late autumn (Clapham and Mattila, 1990; Charif *et al.*, 2001). Songs have also been detected during summer and autumn on Alaskan feeding grounds (58°N) (McSweeney *et al.*, 1989). Similar humpback whale singing events have been detected on feeding grounds in Antarctica during the Austral fall (Garland *et al.*, 2013). These songs are often similar to those sung in breeding grounds within the same ocean basin the previous winter but sometimes appear somewhat shorter in duration (McSweeney *et al.*, 1989). The purpose of the songs on feeding grounds is not fully understood, but they may be related to continued breeding activity into spring and summer. Garland *et al.* (2013) implied that "off season" songs on feeding grounds aid rapid horizontal cultural transmission of songs between distinct breeding populations, which meet at common feeding grounds. At a subarctic feeding ground (66°N), off North Iceland, active singing was detected during December–February (Magnúsdóttir *et al.*, 2014), no singing was recorded during the summer, and sporadic singing activity was recorded during early and late autumn. It has been shown that female humpback whales, which have approximately a 2 yr reproductive cycle (Steiger and Calambokidis, 2000) sometimes appear to overwinter at high latitudes (Craig and Herman, 1997). That has led to the speculation that mating behaviour, including singing, sometimes occurs in high latitude feeding grounds during the breeding season as a trade-off strategy for both sexes (Magnúsdóttir *et al.*, 2014). Overwintering individuals, or those that migrate late, could attempt at mating while still having access to an abundance of food. Similar phenomena have been found for fin whales (*Balaenoptera physalus*) in the Davis Strait (67°N) during the winter (Simon *et al.*, 2010).

Humpback whale song analyses have traditionally focused on the song structure and patterns where the cyclical repetitions of themes or phrases are investigated (Payne and McVay, 1971). Measurements of variation both on the overall pattern level, as well as on the level of individual song units, are important for understanding the characteristics of humpback whale song progression over time (Cholewiak *et al.*, 2013). To date, limited information exists about the song structure and song unit characteristics of humpback whale songs in the subarctic North Atlantic. In this study, song unit repertoires in the same subarctic location as songs reported by Magnúsdóttir *et al.* (2014) were examined across three consecutive winter seasons. The aim was to verify that singing by humpback whales on a subarctic feeding ground is comparable to singing on breeding grounds in terms of consistent song production across years and the songs dynamics over time. Also, the aim was to measure and classify song unit characteristics with statistical methods to examine the variation of song units within and between years. Such analysis can reveal the variation of song structure and the rate of changes within the songs in terms of modification and replacement of units. The findings carry implications with respect to the importance of northern Icelandic waters as a stopover during or before migration, the evolution of song, and the possibility that this subarctic region could serve as an alternative mating ground for non-migrating whales.

II. METHODS

A. Acoustic recordings

Acoustic recordings were collected from the same area as described in Magnúsdóttir *et al.* (2014) in Skjálfandi Bay, NE-Iceland (see Fig. 1 in Appendix A in the supplementary material for further details), during three consecutive winters: September 2008–February 2009, November 2009–April 2010 and January–March 2011. The recordings were made with two bottom-moored ecological acoustic recorders (EARs). The EAR is a microprocessor-based autonomous recorder with a Sensor Technology SQ26-01 hydrophone with a response sensitivity of −193.5 dB that is flat (±1.5 dB) from 1 Hz to 28 kHz (Lammers *et al.*, 2008). Before being digitized, the input signal is amplified by 20 dB gain and filtered with an eighth-order low-pass filter with a cutoff frequency that is set via software as a fractional percentage value of the Nyquist frequency, for example 80%. The signal is then digitized by a 16 bit analog to digital converter (Lammers *et al.*, 2008). The recordings are stored as raw binary files and converted to wave files using custom written MATLAB script. The detection range of the EARs for humpback whale signals below 1 kHz, based on the minimum (171 dB) and maximum (189 dB) source levels, are 12 and 28 km, respectively, assuming spherical spreading.

One of the EAR recording units did not record during the 2009–2010 and 2011 recording periods due to unexplained malfunction, and thus data from only one recording unit were used in these two recording periods. During the first two winter seasons, whale acoustic data were collected over approximately 5 months periods using a duty-cycled recording schedule of 1 min "on" every 15 min at a sampling rate of 64 kHz. During these first two seasons, the aim was to collect a broad range of sounds from as many cetacean species as possible. The recordings made during the 2011 winter season were made using a recording duty cycle of 10 min recordings "on" every 15 min at a sampling rate of 16 kHz to obtain longer humpback whale song samples. Only recordings from the EAR that contained the greater number of humpback whale detections were used in analyses of the 2008–2009 dataset. This EAR unit was placed on an outcrop called Lundey (66°03′N, 17°40′W) at a depth of roughly 65 m. In 2009–2010 and 2011, the functional EAR unit was located approximately 12.5 km away from Lundey, at a site called Fiskisker (66°05′N, 17°25′W) on a slope at about 62 m depth (see Fig. 1 in Appendix A in the supplementary material for further details).

B. Song unit analysis

The software package ISHMAEL 2.0 (Mellinger, 2002; Mellinger *et al.*, 2011) was used to automatically detect humpback whale song units in the datasets as described in Magnúsdóttir *et al.* (2014). The automatic detector was used to find sound files with possible singing events. Each detected sound file was inspected to confirm the occurrence of phrases. Song units within complete phrases were selected for measurements based on clarity (>10 dB above background noise). Signals were not included in the analysis if they were found within incomplete phrases, i.e., phrases where not all units were visible, to minimize overrepresentation of high amplitude signals. Recordings from 2011 contained substantially more song detections. Therefore a random sample of high quality recordings was selected from that period that approximately matched the duration of high quality recordings from the previous years. The peak frequency for all sounds was measured from a spectrogram every 0.05 s throughout the signals with the software RAVEN PRO 1.4 (Cornell Lab of Ornithology, Ithaca, NY).[1] The program measures the maximum power within a selection window as decibels relative to 1 dimensionless sample unit (re 1 su). The peak frequency of the signal's fundamental frequency (f0) was measured when distinguishable. In cases where harmonics were much clearer than the f0 or when the f0 was not visible, then the peak frequencies of the clearest harmonic were measured, including the harmonic interval to assess the frequency of the f0. Spectrographic analyses for song units that did not contain discrete pulses and had a clear f0 were performed using 50% overlap with a 30–50 ms/10–15 Hz resolution Hanning window. For lower frequency signals (<100 Hz) where the f0 was not visible and/or the signals included discrete pulses, the pulse rate was measured from the spacing of spectral bands (Watkins, 1968) using a Hanning window with no overlap and 200 ms/3 Hz resolution. From the frequency measurements, the peak frequency at 1/4 of duration, at 1/2 of duration, and at 3/4 of duration of the signals f0 were extracted to describe the distribution of spectral energy over time. Other measurements made included the duration, the start and end frequency, the peak frequency, the maximum and minimum frequency, the ratio of start to end frequency (frequency trend), the ratio of maximum to minimum frequency (frequency range), the frequency modulation (standard deviation of signal frequency/mean signal frequency), and the percentage of duration to the maximum frequency of the signal (Table I). Approximately ≥100 ms silence had to occur between sounds to be considered discrete song units. The start and end points of each sound was determined manually by visually designating sample points jointly from the spectrogram (15 Hz resolution) and the sound's waveform. Spectrogram measurements were included because the precise duration of the units could not always be evaluated from a waveform alone due to a gradual increase and decrease in amplitude at the beginning and end of the units, respectively. Also, background noise affected the measurement precisions when using the waveform envelope. Ratios of frequencies were measured because they better match mammal perception of pitch rather than differences of frequencies (Dunlop *et al.*, 2007). A low value for frequency trend (<1) indicates an upsweep angle and a high value for frequency trend (>1) indicates a down-sweep angle, while a frequency trend close to 1 indicates no or small difference between start and end frequency. Low values of frequency modulation (close to 0) indicate less frequency variation in the signals, whereas high values (close to 1) indicate more frequency variation in the signals. Similar measurements were made by Maeda *et al.* (2000) and Dunlop *et al.* (2007). Phrases were identified based on previously defined protocols by Cholewiak *et al.* (2013).

Because different individuals were not confirmed by eye or by using photo identification, the number of different singers could only be assumed hypothetically where recordings greater than 24 h apart were assumed to represent different individuals. Additionally, the minimum number of singers per recording was estimated by investigating overlapping phrases that could not have been produced by the same animal. This assumption has previously been applied as a referent in studies on humpback whale songs (Payne and Payne, 1985; Murray *et al.*, 2012).

TABLE I. Measurements including description of measurements made on each song unit.

Measurement	Abbreviation	Description
Duration (s)	Dur	Duration of sound signal
Minimum frequency (Hz)	FMin	Minimum fundamental frequency of sound signal
Maximum frequency (Hz)	FMax	Maximum fundamental frequency of sound signal
Start frequency (Hz)	FStart	Initial fundamental frequency of sound signal
Frequency at $\frac{1}{4}$ (Hz)	F25	Peak fundamental frequency at 25% of the signal's duration
Frequency at $\frac{1}{2}$ (Hz)	F50	Peak fundamental frequency at 50% of the signal's duration
Frequency at $\frac{3}{4}$ (Hz)	F75	Peak fundamental frequency at 75% of the signal's duration
End frequency (Hz)	FEnd	Terminal fundamental frequency of sound signal
Peak frequency (Hz)	PeakF	Frequency of the maximum amplitude in the signal
Percentage to maximum frequency (%)	PMax	Percentage of duration to the maximum fundamental frequency within the signal
Frequency trend ratio	FTrend	StartF/EndF
Frequency range ratio	FRange	MaxF/MinF
Frequency modulation ratio	FMod	Standard deviation of fundamental frequency parameters (StartF, F25, F50, F75, EndF) divided by the mean of the frequency parameters

C. Statistical analysis

Principal component analysis (PCA) was used to estimate groupings of the data and to assess which parameters contributed the most to the variance between song unit groups. The collection of parameters used in the PCA analyses was accepted when the principal components, with eigenvalues greater than 1, accounted for more than 80% of the total variance. This was achieved by discarding parameters with weak loadings. The measured frequency parameters were converted to a logarithmic scale prior to the PCA as this better matches mammalian perception of pitch (Deecke and Janik, 2006). Other parameters were log-transformed to increase the normality of their distribution when needed. Also the variable dataset was scaled to account for different measurement scales by centering each column of the matrix. Centering is done by subtracting the column means (omitting NAs) of the matrix from their corresponding columns.

The dataset was clustered separately with hierarchical clustering (Stimpert *et al.*, 2011) and a *k*-means algorithm (Brown and Miller, 2007). These two methods were compared to find which provided clearer cluster patterns for the dataset. The hierarchical clustering defines the distance between two clusters to be the maximum distance between their individual components. At each stage of the clustering process, the two nearest clusters are merged into a new cluster. The process is repeated until the whole dataset is agglomerated into one single cluster (Yau, 2012). The *k*-mean clustering algorithm, on the other hand, finds a given number (*k*) of groups maximizing the variation between groups. To identify the optimal number of clusters, *k*-means is run sequentially with increasing values of *k*, and different clustering solutions are compared using Bayesian Information Criterion (BIC) (Jombart *et al.*, 2010). The optimal clustering solution should ideally correspond to the lowest BIC. The optimal clustering number was evaluated from a scatterplot of the clusters. The *k*-means gave a better clustering fit and was therefore used to describe groupings in the sound data based on the selected acoustic parameters.

A discriminant analysis of the principal components (DAPC) as described by Jombart *et al.* (2010) was applied using the program R (version 3.1.2) and the R-based *adegenet* package (version 1.4-2) to verify the optimal number of song unit clusters in the dataset. The discriminant functions (DFs) are constructed as linear combinations of the original measured parameters that have the largest between-group variance and the smallest within-group variance. Carrying out a DAPC requires the user to define the number of PCs retained in the analysis. Retaining too many PCs for the DAPC could lead to over-fitting the DFs that would discriminate any set of clusters; however, too few PCs would lead to the loss of useful information (Jombart *et al.*, 2010). A procedure, named the a-score, provided by the *adegenet* package, was used to evaluate the optimal numbers of PCs to retain from the whole set of PCs. This procedure measures the difference between the proportion of successful reassignment of the analysis (observed discrimination) and values obtained using random groups (random discrimination). Since the fundamental frequency of humpback whale signals can vary greatly, from approximately 8 to 10 000 Hz (Cerchio *et al.*, 2001; Mercado *et al.*, 2010), the dataset was primarily separated into the lowest optimal number of clusters. Each of the major clusters was then separated with more detail into sub-clusters using *k*-mean, from now on called subgroups.

Discriminant analysis provided membership probabilities of each song unit for the different subgroups based upon the retained discriminant functions. The subgroups providing the best membership fit were chosen for the dataset. This grouping was verified with visual spectrographic inspection of subsamples from each group to find possible anomalies caused by measurement errors. One-way analysis of variance (ANOVA) and Tukeys *post hoc* tests were used to investigate differences in measured parameters between and within the major groups. The occurrences of song unit groups per winter season were examined for January and February since recordings were made during these months in all years.

A larger sample size, with higher average signal to noise ratio, was obtained from the 2011 season compared to the two preceding study seasons. To test for possible bias in the occurrence of different song unit groups per year, due to unequal sample sizes, several random measurements were subtracted from the 2011 dataset to create smaller subsets. The results from each subset were compared to the results from the whole dataset. Also to correct for overrepresentation of high amplitude song units, a subsample of data with units ranging between 60 and 75 dB (re 1 su) was extracted from all seasons. The decibel range extracted was decided based on where the decibel frequency distribution slopes, from each year, overlapped. By doing so, we could test whether certain signal types were left out when eliminating the lowest and the highest amplitude signals. The song unit group occurrence, resulting from each subset, were compared between each other and with the complete dataset to search for inconsistencies in the results.

To look for overall changes in song unit characteristics across years, the frequency distribution of measured parameters was evaluated quantitatively. The range for each parameter was divided into 21 intervals, both for each year separately and for the whole dataset (Mercado *et al.*, 2005). The number of units with certain acoustic features, represented by each interval, was used to form a frequency distribution for each parameter. A Euclidean distance measure was applied to examine the variability of the frequency distribution for each parameter between years. That was done by comparing the frequency distributions for each song unit parameter per year with the distribution representing measurements of that parameter from all years (Mercado *et al.*, 2005). When two frequency distributions were similar, the Euclidean distance would return values close to zero, whereas an increasing Euclidean distance would indicate non-identical distributions. All frequency distributions were normalized prior to the analysis using the R-based *som* package (version 0.3-5).

III. RESULTS

A total of 1262 h of recordings were collected from all three winter seasons of which 259 h were collected in 2008–2009, 289 h in 2009–2010, and 714 h in 2011. From 2008 to 2009, a total of 540 min of songs were collected with 130 min of high quality recordings (∼24% of the recorded songs) during 25 different days in total. During 2009–2010, a total of 290 min of songs were collected with 83 min of high quality recordings (∼29% of the recorded songs) during 18 different days in total. Minutes with songs increased substantially in 2011 due to increased recording effort per hour, or approximately 12 640 min of songs with 4270 min of high quality recordings (∼32% of the recorded songs). A random sample of 150 min was analyzed from the 2011 dataset from 10 different days throughout the season. The minimum hypothetical number of different singers analyzed in 2008–2009 was 32 singers, 18 singers in 2009–2010, and 28 singers in 2011. A total of 2810 song units were measured with 980 song units from 2008 to 2009, 541 song units from 2009 to 2010, and 1289 song units from 2011.

The average automatic detection rate during January–February decreased between 2008–2009 and 2009–2010, from 0.176 (±0.26 SD) detections/min of effort per month to 0.04 (±0.07) detections/min of effort per month, respectively, but increased intensely in 2011 to 3.75 (±2.72) detections/min of effort per month. The received signal level (dB re 1 su) was similar during 2008–2009 and 2009–2010 (Tukey differences of means = 0.2 dB, $P = 0.77$), whereas the received signal level was significantly higher in 2011 compared to the previous two winter seasons (Tukey differences of means = 14 dB, $P < 0.001$).

The peak fundamental frequency of all the observed song units averaged at 431 (±268) Hz and ranged from ∼15 to 2200 Hz, including signals with discrete pulses, not discrete pulses or a mixture of both. The duration of the song units ranged from 0.1 to 4.6 s and averaged at 1.2 (±0.5) s. The variables excluded from the PCA due to weak contribution to the PCA analysis when grouping the whole dataset into major groups were duration (Dur), peak frequency (PeakF), frequency range (FRange), and frequency modulation (FMod). The first four PCs, explaining 98% of the variance, were retained for the DAPC. The *k*-mean clustering was used to partition the combined dataset from the three winter seasons into five sets of sounds that were primarily separated by the frequency parameters of the f0, the frequency trend and the timing of maximum frequency in the signals (Fig. 1). The first DF explained 82% of the variance and the second explained 16% of the variance. The parameters contributing the most (>10%) to the variance according to the first DF were the maximum f0 frequency and the f0 frequency from the start to the end of the signals, i.e., FStart, F25, F50, and FEnd. The parameters contributing the most to the second DF were the PMax and the FTrend (see Table I in Appendix B in the supplementary material for further details).[2]

The five major groups were (1) high frequency harmonic wails and moans (H-groups, $n = 421$), (2) mid-frequency harmonic moans with down swept trend (Md-groups, $n = 1171$), (3) mid-frequency harmonic moans with upswept trend (MUp-groups, $n = 757$), (4) low-frequency tonal harmonic moans (Lt-groups, $n = 266$), and (5) complex and impulsive low frequency signals (Li-groups, $n = 195$). The DAPC

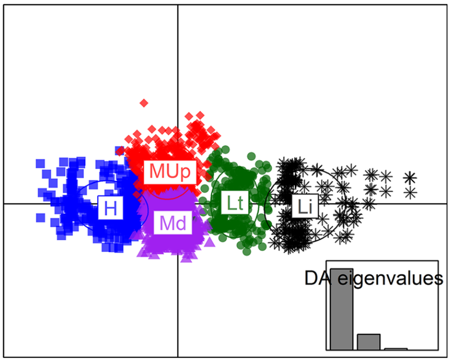


FIG. 1. (Color online) Discrimination of the whole song unit dataset into the five main sets by the discriminant analysis of principal components (DAPC) using two discriminant functions (DFs). The groups were created using *k*-mean analysis prior to the DAPC.

assigned 96% of the song units into correct main groups using the four PCs and two DFs.

Each of the five sets of sounds was clustered further with *k*-means into three sub-groups, apart from the Li-group, which was clustered into 2 sub-groups, resulting in 14 different song unit sub-groups (Fig. 2).

A total of 25 different phrases were identified from the three winter seasons pooled together (Fig. 3). Of these, 9 different phrases were found in the 2008–2009 songs, 10 different phrases in the 2009–2010 songs, and 14 different phrases in the 2011 songs.

A. Song unit cluster identification and characteristics

1. High frequency wails and moans (H-group)

High frequency signals were separated into three subgroups, i.e., H1, H2, and H3 (Fig. 2). The Dur parameter was excluded from the PCA analysis due to weak loadings. The first three PCs from the PCA were retained for the DAPC analysis, which conserved 94% of the variance. The first DF explained 85% of the conserved variance while the second DF explained 15%. The parameters contributing the most to the variance according to the first DF were the PeakF, the FMax, and the f0 frequency at the first half of the signals (FStart–F50). The most effective parameters, according to the second DF, were the FRange, FTrend, and FMod (see Table I in Appendix B in the supplementary material for further details).[2]

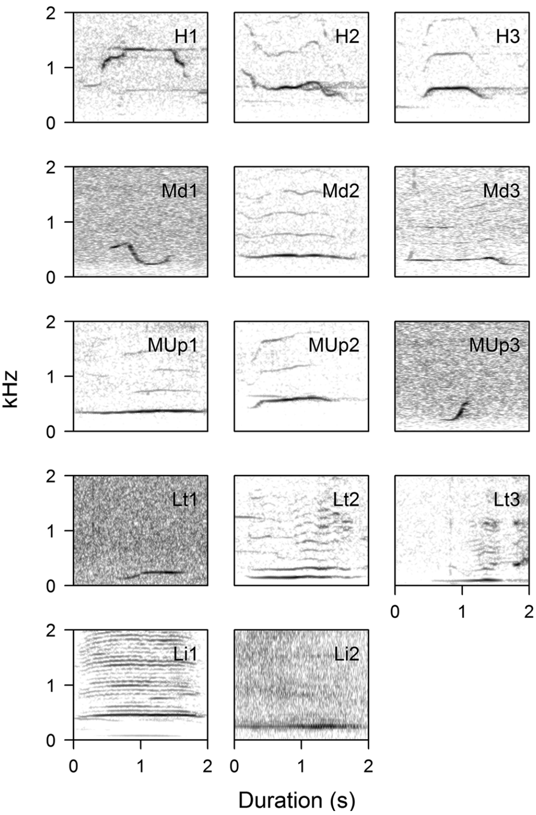
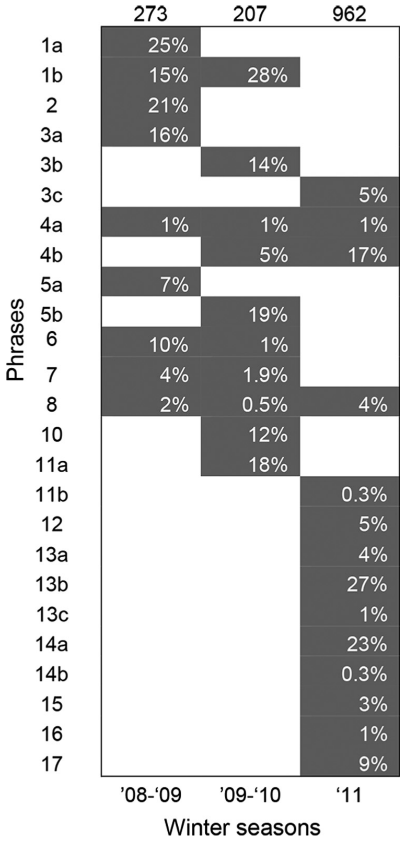


FIG. 2. Spectrograms of representative examples for each song unit subgroup. Each spectrogram is labelled with a subgroup name. In sound signal Li1, the fundamental frequency was very faint and emphasis was on higher frequencies, most notably the fifth through seventh harmonic. Spectrograms for the H-groups, and the subgroups Md2, MUp1, MUp2, Lt2, Lt3, and Lt1 were generated using fast Fourier transformation (FFT) size 1024 Hanning window, a frequency resolution of 15.6 Hz and 95% overlap. Spectrograms for the subgroups Md1, Md3, MUp3, and Lt1 were generated using FFT of 512 Hanning window, a frequency resolution of 9.8 Hz and 95% overlap. The Li2 spectrogram was generated using FFT of 512 with 95% overlap and a frequency resolution of 31 Hz to make the discrete pulses visible.



Phrases	'08-'09 (273)	'09-'10 (207)	'11 (962)
1a	25%		
1b	15%	28%	
2	21%		
3a	16%		
3b		14%	
3c			5%
4a	1%	1%	1%
4b		5%	17%
5a	7%		
5b		19%	
6	10%	1%	
7	4%	1.9%	
8	2%	0.5%	4%
10		12%	
11a		18%	
11b			0.3%
12			5%
13a			4%
13b			27%
13c			1%
14a			23%
14b			0.3%
15			3%
16			1%
17			9%

FIG. 3. The occurrence of observed phrases from each study period. The shaded cells indicate that the phrase was observed that given winter. The values within the cells show the percentage of the occurrence for each phrase relative to other observed phrases during each winter season. The numbers at the top of the figure show how many phrases (*N*) constitute the dataset for each winter season.

Subgroup H1 was composed of high frequency wails and included the highest observed fundamental frequencies (∼800–2000 Hz). These song units commonly consisted of an up and down contour with similar start and end frequency and maximum frequency occurring approximately mid-way through the signals. Subgroup H2 included high frequency signals (∼400–1300 Hz) with moderate modulation and a down-swept trend where the maximum frequency occurred early in the signals. Subgroup H3 included mid to high frequency signals (~350–900 Hz). These signals were moans with small modulation and maximum frequency generally occurring around the middle of the signal (see Table II in Appendix C in the supplementary material for further details).[2] The parameters used in the DAPC that were statistically different between all H-groups were FMax and PeakF, and the frequency parameters from the start to the latter half of the signals (FStart–F75) ($F_{2,418} \geq 5$, $P < 0.01$).

2. Mid-frequency down swept moans (Md-groups)

These mid-frequency song units had a down swept characteristics where the maximum frequency occurred relatively early in the signals. The steepness of the slope varied between subgroups. The Md-group was divided into three subgroups according to the *k*-means, i.e., Md1, Md2, and Md3 (Fig. 2). The Dur and PMax parameters were excluded from the PCA analysis due to weak loadings. The first three PCs from the PCA were retained for the DAPC analysis, resulting in 84% of the variance being conserved. The first DF explained 58% of the variance while the second DF explained 42% of the variance. The most discriminating parameters according to the first DF were the FMax, FRange, PeakF, FMod, and the f0 frequency at the start (FStart) and at the first half (F25) of the signals. According to the second DF, the most discriminating parameters were the FMin and the f0 frequency at the latter half (F75–FEnd) of the signals (see Table I in Appendix B in the supplementary material for further details).[2]

The subgroup Md1 included modulated, mid-frequency moans with relatively large range (~150–700 Hz) and a steep down swept slope. The Md2 subgroup included mid-frequency moans that had the highest minimum frequency of the Md-groups (~300–550 Hz). These signals ranged from being almost flat to having a slightly down-swept contour. The Md3 subgroup included mid-frequency moans with rather sharp down sweep contour but a much smaller range (~100–450 Hz) than the Md1 subgroup (see Table II in Appendix C in the supplementary material for further details).[2] All measured parameters used in the DAPC were significantly different between the subgroups ($F_{2,1168} \geq 23$, $P < 0.001$).

3. Mid-frequency up-sweep calls (MUp-groups)

The MUp-group consisted of mid-frequency song units with an upswept contour where the maximum frequency occurred close to the end of the signals. The sharpness of the upward slope varied between subgroups. The MUp units were divided into three distinct subgroups according to the *k*-means, i.e., MUp1, MUp2, and MUp3 (Fig. 2). The Dur and the PMax parameters were excluded from the PCA due to weak loadings. The first eight PCs from the PCA were retained for the DAPC that resulted in 99% of the variance being conserved. Two DFs were used to discriminate between the MUp-calls. The first DF explained 60% of the variance where the f0 frequency at the center of the signal's duration (F50) and the FTrend were the most discriminating parameters, followed by the FMod and FStart. The second DF explained 40% of the variance and the most discriminating parameters were again the F50, the FTrend, and additionally the FMax (see Table I in Appendix B in the supplementary material for further details).[2]

Song units in the MUp1 subgroup (~200–500 Hz) had a longer duration, lower modulation, and a slower upward gradient than the other MUp signals. The MUp2 song units had a sharper upsweep trend and generally higher frequency range (~250–600 Hz) than the MUp1 units but less modulation and generally less frequency range than the MUp3 units. The MUp3 subgroup consisted of song units starting at a lower frequency (~100–550 Hz) than the other MUp units and had a sharper upsweep trend, larger modulation value and larger frequency range (see Table II in Appendix C in the supplementary material for further details).[2] All measured parameters in the DAPC were significantly different between the subgroups ($F_{2,757} > 26$, $P < 0.001$).

4. Low-frequency tonal and harmonic moans (Lt-group)

The Lt-group was composed of low-frequency moans with tonal characteristics and harmonic components. These song units were divided into three different subgroups according to the *k*-means, i.e., Lt1, Lt2, and Lt3 (Fig. 2). The Dur, PeakF, and PMax parameters were excluded from the PCA due to weak loadings. The first two PCs from the PCA were retained for the DAPC that resulted in 83% of the variance being conserved. The first DF explained 64% of the conserved variance and the second DF explained the remaining 36% of the variance. The primary discriminating variables for the first DF were the FRange, FTrend, and FMod, followed by the FMax. The most discriminating variables for the second DF were the FMin and the f0 frequency from the start to the latter half of the signals (FStart–F75) (see Table I in Appendix B in the supplementary material for further details).[2]

The Lt1 song units were low-frequency upsweep calls with a sharp onset ranging between ~90 and 300 Hz; these units were not frequently observed. The Lt2 subgroup consisted of relatively flat, low frequency moans with a very small frequency range (~120–200 Hz). The Lt3 song units had a very small to no modulation, similar to the Lt2 group but had the lowest average frequency (93.3 ± 32.1 Hz) of the Lt groups (see Table III in Appendix C in the supplementary material for further details).[2] All measured parameters in the DAPC were significantly different between subgroups ($F_{2,111} > 9$, $P < 0.001$) apart from the FTrend which was not statistically different between groups Lt2 and Lt3.

5. Low-frequency impulsive and complex moans (Li-groups)

Song units grouped into the Li-groups were either impulsive moans with no clear harmonics (Li2) or harmonic and impulsive moans (complex) with energy distributed over a broad harmonic spectrum (Li1) (Fig. 2). The first three PCs from the PCA were used in the DAPC that explained 98% of the variance. Only one DF was needed to explain the variance between the Li-groups. The FMin and the FMax, FTrend and the f0 frequency from the start until the middle of the signal's duration (FStart–F50) explained the majority of the variance between the subgroups (see Table I in Appendix B in the supplementary material for further details).[2]

The Li1 subgroup was composed of signals with low fundamental frequency (∼50–100 Hz) and small modulation. These song units were usually a combination of pulsed and tonal periods where the received energy was higher for particular harmonics than the fundamental frequency. Commonly, the fifth to seventh harmonics were the most visible components of the signal. The Li2 subgroup was composed of moans with discrete pulses, no clear harmonics and the lowest observed fundamental frequency among the song units (∼15–50 Hz). These signals were relatively broadband with rumble or gurgle-like qualities (see Table III in Appendix C in the supplementary material for further details).[2] All measured parameters in the DAPC were significantly different between Li1 and Li2 ($F_{2,195} > 7$, $P < 0.01$) apart from the FTrend.

B. Song unit progression between three winter seasons

When testing for possible bias in the occurrence of different song unit groups per winter season, due to unequal quality of recordings, there was a complete consistency between the full dataset and the subsampled datasets. Thus the resulting song unit group occurrences should represent relatively unbiased comparison between years despite the apparent sampling issues.

Pooled data from all years showed that the number of different song unit subgroups detected per day increased within the song repertoire from January to February (Tukey's differences of mean = 3.4 units/day, $F_{1,38} = 12.6$, $P = 0.001$). In other words, the variation of song units increased over the course of the breeding season. The parameter being most prominently modified between years according to the Euclidean distance measurements was the PMax, which was followed by the FStart and the frequency measurements at the latter half of the signals (F50 and F75). However, the most stable signal features were the Dur, the PeakF, and the FTrend (Table II).

The data do not support there being a significant difference at the $P = 0.05$ level between the occurrence of song unit groups during the first two winter seasons ($\chi^2 = 20.5$, $P = 0.08$) but there was a pronounced difference between the third season and the first two winter seasons ($\chi^2 \geq 73$, $P < 0.001$). The mid-frequency down swept harmonic moans (Md) were a rather stable component of the songs in all years (Fig. 4) and were found in 56% (14) of the observed phrases. The MUp group was the other dominant group found in the songs in 2009 and 2010, but became the most infrequently observed song unit group in 2011 (Fig. 4). The sharp upsweep song units MUp2 and MUp3 were dominant in phrases 1a and 1b, which were the most common phrases during the first two winter seasons (Fig. 3). The MUp-group was only observed in phrase 12 during 2011. The H-groups were much more commonly observed in 2011 than during the previous two winter seasons (Fig. 4). The H-group was found in six different phrases during the 2011 winter (11b, 13c, 14b, 15, 16, 17), but only in one phrase in 2009 (6) and in two phrases in 2010 (6 and 11b). The Lt-group comprised

TABLE II. The table shows a Euclidean distance measure applied to examine the variability of the frequency distribution for each parameter between years. The distance shown is the Euclidean distance between the overall frequency distribution of song unit parameters pooled together from all years and the frequency distribution of song unit parameters for each year. The variables are ordered from largest to smallest mean Euclidean distance value.

	Distance from			
Variables	2009	2010	2011	Mean ± SD
PMax	3.2	1.9	1.0	2 ± 1.1
F50	1.9	2.9	1.0	1.9 ± 0.9
FStart	1.4	1.7	1.8	1.6 ± 0.2
F75	1.7	1.7	1.2	1.5 ± 0.3
F25	0.7	2.1	1.4	1.4 ± 0.7
FMax	1.1	1.9	1.3	1.4 ± 0.4
FEnd	0.8	1.5	1.6	1.3 ± 0.4
FMod	1.0	1.9	0.8	1.2 ± 0.6
FRange	1.0	1.6	0.8	1.1 ± 0.4
FMin	1.0	0.8	1.5	1.1 ± 0.4
FTrend	0.5	1.8	0.8	1 ± 0.7
PeakF	1.2	0.4	1.2	0.9 ± 0.5
Dur	0.6	1.0	0.9	0.8 ± 0.2

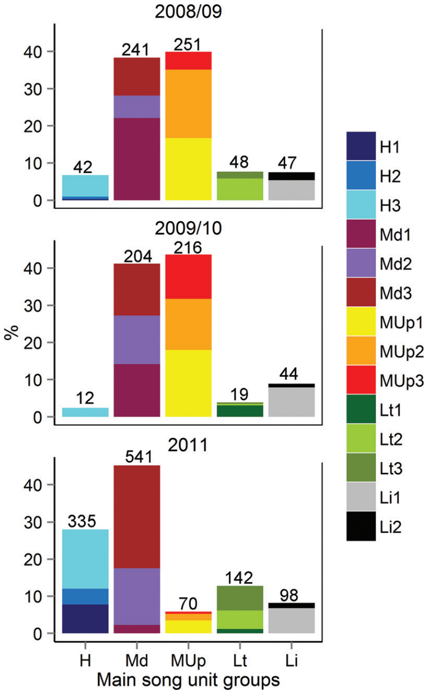


FIG. 4. Percentage of song unit subgroups in songs during January and February for each winter season. The numbers at the top of each bar show the number of song units (N) analyzed for each group during each winter season.

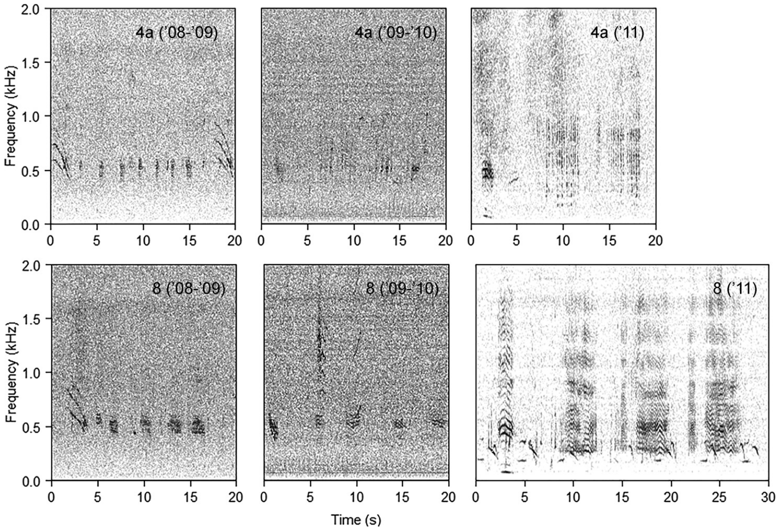


FIG. 5. Spectrograms of the two phrase types found during all winter seasons, i.e., phrase 4a and phrase 8. Phrase 8 from 2011 (bottom right) is overlapped with phrase 13b from another whale. The top right and bottom right spectrograms, from the 2011 season, were generated using fast Fourier transformation (FFT) size 2048 Hanning window, a frequency resolution of 7.8 Hz, and 95% overlap. All the other spectrograms were generated using fast Fourier transformation (FFT) size 1024 Hanning window, a frequency resolution of 4.8 Hz, and 95% overlap.

a relatively low percentage of the song unit repertoires in all years with decreased occurrence between 2009 and 2010 but increased occurrence in 2011 (Fig. 4). The Li-group had a rather stable but rare occurrence in all years. Of these, the complex Li1 song units were more frequent than the impulsive Li2 song units throughout the three winter seasons (Fig. 4).

Off the 25 observed phrases, two occurred with small or no modification in all years, i.e., phrases 4a and 8 (Fig. 5), which were rare in all years (Fig. 3). Few phrase types were possibly modified versions from previous years, these were assigned the same number but separated with letters as different phrase types, i.e., phrase 3a, 3b and 3c, phrases 5a and 5b, and phrases 11a and 11b (Fig. 6). Six phrases (60%) found in the 2009–2010 songs were also observed the previous winter while four phrases (40%) had not been found before. In total, 4 of the 14 phrases (29%) identified from 2011 had been observed the previous seasons, whereas the remaining phrases (71%) appeared to be new (Fig. 3).

IV. DISCUSSION

This study shows for the first time regular singing by humpback whales during three consecutive winters on a North Atlantic subarctic feeding ground, with increased detections and variability in song units between January and February in all years. In 2011, continual singing was recorded until mid-March (when recordings ended). Occasional songs were heard in October and November in 2008 and in April 2010, i.e., during shoulder seasons. This is in contrast with a study from a mid-latitude feeding ground in the North Atlantic (Vu *et al.*, 2012), where singing activity generally decreased or was non-existent during the time of increased singing in Iceland. The increased singing activity in Iceland coincides with the peak breeding season of humpback whales in the northern hemisphere (February), although the period extends at least from January to April (Nishiwaki, 1966). Singing on low latitude breeding grounds in the Northern hemisphere has also been documented to be most active during this period (Winn and Winn, 1978; Au *et al.*, 2000; Herman *et al.*, 2013).

Commonly, subjective human aural classification has been used to group humpback whale signals (Maeda *et al.*, 2000; Au *et al.*, 2006; Dunlop *et al.*, 2007; Garland *et al.*, 2011). However, quantitative, statistical studies or automatic classifications on large datasets of humpback whale sounds have become increasingly common (Stimpert *et al.*, 2011; Ou *et al.*, 2013). Automatically categorizing the song unit dataset using statistical methods likely results in fewer distinct groups compared to completely subjective categorization with aural and visual methods. The aural perception of frequency and changes in frequency, as well as the ability to visually categorize signals from spectrograms, can vary between observers. That can often result in individually specific and sometimes too detailed classification of similar signals that cannot be perfectly replicated. Therefore it is important to include automatic classifications for large datasets, primarily to expedite the clustering process and to promote consistency between observers. Nonetheless, the variables used to objectively categorize sounds are selected subjectively because they are believed to be important for human observers and may not necessarily be of importance to the whales (Dunlop *et al.*, 2007). Notably, such bias could not be avoided in this study. Although there is currently no way to determine how a whale would categorize song units (Mercado *et al.*, 2010), it is important to include statistical methods for categorization to minimize sorting errors and increase the reliability of the sorting results. That allows for more effective comparison between studies conducted by different observers.

The observed units were grouped into five main sets of sounds that were primarily based on fundamental frequency and secondarily according to the sweep of the signals, i.e.,

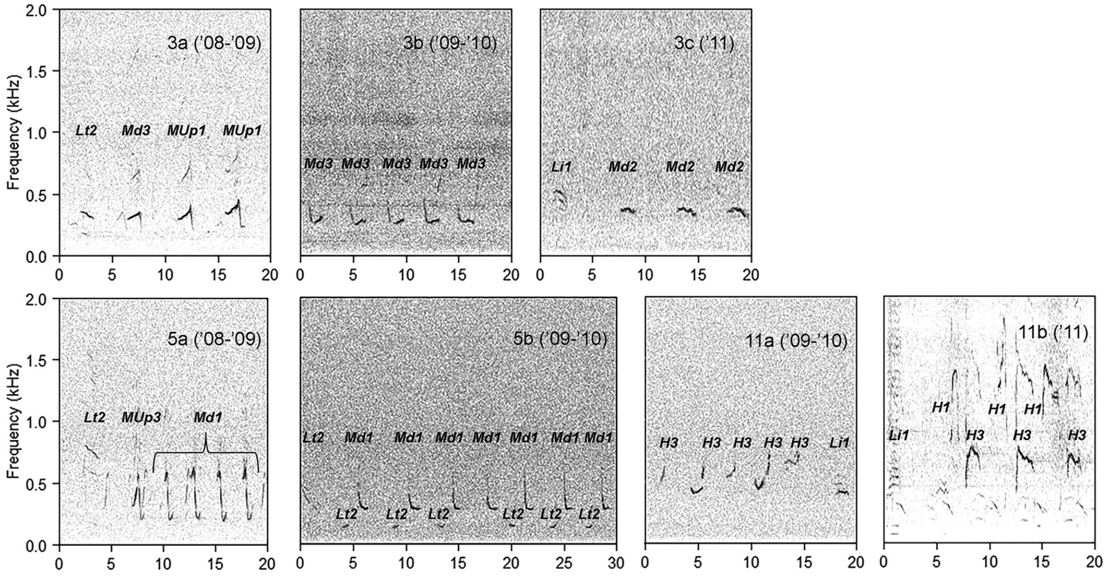


FIG. 6. Spectrograms of similar phrases found in different years. The phrases from 2009 to 2010 (i.e., 3b and 5b) and from 2011 (3c and 11b) are possibly modified versions of phrases from previous years. Similar phrases were assigned the same number but separated with letters to discriminate them as different phrase types. The top right and bottom right spectrograms, from the 2011 season, were generated using FFT size 2048 Hanning window, a frequency resolution of 7.8 Hz and 95% overlap. All the other spectrograms were generated using FFT size 1024 Hanning window, a frequency resolution of 4.8 Hz and 95% overlap.

upward or downward contour. These major groups were further divided into subgroups where the types of parameters contributing substantially to the variance within each of the major groups often differed widely. That can be explained by the wide variety of signal characteristics found within the humpback whale songs and that the variety can be simplified with grouping into broad categories. The duration and frequency range of the units were 0.1–4.6 s and 15–2166 Hz, respectively. The duration of the signals resembled measurements of units from distant breeding grounds in the Pacific (Maeda *et al.*, 2000; Au *et al.*, 2006; Mercado *et al.*, 2010). Also the minimum frequency was similar to what has been observed in other locations; however, the maximum frequency was sometimes lower compared to studies applying short range recordings (Mercado *et al.*, 2010; Stimpert *et al.*, 2011). In studies where the recordings are made from stationary recorders, some signal types such as high frequency signals and low amplitude signals, might be lost due to attenuation since the sound source is generally further away from the recording unit. There is also a possibility that whales, singing on this high-latitude feeding ground, might be using a lower range of frequencies compared to when singing on traditional breeding grounds.

Humpback whale songs usually consist of a variety of song units with different acoustic characteristics. Commonly observed song units are tonal, harmonic sounds (e.g., chirps, cries, moans, and wails), broadband, impulsive signals with often no or weak harmonics and where the peak amplitude is distributed over a large spectrum (e.g., gulp, whop, yup, purrs, trills, snores, ratchets) or a mixture of both, i.e., amplitude modulated sounds with harmonics (complex sounds: e.g., barks, bellows, creaks, screeches) (Winn and Winn, 1978; Au *et al.*, 2006; Dunlop *et al.*, 2007; Mercado *et al.*, 2010). Song units from these previously described categories were found in the humpback whale songs in Iceland. The song units observed from this study period were primarily harmonic, tonal sounds (H-, Md-, MUp-, and Lt-groups) and also complex sounds (Li1 subgroup), whereas broadband impulsive sounds (Li2 subgroup) were infrequent within the songs. The complex signals (Li1) were only found at the end or start of a phrase (i.e., in between phrases), whereas the harmonic tonal sounds and the impulsive sounds were repeated throughout the majority of the phrase's duration. Impulsive, broadband song units (Li2) were only found in two phrase types, i.e., phrase 4a and phrase 8. These phrases were, however, found in all three winter seasons. Despite being rarely observed in all years, these impulsive characteristics of the Li units may be stable features in humpback whale song repertoires.

Mid-frequency moans were the most common constituents of the song unit repertoire for these three winter seasons in Iceland while other signal types were replaced and added more quickly. Of these, the Md-group, which was composed of mid-frequency song units with moderate to large down swept trend, was frequent during all of the three winter seasons. Modulated, mid-frequency moans have commonly been reported from humpback whale songs around the world (Winn and Winn, 1978; Maeda *et al.*, 2000; Mercado *et al.*, 2010; Vu *et al.*, 2012).

It is unlikely that the whole phrase repertoire, including uncommon phrases, was captured each year due to the intermittent sampling technique. However, the progression of song changes was evident between years in the study area based on the changes in song unit repertoire and changes or replacement of phrases. Approximately half of the phrases from the 2009–2010 winter season were either the same or sharing similar spectral features with phrases found the previous winter. Only a small proportion of the phrases found in 2011 were from previous winter seasons, whereas the remaining phrases were all newly observed. Several phrases in both 2009–2010 and 2011 appeared to be a modified version of phrases from a previous year. These modifications were due to the introduction of new units into the phrases or modifications of previously used units. Humpback whales are known for modifying song units throughout a single season and also between seasons (Payne and Payne, 1985; Cerchio *et al.*, 2001; Garland *et al.*, 2011). Individual differences have also been reported (Au *et al.*, 2006) that could result in a greater variety of song units being produced as the number of whales increases in an area.

Although the humpback whale song unit repertoire is constantly modified within and between years, they appear to do so within boundaries that can be stable for at least a decade. The comparison of the frequency distributions of each measured parameter between years showed that there was a stronger tendency among singing humpback whales to modify the frequency characteristics of the song units between years, while the duration, the peak frequency, and the frequency trend of the signals were more predictable. Similar results were found for humpback whales singing off the Hawaiian Islands where spectral characteristics of song units varied more than temporal characteristics both within and across years (Mercado *et al.*, 2005). Ultimately, the findings clearly show a song progression similar to what has been observed in known breeding locations in this unique subarctic habitat.

Studies have shown that the degree of change in humpback whale songs varies between years where in some years the songs progress so rapidly that almost all older themes are replaced for new ones (Payne and Payne, 1985; Noad *et al.*, 2000; Garland *et al.*, 2011). What initiates these changes has not been explained but is probably related to circumstances that favor cultural transmission, e.g., more overlap between different feeding and/or breeding populations during or before migration (Payne and Guinee, 1983; Garland *et al.*, 2011; Garland *et al.*, 2013). Mercado *et al.* (2005) has suggested that song copying is an open process in the spectral domain and that individual whales select units as well as patterns to include in their songs based on recent experience. The larger variety of phrases observed in 2011 compared to the previous two winter seasons of this study could be partly explained by humpback whales singing closer to the recording units for a longer continual time, thus, providing a better chance of collecting larger proportions of the songs. However, because the majority of the phrases in 2011 were not observed the two previous years and substantial changes in the song unit repertoire were observed that year, it is possible that the songs from this season represented an increased level of song exchange. It must be kept in mind that though the estimated number of singers analyzed per year was quite similar between winter seasons, the true number of singers could have varied more. If so, it could have affected the difference in phrase variability between 2011 and the previous 2 years. Indeed these frequent changes might reflect the variability of singers passing through or stopping by in this area or possibly dynamic changes in songs between years as a result of cultural transmission.

Humpback whales were singing within the detection range of the EARs in all years for a considerable amount of time. The results indicate that humpback whales aggregate in this area annually, for a purpose still unknown, and sing. Differences in detection rate between months and years might be explained by movements in and out of the detection area that could be driven by food availability, sea conditions, and location of other humpback whales at each time. An ongoing study in Iceland (The Marine Research Institute, Reykjavik, Iceland)[3] revealed that two satellite-tagged humpback whales stayed close to the study area during November 2014–January 2015 swimming back and forth. During the time of tagging, the whales were found in a large group of 7–13 individuals (Víkingsson, 2015). That supports previous findings where humpback whales from Greenland, Norway, and Iceland generally arrived later on the breeding grounds in the West Indies (Stevick *et al.*, 2003). Thus, they might be forced to choose between incomplete or no southward migration, a truncated breeding season, or a truncated feeding season (Kennedy *et al.*, 2013). Studies have also shown that migratory timing varies with age, sex, and reproductive status (Dawbin, 1966; Craig *et al.*, 2003; Stevick *et al.*, 2003). Humpback whale females seem to overwinter occasionally at high latitude feeding grounds (Craig and Herman, 1997) and might thus become available to males that migrate late or overwinter in such high latitude areas. These apparent anomalies in migration behavior could also be explained by food availability in Arctic and subarctic feeding grounds compared to lower latitude feeding grounds. Iceland is located between western and eastern North-Atlantic feeding grounds where pelagic fish species such as herring (*Clupea harengus*) (Óskarsson *et al.*, 2009) and capelin (*Mallotus villosus*) (Vilhjálmsson, 2002) are found in or close to coastal waters during the winter. Humpback whales have been reported following the capelin migration in Icelandic waters during winter (Magnúsdóttir, 2007). Such a location could be a suitable aggregation area for humpback whales travelling south from other more northerly locations and for those whales that do not migrate. There, singers could both forage and adopt new sounds and patterns into their songs from other nearby humpback whales. This study suggests that subarctic feeding grounds may, therefore, be important for song exchange and possibly as an opportunistic mating ground for migrating or overwintering humpback whales.

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[1] Information available on RAVEN PRO at http://www.birds.cornell.edu/brp/raven/ravenoverview.html.

[2] See supplementary material at http://dx.doi.org/10.1121/1.4935517 for a map of the study area and tabled results from the DAPC analysis and the measurements of the song unit parameters.

[3] Information on study by The Marine Research Institute in Reykjavik, Iceland, is available at http://www.hafro.is/undir.php?REFID=15andID=210andREF=2.

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Paper III

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Why sing in the subarctic? Humpback whale (Megaptera novaeangliae) song structure and progression from an Icelandic feeding ground during winter

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Authors' contribution
Prepared recording units for data collection: EEM.
Deployed and retrieved recording units: EEM RL.
Analysed the data: EEM RL.
Wrote the paper: EEM RL.
Reviewed the manuscript: EEM RL.

Why sing in the subarctic? Humpback whale (*Megaptera novaeangliae*) song structure and progression from an Icelandic feeding ground during winter

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ABSTRACT

Humpback whale songs associated with breeding behaviors are increasingly reported outside of traditional low latitude breeding grounds. Here, we quantitatively characterize the structure and temporal changes of humpback songs in a subarctic feeding ground during the winter months. Recordings were collected from the end of January to mid-March, 2011, using a bottom mounted Ecological Acoustic Recorder deployed in Northeast Iceland. Humpback songs were detected on 91% of the recording days with peak singing activities in February. The majority of the recordings included multiple chorusing singers. To account for fractioned recordings (10 minute durations) a Markov transition analysis was applied to investigate if consistent cyclical patterns could be found in the songs and a Fisher's Exact Test was applied to investigate the predictability of theme transitions in the Markov matrices. Levenshtein Distance Analysis was used to investigate the similarity of song types observed throughout the period and Dice's Similarity Index was used to determine the consistency in the application of themes throughout the period. As a result, most themes transitioned consistently to predictable themes, indicating a consistent song type for this location and particular time period. All the delineated songs formed a single cluster of similar songs and changes were found in the application of themes in the songs throughout the recording period. These subarctic winter songs, thus, represent a characteristic song type for this region with indications of gradual progression during the 2011 winter season. The identified song structure and progression were comparable to extensively studied songs from traditional low latitude breeding grounds. The results confirm that continual singing of sophisticated and consistent songs occur during the breeding season in the subarctic. This also indicates the importance of this summer feeding ground as a winter habitat where cultural transmission of songs could occur, and as a potential mating ground for overwintering humpback whales.

Keywords: Humpback whale song, song units, song progression, song unit repertoire, song phrase repertoire, subarctic, North Atlantic, Iceland, migration

INTRODUCTION

Coastal Icelandic waters are a common subarctic summer feeding ground for humpback whales (*Megaptera noveangliae*) as well as other mysticete cetaceans, including blue whales (*Balaenoptera musculus*), fin whales (*Balaenoptera physalus*) and minke whales (*Balaenoptera acutorostrata*) (Gunnlaugsson *et al.* 1988). Humpback whales are a well-studied migratory species, travelling annually between summer feeding areas in subpolar waters to tropical wintering areas (Dawbin 1966). A high degree of maternally-directed site fidelity is observed when individuals feeding in productive high latitude waters migrate to low latitude waters to calve or mate (Clapham *et al.* 1993; Stevick *et al.* 2006). The North Atlantic humpback whales feeding off productive coastal waters in Iceland and other eastern and central North Atlantic feeding grounds usually make annual migrations to low latitude wintering grounds in the West Indies and off the Cape Verde Islands to breed (Jann *et al.* 2003; Stevick *et al.* 2003; Kennedy *et al.* 2013).

Studies have shown that the location of feeding grounds, sex, age, and reproductive status of an individual whale can affect the timing of migration (Dawbin 1966; Craig *et al.* 2003; Stevick *et al.* 2003). Humpback whales originating from the eastern and central North Atlantic feeding grounds have been observed to arrive at their breeding grounds much later than whales migrating from western feeding

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grounds, such as from the east coast of North America (Stevick *et al.* 2003). To date, only whales from these eastern and central feeding grounds have been sighted in the Cape Verde area as well as in the Guadeloupe area, a particular breeding assembly in the West Indies (Kennedy *et al.* 2013; Stevick *et al.* 2016). Humpback whales rarely arrive in these two areas before March, with the mean sighting date in the Cape Verde area estimated to be April 11th , and April 3rd for Guadeloupe (Stevick *et al.* 2016). The mean sighting date off the coast of the Dominican Republic in the West Indies is much earlier in the month of February (Whitehead & Moore 1982; Stevick *et al.* 2003). Despite a mere 1000 km distance between the Guadeloupe and the Dominican Republic breeding grounds, there appears to be very little interaction between individuals visiting the two breeding areas (Stevick *et al.* 2016).

Magnúsdóttir *et al.* (2015) recently reported that individuals acoustically detected in Iceland's feeding grounds engage in singing during the winter until at least mid-March. The recent findings on late migration patterns, suggest that the North Atlantic humpback whales recorded singing in Iceland are not leaving their high latitude feeding grounds until considerably later than previously believed. Therefore, the humpback whales that remain in Iceland's feeding ground until mid-March could still arrive on time to their breeding grounds in the spring. In the northern hemisphere, occurrence of songs on low latitude breeding grounds have been shown to increase between mid-February and mid-March (Au *et al.* 2000). This coincides with the female ovulation period, increased testis weight (Nishiwaki 1959; 1960; 1962) and agonistic behavior of male humpback whales, suggesting that these songs have a role in reproduction (Tyack 1981; Mobley *et al.* 1988; Darling & Bérubé 2001; Smith *et al.* 2008). The extended stay in feeding grounds and active singing could allow them to build up energy reserves and increase the possibility of successful mating. Another plausible explanation could be that some of the whales are overwintering and the singing behavior recorded in the subarctic represents non-migrating whales that remain in the prey abundant coastal waters of Iceland throughout the year. The overwintering behavior of humpback whales in feeding grounds is not unusual for mysticete species. Humpback whales and fin whales were sometimes found overwintering in high latitude feeding grounds of the Arctic as well as in the Antarctic (Simon *et al.* 2010; Van Opzeeland *et al.* 2013). In the Southern Hemisphere, Van Opzeeland *et al.* (2013) observed an acoustic presence of humpback whales throughout austral winter and summer, indicating that they are overwintering in the area despite the presence of accumulating sea ice. Therefore, migration appears to vary by individuals and is evidently affected by multiple ecological factors. Although the recordings of humpback whale singing activity indicates male presence, it is possible that female humpback whales are also overwintering to avoid the energetically costly migrations (Brown *et al.* 1995; Craig & Herman 1997; Smith *et al.* 1999).

To date, singing has only been associated with males, linking the behavior to mating and male-male social organization (Smith *et al.* 2008; Darling *et al.* 2012; Herman *et al.* 2013). Social and feeding calls vocalized by both males and females do not have the distinct repetitive structures or patterns and consequently not characterized as songs (Silber 1986; Smith *et al.* 2008; Stimpert *et al.* 2011). Humpback whale songs are characterized by high intensity vocal signals ranging from low to mid-frequencies between at least 8 Hz and 10 kHz (Cerchio *et al.* 2001; Mercado *et al.* 2010), and at source levels between at least 151 and 173 dB re 1µPa at 1m (Au *et al.* 2006). Although descriptions of humpback whale songs vary across literature and delineation methods, the essential foundation for song characterization is generally based on the criteria first proposed by Payne and McVay (1971). The hierarchical song is characterized by the shortest, most basic element in the song called a 'unit' which combine to form 'sub-phrases' and 'phrases'. These phrases are repeated in succession to form 'themes' that, when sung continuously, form a 'song session'.

Humpback whale songs are a well-studied behavioral phenomena, however, a growing body of literature challenges what is traditionally understood as typical singing and migratory behavior. In addition to the recent recordings of singing during winter in the subarctic feeding grounds of Iceland (Magnúsdóttir *et al.* 2014; Magnúsdóttir *et al.* 2015), humpback whales have been discovered singing along migration routes and at mid-latitude feeding grounds in the North Atlantic during shoulder seasons (i.e., spring and autumn) (Mattila *et al.* 1987; Clark & Clapham 2004; Vu *et al.* 2012) and to some extent during winter (Vu *et al.* 2012). Songs have also been recorded during the austral fall in the Antarctic (Stimpert *et al.* 2012). Prior to Clark and Clapham's 2004 study (Clark & Clapham 2004), many of the earlier studies of whale songs were short-term, opportunistic findings. Intermittent recordings of songs were discovered by Mattila *et al.* (1987) from March through November in 1983–1984, in the Stellwagen Bank National Marine Sanctuary (mid-latitude feeding ground). One full song was recorded in Southeastern Alaska by McSweeney *et al.* (1989) on one day in August, 1979 and in one day of September, 1981. Findings from both of these studies indicated that singing usually occurred during late autumn months on feeding grounds prior to the start of migration. Clark and Clapham (2004) were, to the best of our knowledge, the first to employ a long-term continuous acoustic monitoring program for humpback whales feeding in the Stellwagen Bank National Marine Sanctuary. In contrast to earlier findings, they observed a daily occurrence of singing during the spring months of May to June. Finally, a more recent study by Vu *et al.* (2012) described continuous singing almost every month of the year from a mid-latitude feeding ground, with increased singing detected during the shoulder seasons of spring (from April to May) and late fall (from October to December) of 2006 to 2008. In the high latitude feeding grounds of Antarctica humpback whales were recorded singing into late austral fall, between May and June, i.e. during a shoulder season (Stimpert *et al.* 2012). In contrast to these findings, however, the most active singing behavior recorded in the high latitude feeding grounds of Iceland did not occur during a shoulder season but during the peak of the breeding season (Magnúsdóttir *et al.* 2014; Magnúsdóttir *et al.* 2015).

These findings raise questions as to what advantages could be gained from singing away from traditionally known breeding grounds. The behavioral flexibility suggests that singing in these areas could offer a positive trade-off strategy for late migrating individuals and individuals that overwinter in an area with available prey and continued mating opportunity (Magnúsdóttir *et al.* 2014; Magnúsdóttir *et al.* 2015). Garland *et al.* (2013a) hypothesized that different breeding populations meeting and singing “off-season” on feeding grounds could also allow for the rapid horizontal cultural transmission of songs.

Cultural transmission is the social learning and sharing of information or behaviors between conspecifics within a population or subpopulation (Rendell & Whitehead 2001; Garland *et al.* 2011). Cultural traits can change the way in which individuals interact with their environment within and over generations, directly and indirectly affecting feeding success, survival rates, and fitness (Marcoux *et al.* 2007). Different modes of cultural transmission exist within the humpback whale species and can include both vertical (parent-offspring) and horizontal transmission. Humpback whale songs are constantly changing within a population over time, and these changes are recognized as cultural evolution or revolution, learned through horizontal cultural transmission across unrelated individuals. A population will therefore conform to singing similar dialects or song types within a shared ocean basin. Differences begin to appear and increase with distance of proximity between populations (Helweg *et al.* 1998; Darling *et al.* 2014) but are distinctly different between geographically isolated populations (Winn *et al.* 1981). Song similarity has been described between breeding grounds in the North Atlantic, i.e. West Indies and Cape Verde Islands (Winn *et al.* 1981), suggesting that song exchange could occur in Icelandic waters before the whales reach their two separate breeding grounds.

Authors often define varying start and end points for the song sequence, because of the variable and continuously evolving song sequence of humpback whales. Cholewiak *et al.* (2013) advised against performing durational analyses on such variable data, and instead recommended that the methodology from established avian literature be applied to humpback whale songs. This involves focusing on phrase sequences and maintaining a consistent phrase description in the song analysis. Phrases are fundamental repeated patterns of 2 to over 20 units, and range from under 10 seconds to over 30 seconds in duration (Payne & McVay 1971; Cerchio *et al.* 2001), with a full song comprising of approximately 180 to 400 song units (Suzuki *et al.* 2006). The complexity and variation of phrases depend both on the number of unit repetitions as well on the composition of unit types and sub-phrases (Cerchio *et al.* 2001). In this study, phrase delineation is considered to be the most effective and stable element for song structure analyses.

A new theme is initiated with a new type of phrase since themes are composed of repeated phrases. Transitional phrases are often observed between two phrase types, when one theme ends and another theme starts. These phrases combine features of both the preceding and succeeding themes (Payne & McVay 1971). Transitional phrases are characterized as unusual and complicated, and generally increase the entropy, i.e. decrease the predictability, of songs (Payne *et al.* 1983; Suzuki *et al.* 2006). Therefore, songs with less entropy have increased predictability (Suzuki *et al.* 2006). Payne *et al.* (1983) observed in their study that the number of transitional phrases would generally decrease, thus increasing song stability, throughout the course of a breeding season. In contrast, since transitional phrases were found between almost all themes in the songs of the present study, it was possible to use transitional phrases to delineate the songs from the recordings. The advantage here is that transitional phrases unmistakably represent a correct order of themes from a singer when songs are overlapped by multiple singers. Transitional phrases indicate the changes and patterns found in the songs by different singers. To obtain the correct sequences of phrases, and ultimately themes, it is important to verify that the phrases within the delineated sequence belong to the same singer.

By further expanding the findings in Magnúsdóttir *et al.* (2015), this study seeks to find evidence of whether the songs examined during the breeding season in Iceland could serve as mating displays and used as a mode of cultural transmission for humpback whale songs in the North Atlantic. To do so we aim to provide a comprehensive description of the Icelandic songs and their evolution during a single winter season. If singing in this subarctic region resembles the singing behavior on a traditional low-latitude breeding ground, we suggest that subarctic songs have a role in humpback whale mating behavior.

We apply quantitative analyses on the delineated songs to 1) uncover if there is a structure and a pattern present, 2) investigate temporal changes and 3) characterize the song type vocalized in this high latitude feeding ground. The main purpose is to investigate whether these songs occur continually and resemble the defined descriptions of breeding songs where all the singers adhere to the current content and pattern of the song (e.g. (Payne & McVay 1971; Frumhoff 1983; Payne *et al.* 1983; Payne & Payne 1985)). We also investigate temporal changes in the songs during this single winter season to search for an indication of gradual development in the songs as shown by previous studies from traditional breeding grounds (e.g.(Payne *et al.* 1983; Payne & Payne 1985; Eriksen *et al.* 2005; Garland *et al.* 2013b)). The evolution of songs usually occur when the acoustic structure of song elements change, new elements are adopted or the song units are reordered, ultimately leading to the insertion of new themes and deletion of older themes in the songs (Payne & Payne 1985; Cholewiak *et al.* 2013). To investigate temporal changes of the songs, i.e. phrase and theme order and application of different phrases within the songs we 1) use a Fisher's Exact test on Markov matrices to uncover transition consistency between phrases throughout the whole period, 2) evaluate the similarity of sequences from the beginning and to the end of the period using Levenshtein Distance Analysis and 3) investigate the consistency of the phrase repertoire throughout the period using Dice's Similarity Index.

METHODS

Acoustic recordings

Humpback whale songs were collected from January, 26, to March, 12, 2011 in Skjálfandi Bay, Northeast Iceland using the methods described in Magnúsdóttir *et al.* (2014; 2015). The recordings were made with a single bottom-moored ecological acoustic recorder (EAR) located approximately 62 m in depth on the slope Fiskisker (66°03'N, 17°40'W) (Fig 1). The EAR is a microprocessor-based autonomous recorder containing a Sensor Technology SQ26-01 hydrophone that has a response sensitivity of -193.5 dB (±1.5 dB) and is flat from 1Hz to 28 kHz (Lammers *et al.* 2008). EARs are described in detail in Magnúsdóttir *et al.* (2015) and Lammers *et al.* (2008). EAR detection ranges are estimated to be from 12 to 28 km for humpback whale signals below 1 kHz. This is based on a minimum (171 dB) and maximum (189 dB) source levels and assumes spherical spreading. The EAR was set to record for 10 minute intervals every 15 minutes at a sampling rate of 16 kHz to capture the fundamental range of humpback whale songs (approximately 8–8000 Hz) (Mercado *et al.* 2010; Stimpert *et al.* 2011) for approximately two month period.

Song detection

A frequency contour detection algorithm from the Ishmael 2.0 software package was applied to search for tonal signal frequencies in recordings that ranged from 100 to 1000 Hz (Mellinger 2002; Mellinger *et al.* 2011). Detection thresholds were set to 0.25 seconds (FFT 0.2048 s., 75% overlap, Hamming window). Despite spanning only a part of the humpback whale tonal frequency range, the detector primarily detected humpback whale signals with minimal false positive detections. The signal detection rate per minute of effort for each day of recording was obtained using the Ishmael 2.0 software. All sound files with detections were checked for humpback whale songs. Sound files with more than 15 detections per minute usually indicated multiple singers 'chorusing' during a section of the file. Sound files containing more than 30 detections per minute usually indicated that multiple singers were chorusing throughout the entire file. Additionally, the proportion of files containing songs was used as an indicator for how much singing occurred each day.

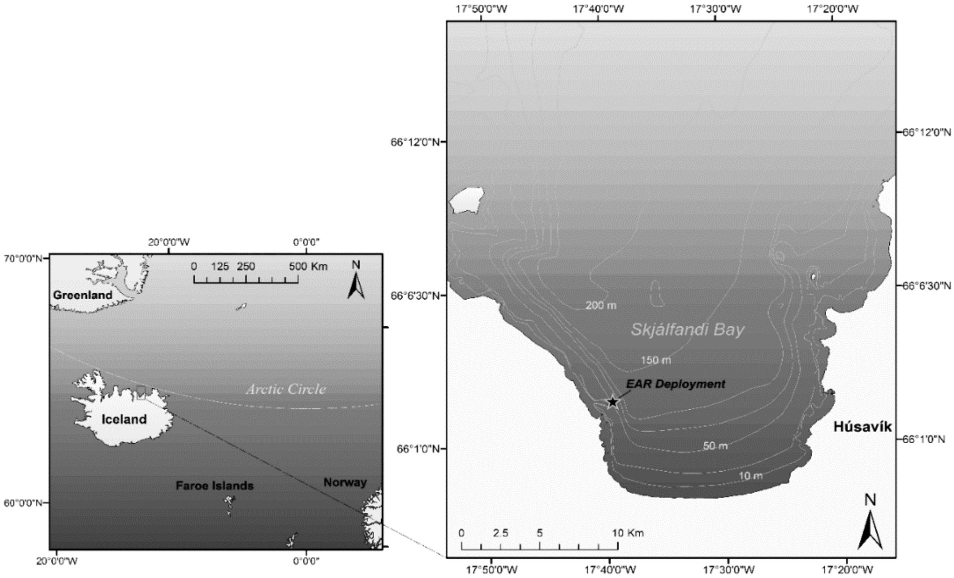

Fig 1 Study area in Skjálfandi Bay, NE Iceland. The star symbol indicates the EAR deployment location at 66°03´N, 17°40´W. The map was created using ArcGIS software. Source: 1) Hydrographic Department of the Icelandic Coast Guard, 2012, 2) National Land Survey of Iceland, 2012.

By comparing the detection activity per day with the percentage of song sound files per day it is possible to determine multiple singer activity, and also which days had few but active singers (low detection activity and high percentage of sound files with songs) or few and inactive singers (low detection activity and low percentage of sound files with songs).

The signal to noise ratio and audibility of the signals in each recording were manually inspected for recording quality. The sound files were graded and categorized as very poor, poor, medium, good, and excellent (Lim 2014). Files where all signal details were distinctly visible with high amplitude units and harmonics (i.e. good signal to noise ratio with a minimum of 10 dB above the background noise) were marked as good to excellent quality.

Dataset creation from fractioned song recordings

Due to the long-term application and data storing limitations of the EAR recordings, the dataset was not continuous (i.e., each 10 minute recording contained 5 minute break intervals). The dataset usually did not contain many complete songs and never contained a full song cycle within a single recording, so complete songs could not always be extracted directly from the recordings. To create a dataset for a group of singers, four to six adjacent sound files of excellent quality were acquired from 16 different days throughout the course of the recording period. These 16 different days were divided into four distinct periods of four days each. By subsetting the dataset into even sets (periods) we could avoid biasing the results towards group of singers for which we had a higher number of song sequences. This allowed for comparison of songs between the quarters to search for temporal changes in the songs. Division into fewer periods could result in too low resolution of the data and, thus, higher risk of averaging out possible changes while greater number of periods would include too small dataset each. To provide a credible comparison between the four periods the same number of days was required for each period. Though most of the sound files included humpback whale songs it was not always possible to find many excellent quality sound files in a consecutive order. The number of excellent sound files also varied considerably between the four periods. It was, however, possible to extract at least four sets of consecutive high quality sound files from each period. Each day represented the same or similar set of singers with 4–6 adjacent recordings, resulting in 40–60 minutes of singing during a period of 60–70 minutes (due to 5 minutes break between the recordings). Each set of sound file could cover at least a single song cycle, which usually lasts for 30 minutes or more (Payne & McVay 1971). It is considered likely that each collection of adjacent sound files contains songs from the same individual or the same group of whales. Sound files separated by a minimum of 24 hours were considered more likely to contain a different set of singers (Payne & Payne 1985; Murray *et al.* 2012). As a result, this method created a dataset containing songs likely to have been produced by several different groups of singers, with each set comprising of 40–60 minutes of recordings from one given group of singers. This, additionally, allows for an inspection of variations within a set of the same individuals as well as variations from the total observed singers throughout the recording period.

Songs were inspected using the spectrographic view of the Raven Pro 1.4 program (Cornell Lab of Ornithology, Ithaca, NY) (Hanning window, 2048 DFT size, 50% overlap) and phrases were logged and labeled in a time sequence as they occurred on the spectrogram. Phrase names used in this dataset are consistent with the naming conventions used in the Magnúsdóttir *et al.* (2015) study. In that study, units constructing song phrases were measured with statistical methods, categorized into groups, and named accordingly. The present study also uses these unit groups to categorize phrases, i.e. 1) high frequency harmonic wails and moans were named H1–H3 depending on the counter shape, slope, and frequency range, 2) mid-frequency harmonic moans with down sweeping trends were named Md1–Md3 depending on the frequency range, angle, and shape of the slope, 3) mid-frequency harmonic moans with upsweeping trends were named MUp1–MUp3 depending on the frequency range, angle, and shape of the slope, 4) low-frequency tonal harmonic sounds were named Lt1–Lt3 depending on the frequency range, angle, and shape of the slope and finally 5) low-frequency impulsive and complex moans were named Li1–Li2 depending on the frequency range and the angle of the slope. Two observers (RL and EEM) verified the categorization of the phrases.

Delineation and analysis of phrase sequences

To account for the fractioned recordings, instead of continual recordings, a Markov transition analysis was applied to each of the four periods to estimate the most likely sequence of phrases belonging to a full song cycle. The Markov matrices calculate probabilities for each occurring transition, providing results that can be used to determine whether or not the phrase belongs to the same sequence. This is a common method used to interpret bird song organization and predict dependent behavioral states (Lemon & Chatfield 1971; 1973; Dobson & Lemon 1979; Katahira *et al.* 2011).

Where multiple singers were recorded singing simultaneously, the phrases from each singer were tracked manually if transitions between phrases were clearly visible on the spectrogram (Fig 2). Delineation was terminated when there was too much overlap of similar phrases sung by different whales.

A Fishers Exact test was used to estimate the consistency of phrase transitions between periods to investigate the progression of songs in the area throughout the recording season. To do so, a contingency table was created for each phrase type, with table rows representing the periods and columns representing each phrase from which the phrase of interest was transitioning to. A *P*-value was calculated for each contingency table and assessed. If $P > 0.05$ then the null hypothesis was rejected and it could be stated that the phrase of interest transitioned consistently to the same phrase or phrases, i.e. the transitions were non-random between periods. However, if $P < 0.05$ then the null hypothesis was accepted and it could be stated that the phrase of interest did not transition consistently to the same phrase or phrases between the four periods, i.e. transitions occurred randomly between periods.

A quantitative method based on the Levenshtein distance (LD) technique (Garland *et al.* 2012; Garland *et al.* 2013b) was used to evaluate the similarity of observed transitional sequences between periods, i.e. sequences with a minimum number of four transition phrases that were extracted directly from the recordings (Fig 2). This method was applied to exclude small sequence fragments which are unlikely representatives of song sequences. Since the start and end of the sequence is not always clear, the start and end was determined visually by the observers. The Markov analysis revealed the most likely starting phrases (i.e. phrase 17 and 15) and ending phrases (i.e. phrases 4a and 4b) of the sequences, referred to as the “start label” and “end label”. Furthermore, if the same phrase reoccurred within a sequence, the sequence was considered terminated, with the subsequent phrase beginning a new sequence, e.g.:

[**15**-14a-13b-12-4b-**15**-14a] → [**15**-14a-13b-12-4b], [**15**-14a]

where each character (number or number and letter) represents a single phrase and the hyphen indicates the transitioning event between the phrases. Sequences are shown within the brackets. Since ‘15’ occurs twice within the first sequence, this sequence is terminated at the phrase ‘4b’ which is the phrase directly preceding the second incidence of ‘15’. This results in two shorter sequences.

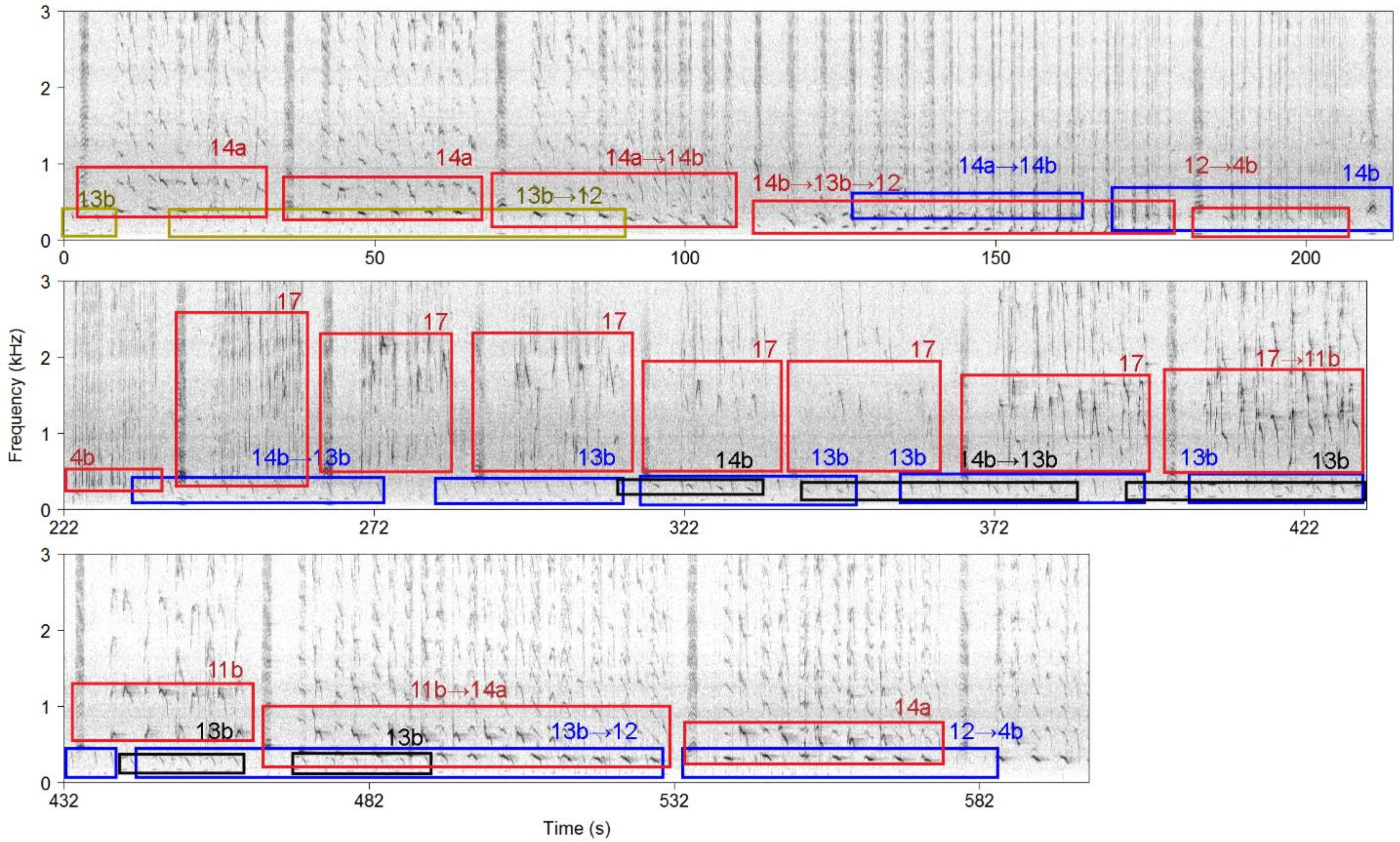

Fig 2 A spectrographic view of a 10 minute recording where phrase sequences from at least 3 different singers have been recorded. Each singer has an assigned color, with a single phrase identified using both a colored box and a corresponding colored phrase label (singer A = red, singer B = green, singer C = blue, singer D = black). Arrows between phrase labels indicate a transitional phrase. Singer B's signal attenuates at the beginning of the recording and because it is not certain if singer D is the same singer, a new label is assigned. At least 3 songs overlapped at time periods within the recording, indicating that a minimum of 3 singers were singing within the detection range of the EARs during this recording. A full song sequence captured from singer A, measured from phrase-14a to phrase-14a, lasted approximately 8 minutes and 50 seconds.

The LD calculates the minimum number of changes, i.e. insertions, deletions and substitutions, needed to transform one string of phrases into another (Kohonen 1985; Garland *et al.* 2012; Garland *et al.* 2013b). A representative string, called the *Set median* (SM), was found for each of the four periods (sets) and used to compare sequence similarity between periods (Kohonen 1985; Helweg *et al.* 1998; Tougaard & Eriksen 2006; Garland *et al.* 2013b). Each string of phrases within a given period was compared to all other strings within that period. The SM was the string of phrases with the smallest summed LD compared to all other strings in the set. To ensure that the SM was the best representation of each period, a set of hypothetical medians, called *Kohonen medians* (KM) (Kohonen 1985; Garland *et al.* 2012; Garland *et al.* 2013b), were created to find if a smaller summed LD score could be obtained. The KM is created by systematically substituting each phrase in the sequence with all possible phrases found within the set (period). If the KM had a smaller summed LD than the SM, the KM would be used instead of the SM as a representative sequence for that period.

To investigate the similarity between the representative strings (SM or KM) for each period a Levenshtein distance similarity index (LSI) was used. The LSI normalizes the LD score against the longest string (Helweg *et al.* 1998; Petroni & Serva 2010; Garland *et al.* 2012; Garland *et al.* 2013b). The incorporation of the string length into the analysis allows the LD scores to be standardized so that the length of strings being compared does not increase the difference between the two strings. This enabled the difference in phrase types and phrase order to be the primary determinant of string differences. The LSI produced a proportion of similarity that ranged from 0 (0%) for no similarity to 1 (100%) for complete similarity between a pair of strings. The resulting LSI scores formed a matrix of LSI similarity which was converted to dissimilarity by subtracting each score from 1.

Using the dissimilarity matrix and the statistical program, R (version 3.1.2), the representative sequences (SM/KM) for each period were hierarchically clustered. The single-linkage clustering (nearest neighbor clustering) method was employed to place the most similar sequences together. These sequences were then successively linked to other sequences/clusters of sequences (Garland *et al.* 2013b). This method analyzed how similar the representative sequences were between periods, allowing for evaluation of song sequence progression.

The presence and sharing of phrases within the songs and between periods was inspected using Dice's similarity index (Garland *et al.* 2015). Note that this analysis does not consider the sequential characteristics of the songs. Dice's coincidence index was originally designed as a measure of the amount of association between two species (Dice 1945). Here, the index is used as a measure of phrase sharing (a method that was previously used by Garland *et al.* (2015)) between the four defined periods:

$$\mathrm{SI} = 2A/(B + C)$$

where SI is the song phrase similarity between population pairs, A is the number of shared phrases, B is the total number of phrases present in population-1 (e.g. period-1), and C is the total number of phrases present in population-2 (e.g. period-2).

RESULTS

Humpback whale winter singing activity

During the 46 day recording period, from January 26th to March 12th, 2011, songs were detected in 42 days (91.3%). Songs could not be confirmed during only 4 days out of the 46 (8.7%). High rates of detection were captured every day from February 9th to February 26th 2011. Humpback whale songs were detected until mid-March when recordings ended (Fig 3).

In total, 70 medium to high quality 10 minute sound files were used for song analysis during the four defined periods (Table 1). This resulted in approximately 11:20:00 h of analyzed song detection files. From these recordings a total of 1683 phrases were logged and identified, resulting in 15 different song phrases (Fig 4), and consequently 15 theme types. In total of 281 phrase sequences (song parts) were extracted from the dataset. Of these, 12 full songs were captured which fitted within the 10 minute sound files. Sequence of themes, represented by phrases, would be considered a "full song" when a phrase type reoccurred in the sequence. The song would end on the phrase occurring before the first phrase type re-occurred in the sequence. The average number of different phrase types in these full songs were 5.6 (SD=±0.6), ranging between 5–7 phrases. Two rare phrases were detected in this dataset which had not yet been assigned to the 2011 dataset in the previous Magnúsdóttir *et al*. (2015) study where the same recordings were used. Because the present study collected a larger sample size, rare phrases were more likely to be observed.

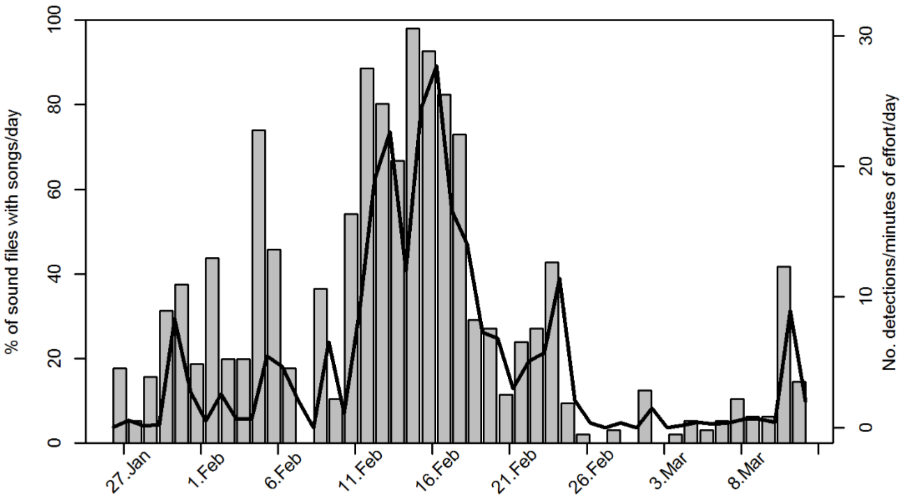

Fig 3 Humpback whale song detections during complete days of recordings, i.e. during January 27th to March 12th 2011. The grey bars show the percentage of sound files containing humpback whale songs per day whereas the black line shows the detection activity by the automatic detector per minute of effort per day. Lower detection rates within sound files in early February indicated less singing activity per minute, with fewer singers per sound file these days despite sometimes a high percentage of sound files containing songThese two phrases (phrase-3a and phrase-6) had previously been observed during the winter seasons of 2009 and 2010 (Magnúsdóttir *et al.* 2015). Each phrase type represented a theme, where the phrase was repeated several times before transitioning into a new theme, most commonly via a transitional phrase. A total of 438 transitional phrases were obtained from the dataset (26% of the observed phrases) and used in the Markov analysis. A total of 77 transitional sequences were used in the Levensthein distance (LD) analysis (Table 1), with a minimum of four phrase transitions required for analysis.

The captured sequences with repeated phrases ranged up to 22 phrases within the 10 minute sound files. When only including sequences with a minimum of four phrases, the average length of the captured phrase sequences was 8.9 phrases (± 4.6) per observed sequence. The total length of the observed phrase sequences increased from period-1 to period-4 (Tukey's differences of mean = 4.3 increase in no. phrases, $F_{3,163}$ = 8.7, $P<0.001$) while the percentage of transitional phrases within the phrase sequences decreased from period-1 to -4, however, this change was not significant on the *P*-level (Tukey's differences of mean = 4.6% decrease, $F_{3,163}$ = 1.5, $P=0.2$) (Fig 5).

Multiple singers, i.e. ≥2 singers, were detected on 77.6% of the analyzed sound files where the average number of singers per sound file was 2.6 (±1.1). Singers were rarely synchronized when chorusing. However, the singers usually conformed to the same song, but not necessarily to all the same components of the songs.

Phrase development within songs and periods

Phrases were added and deleted from the songs as the recording period progressed (Fig 6; Fig 7). During period-1, a total of 11 different phrases were observed, while 14 different phrases were observed during period-2, 13 during period-3 and 14 during period-4.

Dice's similarity index (DSI) showed a high similarity of phrase composition between all periods (88% – 97% similarity). Though small, the greatest difference in phrase usage was between the first and the last two periods, i.e. 88% similarity between periods 1 and 3 and 89% similarity between periods 1 and 4. The smallest difference in phrase usage according to the DSI was between period-1 and -2 (92% similarity), period-2 and -4 (97% similarity) and period-3 and -4 (93% similarity). The occurrence of the most common phrases, i.e. phrase-14a, 13b, 12 and 4b remained relatively stable between periods. The occurrence of phrase-3c gradually decreased while the occurrence of phrase-17 gradually increased from the first to the last period (Fig 6). The occurrence of the less common phrases, such as phrase-6, -8, -4a, -13c and -11b, fluctuated more between periods (Fig 6). Two transitional phrases were sometimes repeated once or twice by some singers before the transition completed. During these events the transitional phrases were categorized as regular phrases and assigned the phrase names '14b'

Table 1. The date, time, and number of consecutive song files analyzed per selected day including the number of confirmed singers per day. The range of the number of singers detected in the sound files per day is shown in parenthesis. A minimum of 24h intervals passed between detection dates to allow for the estimation of the total hypothetical number of singers. Only song sequences with a minimum of four different phrases were included in the Levenshtein distance analyses (LD).

Period	Dates	Time	No. sound files	Estimated no. singers (range)	No. song seq. analyzed for LD
1	27-Jan-11	22:30-23:15	4	3 (*1-3*)	3
	30-Jan-11	13:00-17:15	6	3 (*1-3*)	3
	31-Jan-11	04:15-05:00	4	3 (*3*)	8
	2-Feb-11	02:45-03:30	4	5 (*4-3*)	3
	Total		*18*	*11*	*17*
2	5-Feb-11	03:15-04:00	4	2 (*2*)	4
	7-Feb-11	05:45-06:30	4	3 (*2-3*)	3
	9-Feb-11	19:30-23:15	4	4 (*4*)	2
	10-Feb-11	00:00-00:45	4	2 (*2*)	7
	Total		*16*	*9*	*16*
3	18-Feb-11	21:00-22:15	6	4 (*3-4*)	6
	20-Feb-11	00:45-01:30	4	4 (*3-4*)	6
	24-Feb-11	17:45-18:30	4	3 (*1-3*)	7
	2Feb-11	06:15-07:00	4	4 (3-4)	9
	Total		*18*	*12*	*28*
4	2-Mar-11	15:15-16:00	4	2 (*1-2*)	4
	8-Mar-11	01:30-02:15	4	1 (*1*)	4
	11-Mar-11	14:15-15:00	4	3 (*3*)	6
	12-Mar-11	06:30-07:15	4	1 (*1*)	2
	Total		*18*	*6*	*16*
Total song time examined	11h 20m				

and ‘13a’, these are two versions of a typical transition between phrase-14a and -13b (Fig 4). These were the only transitional phrases observed to be repeated sequentially as if they were regular phrases.

The Markov matrices revealed each period’s fundamental phrase sequences and their consistency within the songs (Fig 7). The variation within the song sequences, in terms of transitional variation, increased notably during period-2 and-3 but decreased again during the last (4th) period (Fig 7). However, the Fishers Exact test showed very small variations in transition occurrence between the four periods, with most phrases transitioning rather consistently to certain phrases during the course of the recording period (Table 2).

Phrase sequence progression

Three of the most common phrases, i.e. phrase-13b, 12 and 4b, transitioned predictably to certain phrases in all periods and thus represented static themes. Four phrase types (phrase-17, -13c, -14a, and -3c) were less static and transitioned more inconsistently to various phrases. Phrase-17 and -13c, showed significant inconsistencies between the compared periods in to which phrases they transitioned to (Table 2). Phrases 3c and 14a contributed to the variation in transitions between periods though not statistically significantly. Less common phrases occurred rarely enough that they did not affect the results of the ’Fishers’s Exact test (Table 2).

Though phrase-17 was not common during the first two periods, it became more prevalent during period-3 and -4. During period-1, phrase-17 was found to only transition to phrase-14a. In period-2, however, phrase-17 transitioned most frequently to phrase-13c and also to phrase-15 and -14a (Fig 7). Phrase-17 then transitioned to phrase-13c, phrase-11b and phrase-14a during period-3, but primarily to phrase-15 and also to phrase-11b and -14a during period-4 (Fig 7). Phrase-17’s inconsistent transitions indicate it was an irregular theme that transitioned to a variety of different themes. Phrase-13c was first observed in period-2 where it only transitioned to phrase-13b. During period-3 this phrase continued to transition to phrase-13b, as well as phrase-14a and -14b. During period-4, however, it transitioned only to phrase-13a (Fig 7). Phrase 4b was a common terminal phrase (end phrase) within the sequences during the first two periods but started to transition more frequently to phrase-17 (a common starting phrase), during the two latter periods. A fundamental phrase sequence, i.e. [13b-12-4b], occurred at the end of the majority of extracted sequences and was also the most common

Markov sequence (Fig 7; Table 3). Phrase sequences occurring before this fundamental sequence varied within the songs between periods (Fig 7; Table 3). The designated starting themes or themes early in the songs (17, 15, 11b and 13c) included high frequency units which had rather varying contours between singers, these were followed by themes which gradually lowered in frequency (14a, 14b, 3c, 13a and 13b) and transitioned into themes composed of repeated short upcall units (12, 4b and 4a) which sometimes were followed by themes made from low frequency impulsive units (8 and 6) (Fig 4). The set median sequences obtained from the sequences extracted directly from the recordings were consistent with the most common sequences produced by the Markov matrices (Table 3). The hypothetical Kohonen set median sequences did not produce better representatives of sequence sets for any period, thus, the set medians obtained from the true data were the best representatives for all periods.

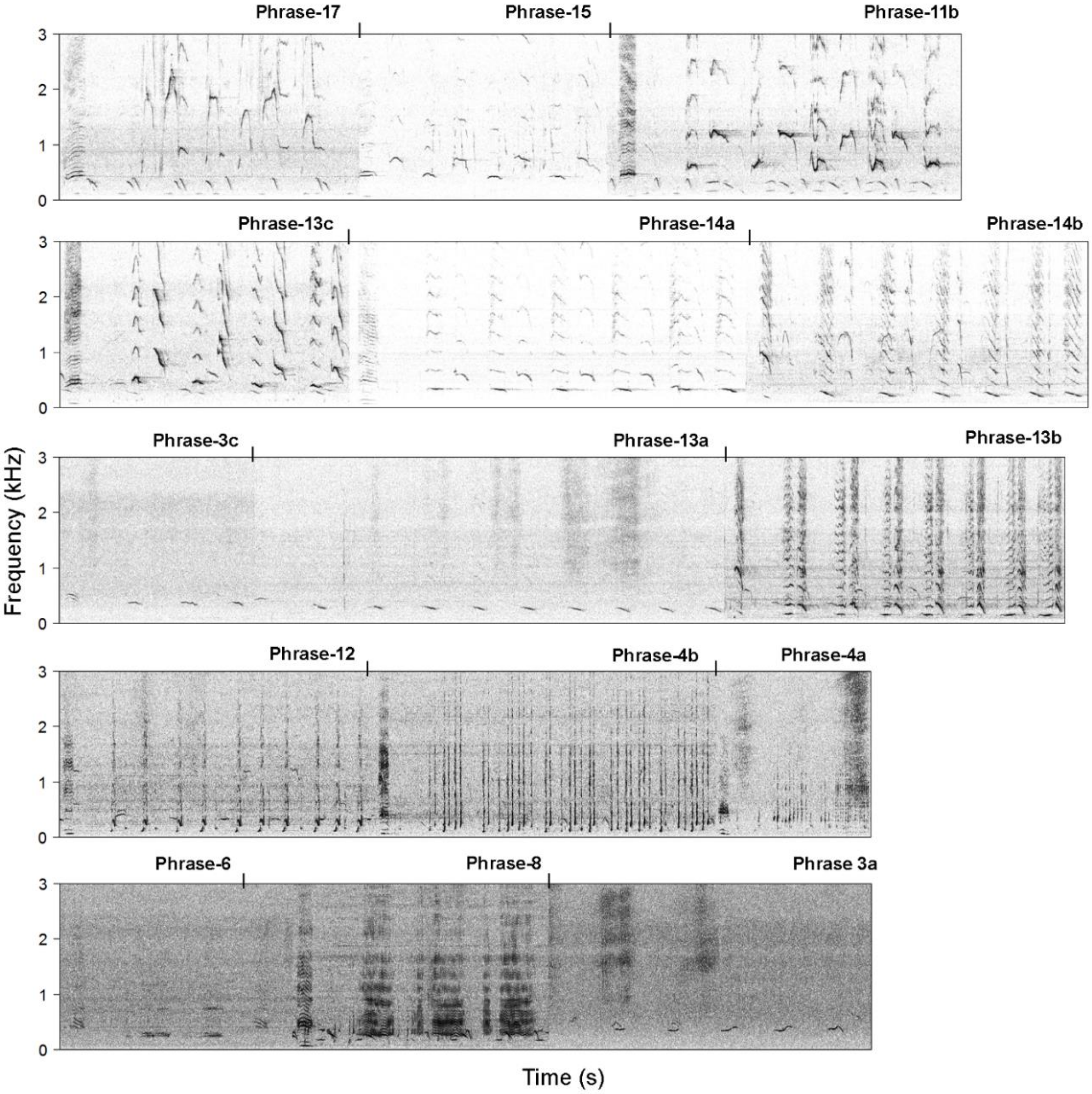

Fig 4 Spectrographic representations of the observed phrases from the complete recording period. The spectrograms were generated using fast Fourier transformation (FFT) (size 2048 Hanning window) with a frequency resolution of 7.8 Hz and a 95% overlap. The vertical, black lines indicate the division between the phrases.

The set median sequences for period-1,-2 and -4 were the same, i.e. 14a-13b-12-4b. The set median sequence from period 3 was almost the same. only phrase-17 was also included, i.e. 17-14a-13b-12-4b. Since the set median sequences from all periods displayed 80–100% similarity between each other according to the LSI analysis, the songs analyzed from these four periods could be considered a single cluster of songs (Garland *et al.* 2013b)

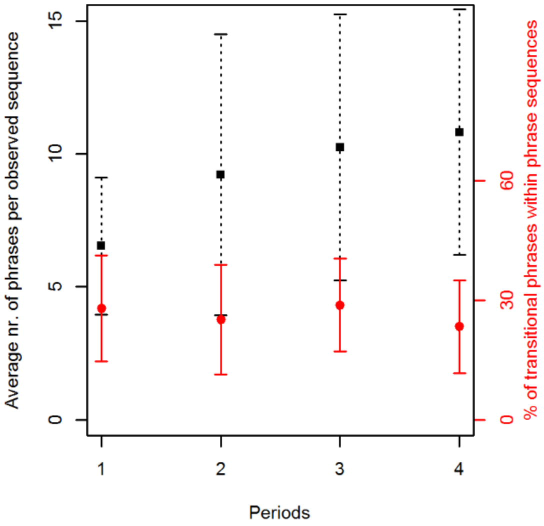

Fig 5 An increase in the length of the phrase sequences was observed when including all repeated phrases within the 10 minute recordings (y-axis in black). Sequences with fewer than four phrases were not included in this dataset. The secondary y-axis (red) represents the percentage of transitional phrases within the observed phrase sequences from period-1 to -4.

DISCUSSION

This study provides, to the best of our knowledge, the first description of the structure and evolution of humpback whale mating songs from a subarctic feeding ground during the breeding months of winter. The findings demonstrated a characteristic song type for this region adopted by the majority of the singers recorded during the study. A fundamental theme sequence was included in the vast majority of the observed songs. Other themes were also included consistently, though not as rigidly, as these fundamental themes.

When implemented in the songs, despite being predominant or rare, most themes were found to be in a similar pattern or place in the songs. The transition from one theme to the next was relatively consistent throughout the recording period for the majority of the themes. Only four common phrases transitioned somewhat inconsistently to different phrases. The lack of predictability, or entropy, of the songs increased close to and around the middle of the period but returned again to a more homogenous cluster of songs close to the end of the recording period. Some variation in the usage of themes was observed throughout the period. Evidences of song evolution, primarily recognized in the change of theme use as the period progressed, was identified during the course of the recording period.

Characteristics of subarctic winter songs

The song characteristics observed in this study closely resemble reported songs quantified from low latitude breeding grounds. In particular, songs recorded in this subarctic feeding region displayed a sophisticated, hierarchical structure and a fundamental theme order shared by almost all of the observed singers. Themes were generally sung in the same order by all the detected singers but not in synchrony which has shown to be typical for humpback whale singers on breeding grounds (Payne & McVay 1971; Payne 2000). The observed songs were comprised of 14 unique song units, as discussed in the previous publication by Magnúsdóttir *et al.* (2015).

Table 2. Results from the Fishers Exact test indicating whether a single phrase transitioned consistently (P>0.05) or inconsistently (P<0.05) to other phrases throughout the course of the recording period, i.e. from period-1 to period-4. The asterisk indicates the phrases that were significantly inconsistent in their transitions to the next phrase across the four periods. The ‘Occurrence during transitions’ column indicates how often each phrase was included in a transition within the Markov matrices.

Phrase type	Occurrence during transitions	Difference in transitions between periods (*P* - value)
17	36	<0.001*
15	23	0.88
11b	10	1.00
13c	15	0.01*
14a	84	0.06
14b	11	0.29
13a	17	0.65
3c	34	0.07
13b	112	1.00
12	84	1.00
4b	23	0.34
4a	5	1.00
8	7	1.00
6	3	1.00
3a	1	1.00

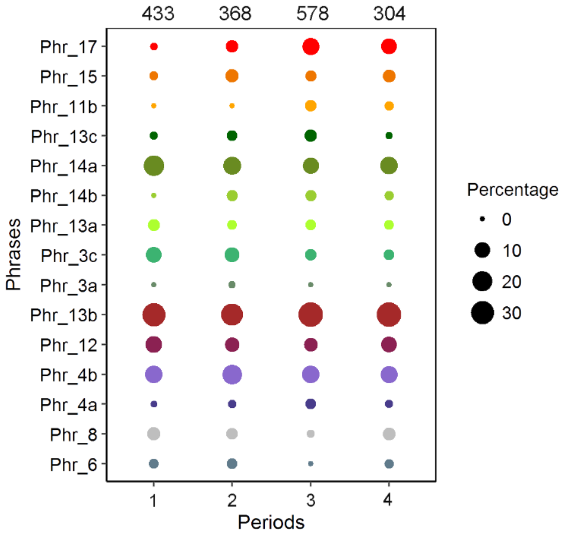

Fig 6 Percentage of phrase occurrence within the songs per period. The values above each period column represents the sample size for each period (n).

These units subsequently made up 15 phrase types which were observed to combine and form 15 different themes. These song characteristics could therefore be recognized, quantified, and used for defining the recorded songs.

Many song sequences exceeded the 10 minute recording, thus falling within the previously published average song duration range, i.e. approximately 6–30 minutes (Payne & McVay 1971; Payne 2000; Eriksen *et al.* 2005). Additionally, reviewing consecutive sound files provided evidence for song cycles that lasted 40–70 minutes.

Transitional phrases represented a relatively large part of the observed songs. This is in comparison with a previous study by Payne *et al.* (1983) which reported that Hawaiian humpback songs were only 5% transitional phrases, with the proportion decreasing towards the end of the season. This was observed to decrease the songs' entropy (Suzuki *et al.* 2006). The songs analyzed in this study included a total of 26% transitional phrases with an average representation of 23–29% per period. The majority of changes between themes occurred through the use of transitional phrases with a slight proportional change found towards the end of the season, indicating a possible decrease in the songs' entropy. However, as the present study covered approximately 1.5 months of the breeding season, it may not have captured a true trend in decreasing entropy. In Payne *et al.* (1983), songs were described as becoming more predictable and organized as transitional phrases were phased out. According to these characteristics, the subarctic Icelandic humpback whale songs recorded from the end of January until mid-March would be categorized as less stable.

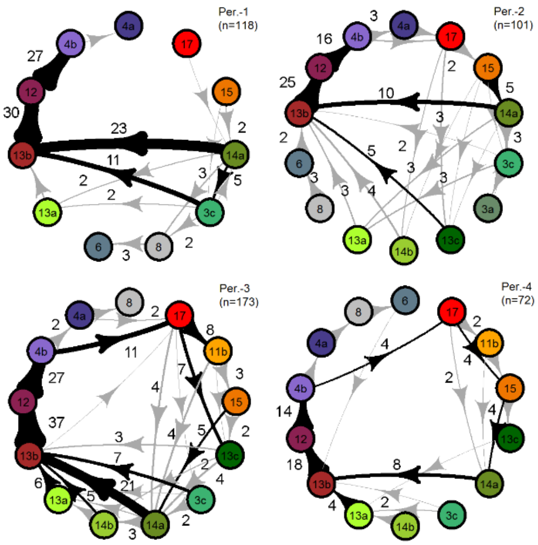

Fig 7 A diagram based on Markov transition matrix of song sequences during each period. The data points (n) represent the number of analyzed transitions observed during each period. The numbers within each diagram represents transition counts represented by the different arrows. Single transition events are represented with narrow gray lines, but not labeled. Black lines represent transitions occurring a minimum of 5% of the time while gray lines represent transitions occurring less than 5% of the time. The line thickness indicates the prevalence and frequency of the transitions observed, i.e. thicker lines indicate more common transitions.

The transitions observed in the present study between the more common phrases were actually found to be stable across all four periods with the clear exception of four phrases, i.e. 17, 13c, 14a and 3c. This indicates that there is an apparent pattern of predictable phrases attributed to all periods. The consistent transition order found using Markovian sequencing showed that the sequences were fairly invariant and phrase transition reversals were rare throughout the entire recording period. In instances of varying phrase transitions between particular phrase types, a modified transition order would occur instead of the more common phrase transition. Such variation in theme orders are not uncommon in humpback whale songs and has for example been shown in songs from South Pacific breeding grounds (Helweg *et al.* 1998; Eriksen *et al.* 2005). The greatest transition variations were found during

Table 3. The table summarizes the most likely sequences per period according to the Markov matrices. The set median sequences from each period are shown

Period	Common Markov sequences	Set median sequences
1	a) 14a-3c-13b-12-4b	14a-13b-12-4b
	b) 14a-13b-12-4b	
2	a) 14a-13b-12-4b	14a-13b-12-4b
	b) 15-14a-13b-12-4b	
	c) 13c-13b-12-4b	
3	a) 17-11b-14a-13b-12-4b	17-14a-13b-12-4b
	b) 17-13c-14a-13b-12-4b	
	c) 15-14a-13b-12-4b	
	d) 14b-13b-12-4b	
	e) 13a-13b-12-4b	
4	a) 14a-13b-12-4b	14a-13b-12-4b
	b) 17-15-14a-13b-12-4b	
	c) 13a-13b-12-4b	

periods that had the highest numbers of detections, i.e. period-2 and -3. The increased variations during these periods (Fig 7) could have been caused by individual variation due to a greater number of singers present in the area.

The most evident evolution identified from the songs of this study was the gradual increase in occurrence of particular phrases, while other phrases were gradually removed from the songs as the period progressed. The set median song sequences were identical between all but one period, i.e. period-3 where the high frequency phrase “phrase-17” was also included in the set median sequence. That phrase was removed again from the set median for period-4. Overall, the set median sequences for all the periods displayed at least 80% similarity between each other (LSI) and 85–97% of the themes were shared between all periods (DSI), suggesting that the songs analyzed from these four periods represent a single song type. In comparison to other studies, songs from six different breeding grounds in the South Pacific showed four different vocal clusters based on the LSI and DSI methods where similarity within clusters were minimum of 60% (Garland *et al.* 2013b). This implies that the general song characteristics observed here on this high-latitude feeding ground could be representative of the population. In Magnúsdóttir *et al.* (2015) , the repertoire of song units analyzed from this study area noticeably evolved during the course of three winter seasons while new phrases were being formed every year. Particular phrases from previous years were observed to be carried over to the next while other phrases were completely omitted after one season. These conformed changes over time indicate that humpback whale singers feeding in the central North Atlantic share a repertoire of sounds. Such cultural development within and between years is continually shown on many traditional breeding grounds (e.g. Winn & Winn 1978; Payne & Payne 1985; Noad *et al.* 2000; Eriksen *et al.* 2005; Mercado *et al.* 2005) and evidently occurs in this subarctic feeding ground.

Why sing in the subarctic?

The feeding grounds off Iceland’s coast are considered important habitat for North Atlantic humpback whales since a large proportion (approximately 80% of the North Atlantic population) are found to occur in Icelandic waters (Reilly 2008; Smith & Pike 2009). A comprehensive photo-identification database is available for this region’s humpback whales identified in the summer but limited in the winter by the high subarctic location of this area. This particular location is characterized by polar nights (with darkness lasting up to 22 hours) and persistent adverse weather conditions throughout the winter season. Photo-identification matches of 50 humpback whale individuals were confirmed between summer and winter months of the same year in the Northeast coast of Iceland which indicated that those identified could be the same individuals recorded singing in the winter months (de Heus 2014). Despite the difficulties of making visual observations during winter, deployments of hydrophones in this area has given a new and unique insight into the plasticity of humpback whale breeding behavior in a non-traditional feeding ground.

In this study, humpback whale song vocalizations were detected almost every day (42 out of 46 days), from late January to the middle of March, 2011. Though song occurrences are mainly associated with traditional mating and breeding grounds of tropical low latitude aggregation areas, more findings confirm that singing is no longer an explicit behavior confined to such areas. Frequent reports of singing during migration already demonstrate the flexibility of singing behavior outside of regular breeding grounds

(Clapham & Mattila 1990; Norris *et al.* 1999; Charif *et al.* 2001) and songs have been recorded in numerous mid-to-high latitude feeding grounds, including feeding grounds located in the North Atlantic and North Pacific (Baker *et al.* 1985; Mattila *et al.* 1987; McSweeney *et al.* 1989; Clark & Clapham 2004; Vu *et al.* 2012). Singing humpback whales have recently been tagged and observed during periods of active foraging behavior in the high latitude feeding grounds of the Antarctic during austral spring and fall (Stimpert *et al.* 2012; Garland *et al.* 2013a). Findings by Stimpert *et al.* (2012) demonstrated song production in close overlaps between singing and feeding behavior during periods of active dives at depths greater than 100 m. Their studies indicated that a trade-off strategy between foraging and mating behavior is highly applicable to the humpback whale species while on winter feeding grounds where spatial and temporal limitations are not as restrictive as previously assumed.

At this time, it is not certain whether the individuals remaining in the high subarctic waters are immature males rather than mature males singing throughout the winter breeding period. In Herman *et al.* (2013), the majority of the singers during winter breeding seasons in Hawaiian waters from 1998 to 2008 were reportedly sexually mature, with relatively few immature singers recorded. In their study, the participation of many male singers in the asynchronous singing chorus was interpreted as a lekking aggregation which could attract more females to the area with the heightened signal levels. The recordings from this present study included hours of singing, frequent chorusing of multiple singers, and long durations of complex song characteristics. Therefore, these recordings strongly suggest that sexually mature males were present in the recordings and that the songs in the subarctic have a mating purpose.

Magnúsdóttir *et al.* (2015) proposed that these subarctic feeding grounds may be important for song exchange and as a possible opportunistic mating ground for humpback whales. Direct transmission and sharing can take place through mixing and communication between individuals sharing feeding grounds or during migration (Payne & Guinee 1983; Garland *et al.* 2013a). The potential interaction and song exchange at the high latitude feeding grounds of Iceland could be a key driving force behind continued cultural transmission and song exchange between North Atlantic populations of humpback whales. Future investigations will quantitatively compare this study's song recordings with songs collected from known breeding grounds in the Cape Verde Islands and West Indies. Data collected from such a comparison would enable a confirmation of whether breeding ground songs are culturally transmitted in Icelandic waters.

On a global scale, perhaps humpback whales have always overwintered and partaken in late migrations from many or most mid to high latitude feeding grounds. Equipment used in the past may have had limiting capabilities that hindered the ability to detect songs at high latitude feeding grounds. Though these considerations as well as the ecological contexts of an individual humpback whale complicate our understanding of the humpback whale behavior, it also presents a remarkable new perspective that demands further exploration.

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Paper IV

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The importance of a subarctic feeding ground for humpback whale song transmission to subtropical breeding grounds in the North Atlantic Ocean

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Authors' contribution
Collected sound recordings: EEM CR STG.
Designed the study: EEM ECG.
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The importance of a subarctic feeding ground for humpback whale song transmission to subtropical breeding grounds in the North Atlantic Ocean

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ABSTRACT

The cyclically-repeated song of the male humpback whale is an important social display on their breeding grounds, functioning in male-male interactions and/or as a reproductive display to attract females. Either way, these songs, containing phrases repeated within sequential themes, ultimately influence the reproductive success of the singers. Humpback whales are capable of song copying and innovation, which results in continual song evolution and horizontal transmission between individuals. Song transmission is important for vocal convergence within a population, and for sharing song components with other breeding populations within the same ocean basin. Here, we present evidence of cultural transmission of songs between a subarctic feeding ground (Iceland) and both of the known subtropical breeding grounds (Cape Verde Islands and the Caribbean) in the North Atlantic. Recordings of humpback song from these locations were decomposed to the phrase level. Utilising Markov matrices and similarity analyses (Levenshtein Distance, Levenshtein Distance Similarity Index and Dice's Similarity Index (DSI)), the level of song exchange between Iceland, the Cape Verde Islands and the Lesser Antilles in the Caribbean was quantified. Songs recorded in the Icelandic feeding ground and at the same time on the Cape Verde breeding ground formed a single song cluster, demonstrating pronounced song similarity. Songs recorded in the Cape Verde and the Caribbean the following year formed different song clusters but shared 53% of the phrase repertoire according to the DSI. Songs from the Caribbean in one year shared 82% of the repertoire with songs from Iceland the following year. Results clearly suggest that songs are transmitted between individuals on the joint Icelandic subarctic feeding ground, producing a similar pattern to the North Pacific. This highlights the importance of Iceland as an area for song exchange in the North Atlantic.

Keywords: Humpback whale song, cultural transmission, song sharing, song evolution, migration, reproductive behaviour, feeding ground, subarctic, Iceland, North Atlantic

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INTRODUCTION

The humpback whale has a worldwide distribution extending from high latitude polar feeding grounds to tropical mating grounds (Clapham 2000). Traditional humpback whale feeding grounds in the western North Atlantic stretch northwards from the east coast of North America from the Gulf of Maine and towards West Greenland. Central North Atlantic feeding grounds are found off Iceland and Jan Mayen, while eastern feeding grounds span the north coast of Norway extending towards the Barents Sea (Stevick *et al.* 2016). Most of these feeding grounds are characterized by high maternally directed site fidelity where little interchange has been observed between aggregations (Clapham *et al.* 1993; Stevick *et al.* 2003a; Stevick *et al.* 2006). The feeding ground off Iceland is considered important for North Atlantic humpback whales given a large proportion (~ 80%) of the estimated abundance in the North Atlantic has been observed in Icelandic waters, or approximately 11,000 whales (Stevick *et al.* 2003b; Reilly 2008; Paxton *et al.* 2009; Øien 2009).

North Atlantic humpback whales are known to aggregate on breeding grounds off the Caribbean Islands in the West Indies and around the Cape Verde Islands, northwest Africa during winter and spring (Charif *et al.* 2001). The Cape Verde breeding population is currently very small, with a recent estimation of approximately 260 individuals (Ryan *et al.* 2014) while the estimates for the West Indies breeding population is in excess of 11,000 individuals (Stevick *et al.* 2003b). The largest breeding assembly in the West Indies occur on Silver Bank and Navidad Bank near the Dominican Republic while lower numbers of whales have been found further east off Puerto Rico, the Virgin Islands and the Lesser Antilles (Stevick *et al.* 2003b; Reilly 2008).

Humpback whales from central and eastern feeding grounds, such as Iceland and Norway, appear to be underrepresented in these large western Caribbean breeding assemblies, such as the Dominican Republic (Stevick *et al.* 2003a). However, only whales from these feeding grounds have been identified on other smaller breeding grounds, i.e. Guadeloupe and the Cape Verde (Jann *et al.* 2003; Stevick *et al.* 2003a). Guadeloupe is a breeding assembly within the eastern Caribbean Island clusters and belongs to the Lesser Antilles. In spite of the small distance (~1000 km) for such mobile species, there is surprisingly low interchange between the Dominican Republic and Guadeloupe breeding assemblies (Stevick *et al.* 2016). A small number of individuals from the eastern North Atlantic feeding grounds have been sighted in both Guadeloupe and the Cape Verde during different winter breeding seasons, though none were sighted in both locations during the same winter season (Stevick *et al.* 2016). Additionally, two satellite-tagged humpback whales have been tracked migrating from Guadeloupe towards central and eastern North Atlantic feeding grounds (Kennedy *et al.* 2013). These findings indicate migration affinity of central and eastern North Atlantic humpback whales towards the Cape Verde and the Lesser Antilles.

Humpback whales sing complex and patterned songs while on their low latitude breeding grounds. To date, singing has only been associated with males, linking the behaviour to mating and male-male social organization (Smith *et al.* 2008; Darling *et al.* 2012; Herman *et al.* 2013). Humpback whale songs are characterized by high intensity vocal signals forming a hierarchical song. The song is further characterized by the ordering of the shortest, most basic element in the song called a 'unit' which combine to form 'sub-phrases' and 'phrases'. These phrases are repeated in succession to form 'themes' that, when sung continuously, form a 'song' which can also be repeated to form a 'song session'(Payne & McVay 1971).

The purpose of humpback whale song and the reason for its hierarchical structure composed of diverse sound units remains largely unexplained. Males sing actively during the breeding season where the songs are gradually synchronized into a predominant pattern shared by the majority of the singers (Payne & McVay 1971). The songs develop during the course of the breeding season and often change quite dramatically between years (Payne & Payne 1985; Noad *et al.* 2000; Eriksen *et al.* 2005; Garland *et al.* 2011). It has been suggested that the continual song development is a result of this species ability to copy song elements from other singers (Mercado *et al.* 2005) and their ability to innovate (Noad *et al.* 2000; Cerchio *et al.* 2001).

Females have rarely been observed approaching male singers, whereas several studies have confirmed that the majority of individuals approaching singers are males (Smith *et al.* 2008; Darling *et al.* 2012; Herman *et al.* 2013). Behavioural studies from low-latitude breeding grounds have also shown that some males form cooperative alliances while others display agonistic behaviour towards one another (Tyack 1981;

Clapham *et al.* 1992; Darling *et al.* 2006) which has led to suggestions that the songs organize males on the breeding grounds. When males escort females on the breeding grounds they often sing and often continue to do so even if the escort duo is joined by other males (Smith *et al.* 2008). Smith *et al.* (2008) suggested that males approach other singers as a low-cost strategy to locate females, however, singers escorting females continue to sing since the song is an important reproductive display during courtship. Furthermore, it has been proposed that the lower frequency components of the songs could indicate the size, robust health and sexual maturity of the singer (Adam *et al.* 2013) which would allow for a female choice mechanism, and be an advertise for rivals (Tyack 1981). Herman *et al.* (2013) suggested that the broad participation of males in singing on breeding grounds is a lekking aggregation. Leks have been defined as male display aggregations that females attend primarily for the purpose of mating (Jiguet *et al.* 2000). The participation of many singers yields a heightened signal level (Au *et al.* 2000) that could attract more females into the area. Also, the songs advertise the sex of the singers and possibly a readiness to mate (Tyack 1981). Furthermore, a recognizable song pattern could serve as a beacon to guide the whales into a hotspot breeding area occupied by animals of their own species and possibly of their own population. Darling *et al.* (2006) proposed that the continuous change in songs and the adoption of these changes by all nearby singers is a real time measure of association between individuals which might provide a means of reciprocity for mutual assistance in mating. Despite the variability in the abovementioned song mechanism hypothesis it is evident that a cultural transmission of songs between male singers, consequently leading to a mutual song each breeding season, is important for reproduction in this species.

Song similarity has been observed between populations within the same ocean basin (Payne & Guinee 1983; Helweg *et al.* 1998; Garland *et al.* 2011; Garland *et al.* 2013a). Payne and Guinee (1983) hypothesized three possible song sharing mechanisms, i.e. that 1) individuals could move from one breeding population to another between seasons, which has now been shown to be quite common (e.g. (Calambokidis *et al.* 2001; Garrigue *et al.* 2011a; Garrigue *et al.* 2011b)), 2) individuals could move between two breeding populations within a single breeding season, which has, however, only rarely been observed (Garrigue *et al.* 2002; Garrigue *et al.* 2011a)) and 3) the synchronization of songs could start during migration and possibly when the whales are still on their feeding ground. A study by Garland *et al.* (2013a) supported the 3rd hypothesised mechanism by showing how songs were transmitted between a Southern Ocean feeding ground and breeding grounds in the western and central South Pacific.

Accumulations of singing humpback whales have been recorded at mid-to high-latitude feeding grounds (Baker *et al.* 1985; Mattila *et al.* 1987; McSweeney *et al.* 1989; Clark & Clapham 2004; Vu *et al.* 2012; Stanistreet *et al.* 2013). Magnúsdóttir *et al.* (2015) recently reported that individuals acoustically detected on Iceland's feeding grounds engage in singing during the winter from January until at least mid-March. This timing overlaps with the estimated breeding period of northern hemisphere humpback whales (Nishiwaki 1966). Additionally, Magnúsdóttir and Lim (2017) demonstrated that humpback whale songs were detected in northeast Iceland almost every day (42 out of 46 days), from late January to the middle of March in 2011. During that time humpback whales chorused actively, singing complex and sophisticated songs in an asynchronous manner as has been shown on traditional low latitude breeding grounds. Such investment in singing on a feeding ground is likely beneficial for the species, probably for the cultural transmission of songs and also for mating opportunities.

Cultural transmission is the social learning and sharing of information or behaviours between conspecifics within a population or subpopulation and has been observed among humpback whales (Rendell & Whitehead 2001; Garland *et al.* 2011). Different modes of cultural transmission exist within the humpback whale species and can include both vertical (parent-offspring) and horizontal transmission. The song of the humpback whales is learned through horizontal cultural transmission across unrelated individuals. Humpback whale songs are constantly changing within a population over time, and these changes are recognized as cultural evolution and if the changes are complete they are referred to as cultural revolution. A population will therefore conform to singing similar dialects or song types within a shared ocean basin. Differences begin to appear and increase with distance of proximity between populations (Helweg *et al.* 1998; Darling *et al.* 2014) but are distinctly different between geographically isolated populations (Winn *et al.* 1981).

The potential interaction and song exchange at the high latitude feeding grounds could be a key driving force behind continued cultural transmission and song exchange between North Atlantic humpback whale populations. Winn *et al.* (1981) previously described a similarity of humpback whale songs from the West Indies and the Cape Verde Islands where the songs shared at least six themes. However, to date, this comparison has not been validated with other studies. The aims of the present study were to compare the previously described song structure from Iceland by Magnúsdóttir and Lim (2017) with songs from the Cape Verde and, the Lesser Antilles, to understand ocean-basin scale song transmission in the North Atlantic in addition to the linking of these feeding and breeding grounds. Ultimately, this study aims to find if subarctic feeding grounds are important for cultural transmission of humpback whale songs in the North Atlantic.

METHODS

Study areas

Humpback whale songs were recorded off the northeast coast of Iceland in Skjálfandi Bay (66°03'N, 17°40'W), a subarctic feeding ground in the central North Atlantic, and from two distinct North Atlantic breeding grounds for humpback whales. The breeding ground recordings were taken at 1) the Cape Verde archipelago (eastern Atlantic); specifically west off the island Boa Vista (16°5'N, 23°5'W), and 2) the Lesser Antillean archipelago in the Caribbean Sea; specifically off the leeward, western coast of the island of Dominica (15°23'N, 61°30'W) (Fig 1).

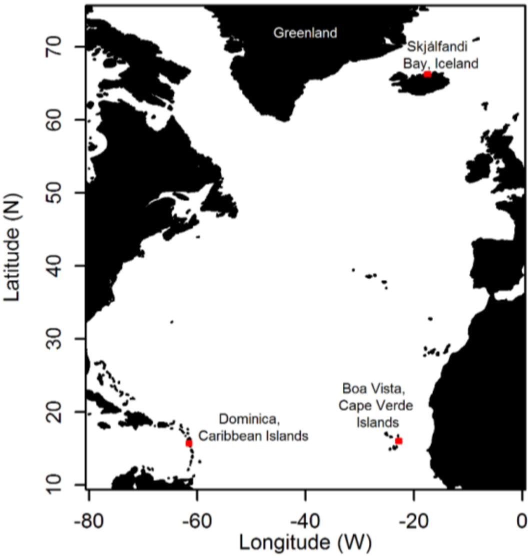

Fig 1 The locations where humpback whale songs were recorded between 2008–2012 are labelled with read squares.

Dominica lies south of the island of Guadeloupe and north of the island of Martinique. The recordings from Iceland (ICE) were collected in Skjálfandi Bay during three consecutive winters: September 2008–February 2009, November 2009–April 2010 and January–March 2011. The recordings from the subtropics were recorded during shorter periods; recordings from Boa Vista in the Cape Verde (CVI) were collected between April 2nd and May 11th 2011, and the following year between April 17th and May 15th 2012. The songs from Dominica in the Lesser Antilles, Caribbean (CAR), were recorded during two separate years, i.e. in 2008 and 2012. The recordings from 2008 were collected during March 2nd, March 28th and April 4th and a single recording was collected in May 9th in 2012.

Acoustic recordings

The recordings in Skjálfandi Bay, Iceland were made with two bottom-moored ecological acoustic recorders (EAR) moored at approximately 62 m. However, only one of the EAR units recorded during the last two periods, therefore, the recordings from that single unit was used in all years for this study. During the first two winter seasons, whale acoustic data were collected over approximately 5 months periods and the EAR was set to record for 1 min every 15 min at a sampling rate of 64 kHz. During these first two seasons, the aim was to collect a broad range of sounds from as many cetacean species as possible. In 2011, the EAR was set to record for 10 minutes every 15 minutes at a sampling rate of 16 kHz to capture the fundamental range of humpback whale songs (approximately 10-8,000 Hz) (Mercado *et al.* 2010; Stimpert *et al.* 2011). This duty cycle was chosen to obtain phrase sequences and themes without necessarily collecting full songs or song cycles. That setting allowed for longer recording period due to data storage limitations and an optimisation of battery life. The EAR is a microprocessor-based autonomous recorder containing a Sensor Technology SQ26-01 hydrophone that has a response sensitivity of -193.5 dB and is flat (±1.5 dB) from 1 Hz to 28 kHz (Lammers *et al.* 2008). Previous work (Magnúsdóttir *et al.* 2014; Magnúsdóttir *et al.* 2015; Magnúsdóttir & Lim 2017) has described the song recordings from Iceland in further detail. Here, the Icelandic (ICE) recordings are used in a comparative study to assess their similarity to songs recorded in the major breeding grounds located on either side of the North Atlantic, CVI and CAR.

The recordings in the CVI were collected during dedicated humpback whale sighting and biopsy surveys in the continental shelf waters to the west of Boa Vista during two consecutive breeding seasons (10 April–17 May 2011 and 14 April–15 May 2012). The study area, comprising 206 km^2 of inshore waters (up to 8 km from shore) off western Boa Vista, was chosen based on high sightings rates of humpback whales from previous expeditions (Wenzel *et al.*

2009). The recordings where collected from a stationary 5 m vessel using a dipping hydrophone at a 32 kHz sampling rate using a MAGREC HP30 with a flat response between 200Hz and 20KHz. The hydrophone signal was amplified through a MAGREC HP-26 SB amplifier box with high-pass filter at 1kHz.

The recordings from the Caribbean were obtained from near the island of Dominica in the Lesser Antilles during research conducted by the Dominican Sperm Whale Project. The recordings were collected using a custom built towed hydrophone array based on two Benthos AQ-4 elements with a frequency response between 100Hz and 30kHz. A filter box with high-pass filters up to 1 kHz was used resulting in a recording chain with a flat frequency response across a minimum of 2–20 kHz (Gero *et al.* 2016) deployed from a 12 m sailboat. The recording was made on a laptop PC using a Fireface 400 sound card and Pamguard software (Gillespie *et al.* 2008) with a sampling rate of 96 kHz. All recordings covered the frequency range of the humpback whale song.

Song analysis

A frequency contour detection algorithm from the Ishmael 2.0 software package was applied to search for tonal signal frequencies in recordings from Iceland that ranged from 100 to 1000 Hz (Mellinger 2002; Mellinger et al. 2011). Detection thresholds were set to 0.25 seconds (Fast Fourier Transform (FFT) 0.2048 s., 75% overlap, Hamming window). Despite spanning only a part of the humpback whale tonal frequency range, the detector primarily detected humpback whale signals with minimal false positive detections. The signal to noise ratio and audibility of the signals in each recording were manually inspected for recording quality. The sound files were graded and categorized as very poor, poor, medium, good, and excellent (Magnúsdóttir & Lim 2017). Files where all signal details were distinctly visible with high amplitude units (i.e., good signal to noise ratio with a minimum of 10 dB above the background noise) were marked as good and excellent quality and used for further analysis.

The Icelandic dataset was not recorded continuously (i.e., each 10 minute recording was followed by a 5 minute break and each 1 minute recording was followed by a 15 minute break before the start of the next recording). The datasets from 2009 and 2010 included a large sample of 1 minute long sound files which allowed for phrase inspection but not of phrase sequences and was thus only used to compare the phrase repertoire to other sets. However, the 10 minute long recordings from 2011 included sequences of phrases which allowed for song sequence analysis. The 2011 dataset usually did not contain complete songs, i.e. sequences of phrases that ends when the same phrase as the first one in the sequence is repeated; therefore the complete song could not always be extracted directly from the recordings. To create a dataset for a group of singers, four to six adjacent sound files of excellent quality were acquired from 16 different days throughout the course of the recording period (Magnúsdóttir & Lim 2017). These 16 different days were divided into four distinct periods of four days each (Table 1). By dividing the Icelandic dataset into even time periods (subsets) we could avoid biasing the results towards the same group of singers for which we had a higher number of song sequences (series of phrases). The Icelandic (ICE) and the Cape Verde (CVI) recordings were consecutive in 2011, while there was a seperate CVI and CAR sample recorded in 2012 with no corresponding ICE sample. The song sequences recorded in the subtropics (CVI and CAR) during 2011 and 2012 were used in song similarity analysis along with the recordings from Iceland in 2011 since these mating seasons, i.e. 2011 and 2012, are aligned and can, therefore, provide information about song sharing between these locations. The song recordings from the Caribbean in 2008 were only used for phrase repertoire analysis since they were not close enough in time from the 2011 and 2012 songs to contribute evidences to the analysis of song sequence sharing between Iceland and the subtropics. However, the Caribbean dataset from 2008 was used to investigate the similarity of phrase repertoire between the Caribbean (in 2008) and in Iceland during 2009 and 2010. Songs were inspected using the spectrographic view of the Raven Pro 1.4 software (Cornell Lab of Ornithology, 2010) using a Hanning window, 2048 Fast Fourier Transform (FFT) size, and 50% overlap. Phrases were noted and labelled in a time sequence as they occurred on the spectrogram. Phrase labels followed those previously assigned by Magnúsdóttir *et al.* (2015) to maintain consistency. Where multiple singers were recorded singing simultaneously, the phrases from each singer were tracked manually if transitions between phrases were clearly visible on the spectrogram (Magnúsdóttir & Lim 2017)

Table 1 A summary of the datasets from Iceland (ICE), Cape Verde (CVI) and the Caribbean (CAR). The ICE sets from 2008–2010 included multiple 1 min sound files. The total duration of recordings is provided on the format min:sec. The recordings from the CAR-08 and ICE between 2008 and 2010 were only used to compare phrase repertoire using DSI analysis. Other sets were used for both DSI and LSI analysis. The table includes the number of confirmed singers per day. A minimum threshold of 24 h intervals passed between detection dates to allow for estimation of the total hypothetical number of singers per set. Only song sequences with a minimum of four phrases were included in the LD analyses. Hyphens indicate that the data was not available.

Study Site	Year	Set ID.	Dates	Total duration of recordings	Estimated no. singers (range)	No. song seq. analyzed
CAR	2008	CAR-08	2-Mar-08	10:00	2	-
			28-Mar-08	28:53	2	-
			3-Apr-08	07:05	3	-
			Total	*45:53*		
ICE	2008–09	ICE-09	15-Dec-08 to 09-Feb-09	231:00	-	-
			Total	*231:00*		
ICE	2009–2010	ICE-10	28-Dec_09 to 11-Feb-10	174:00	-	-
			Total	*174:00*		
ICE	2011	ICE-11-1	27-Jan-11	40:00	3 (*1-3*)	3
			30-Jan-11	60:00	3 (*1-3*)	3
			31-Jan-11	40:00	3 (*3*)	8
			2-Feb-11	40:00	5 (*4-5*)	3
			Total	*180:00*	*11*	*17*
ICE	2011	ICE-11-2	5-Feb-11	40:00	2 (*2*)	4
			7-Feb-11	40:00	3 (*2-3*)	3
			9-Feb-11	40:00	4 (*4*)	2
			10-Feb-11	40:00	2 (*2*)	7
			Total	*160:00*	*9*	*16*
ICE	2011	ICE-11-3	18-Feb-11	60:00	4 (*3-4*)	6
			20-Feb-11	40:00	4 (*3-4*)	6
			24-Feb-11	40:00	3 (*1-3*)	7
			25-Feb-11	40:00	4 (3-4)	9
			Total	*180:00*	*12*	*28*
ICE	2011	ICE-11-4	2-Mar-11	40:00	2 (*1-2*)	4
			8- Mar-11	40:00	1 (*1*)	4
			11-Mar-11	40:00	3 (*3*)	6
			12-Mar-11	40:00	1 (*1*)	2
			Total	*160:00*	*6*	*16*
CVI	2011	CVI-11	2-Apr-11	19:11	2 *(1-2)*	3
			3-May-11	56:40	2 *(1-2)*	8
			10-May-11	10:14	1 *(1)*	2
			11-May-11	12:09	1 *(1)*	2
			Total	*132:00*	*6*	*15*
CVI	2012	CVI-12	17-Apr.-12	11:09	1 *(1)*	2
			18-Apr.-12	34:22	3 *(2-3)*	12
			19-Apr.-12	17:29	1 *(1)*	4
			22-Apr.-12	11:25	2 *(2)*	5
			Total	*87:02*	*7*	*23*
CAR	2012	CAR-12	9-May-12	21:40	*1*	*2*
			Total	*21:40*	*1*	*2*
			Total song time examined	*22:16:26*		

If at any point the song overlap resulted in ambiguity as to which singer was singing what song, transcription was terminated. Since themes are composed of the same or similar phrase repeated several times and the repetition of phrases within themes can vary considerably between song sessions and even by the same whale (Cholewiak et al. 2013), only one phrase was used to represent each theme in the song sequences.

The CVI and CAR datasets were composed of opportunistic recordings of varying durations. Few longer recordings contained full songs (n=11) while shorter recordings (n=9) did not always contain a full song. To enable similarity analysis on these different datasets, i.e., primarily the Icelandic and the CVI (though the single CAR 2012 recording was also included for song sequence comparison), Markov matrices were created to find the most common transitions between phrases, and consequently themes, in all data sets. Markov matrices are useful when predicting behavioural states by quantifying the dependence of an event on the preceding ones and provide probabilities of transition from one event to the next (Lusseau 2003). Markov models of phrase transitions were constructed based on the values from the Markov matrices for visual representation of transitional characteristics of the songs in each set and of temporal changes in the song sequences. To better visualise the changes occurring in the songs from the first period in Iceland until the last period in the CVI and CAR recordings, all phrases were included in the diagrams and in the same order in each diagram. Song changes were, thus, displayed by the changes in the direction and width of the arrows between subsequent phrases. The width of the arrows were used to represent percentage weight, i.e., the likelihood of a transition to occur between two phrases. Thicker arrows represented a greater likelihood of the particular transition to occur in songs from that period.

When the phrases were delineated for a spectrographic comparison each unit within a phrase was labelled with the corresponding unit group name previously published in Magnúsdóttir *et al.* (2015). These groups were 1) high frequency harmonic wails and moans named H1–H3 depending on the counter shape, slope, and frequency range, 2) mid-frequency harmonic moans with down sweeping trends named Md1–Md3 depending on the frequency range, angle, and shape of the slope, 3) mid-frequency harmonic moans with upsweeping trends named MUp1–MUp3 depending on the frequency range, angle, and shape of the slope, 4) low-frequency tonal harmonic sounds named Lt1–Lt3 depending on the frequency range, angle, and shape of the slope and finally 5) low-frequency impulsive and complex moans were named Li1–Li2 depending on the frequency range and the angle of the slope. The displayed units were measured and subjectively fitted into these unit groups based on the published description of the groups by Magnúsdóttir *et al.* (2015). The phrases were constructed by one or two sub-phrases whereas in the majority of the phrases the latter sub-phrase was repeated. When the phrases were long (ca. ≥ 15 min) and included a repeated sub-phrase, which did not change throughout the phrase, only the first part of the phrase, including both sub-phrase types, was demonstrated in the spectrogram and the whole phrase structure indicated instead with descriptive symbols (Fig 2). The parenthesis defined a sub-phrase which was repeated within the phrase. The superscript numeric value to the right of the parenthesis, e.g. [Li1 (MUp3 x5-8)$^{4/5}$], indicated the number of repetitions of the sub-phrase within the parenthesis (Fig 2). Different repetition values were presented and separated with a solidus (/), also if the unit type produced would vary within a phrase the unit types were both presented and separated with a solidus, e.g. [Li1 (Md2/Md3)^{4}]. Also, if the repetition value of the unit varied within the sub-phrase the repetition range was indicated with a hyphen. Song units are sometimes composed of sub-units (Cholewiak *et al.* 2013), if that was the case each sub-unit was identified by a corresponding song unit group and were connected with a '+' symbol (Fig 2). A quantitative method based on the Levenshtein distance (LD) technique (Garland *et al.* 2012; Garland *et al.* 2013b) was conducted. An LD score between two sequences is found by calculating the minimum number of changes, i.e. insertions, deletions and substitutions, needed to transform one string of phrases into another (Kohonen 1985; Garland *et al.* 2012; Garland *et al.* 2013b). To obtain the most representative string for each analysed set the *Set Median* (SM) sequences for each set (i.e. form ICE-11 to CVI-12) was calculated to measure the song similarity between these periods and locations. A quantitative method based on the Levenshtein distance (LD) technique (Garland *et al.* 2012; Garland *et al.* 2013b) was conducted. An LD score between two sequences is found by calculating the minimum number of changes, i.e. insertions, deletions and substitutions, needed to transform one string of phrases into another (Kohonen 1985; Garland *et al.* 2012; Garland *et al.* 2013b). To obtain the most representative string for each analysed set the *Set Median* (SM) sequences for each set (i.e. form ICE-11 to CVI-12) was calculated to measure the song similarity between these periods and locations.

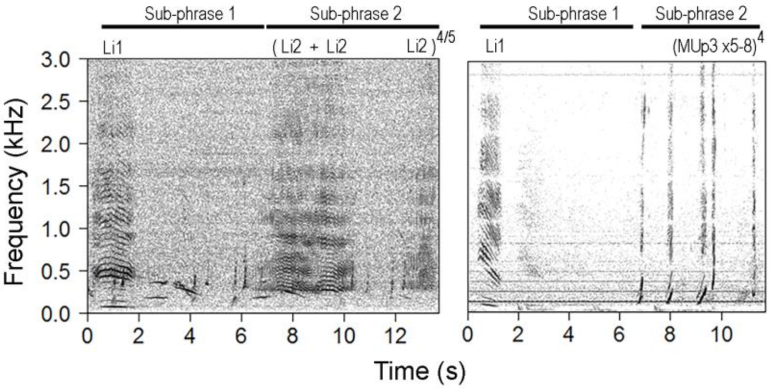

Fig 2 Examples of spectrographic representations of two different phrases. The horizontal lines represent the duration of each sub-phrase. Sub-phrase 1 is composed of a single unit, i.e. Li1. A sub-phrase which was repeated within a phrase was defined with a parenthesis where the repetition value was presented to the right of the closing parenthesis. The labels on top of each song unit represent the name of the unit group of which the unit was assigned to. The repetition value of the unit MUp3 in the right spectrogram varied within the sub-phrase, thus, the repetition range was indicated with a hyphen. Song units composed of sub-units (e.g. Li2+Li2) were identified by the two corresponding groups of which the sub-units belonged to and were connected with a '+'.

The SM is found by calculating the LD for every pair of sequences (strings) within a set. The sequence with the smallest Levenshtein distance (LD), i.e. the highest similarity, to all other sequences in the set becomes the SM (Kohonen 1985; Helweg *et al.* 1998; Tougaard & Eriksen 2006; Garland *et al.* 2013b). Since only one sequence was obtained from the CAR-12 data it was not possible to find a SM for that dataset, instead the single sequence was used in the comparison analysis. To ensure that the SM was the best representation of each period, a set of hypothetical medians, called *Kohonen median* (KM) (Kohonen 1985; Garland *et al.* 2012; Garland *et al.* 2013b), were created to find if a smaller summed LD score could be obtained. The KM is created by systematically substituting each phrase in the sequence with all possible phrases found within the set. This was not necessary for the CAR-12 dataset as previously stated since an SM was not created for that set.

To investigate the similarity between the representative strings (SM or KM) for each period a Levenshtein Distance Similarity Index (LSI) was used. The LSI normalizes the LD score by dividing it by the length of the longest string (Helweg *et al.* 1998; Petroni & Serva 2010; Garland *et al.* 2012; Garland *et al.* 2013b). The incorporation of the string length into the analysis allows the LD scores to be standardized so that the length of strings being compared does not increase the difference between the two strings. This enabled the difference in phrase types and phrase order to be the primary determinant of string differences. The LSI produced a proportion of similarity that ranged from 0 (0%) for no similarity to 1 (100%) for complete similarity between a pair of strings. The resulting LSI scores formed a matrix of LSI similarity which was converted to dissimilarity by subtracting each score from 1.

Using the statistical program, R (version 3.1.2), the representative sequences (SM/KM) for each period and the CAR-12 sequence were hierarchically clustered based on a dissimilarity matrix. The single-linkage clustering (nearest-neighbour clustering) method was employed to place the most similar sequences together. These sequences were then successively linked to other sequences/clusters of sequences (Garland *et al.* 2013b). This method analysed how similar the representative sequences were between periods, allowing for evaluation of song sequence progression.

Frumhoff (1983) defined a song being composed of a minimum of three different themes. Therefore, sequences with a minimum number of four different representative phrase types were used in the LD and LSI analysis to exclude with confidence the short sequence fragments, which were unlikely representatives of song sequences. These phrase sequences were extracted directly from the recordings. Since the start and end of the sequence is not always clear, the start and end was determined visually. The Markov analysis of the Icelandic data revealed the most likely starting phrases (i.e. phrase 17 and 15) and ending phrases (i.e. phrases 4a and 4b) of the sequences, referred to as the "start label" and "end label". Due to the smaller sample sizes of the CVI and the CAR-12 datasets the likely start and end labels had to be subjectively assessed. Phrases in the CVI and the CAR-12 dataset similar to the start label phrases in the

Icelandic dataset were anchored as the “start labels” in the CVI and CAR-12 sequences. Phrases that commonly occurred before the start labels in the CVI and the CAR-12 datasets were assigned an “end label”. Furthermore, if the same phrase reoccurred later within a sequence, the sequence was considered terminated, with the subsequent phrase beginning a new sequence, e.g.:

[**15**-14a-13b-12-4b-**15**-14a] → [**15**-14a-13b-12-4b], [**15**-14a]

where each character (number or number and letter) represents a single phrase and the hyphen indicates the transitioning event between the phrase types. Sequences are shown within the brackets. Since ‘15’ occurs twice within the first sequence, this sequence is terminated at the phrase ‘4b’ which is the phrase directly preceding the second incidence of ‘15’. This results in two shorter sequences.

To further investigate song similarity between time periods, the presence and sharing of phrases (phrase repertoire) was calculated using Dice‘s similarity index (DSI) (Garland *et al.* 2015). The DSI does not consider sequential characteristic of the songs such as the LD analysis, instead it shows presence or absence of phrases.

RESULTS

A total of 77 song sequences from Iceland in 2011, 38 from the Cape Verde in 2011 and 2012 and one from the Lesser Antilles in 2012 were extracted and analysed from approximately 22 hours of song recordings (Table 1). Additionally, 2778 phrases from all periods and locations were analysed. The average minimum number of singers from each recording used to analyse song sequences from Iceland was 2.6 (±1.1) (previously presented by Magnúsdóttir and Lim (2017)), 1.5 (±0.58) from the CVI in 2011 and 2 (±0.82) from the CVI in 2012 while a single singer was recorded in the Caribbean (Lesser Antilles) in 2012 (Table 1). A total of nine different phrases were identified in Iceland in 2009, ten in 2010 and 14 different phrases were identified in the songs from Iceland in 2011. A total of 12 different phrases were identified in the Cape Verde songs from 2011 and nine in the Cape Verde songs from 2012, finally eight different phrases were identified in the Dominica song from 2008 and six from 2012 (Fig 3).

The hypothetical Kohonen median analysis did not produce better representatives with lower LD scores than the assigned set median sequences (SM). Thus the SMs were the best representative sequences for all analysed sets (i.e. ICE-11-1–4 and CVI-11–12) and utilized in further analysis. A single sequence was extracted from the CAR-12 song. A minimum of 40% similarity was required between set median (representative) sequences to be grouped into the same cluster of songs. Three types of song groups were identified, i.e. 1) the ICE-CVI 2011 songs from Iceland and the Cape Verde in 2011, 2) the CVI-12 from the Cape Verde in 2012 and 3) the CAR-12 song from the Dominica in 2012. The set median sequences for different periods during the winter in Iceland shared 80 to 100% similarity between each other (Fig 4 a-b). The SM from ICE-11-3 differed slightly from the other Icelandic SMs (Magnúsdóttir & Lim 2017). Similarity between the CVI-11 and the ICE-11 SMs sequences ranged from 75% (sets 1, 2 and 4) to 60% (set 3; Table 2; Fig 4a-b). The SM assigned for the CVI-12 set did not share any similarities with any SMs from Iceland and the Cape Verde but shared 27% similarity with the CAR-12 song (Table 2; Fig 4 a-b). The CAR-12 song sequence shared 33% similarity with the ICE-11 SMs and 27% similarity with the CVI-11 SM.

Dice’s Similarity Index (DSI) revealed a general trend of gradual decrease in DSI phrase repertoire similarity from each period and to the period furthest away in time (Fig 5). There was a strong similarity, i.e. 82%, between the phrase repertoire in the Caribbean in 2008 (CAR-08) and in Iceland in 2009 (ICE-09) but the similarity dropped to 33% DSI between CAR-08 and ICE-10 and was 53% DSI between ICE-09 and ICE-10. The songs for each period in Iceland in 2011 shared 88–92% of the phrases with each other (Magnúsdóttir & Lim 2017), and 58–67% were shared with the Cape Verde phrase repertoire in 2011 (CVI-11) according to the DSI. The songs from Iceland in 2011 shared 33–38% of the phrases with the repertoire from the Cape Verde in 2012 (CVI-12), and 29–33% of the phrase repertoire with the CAR-12 song (Fig 5). The CVI-11 songs shared 50% of the phrases with the CVI songs from a year later, i.e. in 2012 (CVI-12), and 47% with the CAR song from 2012 (CAR-12). The CAR-12 song and the CVI-12 songs shared 53% of the phrases with each other (Fig 5). A variant of phrase 5c was present in the CAR-12 song, named phrase 5cc. When 5c and 5cc were combined the similarity (DSI) between the CAR-12 and the CVI-12 songs rose up to 57%.

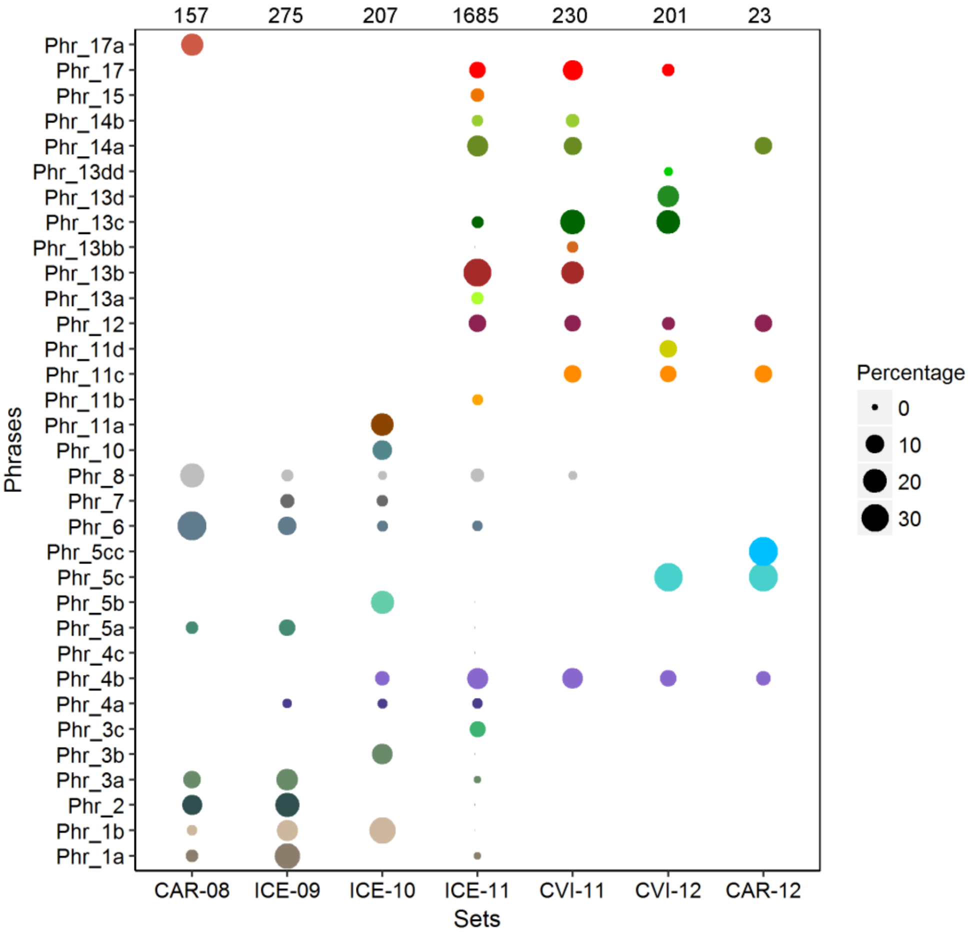

Fig 3 The percentage of occurrence of each observed phrase during each location and period (i.e. within set). The sizes of the dots indicate the percentage of occurrence of each phrase within a set. The values above each set show the sample size (n), i.e. the number of phrases included in the analysis.

In total, the songs from CAR-08 shared eight phrases with the songs from ICE-09 and five phrases with ICE-10 whereas ICE-09 and ICE-10 also shared five phrases The songs from CVI in 2011 shared eight phrases with the Icelandic songs in 2011 (ICE-11) and four phrases with the CVI songs in 2012, where the CVI songs in 2012 and the Icelandic 2011 songs also shared four phrases. The CAR-12 song shared four phrase types with the CVI songs in 2011 and 2012 but three phrase types with the Icelandic songs in 2011. Phrases 4b and 8 were the most consistent phrases observed through the course of this study (Fig 3). Phrase 4b was first observed in the ICE-10 dataset and continued to occur in the songs until the last season studied. Phrase 4b lengthened in 2011 due to increased repetition of the song unit MUp3 (Fig S1 4). Also, phrase 4b was more common in the songs from 2011 compared to other years (Fig 3). Phrase 8 was first observed in the CAR-08 songs and continued to appear in the songs until 2011 but was not observed in the subtropical song in 2012. Phrase 8 was modified between years where the repeated song unit type Li2 lengthen in the 2011 songs (Fig S1 3). Phrase 8 was first observed in the CAR-08 songs and continued to appear in the songs until 2011 but was not observed in the subtropical song in 2012. Phrase 8 was modified between years where the repeated song unit type Li2 lengthen in the 2011 songs (Fig S1 3). Other consistent phrases were phrases 6 (Fig S1 3) and 12 (Fig S1 5). Phrase 6 was observed in the Caribbean in 2008 and occurred until 2011 in both Iceland and the CVI. Phrase 12 was first observed in the 2011 songs and continued in both locations in 2012. In total of 47% of all the observed phrases were shared between one or more years, i.e. phrases 17, 14a, 13c, 12, 11c, 8, 7, 6, 5a, 4b, 4a, 3a, 2, 1b and 1a whereas 44% of all the phrases were shared between Iceland and the subtropics, i.e. phrases 17, 14b, 14a, 13c, 13b, 12, 8,

Table 2 Set median sequences (i.e. representative sequences) obtained from the Levenshtein Distance (LD) calculations and few examples of full song sequences delineated from each period (set). ICE-11-1-4: Songs recorded in Iceland during the first to the fourth period in 2011, CVI-11 and -12: Songs recorded in the Cape Verde in 2011 and 2012, respectively, CAR-12: Song recorded in Dominica in the Caribbean in 2012. Only one continuous theme sequence was obtained from the Caribbean Islands (CAR) in 2012. Since set median could not be calculated from such a small dataset a representative sequence subtracted from the total theme sequence was found according to delineation methods.

Set	Full song examples	A representative sequence	Sum of LD
ICE-11-1	17-14a-13b-12-4b	14a-13b-12-4b	17
ICE-11-2	17-15-14a-13b-12-4b-4a 3c-1a-14a-13c-13b-12-4b	14a-13b-12-4b	28
ICE-11-3	17-13c-14a-13b-12-4b 17-11b-15-14a-14b-13b-12-4b-4a 17-11b-13c-14a-14b-13b-12-4b	17-14a-13b-12-4b	66
ICE-11-4	17-11b-14a-12-4b 17-15-13c-13b-12-4b 17-15-14a-13b-12-4b 8-6-14a-13b-12-4b	14a-13b-12-4b	36
CVI-11	17-11c-14a-13c-13b-12-4b	13c-13b-12-4b	40
CVI-12	17-11d-11c-13c-13d-5c-4d-4b	11d-11c-13c-13d-5c	50
CAR-12	5c-4d-4b-11c-14a-1b	11c-14a-1b-5c-4d-4b	-

6, 5a, 4b, 3a, 2, 1b and 1a (Fig 3; Fig S1 1–8). Phrase 11d from the CVI-12 songs and 11c from CVI-11, CVI-12 and CAR-12 seemed to have developed from 11b in the ICE-11 songs (Fig S3 1). Phrase-11d occurred as a transition between 11c and 14b in CVI-11 and, thus, was not registered as a phrase, the similarity is however noteworthy and demonstrates a possible development from phrase 11c. Phrase 11b was only observed in the ICE-11 songs and may have developed into the two similar phrases, i.e. 11c and 11d, in the Cape Verde. A modified version of phrase 11c was also observed in the CAR-12 song (Fig S1 8).

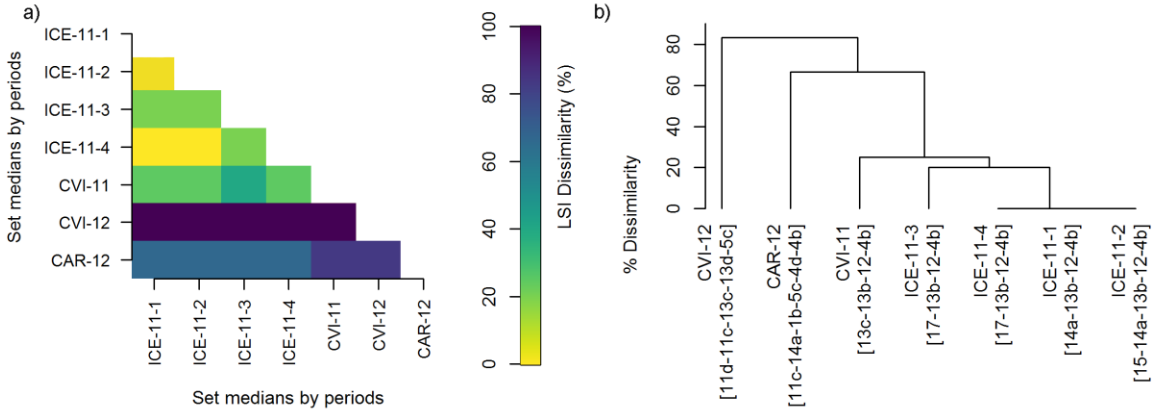

Fig 4. Similarity analysis of song sequences. ICE-11-1-4: Iceland during the first to the fourth period in 2011, CVI-11 and -12: Songs from the Cape Verde in 2011 and 2012, respectively, CAR-12: Song from the Caribbean in 2012. The comparison of set median sequences for each set (period and location) and the single sequence from the CAR is demonstrated in figure a) as a dissimilarity Matrix where identical representative sequences are 0% dissimilar and are assigned a dark purple colour and from that increased dissimilarity evolves into green and finally yellow when two sequences are 100% dissimilar according to the LSI. The dendrogram in b) shows a nearest neighbour clustering of sequences based on LSI values. The SMs from 2011 form a single cluster and the SM for CVI 2012 and the sequence from CAR 2012 form two other separate clusters

Additionally, phrase 5c from the CAR-12 and CVI-12 songs were very similar to themes recorded in Iceland during the winter in 2009 and originally published by Magnúsdóttir *et al.* (2015), these were 1a and 5a respectively (Fig S1 1). Variants of common phrases were found within songs of individual singers. The single singer recorded in the Caribbean in 2012 (CAR-12) sang a variant of phrase 5c, named 5cc, before and after the phrase 5c. Phrase 5cc included a low frequency down swept signal (Lt3) not found in phrase 5c which occurred before an upsweep signal (MUp1). The MUp1 signal from phrase 5cc was very similar to a MUp1 subunit sung within a subunit complex (Md1+MUp1) in phrase 5c, i.e. in terms of frequency range, the frequency modulation and the sloping trend of the signal contour. The singer seemed to skip the Md1 subunit of the Md1+MUp1 subunit complex and the following MUp3 units which resulted in the variant phrase 5cc (Fig S1 8). A singer from the CVI-11 sang a variant of phrase 13b (i.e. 13bb) (Fig S2 1) by skipping the low frequency song units Lt2 from the phrase while another singer in CVI-12 added an additional Lt2 signal into the phrase 13d (i.e. 13dd) (Fig S2 1).

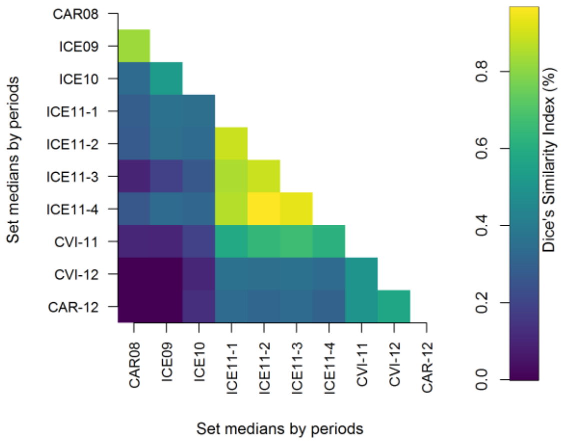

Fig 5 The matrix demonstrates the level of theme sharing between every two sets (period and location) based on the Dice's Similarity Index. CAR08: Songs recorded in Dominica in the Caribbean in 2008, ICE09-10: Songs recorded in Iceland in 2009 and 2010, ICE-11-1-4: Songs recorded in Iceland during the first to the fourth period in 2011, CVI-11 and -12: Songs recorded in the Cape Verde in 2011 and 2012, respectively, CAR-12: Song recorded in Dominica in the Caribbean in 2012. If any two sets shared 100% identical theme repertoire they were assigned a yellow colour. The colour evolved into green and finally dark purple with decreased similarity, i.e. lowering number of shared themes between two sets

The diagrams in Fig 6 show how the song sequences gradually developed from the first period in Iceland (end of January 2011 until mid-March) and until in the Cape Verde (between April–May 2011). The last two diagrams show how the transition trend had developed a year later in 2012 in the Cape Verde and in the Caribbean. The song from the Caribbean (CAR-12) included only single transitions and was, therefore, only used for comparison since a single song cannot represent the complete variation in songs from a particular season and location. The arrow width and direction between representative phrases stayed relatively constant in Iceland from ICE-11-1 to ICE-11-4 while more pronounced changes started to occur later that year in the Cape Verde (CVI-11) and a complete change in the pattern of arrow direction and arrow width occurred a year later in the Cape Verde (CVI-12) and in Dominica (CAR-12) (Fig 6).

DISCUSSION

This study demonstrates strong evidence for humpback whale song sharing between the Icelandic subarctic feeding grounds and the subtropical breeding grounds in the Cape Verde archipelago and the eastern Antilles archipelago (Lesser Antilles) in the Caribbean Sea. With a combination of first-order Markov models and similarity analyses (LD, LSI and DSI) it was possible to investigate what song components were shared between these subarctic and subtropical habitats.

The level of phrase sharing between adjacent sets (location and period) ranged from 34–82% DSI where the strongest phrase repertoire similarity between different locations was, found between the Caribbean in 2008 and Iceland in 2009 (82% DSI). The lowest sharing occurred between Iceland in 2010 and 2011 indicating a pronounced shifting in song phrases in 2011, a phenomenon not uncommon during song evolution in humpback whales (Payne & Payne 1985; Noad *et al.* 2000; Eriksen *et al.* 2005; Garland *et al.* 2011). Since the recordings from Iceland in 2009 and 2010 did not allow for delineation of phrases it was not possible to find set medians from these datasets and compare with sequences from the adjacent season in the Caribbean (CAR-08). However, the strong similarity of the phrase repertoires from the Caribbean in 2008 and Iceland in 2009 indicates potentially high levels of song sharing between these subarctic and subtropical habitats

The theme sequences constituting the songs recorded during winter in Iceland were very similar to the sequences recorded in the Cape Verde Islands the following spring. As a result, all the songs from that breeding season, i.e. 2011, were grouped into a single cluster according to the LSI analysis and hierarchical

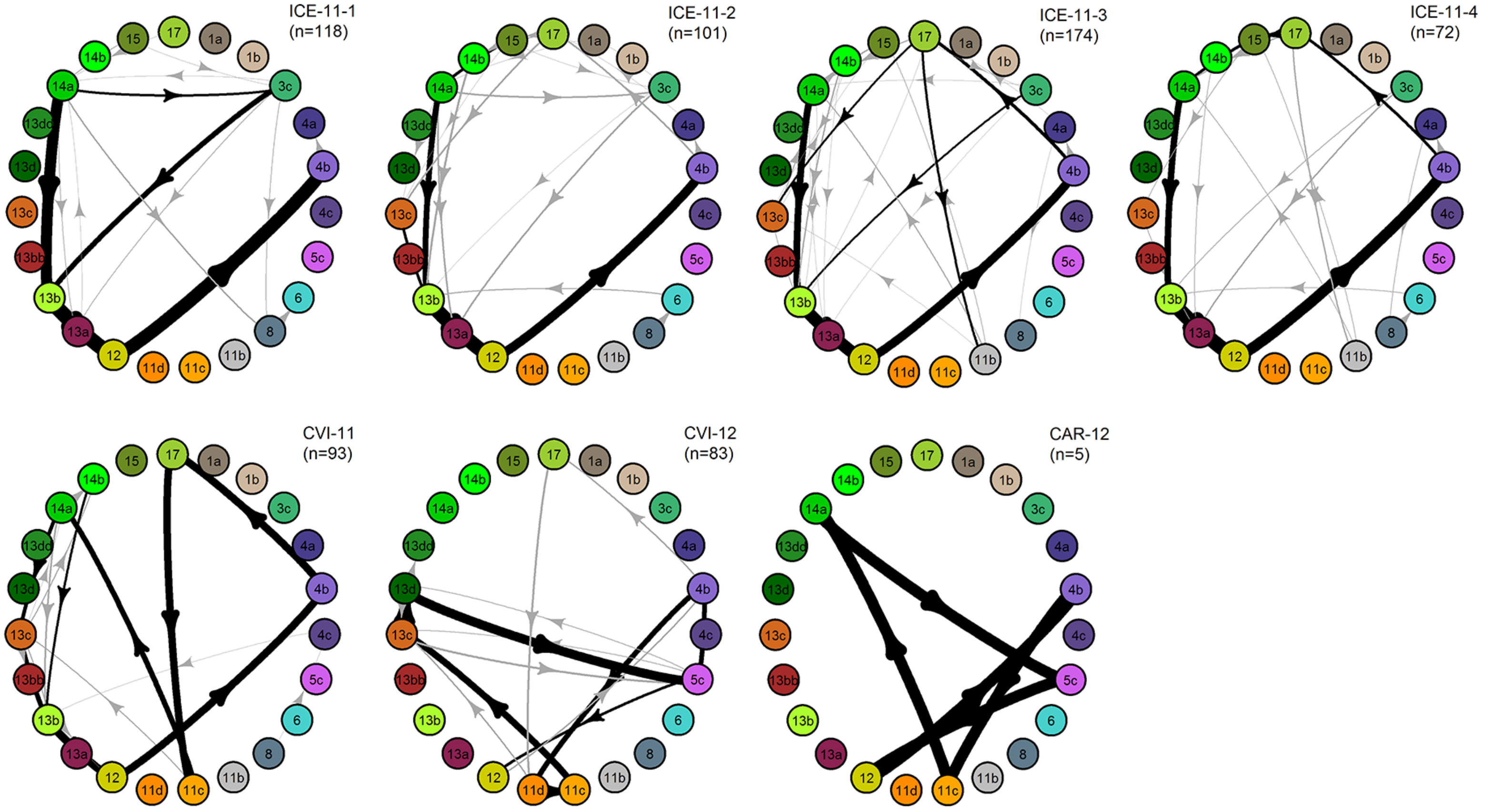

Fig 6 Transition diagrams from each period and location (set) based on Markov transition matrices. The data points (n) represent the number of analysed transitions observed during each period. Each diagram contains all the observed phrases from songs in Iceland, the Cape Verde and one song cycle from the Caribbean (CAR-12). The CAR-12 song includes single transitions and is therefore only used for comparison but does not represent a general trend of songs from this location and period. The phrase 5c and its variant 5cc are merged together in the diagrams. The grey lines represent transitions occurring less than 5% of the time and black lines occurred more than 5% of the time. The line thickness indicates the percentage likelihood of a transition to occur with wider line corresponding to greater percentage.

clustering. These songs evolved as a result of insertion, deletion and modification of themes and some themes became more common and other rarer as the period progressed. For example, common themes from 2011 such as 13b, 12, 4b and 14a stayed relatively constant throughout the season in the subarctic and in the Cape Verde, whereas phrases 17 and 13c became more common as the period progressed and phrase 11b appeared to have been modified into phrase 11c in the Cape Verde (CVI-11) and further into 11d a year later in the Cape Verde (CVI-12) and in Dominica (CAR-12).Modification of phrases occurred as spectral parameters of at least one unit type changed or new units were inserted into older phrases. The rarer phrases 13a, 3c, 15, 11b and 4a from Iceland in 2011 were either deleted from the songs or became even rarer and were thus less likely to be detected in the subtropics. However, a larger sample set from the tropical breeding grounds is needed to describe the development of these rare phrases during the process of cultural transmission. Analysis and comparisons of songs recorded a year later in the same subtropical breeding ground (CVI-12) demonstrated more pronounced substitution and re-ordering of themes. Phrase 5c from the Cape Verde and Caribbean in 2012 was very similar to phrases 1a and 5a recorded in Iceland during the winter in 2009 and published by Magnúsdóttir *et al.* (2015). That could demonstrate a recycling of an older phrase. Even though the set median sequence from the Cape Verde in 2012 was placed in a separate group from the song from the Caribbean the phrase repertoire from these two locations shared considerable similarity (53% DSI). Thus, supporting previous findings by Winn *et al.* (1981) that songs from these different breeding grounds shared thematic similarities some three decades later. The similarity observed in the present study was thus primarily evident in terms of the phrases sung within the songs with four phrases being shared.

The Cape Verde Islands and the Caribbean (West Indies), the only known breeding locations of humpback whales in the North Atlantic, share similar latitudes, or approximately 15–16°N, but are separated by an ocean basin of at least 4000 km. These breeding grounds are situated on opposite sides of the mid-Atlantic ridge which converges at the joint feeding ground off Iceland. Due to different geographical locations of these subtropical breeding grounds and a converse angle from Iceland it is unlikely that the migration routes to these destinations would overlap greatly but singers need to be in acoustic contact in order to share song components. Therefore, it is not possible that sharing could have occurred across ocean basins since the sounds of the songs do not travel that far. Data from satellite tracked humpback whales during migration has, to date, commonly shown that the whales migrate in a relatively straight line with few, if any, detours and layovers on the way (Horton *et al.* 2011; Kennedy *et al.* 2013). If such migration behaviour is general within this species it is less likely that whales en route to the opposite breeding locations in the North Atlantic would associate during migration. Additionally, movements between breeding grounds within-season have only rarely been observed (Garrigue *et al.* 2002; Garrigue *et al.* 2011a). Thus, for these patterns of similarity to be observed the transmission of song components in the North Atlantic would be expected to be most active prior to migration on a joint feeding ground. Continual song sharing between migrating individuals heading for the same breeding assembly would lead to further within-location evolution of the songs, resulting in slightly different songs for these two breeding grounds. To date, only a single study, i.e. Garland *et al.* (2013a), has shown song sharing between two populations on a feeding ground. The active singing in Iceland until mid-March 2011 and a clear similarity with the songs from Cape Verde songs during 2011 strongly suggest that vocal convergence for an undefined unit of humpback whales feeding in central and eastern North Atlantic occurred in this subarctic feeding ground, consequently supporting the previous findings from the Southern Ocean (Garland *et al.* 2013a).

Evolution and variation of the songs

The Markov models demonstrated a greater transition variation in the Icelandic songs compared to the sub-tropical songs. That could be explained with a larger number of singers as well as a larger data set of song sequences. However, the recordings from Iceland occurred from the onset of the breeding season and continued until mid-/late breeding season while the sub-tropical song samples were from near the end of the estimated breeding season, i.e. May (Jann *et al.* 2003). Consequently, the variety in theme transitions found in the songs from Iceland might be explained with that the songs are evolving and the entropy (Suzuki *et al.* 2006) is relatively high as the singers are gradually synchronising their songs. Conversely, the late season songs from the subtropics have evolved further and become more uniform.

(Cerchio *et al.* 2001), individual variation can also be observed. For example, Arraut and Vielliard (2004) described individual variation in the way singers produced certain unit types (referred to as notes). As an example from this study, the same singer singer from the CVI-11 sang a variant of theme 13b (i.e. 13bb) by deleting low frequency units from the phrase, another singer in the CVI-12 added an additional low frequency unit into the phrase 13d (i.e. 13dd) and the single singer recorded in the Caribbean in 2012 seemed to modify phrase 5c within the same song sequence by sometimes mixing low frequency units into the phrase and also by varying the number of MUp3 song units.

Humpback whale singing is a type of production learning (Janik & Slater 2000) where the singers learn and copy sounds from others and can be innovative in sound production, a process which leads to song conversion (Tyack 2008). Such vocal behaviour is likely to result in some variation in signal production and theme order within a singing aggregation. Consequently, greater number of singers and a larger sample of sounds could lead to some variety in songs during the convergence process.

Connection between a subarctic feeding ground and subtropical breeding grounds in the North Atlantic

The apparent song similarity between Iceland and the Cape Verde Islands during the same breeding season strongly suggests that Cape Verde is an active breeding ground during the spring for humpback whales from Icelandic feeding grounds. Also, the level of phrase sharing between the Caribbean (Lesser Antilles) in 2008 and Iceland in 2009 indicate a connection between these habitats. Additionally, the degree of phrase sharing between the two subtropical breeding grounds provides further evidence of a population connection between these two habitats. A larger sample size is needed from these North Atlantic breeding grounds to demonstrate more robustly the level of song exchange between these areas. Nonetheless, this mirrors the findings from the North Pacific where the songs from different breeding grounds within the same ocean basin displayed strong similarity despite of being separated by more than 2000 km (Cerchio *et al.* 2001; Darling *et al.* 2014). As a result, this sharing of phrases and consequently themes and song sequences provides evidence of the level of the sharing of song culture between the subarctic and the subtropics in the North-Atlantic.

A small sample of humpback whales photo-identified in Icelandic waters was re-captured in the Cape Verde Islands (Jann *et al.* 2003). However, no matches have been found, to the best of our knowledge, between Iceland and the Lesser Antilles. A possible explanation could be that the Lesser Antilles are understudied and only a relatively small photographic collection exists from this area compared to the Dominican Republic breeding assembly in the Caribbean. Nonetheless, a single photo-identification has been made between North Norway and the Lesser Antilles (Stevick *et al.* 2016) and two satellite tagged humpback whale were confirmed to migrate from Guadeloupe in the Lesser Antilles and towards Iceland and North Norway (Kennedy *et al.* 2013). The song recordings in this study are consistent with and support these previous findings. The singers in Iceland either migrate to or are at least associated with humpback whales breeding in the Cape Verde and the Lesser Antilles of the Caribbean. Stevick *et al.* (2016) showed that four humpback whales were identified in both the Cape Verde and Guadeloupe in the Lesser Antilles in different years. However, to date, no matches have been found between the more abundant Silver Bank area off the Dominican Republic and the Cape Verde and little interchange appears to be between the Silver Bank area and the Lesser Antilles (Kennedy *et al.* 2013; Stevick *et al.* 2016), indicating a population linkage between the Lesser Antilles and the Cape Verde.

Whales from the central and eastern feeding grounds such as Iceland and Norway have been shown to exhibit longer distance movements over shorter time periods than whales from western feeding grounds in the North Atlantic (Stevick *et al.* 2006). Since the time of singing in Iceland, which extends far into the breeding period, tallies with the average time of arrival in the Cape Verde Islands and the Lesser Antilles, there appears to be an opportunity for these whales to start their southbound migration later. Consequently, these whales can extend the time spent feeding without necessarily delaying mating or at least mating displays. It is therefore possible that the breeding habitat of central and eastern North Atlantic humpback whales is not only limited to the low latitude areas but extends into their subarctic feeding grounds.

Future studies on the social structure, gender ratio and reproductive status of humpback whales wintering in subarctic feeding grounds and more extensive song comparison between feeding and breeding grounds in the North Atlantic would enable confirmation of critical habitats and timings for humpback whales in the North Atlantic. Such knowledge would be essential for addressing management considerations for this species with better understanding of possible segregation into stocks and units within the North Atlantic.

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Supplementary Material

The importance of a subarctic feeding ground for humpback whale song transmission to subtropical breeding grounds in the North Atlantic Ocean

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S1 Phrase comparison between locations and periods (sets)

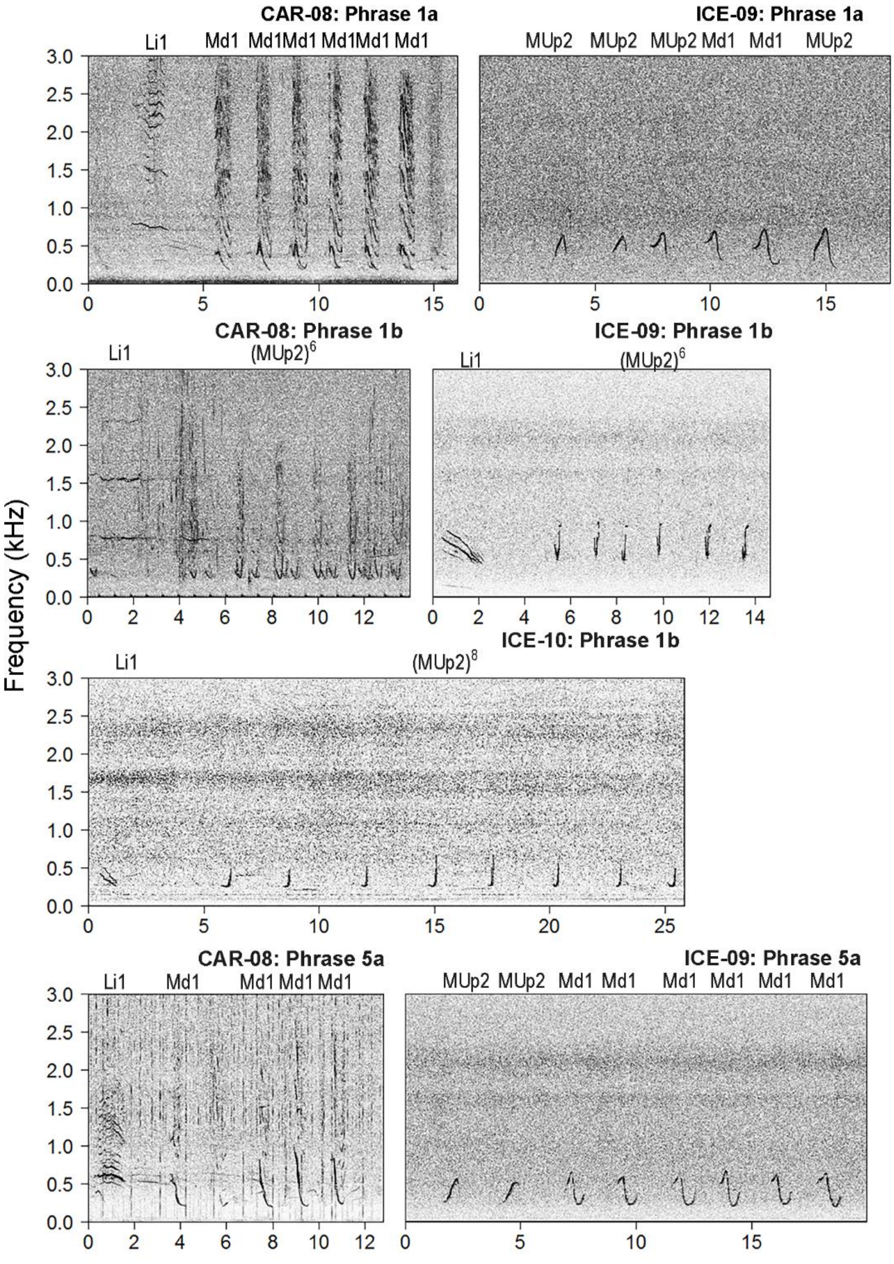

Fig S1 1 Spectrographic representations of the phrase types 1a, 1b and 5a from the Caribbean in 2008 (CAR-08) and Iceland in 2009 (ICE-09) and 2010 (ICE-10). The song units composing each phrase are labelled on top of each spectrogram. A detailed description of the labelling and naming convention of the represented phrases can be found in the methods chapter. The spectrograms were generated using fast Fourier transformation (FFT) (size 2048 Hanning window) with a frequency resolution of 7.8 Hz and a 95% overlap. Each unit within a phrase is labelled with a corresponding unit group name.

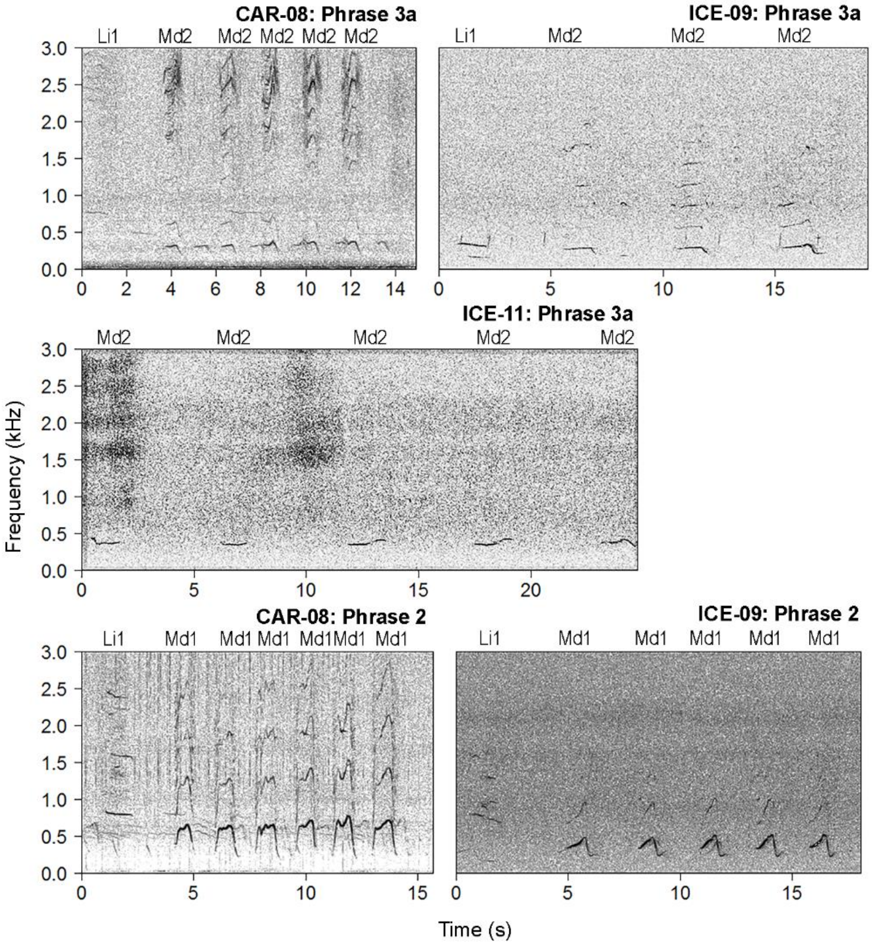

Fig S1 2 Spectrographic representations of the phrase types 3a and 2 from the Caribbean in 2008 (CAR-08) and Iceland in 2009 (ICE-09) and 2011 (ICE-11). The song units composing each phrase are labelled on top of each spectrogram. A detailed description of the labelling and naming convention of the represented phrases can be found in the methods chapter. The spectrograms were generated using fast Fourier transformation (FFT) (size 2048 Hanning window) with a frequency resolution of 7.8 Hz and a 95% overlap. Each unit within a phrase is labelled with a corresponding unit group name.

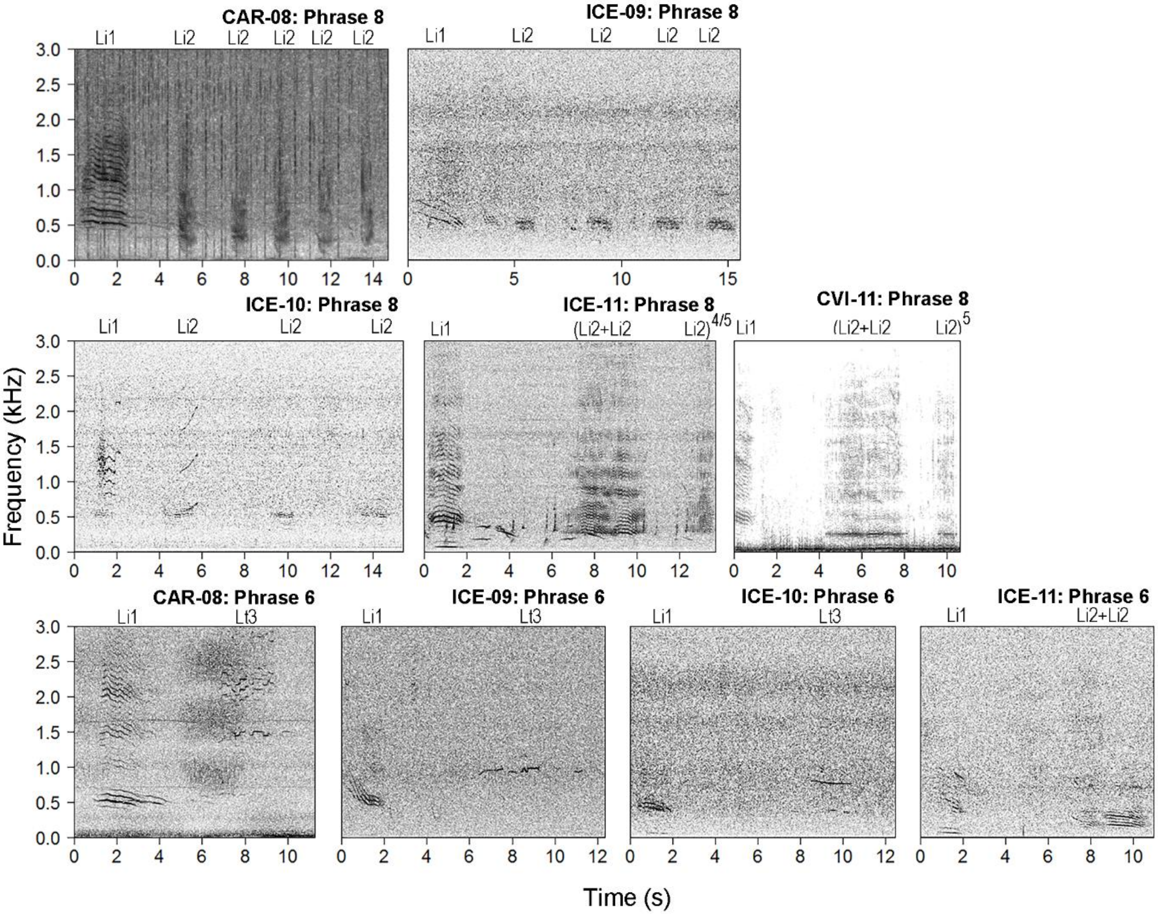

Fig S1 3 The song units composing each phrase are labelled on top of each spectrogram. A detailed description of the labelling and naming convention of the represented phrases can be found in the methods chapter. The spectrograms were generated using fast Fourier transformation (FFT) (size 2048 Hanning window) with a frequency resolution of 7.8 Hz and a 95% overlap. Each unit within a phrase is labelled with a corresponding unit group name. Song units composed of sub-units in phrase 8 from ICE-11 and CVI-11 were identified by the two corresponding sub-unit groups which were connected with a '+' symbol.

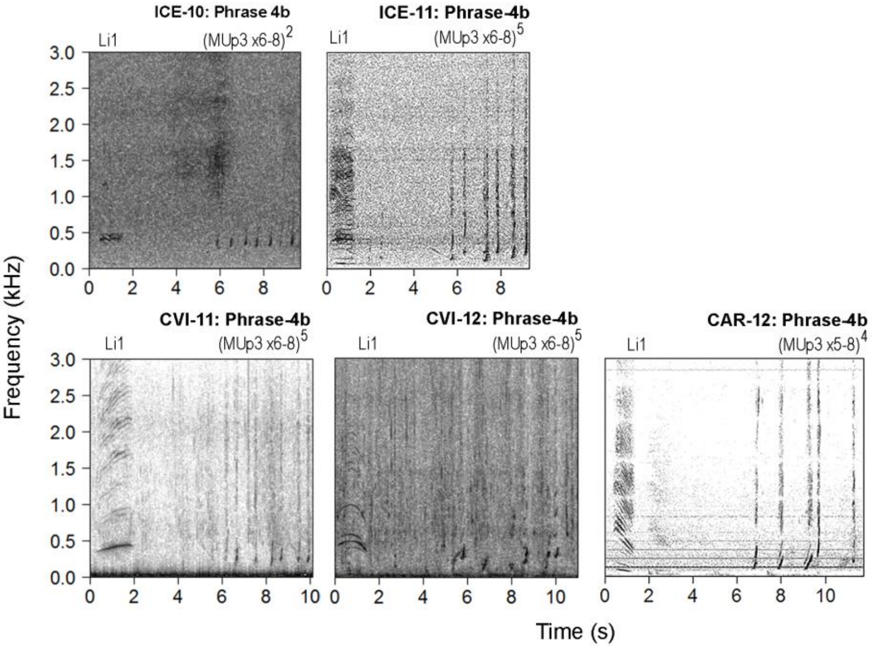

Fig S1 4 Spectrographic representations of the phrase type 4b from different sets, i.e. Iceland in 2009 (ICE-09), 2010 (ICE-10) and 2011 (ICE-11), Cape Verde in 2011 (CVI-11) and 2012 (CVI-12) and the Caribbean in 2012 (CAR-12). The song units composing each phrase are labelled on top of each spectrogram. A detailed description of the labelling and naming convention of the represented phrases can be found in the methods chapter. The spectrograms were generated using fast Fourier transformation (FFT) (size 2048 Hanning window) with a frequency resolution of 7.8 Hz and a 95% overlap. Each unit within a phrase is labelled with a corresponding unit group name. This phrase type was composed of repeated sharp upsweep units (MUp3). This phrase developed further in 2011 and became shorter in duration with shorter interval between each song unit where the song units were repeated in bouts of 5–8 MUp3 units. These MUp3 song units from 2011 and 2012 are similar to previously reported song units often named “Wop” in the literature.

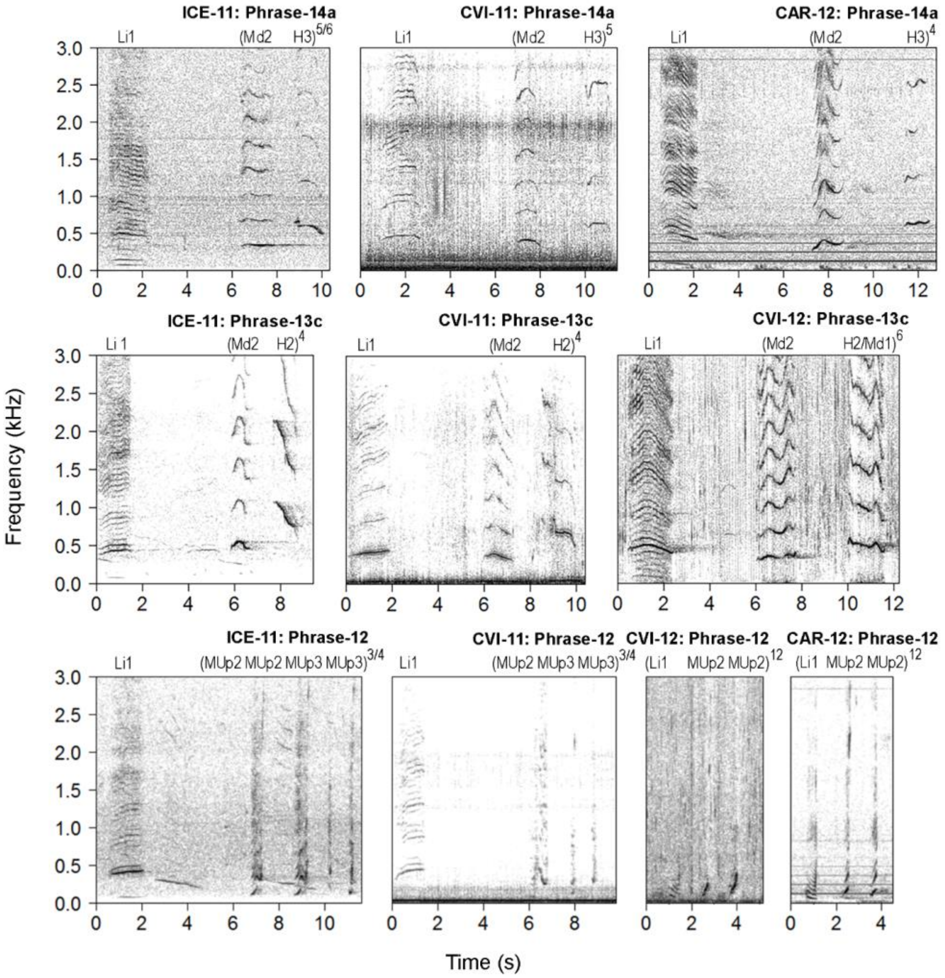

Fig S1 5 Spectrographic representations of the phrase types 14a, 13c and 12 from different sets, i.e. Iceland in 2011 (ICE-11), Cape Verde in 2011 (CVI-11) and 2012 (CVI-12) and the Caribbean in 2012 (CAR-12). The song units composing each phrase are labelled on top of each spectrogram. A detailed description of the labelling and naming convention of the represented phrases can be found in the methods chapter. The spectrograms were generated using fast Fourier transformation (FFT) (size 2048 Hanning window) with a frequency resolution of 7.8 Hz and a 95% overlap. Each unit within a phrase is labelled with a corresponding unit group name.

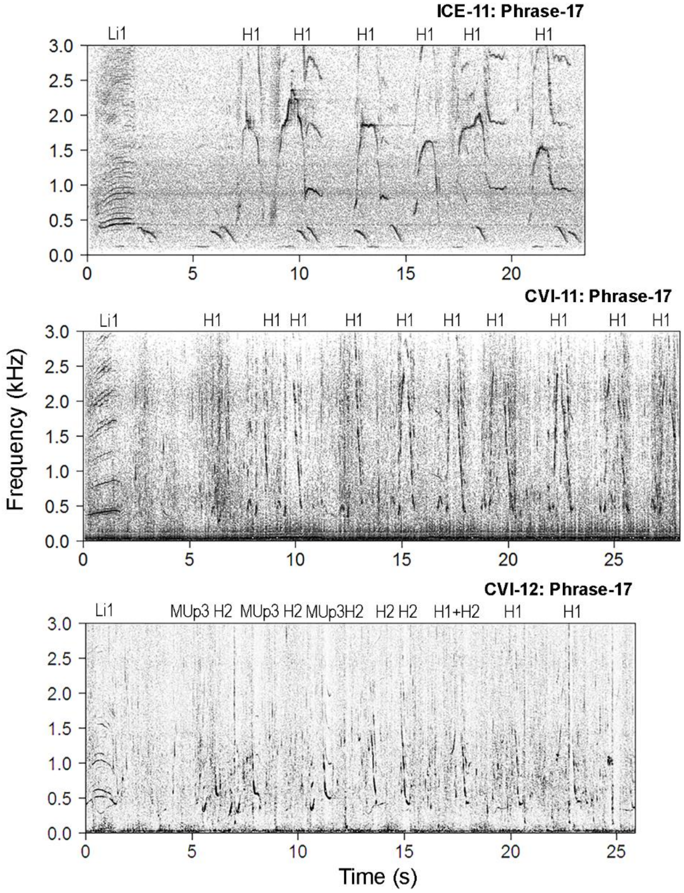

Fig S1 6 Spectrographic representations of phrase 17 from different sets, i.e. Iceland in 2011 (ICE-11), Cape Verde in 2011 (CVI-11) and 2012 (CVI-12). The song units composing each phrase are labelled on top of each spectrogram. A detailed description of the labelling and naming convention of the represented phrases can be found in the methods chapter. The spectrograms were generated using fast Fourier transformation (FFT) (size 2048 Hanning window) with a frequency resolution of 7.8 Hz and a 95% overlap. Each unit within a phrase is labelled with a corresponding unit group name. Song units composed of sub-units (from CVI-12) were identified by the two corresponding sub-unit groups which were connected with a '+' symbol.

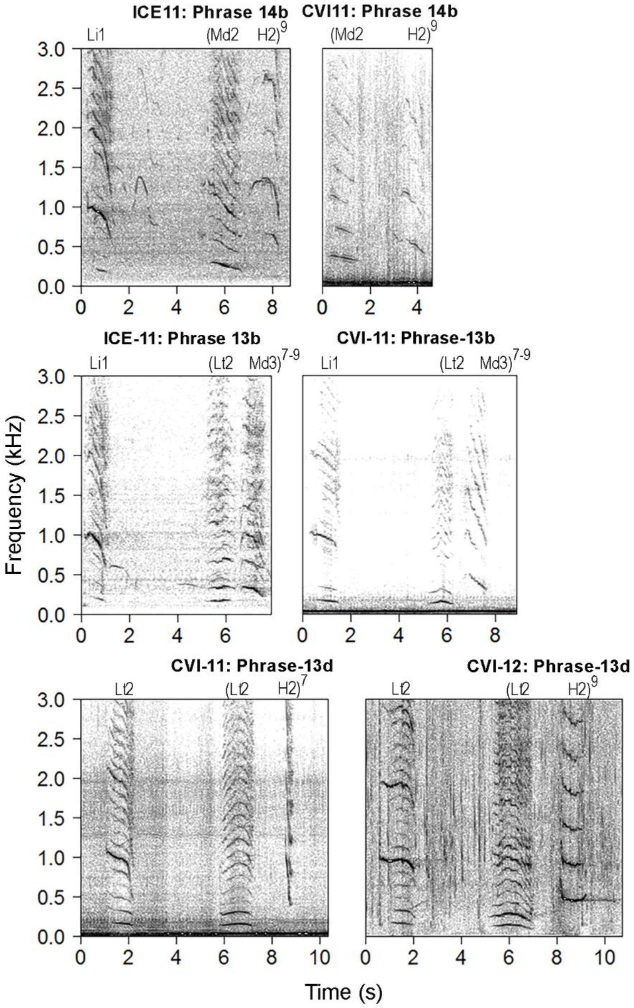

Fig S1 7 Spectrographic representations of the phrase types 14b, 13b and 13d from different sets, i.e. Iceland in 2011 (ICE-11) and Cape Verde in 2011 (CVI-11) and 2012 (CVI-12). The song units composing each phrase are labelled on top of each spectrogram. A detailed description of the labelling and naming convention of the represented phrases can be found in the methods chapter. The spectrograms were generated using fast Fourier transformation (FFT) (size 2048 Hanning window) with a frequency resolution of 7.8 Hz and a 95% overlap. Each unit within a phrase is labelled with a corresponding unit group name.

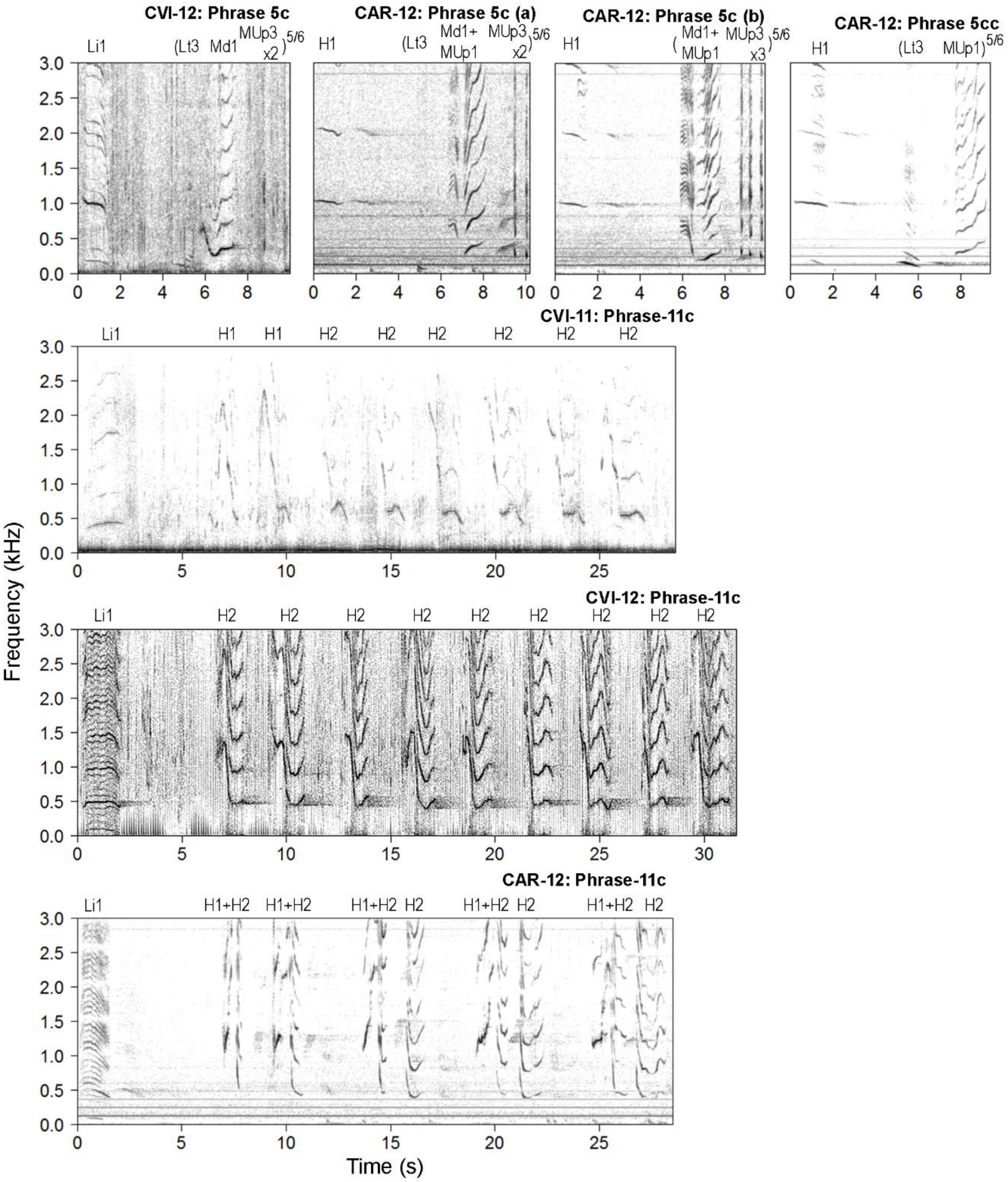

Fig S1 8 Spectrographic representations of 5c and phrase 11c from different sets, i.e. Cape Verde in 2011 (CVI-11) and 2012 (CVI-12) and Dominica (CAR-12). A variant of phrase 5c from CAR-12, i.e. 5cc, is shown. The song units composing each phrase are labelled on top of each spectrogram. A detailed description of the labelling and naming convention of the represented phrases can be found in the methods chapter. The spectrograms were generated using fast Fourier transformation (FFT) (size 2048 Hanning window) with a frequency resolution of 7.8 Hz and a 95% overlap. Each unit within a phrase is labelled with a corresponding unit group name. Phrase-11c was not constructed from a constant repetition during CVI-11 and is therefore presented here in its full length for each set for a better comparison. Song units composed of sub-units (from CAR-12) were identified by the two corresponding sub-unit groups which were connected with a ‘+’ symbol.

S2 Phrase variants and phrase development

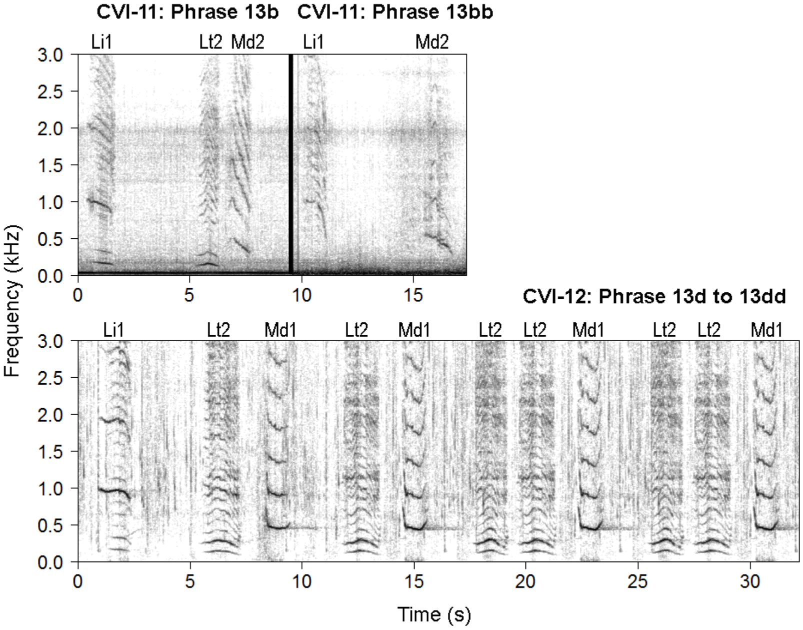

Fig S2 1 Phrase 13bb on the upper spectrogram is a version of 13 b where the low frequency Lt2 units have been discarded. The lower spectrogram shows how phrase 13d changes into its variant, i.e. 13dd, by singing a low frequency unit (Lt2) in between the down swept (Md1) units. The vertical, black line indicates the division between phrases 13b and 13bb, since 13d develops into 13dd within the same phrase no vertical line is used to divide between the phrases.

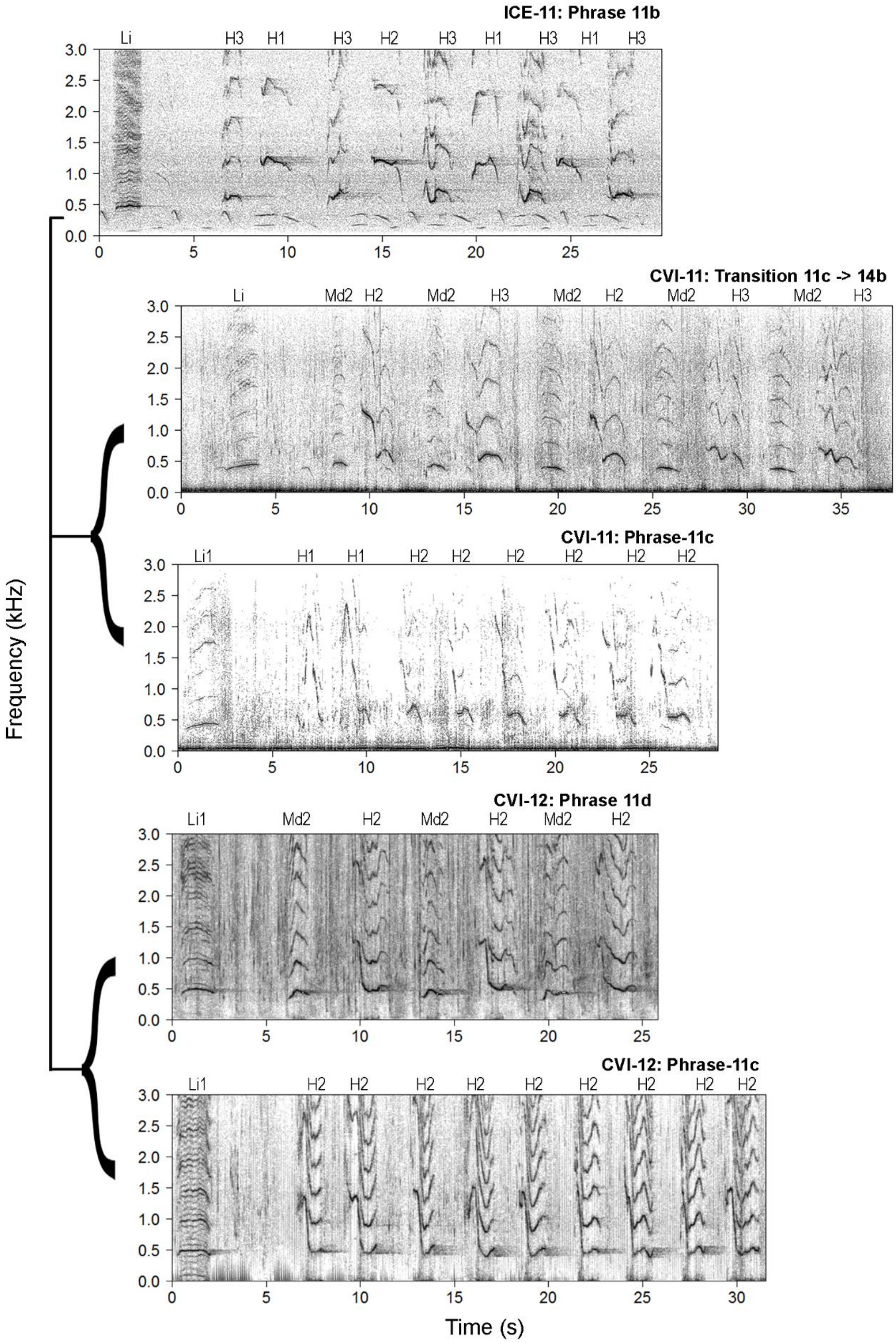

Fig S2 2 Spectrographic representations of the phrases 11b from Iceland (ICE-11), 11c from Iceland in 2011 and the Cape Verde in 2011 (CVI-11) and 2012 (CVI-12) and 11d from CVI-12. Phrase-11d occurred as a transition between 11c and 14b in CVI-11 and was not registered as a phrase, the similarity is however noteworthy and demonstrates a possible development from phrase 11c. Phrase 11b was only observed in the ICE-11 dataset and may have developed into the similar phrases 11c and/or 11d in the Cape Verde and the Caribbean.

Final words

We are one, human and nature. Understanding every aspect of nature and its inhabitants provides us with the whole picture. Therefore, we must continue to learn and understand, understand just a little bit better with every sand grain of knowledge provided by each sufficiently conducted study. Our Earth’s climate is changing more rapidly than ever before, we must pay attention to the signals nature is giving us. With natural science we can find these signals and act accordingly.