Faculty of biosciences, Fisheries and Economics
Department of Arctic and Marine Biology

Decadal changes in distribution, abundance and feeding ecology of baleen whales in Icelandic and adjacent waters.

— A consequence of climate change?

Gísli A. Víkingsson

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Gísli A. Víkingsson

2. Summary

Icelandic waters are characterized by high productivity partly due to it‘s location on the Mid-Atlantic ridge where warm and cold water masses meet south of the Arctic Circle. These waters sustain high diversity and abundance of cetaceans with a total of 23 species documented in the area. Five species of baleen whales are regularly encountered in Icelandic waters during summer. They have all been subject to whaling operations to varying degrees and periods since the so-called modern whaling techniques were introduced to Iceland by Norwegian whalers in 1883. A whaling ban in 1915 marked the end of the first period of commercial whaling in Iceland that left most of the whale stocks highly depleted. The whale populations have recovered to a varying degree and today two species, the common minke whale and the fin whale are exploited sustainably.

Systematic monitoring of distribution and abundance of cetaceans in Icelandic and adjacent waters was initiated in 1987 as a part of the multi-national North Atlantic Sightings Surveys (NASS). Since then, large scale surveys have been conducted at around 6-8 year intervals as recommended by the International Whaling Commission (IWC) and North Atlantic Marine Mammal Commission (NAMMCO). In this thesis, the objecive is to summarize the results of these surveys in relation to changes in the marine environment and the feeding ecology of four baleen whale species. In particular I will explore recent changes in distribution and abundance of fin, common minke, humpback and blue whales in Icelandic waters and the ecological role played by the most abundant species.

The results presented here indicate an important role played by baleen whales in the marine ecosystem around Iceland. Icelandic waters represent summer feeding grounds for these migratory species, which are believed to fast or feed at much lower rates during winter. Deposition of energy reserves during the feeding season differed among reproductive classes in both fin and common minke whales. Pregnant female fin whales stored the largest amounts of energy in tissues s.a. blubber, muscle, visceral fat and bones, thereby increasing the energy content of the body by 80% over an assumed four month feeding season. The difference between reproductive classes was qualitatively similar but less pronounced in common minke whales. Two independent methods to estimate daily feeding rates of fin whales gave similar results that are close to the center of the wide range of values assumed in previous studies on cetacean feeding rates. The consumption by the 12 species of cetaceans regularly occurring in Icelandic waters was estimated at around 6 million tons in the 1990’s. Around two thirds of the total consumption was attributable to fin and common minke whales. The results of satellite tracking of minke whales suggest a somewhat later departure from the feeding grounds in autumn than generally assumed. This indicates that the summer residence time used in the above estimate based on catch statistics may have been underestimated.

The potential effects of variable *per-capita* prey abundance on body condition and fecundity of fin whales was studied by a two stage modelling approach. The results indicate that below a certain threshold, per-capita prey abundance will negatively affect blubber thickness. Whales with thin blubber (<50mm) had lower probability of being pregnant than those with average or higher blubber thickness. These results are consistent with a density dependent response in North Atlantic fin whale pregnancy rate.

Pronounced oceanographic changes have occurred in Icelandic waters since the mid-1990s, including a rise in sea water temperature and increased flow of warm Atlantic water into the area north of Iceland. These changes appear to have caused a northward shift in the distribution of several fish species, a decrease in krill abundance and a collapse in the sand eel population off southern and western Iceland. Considerable changes in distribution and abundance of several cetacean species are apparent from the series of cetacean surveys dating back to 1986. These include a pronounced decrease in the abundance of common minke whales in the Icelandic shelf area since 2001, increase in fin whale abundance in the Irminger Sea and large increase in humpback whale abundance in recent decades. Some of these changes appear to be related to the observed oceanographic and biological changes, while others are harder to explain.

The decrease in common minke whale abundance in the Icelandic continental shelf area after 2001 seems to be related to the decrease in the abundance of the preferred prey species, sand eel in the southern part and capelin in the northern part. These species, together with euphausiids dominated the minke whale diet before the turn of the century but had been largely replaced by herring and gadoids in 2007. Apparently, minke whales have responded to these environmental changes by a) a shift in distribution away from Icelandic coastal waters and b) a change in diet of the animals remaining in Icelandic waters.

Concurrently with increasing sea temperature in the deep waters of the Irminger Sea, the distribution of fin whales expanded into this area and the total abundance of fin whales in the Irminger Sea increased. However, the relationship between the rise in temperature and fin whale abundance is unclear. The warming of these waters could have triggered an increase in euphausiid abundance, the fin whale's dominant prey species in this area. However, due to lack of time series of euphausiid abundance in this area this theory cannot be verified.

Humpback whales were rare in Icelandic waters throughout most of the 20th century but a significant increase occurred between 1970 and 2001 in the Central North Atlantic. Feeding ecology of humpback whales in Icelandic waters is poorly documented but capelin and euphausiids are known to be among their prey species. It is hard to relate the increased abundance of humpback whales since the 1970s to any particular biological changes in the marine environment.

An apparent shift in distribution of blue whales from southwestern to northeastern Icelandic waters may be related to the decrease in euphausiid abundance in the waters south and southwest of Iceland.

The research presented in this thesis indicates that effects of warming are already evident in Icelandic and adjacent waters. The NASS series has revealed appreciable changes in distribution of several cetacean species and studies into feeding ecology and energetics provide possible explanations for these changes. Potential benefits of global warming to subarctic and/or migratory species through increased size of suitable habitat might be offset by increased competition from the south. For example the recent “invasion” of the large Northeast Atlantic mackerel stock into Icelandic waters is likely to have had appreciable impact on the ecosystem, possibly including competition with baleen whales.

Continued monitoring of the distribution and abundance of cetaceans as well as further studies into their feeding ecology are essential for better understanding of the recent and ongoing changes documented here. The value of such monitoring is not limited to conservation and management of the whale stocks. As top predators, cetaceans, and other marine mammals are well suited to serve as indicators of climate change and should be included in future comprehensive schemes for monitoring the effects of climate change.

3. List of papers included in the thesis.

Paper 1. Víkingsson GA, Pike DG, Desportes G, Öien N, Gunnlaugsson T, Bloch D (2009) Distribution and abundance of fin whales (*Balaenoptera physalus*) in the Northeast and Central Atlantic as inferred from the North Atlantic Sightings Surveys 1987-2001. NAMMCO Sci Publ 7:49–72.

Paper 2. Pike DG, Paxton CGM, Gunnlaugsson T, Víkingsson GA (2009) Trends in the distribution and abundance of cetaceans from aerial surveys in Icelandic coastal waters, 1986-2001. NAMMCO Sci Publ 7:117–142.

Paper 3. Pike DG., Gunnlaugsson T., Elvarsson B., and Víkingsson, GA. (2011). Correcting perception bias for Icelandic aerial surveys, 2007 and 2009. NAMMCO SC/18/AESP/08; 12 pp.

Paper 4. Sigurjónsson J. and Víkingsson GA. 1997. Seasonal abundance of and estimated food consumption by cetaceans in Icelandic and adjacent waters. Journal of Northwest Atlantic Fishery Science 22:271–287.

Paper 5. Sigurjónsson J, Galan A, and Vikingsson GA (2000) A note on stomach contents of minke whales (*Balaenoptera acutorostrata*) in Icelandic waters. NAMMCO Sci Publ 2:82–90.

Paper 6. Víkingsson GA, Elvarsson BT, Ólafsdottir D, Sigurjonsson J, Chosson V, Galan A (2014) Recent changes in the diet composition of common minke whales (*Balaenoptera acutorostrata*) in Icelandic waters. – A consequence of climate change? Mar Biol Res 10:138–152.

Paper 7. Víkingsson, GA. (1995). "Body condition of fin whales during summer off Iceland," in Whales, seals, fish and man; Blix, AS, Walløe L. and Ulltang Ø (eds); (Elsevier Science B.V.), 361–369.

Paper 8. Víkingsson GA (1997) Feeding of fin whales (*Balaenoptera physalus*) off Iceland—diurnal and seasonal variation and possible rates. J Northw Atl Fish Sci 22:77–89.

Paper 9. Víkingsson GA., Auðunsson GA., Elvarsson BT. and Gunnlaugsson T. (2013). Energy storage in common minke whales (*Balaenoptera acutorostrata*) in Icelandic waters 2003-2007. -Chemical composition of tissues and organs. IWC. SC/F13/SP10, 13 pp.

Paper 10. Williams R, Vikingsson GA, Gislason A, Lockyer C, New L, Thomas L, and Hammond PS (2013). Evidence for density-dependent changes in body condition and pregnancy rate of North Atlantic fin whales over four decades of varying environmental conditions. ICES J. Mar. Sci. 70, 1273–1280.

Paper 11. Víkingsson GA and Heide-Jørgensen MP (2015). First indications of autumn migration routes and destination of common minke whales tracked by satellite in the North Atlantic during 2001–2011. Mar. Mammal Sci. 31, 376–385.

Paper 12. Víkingsson G, Pike D, Schleimer A, Valdimarsson H, Gunnlaugsson T, Silva T, Elvarsson B, Mikkelsen B, Öien N, Desportes G, Bogason V and Hammond PS (2015). Distribution, abundance and feeding ecology of baleen whales in Icelandic waters: have recent environmental changes had an effect ? Front. Ecol. Evol. 3, 1–18. doi:10.3389/fevo.2015.00006.

4. Introduction

The location of Iceland at the junction of the Mid-Atlantic Ridge and the Greenland–Scotland Ridge where warm and cold water masses meet south of the Arctic Circle contributes to high productivity of the sea around the island . Since the settlement of Iceland over 1100 years ago fisheries have been an important source of food for the inhabitants, and this industry has by far constituted the most important basis for economic prosperity of modern Icelandic society contributing well over half of exported goods during the last century. Historically, large fluctuations have been observed in environmental conditions around Iceland, in particular north of Iceland where the effects of the warm Atlantic water masses have varied widely (Astthorsson et al., 2012; Gislason et al., 2009; Jakobsson, 1992; Malmberg, 1994; Stefánsson, 1962; Stefansson and Jakobsson, 1989; Valdimarsson et al., 2012; Vilhjálmsson, 1994).

Icelandic waters sustain high diversity and abundance of cetaceans which has caught the attention of people for a long time. Thus, the medieval manuscript Konungsskuggsjá or Speculum Regale (Kings mirror) written in Norway in the mid 13th Century places great emphasis on whales in it‘s introduction to Icelandic waters. "Í Íslands höfum þykir mér fátt það vera er minninga sé vert eður umræðu fyrir utan hvali þá er þar eru í höfum" ("Aside from the whales in the ocean, there are, I should say, but few things in the Icelandic waters which are worth mentioning or discussing." (Translation L.A. Larson 1917). The chapter then goes on with descriptions of various species of whales and other sea creatures which are though largely difficult to assign with certainity to the names of species we use today. Konungsskuggsjá remained the main written source of information on Icelandic whales until Jón Lærði (Jón the learned) wrote his description of Iceland's nature ("Ein stutt undirrétting um Íslands aðskiljanlegar náttúrur") around 1640 (Guðmundsson, 1966). There he presented numerous descriptions and drawings of cetaceans around Iceland including the only reliable written account of the now extinct North Atlantic gray whale (*Eschrichtius robustus*)(Fraser, 1970).

The high abundance of cetaceans in Icelandic waters attracted foreign whalers, mainly Basque, Dutch and French from around 1600 (Aguilar, 1986; Einarsson, 1987; Monsarrat et al., 2015). In the subsequent two centuries right whales (*Eubalaena glacialis*) and bowhead whales (*Balaena mysticetus*) were hunted close to extinction in Icelandic waters. The fast swimming rorquals were, however, out of reach for these early whalers until the invention of steam driven vessels and Svend Foyn's explosive harpoon marked the onset of modern whaling (Tønnessen and Johnsen, 1982). In 1883 Iceland became the first country outside Norway where this new whaling technique was applied (Einarsson, 1987; Tønnessen and Johnsen, 1982). Subsequently numerous Norwegian whaling stations were operated in Iceland until 1915, when a total ban on all large whaling agreed by the Icelandic parliament Alþingi took effect (Einarsson, 1987; Sigurjonsson, 1989). The main target species during this first phase of modern whaling in Icelandic waters were blue (*Balaenoptera musculus*) and fin (*B. physalus*) whales while humpback (*Megaptera noveangliae*) and sei (*B. borealis*) whales were also taken. From these old whaling records, notably the distribution of catches and catch per unit effort, it is clear that the main target species were severly depleted by the end of this first period of modern whaling (Sigurjonsson, 1989). With the exception of limited catches during 1935-1939, no whaling for large whales was conducted from Iceland until 1948 when a single landstation started operating in Hvalfjörður, West Iceland. The Hvalfjörður whaling station is still in operation with fin whales as the only target species, but previously sei and sperm (*Physeter macrocephalus*) whales were also caught together with a few blue and humpback whales. Minke (*B. acutorostrata*) whaling was initated in Iceland in 1914. These were small-type operations widely distributed in Icelandic coastal waters and were unaffected by the whaling ban mentioned above (Sigurjónsson, 1982; Víkingsson and Sigurjónsson, 1998). No minke whaling was conducted during 1986-2002 due to the IWC Moratorium.

In historical times, a total of 23 species of cetaceans have been documented in Icelandic waters including 7 baleen whale species and 16 toothed whales (Table 1). Of these, 12 species can be considered regular inhabitants in Icelandic waters while 10 species are regarded as vagrant, having their main distribution in warmer or colder areas and one species is extinct in the North Atlantic (see above). Most of these species (17 out of 23) are mentioned by Sæmundsson (1939) in his general account of Icelandic mammals 76 years ago. Systematic research into the biology and population ecology of cetaceans in Icelandic waters was however limited until the late 1960‘s when the Marine Research Institute (MRI) established research cooperation with the British Antarctic Survey (later Sea Mammal Research Unit). This cooperation led to a wide range of biological studies that were conducted on the exploited species (fin, sei, and sperm whales) regarding age, reproduction and potential effects of the catches (Brown, 1976; Lockyer, 1977, 1991; Lockyer and Brown, 1979; Martin, 1983; Rörvik et al., 1976). The MRI took over these research activities around 1980.

In 1982 the IWC agreed to a moratorium (pause) on commercial whaling taking effect in 1986. The main reason given was that there was insufficient scientific basis for management of whales. Member nations were encouraged to increase their research efforts to strenghthen this basis before the re-consideration of the moratorium that was to take place by 1990 at latest (Gambell 1997). The onset of the moratorium can be considered a watershed in the history of whale research in Icelandic waters. A comprehensive research program was conducted during 1986-1990 (Marine Research Institute, 1985) with a main emphasis on the biology and population ecology of fin and sei whales. The series of the North Atlantic Sightings Surveys (NASS) were initiated as a part of this research program providing the first estimates of absolute abundance of cetaceans in this area. Prior to NASS, no direct estimates of absolute abundance of cetaceans in Icelandic waters were available and information on distribution was largely confined to indirect observations s.a. from catch distributions, discovery marking data and analyses of catch per unit effort (CPUE) (Rørvik, 1980; Rørvik and Sigurjónsson, 1981; Gunnlaugsson and Sigurjónsson 1989). Few systematic cetacean sightings surveys were conducted in the Central North

Atlantic prior to the mid 1980's and these had only partial coverage and/or had other primary objectives than to estimate total population size (Sigurjónsson 1983, 1985, Martin et al. 1984)

In general, the history of whale research in Icelandic waters has largely been related to the whaling operations. As for other natural resources, this has arisen partly out of the necessity to ensure sustainable developement of the whaling industry, but questions concerning the ecological role of cetaceans and potential conflict with fisheries have also received increasing attention in recent decades. Although the variety of research has increased in recent years, including acoustic studies and research on small cetaceans, existing long-term data series are mostly confined to large whales, in particular the recently or presently exploited species. This thesis will examine the distribution and abundance of baleen whales in Icelandic waters in relation to feeding ecology and recent changes in the marine environment. In accordance with data availability the main focus will be on the two presently exploited species, fin and common minke whales as the best studied species, but blue, sei and humpback whales are also considered where data are available.

Table 1. Cetacean species documented in Icelandic waters. Occurrence in Icelandic waters: S: seasonal; Y: Year round; S/Y: partial migration; V: vagrant (rare).

Common name	Species name	Approximate abundance	Notes	Occurrence in Icelandic waters	Source
Baleen whales	**Mysticeti**				
Blue whale	*Balaenoptera musculus*	1,000	Central N-Atlantic	S	(Pike et al., 2009b; Víkingsson, 2004i)
Fin whale	*Balaenoptera physalus*	22,000	East Greenland-Iceland stock	S	(Víkingsson, 2004c; Víkingsson et al., 2009)
Sei whale	*Balaenoptera borealis*	10,000	Central N-Atlantic stock	S	(Cattanach et al., 1993; Víkingsson, 2004g)
Common minke whale	*Balaenoptera acutorostrata*	30,000	Central N-Atlantic stock	S/Y	(Pike et al., 2011(Paper 3); Víkingsson, 2004b);Pike et al. 2010b
Humpback whale	*Megaptera noveangliae*	15,000	Central N-Atlantic	S/Y	(Paxton et al., 2009; Pike et al., 2010a; Víkingsson, 2004a)

North Atlantic right whale	*Eubalaena glacialis*	300-350	Only five sightings in Icelandic waters for the past 100 years.	V	(Víkingsson, 2004h)
Bowhead whale	*Balaena mysticetus*	NA	Not observed in Icelandic waters since 1879	V	(Víkingsson, 2004d)
Gray whale	*Eschrichtus robustus*	0	Extinct in the North Atlantic		(Víkingsson, 2004f)
Toothed whales	**Odontoceti**				
Sperm whale	*Physeter macrocephalus*	11,000	Central N-Atlantic	S/Y	(Gunnlaugsson et al., 2009a; Ólafsdóttir and Víkingsson, 2004b; Skov et al., 2008)
N-bottlenose whale	*Hyperoodon ampullatus*	28,000	Minimum estimate, uncorrected for g(0)	?	(Ólafsdóttir and Víkingsson, 2004a; Pike et al., 2003)
Cuvier's beaked whale	*Ziphius cavirostris*	NA		?	(Ólafsdóttir and Víkingsson, 2004d)
Blainville's beaked whale	*Mesoplodon densirostris*	NA		?	(Ólafsdóttir, 2004)
Sowerby's beaked whale	*Mesoplodon bidens*	NA		?	(Víkingsson, 2004e)
Long-finned pilot whale	*Globicephala melas*	750,000	Central and NE Atlantic	S/Y	(Buckland et al., 1993)
Killer whale	*Orcinus orca*	6,600	Central North Atlantic	Y	(Gunnlaugsson and Sigurjónsson, 1990)
Narwhal	*Monodon monocerus*	80,000 (1,000+)	Circumpolar (E-Greenland)	V	NAMMCO 2005
Beluga	*Delphinaptera leucas*	150,000+	Circumpolar	V	NAMMCO 2005
White-beaked dolphin	*Lagenorhynchus albirostris*	32,000	Icelandic coastal waters	Y	(Pike et al., 2009a (Paper 2)
White sided dolphin	*Lagenorhynchus acutus*	38,000+	Central North Atlantic	Y?	(Sigurjónsson and Víkingsson, 1997)

Common dolphin	*Delphinus delphis*	500,000+	North Atlantic[1]	V	Hammond et al. 2008a
Common bottlenose dolphin	*Tursiops truncatus*	150,000+	North Atlantic[1].	V	Hammond et al. 2012
Striped dolphin	*Stenella coeruleoalba*	150,000+	North Atlantic[1].	V	Hammond et al. 2008b
Harbour porpoise	*Phocoena phocoena*	43,000	Icelandic coastal waters	Y	(Gilles et al., 2011)

5. Objectives

The main objective of this thesis is to describe recent findings on some key aspects in the population and feeding ecology of baleen whales in Icelandic waters. Krebs (1972) defined ecology as: „the scientific study of the interactions that determine the distribution and abundance of organisms". Here I will summarize the available data on distribution and abundance of baleen whales in Icelandic waters. In particular the aim is to explore the ecological role played by the most common baleen whales occurring in Icelandic waters and to examine recent changes in distribution and abundance of three cetacean species and their relationship with concurrent changes in the marine environment.

The specific objectives of the thesis are:

1. Estimation of abundance of baleen whales in Icelandic waters and changes in distribution and abundance during 1987-2009 (Papers 1, 2, 3).

2. Estimation of energetic requirements and food consumption by cetaceans in Icelandic waters (Papers 4, 7, 8 and 9).

3. Examination of diet and feeding ecology of key baleen whale species in Icelandic waters. (Papers 5, 6, and 8).

4. Investigation into autumn migration routes, timing and destination of North Atlantic common minke whales (Paper 11).

5. Potential effects of recent changes in the marine environment on the distribution, abundance and feeding ecology of baleen whales around Iceland. (Papers 6, 10 and 12).

[1] Main distribution area south of Iceland.

6. Results and discussion

6.1. Distribution, abundance and trends

Systematic monitoring of the distribution and abundance of cetaceans in Icelandic and adjacent waters began with the onset of the North Atlantic Sightings Surveys (NASS) in 1987 (Lockyer and Pike, 2009). The NASS constitute the largest series of cetacean surveys conducted to date in both spatial and temporal extent (Pike, 2009). These multi-national surveys have covered large parts of the summer distributions of most North Atlantic baleen whale species. To date, the series includes five large-scale surveys conducted in 1987, 1989, 1995, 2001 and 2007. The most recent one (TNASS) involved participation by Canada (Lawson and Gosselin, 2011) and was coordinated with European (CODA) (Hammond et al., 2009) and US (SNESSA) surveys, extending across the whole North Atlantic from the east coast of North America to the European west coast (NAMMCO, 2009). In all these surveys, the Central North Atlantic stock area (Donovan, 1991) has been covered by Icelandic, Faroese and Norwegian research effort.

In the Icelandic part of NASS, covering Icelandic and adjacent areas in the Central North Atlantic, the continental shelf area has been covered by aircraft (Borchers et al., 2009; Donovan and Gunnlaugsson, 1989; Hiby et al., 1989) while the offshore areas were surveyed by vessels (Sigurjónsson et al., 1989, 1991). The timing of the surveys was centered around the month of July, corresponding to the assumed peak abundance of the main target species, fin and common minke whales. Irrespective of the primary target species declared by each participating country in NASS, sightings of all cetaceans were systematically recorded in all surveys using the same basic protocols.

6.1.1. Fin whales

Fin whales have a worldwide distribution although they are rarely seen in tropical waters. They occur mostly, but not exclusively in offshore waters. Two subspecies are now recognized *Balaenoptera physalus physalus* in the Northern Hemisphere and *Balaenoptera physalus quoyi* in the Southern Hemisphere. (Committee on Taxonomy, 2011). In the North Atlantic fin whales occur as far as Baffin Bay and Davis Strait in the the northwest, Svalbard in the northeast and the Antilles and Canary Islands in the southwest and southeast respectively (Reilly et al. 2008a; Aguilar 2009).

Traditionally North Atlantic fin whales were divided into seven populations or management areas, based mainly on distribution of historical catches and marking experiments (Donovan, 1991). Fin whales in Icelandic waters belong to the so-called East Greenland-Iceland (EGI) stock. In recent assessments within the IWC, several other stock structure hypotheses were explored assuming 2-4 breeding stocks in the North Atlantic (IWC, 2009; IWC and NAMMCO, 2006).

Fin whales were a primary target species in all NASS except in 1989 when efforts were made to estimate sei whale abundance by later timing (July-August) and more southern coverage of the survey (Víkingsson et al., 2009 hereafter Paper 1).

Abundance estimates from NASS were dervied using standard stratified line transect methods (Buckland et al., 2001). The Icelandic and Faorese datasets were combined for estimation of fin whale abundance in the Central North Atlantic.

Abundance

Prior to NASS, no reliable estimates were available for the EGI population of fin whales. Based on mark-recapture experiments on fin whales, mainly on the whaling grounds west of Iceland, Sigurjonsson and Gunnlaugsson, (1985) came to an estimate of around 7,000 whales in the late 1960‘s. This and other mark-recapture estimates of absolute abundance based on discovery markings were surrounded by large uncertainty. In particular, these marking studies (Gunnlaugsson and Sigurjonsson, 1989) and subsequent photo-id studies (Agler et al., 1993; Clapham and Seipt, 1991; Seipt et al., 1990), showed some degree of site fidelity of individuals, indicating that the fundamental assumption of random mixing within the whole "EGI stock area" was likely violated.

The estimated abundance of fin whales from the first NASS, conducted in 1987 was considerably higher than the mark-recapture estimated mentioned above or 11,285 (c.v. 0.273) (Buckland et al., 1992; Gunnlaugsson and Sigurjónsson, 1990). Based on the 1989 survey (NASS-89), the abundance of fin whales was estimated as 10,378 (c.v. 0.1599), but the difference in timing and coverage of that survey must be borne in mind as mentioned above (Buckland et al., 1992). A combined estimate for the EGI area from the 1987 and 1989 surveys is 15,237 (c.v. 0.22) (Paper 1). From the NASS 1995 survey, 19,672 (c.v. 0.23) fin whales were estimated in the Central North Atlantic, and the estimate in 2001 was 24,887 (c.v. 0.13) (Paper 1). In 2007, 21,628 (c.v. 0.15) fin whales were estimated in the area (Pike et al., 2008).

Trends

To account for variable geographical coverage in different survey years, post-stratification was necessary for analysis of trends (Paper 1). This involved division into smaller areas of similar coverage for which abundance estimates were calculated and subsequently combination of these into larger areas. A log-linear regression analysis revealed a significant increase in fin whale abundance during the survey period 1987-2001. For all areas combined, the estimated annual growth rate was 4%. An estimated annual increase of 10% in the area between Iceland and Greenland was responsible for most of this overall increase in numbers of fin whales in the area (Paper 1). Increase rates of 10% are close to the limit or even higher than those traditionally considered biologically plausible for large baleen whales although similar rates have been reported for humpback whales in recent years (Heide-Jørgensen et al., 2012; Paterson et al., 2004; Sigurjónsson and Gunnlaugsson, 1990; Stevick et al., 2003b; Víkingsson et al., 2015). The high rates of increase in fin whales off West Iceland might be partly explained by a shift in distribution due to changes in the marine environment (see below and Paper 12). The estimate from the 2007 surey was slightly, albeit not significantly lower than the estimate from 2001. This might indicate that the increase in the abundance of fin whales in the East Greenland – Iceland stock area may now have ceased.

Status of the EGI stock of fin whales

There is no estimate of the total number of fin whales in the North Atlantic as large areas have never been covered by systematic surveys, especially in the western part of the ocean. However, from NASS and other available surveys it can be concluded that there are at least 50,000 fin whales in Central and Northeast Atlantic and 60,000-70,000 in the whole North Atlantic (Paper 1). Judging from stock assessments made by the Scientific Committee of NAMMCO and the IWC fin whales have recovered from historic overexploitation in the Central North Atlantic and off Spain (IWC, 2009, 2010; IWC and NAMMCO, 2006; NAMMCO, 2011). The apparent levelling off in abundance of fin whales around Iceland could be an indication of a population nearing carrying capacity. Depletion is, however, still high off Norway where substantial catces were taken historically. The reasons for the lack of recovery in Norwegian waters are not clear.

Fin whales are classified as endangered on the IUCN global redlist (Reilly et al 2008a). This classification could at first sight seem to contradict with the information described above from the NASS surveys and recent assessments by the Scientific Committees of the IWC and NAMMCO (IWC and NAMMCO, 2006; IWC, 2009, 2010; NAMMCO, 2011). While assessments of wild animals are usually made at the population levels, the IUCN listing refers to the species as a whole, lumping together numerous independent population units into a single assessment. Such an assessment will always be dominated by the Southern Hemisphere sub-species of fin whales (*Balaenoptera physalus quoyi*) due to it‘s enormous estimated pre-exploitation size and high depletion levels at present. This is clearly indicted in the report of the IUCN cetacean specialist group (Reilly et al., 2013) and in the more recent IUCN regional assessment for Europe (http://www.iucnredlist.org/details/2478/1), where North Atlantic fin whales are not classified in any of the threatened categories (IUCN 2007a).

6.1.2. Common minke whales

The common minke whale is a cosmopolitan species found in all major oceans. In the North Atlantic, the summer distribution ranges as far north as Baffin Bay, Greenland Sea, Svalbard (Norway), Franz

Josef Land and Novaya Zemlya (Russian Federation), south to 40°N (New Jersey) on the US east coast, and as far south as the Hebrides (northwest British Isles) and the central North Sea in the east. In the Central-North Atlantic summer concentrations of minke whales occur at least south to 50°N (Sigurjónsson et al. 1991). It is likely that at least a part of the minke whale population over-winters in the summer range (MRI unpublished data) , but there have been very little systematic observation efforts in winter to quantify this (Gunnlaugsson and Víkingsson 2014).

Traditionally, four stocks of common minke whales were recognized in the North Atlantic with Icelandic minke whales belonging to the Central North Atlantic stock ranging from East Greenland through Iceland and Jan Mayen.(Donovan, 1991). However, recent genetic work show very little spatial variation across the whole ocean suggesting that there may be only one genetic population in the North Atlantic (Palsbøll, 2014; Quintela et al., 2014; Tiedemann et al., 2014).

The summer distribution of common minke whales is more coastal than that of fin whales and largely confined to continental shelf waters (Horwood, 1990; Víkingsson, 2004b). Within the North Atlantic highest densities are found in the shelf areas off Canada, Greenland, Iceland and Norway.

The Icelandic aerial survey component of the NASS series was designed for abundance estimation of common minke whales. The aerial survey covered the Icelandic continental shelf area subdivided into nine subareas in which survey effort was roughly proporional to known or suspected density of minke whales. Aerial surveys were conducted in all NASS except in 1989, and additional (non-NASS) aerial surveys were flown in 1986 and 2009 (Borchers et al., 2009; Donovan and Gunnlaugsson, 1989; Gunnlaugsson et al., 1988; Pike et al. 2011, hereafter Paper 3). With the exception of the experimental survey in 1986, all the NASS aerial surveys used the same transect lines, although the realized coverage was variable between surveys.

Abundance

The estimated abundance of minke whales in Icelandic shelf waters has varied appreciably during the survey period 1986-2009 (Pike et al. 2009a, hereafter Paper 2; Paper 3). Abundance was highest in 2001 when 43,600 (c.v. 0.19) minke whales were estimated in the Icelandic shelf area (Paper 2). In the 2007 survey, the estimated abundance was less that half of that in 2001 (Paper 3). Because of this sharp decrease in minke whale densities between 2001 and 2007, a partial survey was conducted in 2008 in Faxaflói Bay, a hot spot area for minke whales in all previous surveys. This survey revealed much higher densities, similar to those in 2001(Gunnlaugsson et al., 2009b). However, a full aerial survey conducted in 2009 showed further decrease with estimated abundance 9,588 (c.v. 0.24) animals (Paper 3). This is the lowest estimate of common minke whales on the Icelandic continetal shelf since the beginning of monitoring in 1986 (Paper 3). While there was a decrease in densities all around Iceland, the decrease was most prominent in the southern and southeastern areas. Estimates from the shipboard surveys in deeper waters outside of the aerial survey area varied between 10,800 and 26,600 during 1987 and 2007. The shipboard component of NASS was primarily designed for fin whales and the above estimates for minke whales are considered downward biased to an unknown, but probably substantial degreee (Pike et al. 2009c).

Trends

The aerial surveys conducted during 1987-2009 show large variations in minke whale densities in Icelandic shelf waters. Due to variable realized coverage and minor differences in survey design (1986 v/s later surveys), post stratification was applied in analysis of trends (Paper 2). The point estimate of the rate of increase was positive during 1987-2001, although the trend was not statistically significant. (Paper 2). Although there are indications of higher densities in Faxaflói Bay in 2008, the two full scale surveys in 2007 and 2009 show a drastic decrease, the point estimates being 48% and 22% of the 2001 estimate respectively (Paper 3). This decrease in coastal waters is consistent with incidental evidence from minke whaling and whale watching operations. These sources indicate that minke whale densities are still low in the southwestern coastal waters.

Status of Central North Atlantic common minke whales

The total number of common minke whales in the North Atlantic is estimated as around 180,000 animals (IUCN 2007b, Reilly et al. 2008b).

Common minke whales are classified as „Least concern“ on the IUCN redlist, both globally (Reilly et al. 2008b) and in the North Atlantic (IUCN 2007b). This species was not subject to overexploitation during late 19th Century and the first half of 20th Century at least not to the same extent as the larger balaenopterids. Although catch statistics for the Icelandic small-type minke whaling were not systematically collected before 1974, catches were low during these first 60 years, likely few tens per annum and certainly less than 50 (Sigurjónsson, 1982). Catches increased to 100-200 when export of minke whale products was initiated in 1974 and during 1977-1985 quotas of around 200 animals/year were set by the IWC. After two decates of total protection due to the IWC moratorium, commercial minke whaling was resumed in 2006. Mean annual catches during 2006-2014 were 40 minke whales. According to assessments conducted by the scientific committees of the IWC and NAMMCO, Central North Atlantic common minke whales have not been appreciably affected by past whaling and are today close to pre-exploitation levels (IWC, 2009, 2010, NAMMCO, 2011). These assessments are thus in agreement with the IUCN assessments mentioned above.

6.1.3. Humpback whales

Like fin and common minke whales, humpback whales have a worldwide distribution. In the summer, their distribution ranges from the Gulf of Maine to Davis Strait in the west and from Ireland to the Barents Sea in the east. The summer distribution is largely confined to seven discrete feeding areas: Gulf of Maine, Gulf of St Lawrence, Newfoundland, Labrador, Greenland, Iceland and Norway (Clapham, 2000). Fidelity to these feeding areas appears to be strong and determined matrilineally (Larsen et al., 1996; Palsbøll et al., 1997).

Unlike other North Atlantic balaenopterids, the location of two wintering breeding grounds is known for humpback whales; a large aggregation in the West Indies and a smaller one near the Cape Verde Islands (Reilly et al 2008c). Humpbacks summering in Iceandic waters have been linked to both these breeding areas (Jann et al., 2003; Martin et al., 1984; Smith et al., 1999).

Whereas there is little overlap in the summer distribution of common minke whales (coastal waters) and fin whales (offshore), humpback whales occupy both these habitats. However, they overlap much more with minke whales and are relatively seldomly observed beyond 2,000m depth in Icelandic and adjacent waters (Víkingsson, 2004a).

Abundance

As other large balaeopterids, humpback whale stocks were depleted worldwide by 19th and 20th century whaling operations. Whaling for this species began before the invention of the explosive harpoon in the late 19th century (Reeves et al., 2004). This was made possible by the coastal distribution and relatively slow swimming habits of humpback whales. The total catch of humpback whales in Icelandic waters during 1883-1915 has been estimated as 3,300 animals (Reilly et al 2008c). After the resumption of Icelandic whaling in 1948, only six humpback whales were taken until the species was totally protected in 1955, illustrating the rarity of the species at that time.

The first estimate of absolute abundance of humpback whales in Icelandic waters was 1,816 (c.v. 0.18) derived from the first NASS conducted in 1987 (Gunnlaugsson and Sigurjónsson, 1990). NASS estimates during 1995-2007 were all significantly higher, ranging between 10, 521 and 14,662 thousand animals (Paxton et al., 2009; Pike et al., 2010a; Víkingsson et al., 2015, hereafter Paper 12). According to a large scale international photo-identification study conducted in the early 1990's (YoNAH) the total number of humpback whales occupying the West Indies breeding area was 10,752 (CV = 0.068) in 1992-1993 (Stevick et al., 2003b). This is of the same order of magnitude as the recent estimates of the Icelandic (Central N-Atlantic) feeding area alone. However, recent research has shown that an appreciable proportion of Icelandic humpback whales breed outside the West Indies (Stevick et al 2003a, Jann et al. 2003).

Trend

Sigurjónsson and Gunnlaugsson (1990) reported an annual increase of 14.8% in relative abundance of humpback whales during 1979–1988 west of Iceland. This growth rate, coupled with the small absolute abundance estimate of less than 2,000 humpback whales in 1987 (Gunnlaugsson and Sigurjónsson, 1990) indicates that the number of animals in the area must still have been very small prior to 1970. According to a trend analysis, of the data collected in the aerial surveys of NASS, annual rates of increase in abundance were estimated as 12% for the period 1987–2001 (Paper 2). The most recent data from the 2007 survey (Pike et al., 2010a) suggest that this rapid growth may have leveled off around the turn of the century (after the 1995 survey).

Status

High rates of increase have also been reported for humpback whales elsewhere in the world in recent decades (Barlow and Clapham, 1997; Stevick et al., 2003b; Reilly et al., 2008c). While there is shortage of information from some areas, humpback whales seem to have recovered from overexploitation throughout the world with the exception of a small apparently isolated stock in the Arabial Sea. Humpback whales are therefore now listed as „Least Concern“ on the IUCN redlist (Reilly et al., 2008c).

6.1.4. Other species

The NASS surveys have provided estimates of abundance of several other species of cetaceans (Table 1). With the exception of sei whales in 1989, these were not primary target species of the surveys, hence the abundance estimates are likely downward biased. The estimated abundance of sei whales was 10,300 (c.v. 0.268) in 1989, when the survey was conducted later in the season (July/August) and extended further south in accordance with suspected sei whale distribution (Cattanach et al., 1993). The mid summer surveys (1987, 2001) encountered rather few sei whales with the exception of the 1995 survey that yielded an estimate of 9.249 (Borchers and Burt 1997). High densities of sei whales were encountered in a multi-disciplinary survey along the Mid Atlantic Ridge in June-early July 2004 (Waring et al., 2008).

Blue whales have not recovered to the same extent as fin whales from whaling operations during the late 19th century and early 20th century in the North Atlantic (Reilly et al. 2008d). Although Sigurjónsson and Gunnlaugsson, (1990) reported a significant increase in relative abundance west of Iceland during 1969-1988, numbers were still low when systematic surveys began in 1987 (Pike et al., 2009b; Víkingsson, 2004i). The survey data 1987-2001 show increasing trend with the most recent estimates around 1,000 blue whales in Icelandic waters (Pike et al., 2009b).

The harbour porpoise is the smallest cetacean in Icelandic waters (Halldórsson and Víkingsson, 2003; Ólafsdóttir et al., 2003; Ólafsdóttir and Víkingsson, 2004c). The coastal distribution of this species coupled with small body size complicates the interpretation of sightings from a survey designed for whales that are 100-1,000 times larger by body weight and have a more offshore distribution. The results from the NASS surveys should therefore be treated with caution. In the 2007 aerial survey, some adjustments were made to better capture porppoise sightings including surveys of some selected fjords and a slight decrease in survey altitude. From this survey (Gilles et al., 2011) estimated the abundance of harbour porpoises in the Icelandic continental shelf area as 43,000 animals. Analysis of relative abundance indicated a negative trend during 1987-2001 (Paper 2).

Several other (minimum) abundance estimates of non-target odontocete species, including sperm whales, northern bottlenose whales (*Hyperoodon ampullatus*), killer whales (*Orcinus orca*), long-finned pilot whales (*Globicephala melas*) and *Lagenorhynchus* dolphin species have been derived from the NASS series (see Table 1 for references).

6.1.5. Migration and breeding grounds.

Rorquals are generally regarded as migratory, spending the summer in productive feeding areas at high latitudes, where they are believed to fulfill most of their annual food requirements during a period of 4–6 months (Lockyer and Brown, 1981; Lockyer, 1981). During the winter breeding season they are believed to inhabit lower latitudes although migration routes and wintering areas in the North Atlantic are poorly known except for humpback whales (Smith et al., 1999). The present knowledge on the natural history of Northern Hemisphere balenopterids is therefore largely derived from studies on the summer feeding grounds. This lack of knowledge on breeding grounds and migratory pattern constitutes a major gap in knowledge on the biology of most species of baleen whales (Lockyer and Brown, 1981; Mate et al., 2007). This is a major factor of uncertainty in assessment of baleen whale stocks within an ocean basin such as the North Atlantic as the number of stocks and their boundaries are uncertain (Donovan, 1991). Genetic research based solely on samples from the feeding grounds (e.g. Pampoulie et al., 2008; Olsen et al., 2014; Tiedemann et al., 2014; Palsbøll, 2014; Anderwald et al., 2011; Danielsdottir et al., 1991) can often be interpreted in various different ways, necessiating the inclusion of several different stock structure hypotheses in recent stock assessments (IWC and NAMMCO 2006; IWC 2010; NAMMCO 2010).

Photo-identification studies have proven useful for various types of research including studies on whale movements (e.g. Katona and Whitehead, 1981; Mizroch et al., 1990; Smith et al., 1999). Although theoritically applicable on most species, the technique has yielded most information on species that are readily accessible through relatively coastal distribution and/or with readily identifiable traits. Photo-identification has been used to link humpback whales off Iceland to the Caribbean Sea and Cape Verde

(Jann et al., 2003; Martin et al., 1984; Stevick et al., 2003a), Icelandic killer whales to the Northern Isles of Scotland (Foote et al., 2010) and Icelandic blue whales to the waters off Mauritania (Sears et al., 2005).

In recent decades satellite tracking has greatly increased knowledge of animal movements including migrations. This method is difficult to use on large whales as signals cannot be transmitted below the sea surface where whales spend most of their time (Hays et al., 2007). In addition whales cannot be captured and released so the tags have to be deployed remotely, which further reduces the efficiency of the tags. Despite these technical difficulties satellite tagging has greatly improved our knowledge on whale movements of several species of large cetaceans (e.g. Mate et al., 2007; Kennedy et al., 2014). Common minke whales have proven particularly difficult to apply this method to, with low success rates and relatively short transmission periods compared to larger cetaceans (Heide-Jorgensen et al., 2001; Kishiro and Miyashita, 2011).

Most of the common minke whales summering off Iceland are believed to depart Icelandic waters during the autumn but their whereabouts during the winter breeding season are virtually unknown. Little information exists on the timing of the migration, although data from small-type whaling in the late 20th century indicate the species is present in Icelandic coastal waters at least during March–November, with relatively high densities during April–September and a peak in July (Sigurjónsson and Víkingsson, 1997, hereafter Paper 4). Attempts to track minke whales in Icelandic waters using satellite telemetry were initiated in 2001 with increased effort from 2003 as part of a multifaceted research program (Marine Research Institute, 2003). One element of this program was to obtain information on the routes and destinations of the whales as they move out of Icelandic waters in the autumn. Such information is important, not only for improving the basis for conservation and management of the stock, but also to contribute to filling a major gap in our knowledge of the natural history of the North Atlantic common minke whale (Víkingsson and HeideJørgensen, 2015, hereafter Paper 11).

Between 2001 and 2011, 17 minke whales were instrumented with satellite tags in Iceland (Paper 11). Of these, eight provided position data, with tracking periods ranging 2-101 days and total combined tracking period of 370 days. All the positions received were within the present IWC boundaries for the Central North Atlantic stock. Five of the tagged animals remained within Icelandic waters during the tracking period, while three whales yielded information on fall migration. The results of these tagging experiments cast doubt on the peak of migration being in September, as had previously been assumed from catch data (e.g. in Paper 4) as two of the three migrating whales did not initate migration until November and one was still in Icelandic waters when transmissions stopped in late October. The average traveling speeds during migration (4.6–7.3 km/h) reported in Paper 11 are similar to those recorded from migrating gray whales (*Eschrichtius robustus*), and fin whales (Mate and Urban-Ramirez, 2003; Silva et al., 2013; Swartz et al., 1987) and somewhat higher than those reported for blue and humpback whales (Bailey et al., 2009; Kennedy et al., 2014).

The tracks of the three minke whales that departed from Icelandic waters provide the first documentation of the migration route of North Atlantic common minke whales and indication of winter destination of minke whales summering in Iceland. All three followed an offshore route heading south in the middle of the Atlantic. Contact was lost early with two of the whales but all three were heading in the same direction at the time. The third whale, for which contact was maintained until it had passed the Azores, continued south to a position in the mid Atlantic at about 28°N in early December. This represents the longest tracking record for a common minke whale to date, both in terms of distance traveled (3,700 km) and tracking duration (100 d) (Paper 11).

6.2. Feeding ecology

Questions concerning food consumption of cetaceans and potential interactions between fisheries and cetaceans have been a prominent part of the public debate in Iceland for decades. Although the abundance estimates for non-target species (Table 1) are likely seriously downward biased, it seems clear that cetaceans regularly occurring in Icelandic waters constitute a large biomass and likely play an important ecological role in the Icelandic ecosystem.

6.2.1. Total consumption by cetaceans in Icelandic waters

In addition to abundance, an estimation of consumption requires knowledge on body weight of cetaceans, food ingestion rates, diet composition and for migrating animals residence times in the study area. Food ingestion rates are particularly difficult to estimate for baleen whales. Their large size and feeding habits preclude laboratory experiments under controlled conditions in captivity. In addition their seasonal life history traits with intense feeding season for building up energy reserves during summer and fasting or low level feeding in winter complicates the use of general mammalian energetic models for estimating energy needs.

Lockyer (1981, 1987b) used carcass analysis to quantify energy deposition by large baleen whales during the summer feeding season and concluded that an average pregnant fin whale nearly doubles the energy content of the body over an assumed 13 week feeding period. In Paper 7 similar methods were used on a larger sample to estimate energy deposition and summer feeding rates of fin whales in Icelandic waters using data collected during the 1986-1989 research programme (Vikingsson, 1988, 1990; Víkingsson et al., 1988). A total of 72 fin whales were weighed in parts to create formulae for prediction of total body weight and the weight of tissues that are important for energy storage from simple anatomical measurements.

Seasonal changes in these anatomical measurements, coupled with seasonal changes in energetic density of tissues were then used to estimate energy deposition in various tissue during the feeding season. As previously reported (Lockyer, 1987a; Vikingsson, 1990) pronounced differences were found among reproductive classes in energy deposition pattern, necessiating stratification by sex and reproductive condition (Paper 7). Pregnant females had the highest estimated deposition rates, increasing the energy content of the body by 80% over the assumed 4 month feeding season. The corresponding value for immatures was less than 30%. Significant energy deposition was found in blubber, visceral fat and muscle. Energy storage in muscle tissue seems particularly important for adult females. The deposition rates were slightly lower than those reported by Lockyer, possibly due to the larger sample size reported in Paper 7. However, inter-annual variation (e.g. (Lockyer, 1987b; Vikingsson, 1990) could also contribute to this difference. Energy requirements for a 4 month feeding period were derived by adding energy required for maintenance using basal metabolic rate according to (Kleiber, 1961) with activity coefficient of 1.45 (Markussen et al., 1992). Assuming that fin whales off Iceland feed solely on krill with energy density of 0.93 kcal/g and assimilation efficiencey of 80%, the estimated energy requirements corresponds to daily feeding rates of 2-3% of body weight amounting to 800-1,200 kgs/day for an average sized fin whale. This estimate is in concordance with ingestion rate values most commonly assumed for marine mammals in general (Boyd, 2002; Lavigne et al., 1986; Leaper and Lavigne, 2007; Reilly et al., 2004; Sergeant, 1969; Tsutomu and Ohsumi, 1999).

Another approach, independent from the carcass analysis above, to estimation of feeding rates of fin whales was given by Víkingsson, (1997, hereafter Paper 8). This approach is based on direct observations of quantities of food remains in the stomach and estimation of passage time through the digestive tract. During 1967-1989 the stomach fullness of 1,524 fin whales landed at the whaling station in Hvalfjörður was assessed visually by assignment into seven categories. In 1988–89 attempts were made to quantify the visual assessments by weighing or measuring volumes of the content of stomachs previously assessed by eye. This was done by direct weighings and/or measurements of the volume of the stomach contents and measurements of the inner volume of the forestomach. Passage times through the digestive system (the four stomach chambers and the intestines) was then estimated from diurnal pattern in relative quantities and freshness of food remains in different parts of the digestive tract.

A forestomach visually assessed as full normally contained 5–600 kg of krill, the maximum being 760 kg in the present study (n = 34). Daytime feeding rates declined with the progression of the season, especially in August–September. Pronounced diurnal fluctuations were found in the quantity of forestomach content peaking at 0000–0600 hr, but some feeding activity continued throughout the day. Diurnal variation of food remains found in different parts of the digestive tract suggested that the mean passage time from the forestomach to the fundic chamber (2nd stomach compartment) was 3–6 hr, and that from the forestomach to the rectum around 15–18 hr. The calculated daily feeding rates for fin whales in June–July were between 677 and 1 356 kg, assuming 6 and 3 hr evacuation rates of the forestomach, respectively. The latter value is more likely with respect to studies on seasonal fattening of fin whales off Iceland (Paper 7; Lockyer, 1987b) and studies on ingestion rates in captivity (Innes et al., 1987; Sergeant, 1969). Three hour evacuation rate of the forestomach is also consistent with research on passage times for small and medium sized cetaceans in captivity (Ridgway, 1972; Sergeant, 1962; Tomilin, 1967). Three hour passage time leads to a consumption estimate that is close to the middle of the range of values considered by Leaper and Lavigne (2007) in their review.

Analysis of energy density of tissues in common minke whales gave broadly similar results as for other balaenopterid species (Paper 9). The study demonstrated that in addition to the increase in mass of important energy storage tissues, s.a. blubber and visceral fat (Christiansen et al., 2013c; Víkingsson et al., 2013a), common minke whales store significant amounts of energy by increasing the lipid content of various tissues, thereby increasing the energy density per unit weight. The results are consistent with previous studies on balaenopterids in that the most important blubber storage sites lie dorsally in the posterior part of the body (Lockyer et al. 1985; Vikingsson 1990; Paper 7) and support indications detected by (Næss et al., 1998) regarding common minke whales. In addition, large amounts of energy are apparently stored as visceral fats. Average lipid levels as high as 26% were found in bones. As skeletal tissue comprises around 10% of total body weight in baleen whales (Paper 7; Lockyer and Waters, 1986), the results suggest that the highly porous skeleton serves as an important energy storage site. The pattern of variation among reproductive classes is broadly similar to that found for larger *Balaenoptera spp.* with highest levels of lipids found in pregnant females. The study has also shown interesting spatial variation within the Icelandic continental shelf area, which can be explained by corresponding variation in diet composition (Paper 6). Thus, lipid content was higher in the southern and southwestern areas where sand eel (*Ammodytidae* sp.) dominated the diet than in the northern areas where gadoids were prominent in the diet. A significant decrease over the research period 2003-2007 in lipid content of posterior dorsal muscle could be a result of a decrease in the availability,of lipid rich prey such as the sand eel (Paper 12).

Paper 4 gives an estimate of the consumption by 12 species of cetaceans in Icelandic and adjacent waters from all available data sources by the mid 1990‘s. Abundance estimates were derived from the NASS surveys 1987-1995, recognizing the limitations of the data for non-target species for which estimates are probably downward biased. Data on body weight of the cetacean species were derived from the Icelandic waters where available (Víkingsson et al., 1988, Paper 7; MRI unpublished data), but otherwise from the literature (e.g. Christensen, 1982; Lockyer, 1976). Ingestion rates were estimated for each species on basis of biomass (abundance x mean weights of individuals) using two methods; A). Calculations based on actual feeding rates of cetaceans in captivity (Armstrong and Siegfried, 1991; Lavigne et al., 1986; Sergeant, 1969) and B) Energy requirement model based on assumptions regarding the relationship between physiological parameters and body weight. For the migratory baleen whales, account had to be taken of the seasonal feeding pattern with high feeding rates during summer and very low feeding rated during the winter breeding season. Assumptions regarding summer feeding rates were based on research on energetics of fin and sei whales conducted in Iceland (Lockyer, 1981, 1987a;

Vikingsson, 1990; Víkingsson et al., 1988; Paper 7) and published values for energy content of prey, assimilation efficiency, and activity coefficient (Lockyer, 1987a; Steimle and Terranova, 1985; Hinga, 1979; Overholtz et al., 1989).

Knowledge of diet composition in Icelandic waters was very limited for most of the species involved, allowing only categorization into three prey groups: planktonic crustaceans (krill), finfish and cephalopods. Information on residence time was estimated from the seasonal pattern of catch distribution for the species recently harvested, taking appropriate account of the hunting effort. On the basis of the above information and assumptions, consumption was estimated for each species at half-monthly inervals and these summed up for annual consumption. Total annual prey consumption was estimated as around 6 million tons by both methods, thereof roughly 2 million tons of fish (Paper 4). Fin and common minke whales were the largest consumers, each consuming around 2 million tons of prey. As mentioned above, these estimates are based on several unverifiable assumptions due to data deficiency for many of the species. To increase the precision of the estimates the following areas of increased knowledge were identified of particular importance: diet composition of most species in Icelandic waters, abundance estimates of non-target species (particularly small cetaceans), and seasonal variation in abundance (residence period in Icelandic waters). Further information on feeding habits, including consumption rates are also required to decrease uncertainty. Stefánsson et al., (1997) used these consumption estimates for simulation studies on interactions between some of the largest cetacean consumers and fishery resources. They concluded that increased abundance of cetaceans might decrease the long-term yield of cod (*Gadus morhua*) and capelin (*Mallotus villosus*) fisheries. However, there was large uncertainty associated with these predictions, in particular concerning the likelyhood of growth in whale populations and the diet composition of the cetaceans.

6.2.2. Diet composition

Insufficient knowledge on the diet composition of cetaceans in Icelandic waters was identified as a major source of uncertainty in evaluating the role of cetaceans in the Icelandic ecosystem (Sigurjónsson and Víkingsson, 1997; Stefánsson et al., 1997). Fin and common minke whales were identified as the largest consumers in Icelandic and ajdacent waters and therefore knowledge on their diet composition is especially important in this respect. The distribution of white-beaked dolphins (*Lagenorhynchus albirostris*) and harbour porpoises overlaps largely with the distribution of commercially important species and may thus be important in this context although their total consumption is likely much less than that of fin and minke whales.

6.2.2.1. Fin whales

Globally, fin whales have been shown to feed on a variety of prey species including several species of planktonic crustaceans (krill) and and pelagic fish such as capelin, herring (*Clupea haerengus*), mackerel (*Scomber scombrus*) and blue whiting (*Micromesistius poutassou*) (Aguilar, 2009; Reilly et al. 2013). On the whaling grounds west and soutwest of Iceland fin whales feed predominantly on krill (Papers 4 and 8). Of 1,609 fin whale stomachs examined at the whaling station 96% contained only krill, almost exclusively the species *Meganychtiphanes norwegica*. Other identified prey included capelin, blue whiting and sand eel. Although the sample size of this study was large, it represents a rather restricted geographical area and the diet composition in other parts of the Central North Atlantic is virtually unknown.

6.2.2.2. Common minke whales

Of the baleen whales common minke whales have the widest range of prey species (e.g Haug et al., 1996; Horwood, 1990; Jonsgård, 1982). The feeding habits of the species appear to be opportunistic with large spatial and temporal variations (Haug et al., 1995, 2002; Jonsgård, 1951; Neve, 2000; Tamura and Fujise, 2002; Windsland et al., 2007).

The Icelandic continental shelf constitutes the most important summer feeding ground of the Central North Atlantic population of minke whales judging from the NASS surveys (Borchers et al., 2009; Gunnlaugsson and Sigurjónsson, 1990; Papers 2 and 3). Although common minke whales have been hunted in Icelandic waters since 1914, research on feeding habits were limited at the onset of the moratorium in 1986. Sæmundsson (1932, 1939) concluded from opportunistic observations that herring was the most important prey of minke whales in Icelandic waters.

Sigurjónsson et al., (2000, hereafter Paper 5) examined all available information on minke whale diet in Icelandic waters during 1977-1997. The material comprised a total of 68 forestomachs from commercial catches, net entanglements and strandings. In the overall sample, fish and krill comprised 65% and 35% of the diet, respectively. Four species of fish, sand eel, capelin, herring and cod were identified and two species of krill (*Thysanoessa raschii* and *Meganyctiphanes norvegica*). Despite limitations of the sample, a clear difference was found in diet composition between northern and southern-southeastern Icelandic waters. In the former capelin and krill dominated the diet, whereas sand eel was the most commonly found prey in the southern and southwestern areas. In constrast to fin whales, *M. norvegica* was found in only one minke whales, where *T. raschii* was the dominant krill species. These result are in agreement with other studies showing opportunistic and predominantly piscivorous feeding habits of North Atlantic common minke whales (Christensen, 1974; Haug et al., 1996; Larsen and Kapel, 1982;

Mitchell, 1974). They do not however agree with Sæmundsson‘s (1932, 1939) statement of herring as the most important prey for minke whales in Icelandic waters.

Although the above study constituted a major advancement as the first biological research into minke whale diet in Icelandic waters, Paper 5 concludes that further systematic sampling is required to adequately describe the feeding ecology of this important species in the Icelandic ecosystem. The material had insufficient temporal and spatial coverage to be representative for the minke whale distribution as evident from the NASS surveys (Papers 2 and 3). Paper 4 had identified common minke whales as the most important cetacean species in the marine ecosystem of the Icelandic continental shelf. For any meaningful incorporation of cetaceans in ecosystem modelling of this area, better information on the diet composition of minke whales was therefore of great importance.

In 2003, the MRI initiated a wide ranging research program on common minke whales with the main objective of obtaining better information on the feeding ecology of the species. The program included several secondary objectives including research on biological parameters, stock structure, seasonality of abundance, pollutant levels and parasite burden (Víkingsson et al. 2013b). A total of 200 common minke whales were sampled for this purpose during 2003-2007 (Víkingsson et al., 2014) hereafter Paper 6. To ensure representative sampling, searching effort was distributed temporally and spatially in proportion to densities of minke whales as known from previous surveys. The continental shelf area was divided into 9 subareas based on ecological and oceanographical properties of Icelandic waters which are characterized by the meeting of warm Atlantic water masses from the south and Polar waters from the north (Gislason et al., 2009; Stefansson and Palsson, 1997).

Most (97.4%) of the analysed minke whale forestomachs contained food remains, with a mean weight of 15kg and a maximum of 106kg, the highest recorded for this species (Paper 6).

In general this study confirms earlier findings on the euryphagous and predominantly piscivorous nature of Northern Hemisphere common minke whales (Haug et al., 2002; Jonsgård, 1982; Larsen and Kapel, 1982; Pierce et al., 2004; Tamura and Fujise, 2002; Windsland et al., 2007). In total, 14 prey types were found in the stomachs, including 10 species of fish and 2 species of euphausiids. The size of prey identified in this study ranges from a few millimeters krill and fish fry to 92cm gadoids. The majority of the stomachs contained only one prey species, while the maximum number of species in a single stomach was six. Overall, the diet was primarily composed of fish, with krill contributing only 8-9% to the diet. Sand eel was the single most important prey type overall, with around 46% prevalence in the diet. Other common prey species were herring, capelin, haddock (*Melanogrammus aeglefinus*) and cod. Together, large demersal fish (gadoids) constituted 22% of the diet.

The diet composition varied considerably with geographic location. Sand eel dominated the diet in the southern and western areas, while the diet was more diverse off northern and eastern Iceland where the proportion of gadoids was higher.

Comparison of diet composition with the earlier study (Paper 5), taking account of the difference in temporal and seasonal scope of the two studies, revealed appreciable changes between the two periods. In the former study (1977-1984) capelin and krill were the dominant prey (81% prevalence) compared to only 38% during 2003-2007, when gadoids (30%), sand eel (22%) and herring (9%) contributed appreciably more to the diet.

Large changes in diet composition were also observed within the latter research period. In the southern area the contribution of sand eel decreased from 94% in 2003 to 18% in 2007. This decrease seems to have been largely compensated by herring that increased from being non-existent in the stomachs from 2003 to constituting nearly 80% of the diet in the southern area during 2007. The proportion of haddock also increased during the sampling period.

6.3. Recent oceanographical and biological changes in Icelandic and adjacent waters and their potential effects on baleen whales.

Better understanding of the effects of changing environmental conditions on animal populations is a central task in natural resource management and conservation. While regulation through density-dependent responses have been demonstrated in several studies on terrestrial mammals (Pettorelli et al., 2002; Sæther, 1997), large marine mammals have proven particularly difficult to study in this respect due to their large size and poor accessability (Fowler, 1987; Mizroch and York, 1985; Moore, 2008; Olesiuk et al., 1990; Taylor and DeMaster, 1993). Studies on fin whales in Icelandic waters have indicated a relationship between inter-annual fluctuations in prey abundance, body condition and fecundity (pregnancy rates) (Lockyer, 1987b; Sigurjónsson, 1992; Vikingsson, 1990). Williams et al. (2013, hereafter Paper 10) describe a comprehensive analysis of the available data on fin whale body condition (blubber thickness), fecundity (pregnancy rates) and fin whale abundance. The objective of the study was to quantify the relationship between body condition and *per-capita* prey abundance and between pregnancy rate and body condition as environmental conditions and whale abundance varied between 1967 and 2010. The modelling was performed at two stages: Firstly, day-of-year (Julian day), *per-capita* prey (krill) abundance, fin whale body length, and reporoductive category were used to predict body condition. Secondly, medial blubber thickness of mature females was used to predict probability of pregnancy.

Several potential indices of body condition and prey availability were considered. The best model (according to AIC‘s) for predicting body condition included the covariates day-of-year, body length, *per-capita* prey abundance, zooplankton abundance sampled off Southwest Iceland and reproductive category. Blubber thickness increased with day-of-year upto the end of July, thereafter levelling off. Blubber thickness was lower during low *per-capita* prey abundance than in medium years but did not seem to increase further in years of high *per-capita* krill abundance. In accordance with previous studies, pregnant females had thicker blubber than the other reproductive categories. According to the fecundity model, mature females with blubber thickness less than 50mmm had low probability of being pregnant while those with blubber thickness above 75mm had high probability og being pregnant.

The asymptotic relationship between body condition and per capita prey availability shown here, indicates that below an apparent threshold body condition declines as prey availability declines, but above this threshold surplus prey are not utilised to increase blubber thickness. Paper 10 also demonstrates that pregnancy rate is asymptotically related to blubber thickness in North Atlantic fin whales. Whales with thin blubber had a significantly lower probability of being pregnant than those with average blubber thickness, but extremely thick blubber apparently had little effect on pregnancy rate. This is the first time such a relationship has been demonstrated quantitatively for a large baleen whale species. The combination of the relationship between pregnancy rate and body condition and between body condition and *per capita* prey abundance is consistent with a density dependent response in North Atlantic fin whale pregnancy rate.

As detailed in Papers 1-3 substantial changes have occurred in the distribution and abundance of several baleen whale species since the initiation of systematic sightings surveys in 1987. At the same time large changes have been observed in the diet composition of common minke whales in Icelandic waters (Papers 5 and 6) and an apparent reduction in energy deposition by minke whales was detected between 2003-2007 (Paper 9). Studies combining behavioural observations with data on body condition concluded that common minke whales in Icelandic waters tend to maximize their energy storage and that whale watching activities may disrupt feeding behaviour to an extent that may negatively affect reproduction (Christiansen et al., 2013a, 2013b, 2013c). These studies together with those reported in Paper 10 indicate that fin and common minke whales may be sensitive to changes in prey availability.

Paper 12 summarizes recent changes in cetacean distribution and abundance and investigates to what extent they can be explained by recent biological (prey) and physical (oceanography) changes in the marine environment in this area. A part of this investigation, involves a first attempt at modelling the habitat use of fin whales in the Northeast Atlantic over a 20-year period, as a function of both physiographic and remotely sensed environmental variables.

Substantial warming and salinification has been observed in Icelandic and adjacent waters in the past two decades (Bersch, 2002; Hátún et al., 2005; Malmberg and Valdimarsson, 2003; Mortensen and Valdimarsson, 1999). Following 1995, an increase in temperature and salinity was observed in the waters south and west of Iceland and salinity and temperature have also been higher in the waters north of Iceland since the late 1990s. These changes were associated with a northward shift of fronts following increased flow of Atlantic water to the areas north of Iceland,

Concurrent with these changes, marked changes have occurred in the distribution of several fish species, including a northward shift in haddock and monkfish (*Lophius piscatorius*) (Astthorsson et al., 2007;

Solmundsson et al., 2010; Valdimarsson et al., 2012). At the same time an expansion in mackerel summer distribution westwards and northwards into Icelandic waters took place (Astthorsson et al., 2012). Due to the large size of the stock, this “mackerel invasion” into Icelandic waters represents a substantial change in the ecosystem of the Icelandic continental shelf (Óskarsson et al. 2012). The warm conditions have also been linked with the changed distribution and recruitment of the cold-water species capelin north of Iceland (Pálsson et al., 2012a, 2012b). 0-group capelin retreated northwards on the Icelandic shelf while the mature component has progressively spread along the shelf break off East Greenland (Pálsson et al., 2012a; Vilhjalmsson, 2007). Sand eel abundance in southern and western Icelandic waters was drastically reduced around 2005 because of recruitment failure, with severe consequences for some seabird populations (Bogason and Lilliendahl, 2009; Lilliendahl et al., 2013; Vigfusdottir et al., 2013).

There are limited data available on temporal trends in meso- and macro zooplankton in Icelandic waters. Silva et al., (2014) found a decrease in euphausiid abundance in the oceanic (offshore) waters south and west of Iceland during 1958-2007, while in south Icelandic shelf waters they reported an increase in euphausiid larvae during 1990-2011.

Recent and ongoing oceanographic and ecological changes changes in the Icelandic marine environment have affected several species that are important as prey for cetaceans and are thus likely to have contributed to the changes observed in distribution and abundance of several cetacean populations.

6.3.1. Fin whales

The habitat selection of fin whales was analyzed with respect to physical variables (temperature, depth, salinity) using a generalized additive model. The results suggest that abundance was influenced by an interaction between the physical variables depth and distance to the 2,000m isobaths, but also by sea surface temperature and sea surface height. Fin whales were most likely to be encountered close to the 2,000m isobath (continental slope) and at temperatures between 5°C and 11°C. The distribution of fin whales has changed in the Irminger Sea during this period. Whales aggregated over the continental slope in 1987, 1989, and 1995, but were dispersed throughout the Irminger Sea in 2001 and 2007. This expansion of distribution into the deep waters of the Irminger Sea coincided with appreciable warming of these deep waters after 1995 (Paper 12).

The catch distribution of fin whales in 2014 differed appreciably from all the previous seasons since 1948. Despite considerable effort few whales were found on the traditional whaling grounds west of Iceland and most of the catch was taken in offshore south Icelandic waters where densities are usually low.

As mentioned above, the rate of increase in fin whale abundance was highest in the Irminger Sea, on the tradional whaling grounds and adjacent areas (Paper 1). While recovery following the pause in whaling

1990-2006 could be part of the explanation of the increase, the catch history of the 20th Century and stock assessments suggest that the stock had recovered to a large extent before the period being considered here (Paper 1). The increase in fin whale abundance in the Irminger Sea between 1989 and 2001 coincided with a marked increase in sea temperature in the area (Paper 12). In particular, the expansion of fin whale distribution into deeper waters (>1,000m) of the Irminger Sea seems to be related to appreciable warming of this area between 1994 and 2003. Assuming that the diet of fin whales in the Irminger Sea consists overwhelmingly (> 90%) of euphausiids (Paper 8) it is tempting to conclude that the increased temperatures have facilitated growth in euphausiid abundance and thereby increased carrying capacity for fin whales (Paper 1). However, according to Continuous Plankton Recorder (CPR, SAHFOS) indices there has been a decrease in euphausiids in shelf and oceanic habitats southwest, south and southeast of Iceland from 1958 to 2007 (Silva et al. 2014).

Unfortunately, euphausiid monitoring by the extensive long-term CPR series only reaches as far north as the waters south and southwest of Iceland and is therefore not necessarily representative of the Irminger Sea. After the resumption of fin whaling in 2006 there are indications of decreased proportion of euphausiids in the diet (MRI unpublished data). A shift in diet could explain a less concentrated distribution along the shelf edge and higher observed and predicted numbers of fin whales throughout the Irminger Sea. Increased predation on euphausiids from the growing fin whale population and the recent invasion of mackerel (see below) might also have contributed to the decrease in euphausiid abundance.

6.3.2. Common minke whales

Abundance estimates of common minke whales in the continental Icelandic shelf area have varied widely during 1987-2009 peaking in 2001 (Borchers et al., 2009; Paper 2). The survey in 2007 revealed a reduction in minke whale abundance to less than half that of 2001 and an extra aerial survey conducted in 2009 showed even further decline in numbers. The decrease in abundance was considerably larger in the southern part of the survey area (79%) than in the northern area (46%) indicating a northward shift in relative abundance within the continental shelf area. The shipboard offshore component of the 2007 survey failed to detect a corresponding increase in abundance of minke whales in the offshore regions of the Central North Atlantic stock area. However, large areas north of Iceland and along the coast of East Greenland received no or poor coverage due to unfavorable weather and ice conditions (Pike et al., 2010b). Therefore, the details of a potential shift in distribution are unknown.

Investigations of stomach contents of minke whales have shown pronounced changes in diet composition in recent decades. During 1977-1997, sand eel was the predominant prey in southern and western Iceland while capelin occurred in 42 % and euphausiids in 58% of the stomachs in the northern areas (Paper 5). During 2003-2007 a significant change had occurred in the minke whales’ diet composition with the contribution of euphausiids and capelin decreasing from 45% to 17% and 36% to 22%, respectively in comparable areas (Paper 6). The proportions of large gadoids (mainly haddock and cod) and herring increased correspondingly between these two periods. The overall percentage of sand eel in minke whale stomachs was still high in the latter period, but decreased appreciably within the period from 90% in 2003 to 20% in 2007 in the southern areas (Víkingsson *et al.*, 2014).

These dietary changes coincide well with the documented changes in the local abundance of the prey species sand eel, capelin and euphausiids (Marine Research Institute, 2015; Astthorsson et al., 2007). The decrease in sand eel abundance during 1997-2003 indicated by the analyses of haddock stomachs (Paper 12) is confirmed by decreased breeding success of sand eel-dependent seabirds in southern Iceland (Vigfusdottir et al., 2013; Lilliendahl et al., 2013). The subsequent low levels of sand eels in minke whale stomachs seem to reflect decreased availability of sand eel revealed by a monitoring program initiated in 2006 (Bogason and Lilliendahl, 2009). The low proportion of capelin in the minke whale diet is also consistent with lower availability of capelin in north Icelandic waters during summer and the increased contribution of haddock and herring reflects growth in these stocks during the sampling period (Marine Research Institute, 2015). These diet studies, together with the series of abundance estimates, suggest that minke whales appear to have responded to the environmental changes both by prey switching (from sand eel, capelin and euphausiids to herring and gadoids) and by a shift in distribution away from the Icelandic continental shelf area. While it seems likely that some of the whales followed the capelin to the coast of East Greenland, this cannot be verified because of the lack of coverage of that area by the 2007 survey.

6.3.3. Humpback whales

Catch statistics from the first period of modern whaling in Icelandic waters, the so-called Norwegian whaling period 1883-1915, indicate that humpback whales were hunted down to very low levels before and during that period. Only six humpback whales were caught after whaling was resumed in 1948 until they received total protection again in 1955. Sigurjónsson and Gunnlaugsson (1990) reported an annual increase in relative abundance of 14.8% during 1979-1988 west of Iceland. This growth rate, coupled with the small absolute abundance estimate of around 2,000 humpback whales in 1987 (Gunnlaugsson and Sigurjónsson, 1990) indicates that the number of animals in the area must still have been very small up to the 1970's. Subsequently, annual rates of increase in abundance of 12% were reported for the period 1987-2001 in the shelf area (Paper 2).

The most recent data presented here suggest that this rapid growth may have levelled off around the turn of the century (after the 1995 survey). Feeding habits of humpback whales in Icelandic waters are not well corroborated by stomach contents data. However, visual observations have indicated that capelin and euphausiids likely constitute important parts of the diet (Paper 4; MRI unpublished information). In particular numerous reports from capelin fishermen and capelin research cruises have documented substantial numbers of humpback whales following the migration of capelin in Icelandic waters during winter (Gunnlaugsson and Víkingsson, 2014). In recent years, humpback whale songs associated with mating behavior have been recorded in North Icelandic waters (Magnúsdóttir et al., 2014). Although this acoustic activity does not demonstrate that breeding actually takes place in Icelandic waters, an establishment of a new breeding area, in addition to the two known southern breeding areas, could help explain the large population increase in Icelandic waters and the apparent contradiction between abundance estimates at feeding and breeding grounds of the North Atlantic, as discussed by Smith and Pike (2009).

The increase in humpback whale abundance in Icelandic waters, levelling off around the year 2000, follows a pattern similar to the rise in temperature (Figure 2). However, it is hard to relate this growth to any known biological changes in the marine environment because the presumed most important prey species (capelin, euphausiids and possibly sand eel) have not followed the same trends in abundance. In recent decades, high rates of increase have also been documented for humpback whales in several other areas without a clear explanation (Bannister, 1994; Barlow and Clapham, 1997; Stevick et al., 2003; Findlay et al., 2011; Heide-Jørgensen et al., 2012).

6.3.4. Blue whales

Blue whale populations have not recovered to the same extent as the closely related fin whales or humpback whales, with estimated abundance in the Central North Atlantic of around 1,000 animals (Pike et al., 2009b). However, a significant increase in abundance has been reported for the period 1969-2001 (Pike et al., 2009b; Sigurjónsson and Gunnlaugsson, 1990). During 1987-2001 the increase rate was higher in Northeastern Icelandic waters than west of Iceland (Pike et al., 2009b) indicating a northward shift in relative distribution. Such a shift is consistent with anecdotal evidence from whale watching operations in Icelandic waters. A whale watching company specializing on blue whales was operated from the Snæfellsnes peninsula, West Iceland during 1996-2004. From around 2000, the number of encounters with blue whales decreased appreciably leading the company to give up their special blue whale tours in 2004 due to scarcity of the target species (Pétur Ágústsson pers. comm). During this period of decline in West Iceland, blue whale sightings increased in the whale watching area Skjálfandi Bay in Northeast Iceland. Photo-identification matches have shown that at least some of the whales previously frequenting West Icelandic waters now occur in northeastern Icelandic waters during midsummer (MRI unpublished data).

6.3.5. Other species

During 1986-2001 the relative frequency of harbour porpoises decreased in Icelandic coastal waters (Paper 2). While there are methodological concerns regarding the estimates for this small species, the apparent decrease might be related to decreased availability of capelin, a very important component of the diet of harbour porpoises in Icelandic waters (Víkingsson et al., 2003).

Stranding records maintained at the MRI have shown recent increase in occurrence of striped dolphin (*Stenella coeruleoalba*) strandings (Víkingsson and Halldórsson, 2006). This species is most common in tropical and sub-tropical waters. The first two registered strandings in Iceland were in 1984, and 1998, but since 2004 a total of 10 separate stranding events have been documented (Víkingsson and Halldórsson, 2006; MRI unpublished data). MacLeod *et al.* (2004) report similar findings from Scottish waters where the occurrence of warm water cetacean species increased after 1988.

7. Concluding remarks

Five species of baleen whales migrate annually into Icelandic waters and spend the summer feeding in this productive area. The locations of the winter breeding grounds for these populations are unknown except for the humpback whales that breed in the Caribbean Sea and close to the Cape Verde Islands. Satellite tracking experiments indicate that the deep waters off northwestern Africa (i.e. west of Cape Verde) might be a winter destination for common minke whales summering off Iceland (Paper 11).

Energetic studies of fin and common minke whales show significant energy deposition in blubber, muscle, visceral fat and bones. The energy storage is most intense in pregnant females that increase the energy content of the body by around 80% over the four month feeding season (Papers 4, 7 and 9).

Feeding rates of baleen whales are hard to estimate and represent a major source of uncertainty in most estimates of consumption e.g. (Innes et al., 1987; Leaper and Lavigne, 2007; Markussen et al., 1992). Two methods to estimate feeding rates of fin whales (Papers 7 and 8) gave similar results that are that are close to the middle of the range most commonly assumed in such studies.

The results presented here have demonstrated the important role played by baleen whales in the marine ecosystem around Iceland. The consumption by the 12 species of cetaceans regularly occurring in Icelandic waters was estimated as around 6 million tons, equivalent to around four times the average total Icelandic fishery landings (Paper 4). Fin and common minke whales were the largest consumers with a total consumption of around 2 million tons each species.

Analysis of all available data from 1967-2010 on the abundance, body condition and reproductive parameters of fin whales and indices of zooplankton abundance indicates that *per-capita* prey abundance may affect fecundity through body condition in an asymptotic way (Paper 10).

Pronounced oceanographic changes have occurred in Icelandic waters since the mid-1990s, including a rise in sea water temperature and increased flow of warm Atlantic water into the waters north of Iceland. Although the exact mechanisms remain unclear, these changes appear to have caused a northward shift in the distribution of several fish species, a decrease in krill abundance and a collapse in the sand eel population off southern and western Iceland (Paper 12). Considerable changes in distribution and abundance of several cetacean species are apparent from the series of cetacean surveys dating back to 1986. Some of these changes appear to be related to these oceanographic and biological changes while others are harder to explain. Thus the decrease in common minke whale abundance in the Icelandic continental shelf area after 2001 (Papers 2 and 3) seems to be related to the decrease in the abundance of the preferred prey species, sand eel in the southern part and capelin (and possibly also euphausiids) in the northern part (Papers 5, 6 and 12). The decreased abundance must have led to a dramatic decrease in total prey consumption by minke whales in the Icelandic shelf area. However due to the concurrent changes in diet composition (Papers 5 and 6) predation on some prey s.a. herring and gadoids may have increased during this period.

The apparent shift in distribution of blue whales from southwestern to northeastern Icelandic waters may be related to the decrease in euphausiid abundance in the waters south and southwest of Iceland (Silva et al., 2014, Paper 12).

Concurrently with increasing sea temperature in the deep waters of the Irminger Sea, the distribution of fin whales expanded into this area and the total abundance of fin whales in the Irminger Sea increased (Papers 1 and 12). However, the relationship between the rise in temperature and fin whale abundance is unclear. The warming of these waters could have triggered an increase in euphausiid abundance, the fin whale's dominant prey species in this area. However, this is not supported by CPR data that could instead indicate that fin whales may have switched prey. However, data on euphausiid abundance from the main fin whale feeding grounds are lacking because the CPR data series covers only the southernmost part of that area. Judging from the abundance and feeding ecology of fin whales, the Irminger Sea is a highly productive area in terms of euphausiids abundance. Acccording to recent surveys (e.g. Paper 1) around 15,000 fin whales feed in this area during summer. The feeding rates estimated in Papers 7 and 8 suggest that fin whales consume between 1.4 and 2.2 million tons of euphausiids during a 120 day feeding season. Unfortunately no data on krill biomass is available for this area, but steps are being taken by the MRI to start monitoring the abundance of euphausiids in this important area.

Humpback whales were rare in Icelandic waters throughout most of the 20th century but a significant increase occurred between 1970 and 2001 in the Central North Atlantic (Paper 2). From 1995, abundance has been rather stable at around 10-15,000 whales. Feeding ecology of humpback whales in Icelandic waters is poorly documented but capelin and euphausiids are known to be among their prey species. It is hard to relate the increased abundance of humpback whales since the 1970s to any known biological changes in the marine environment. Using the methods given in Paper 4, the recent increase in abundance amounts to an increase in prey consumption from around 230,000 tons in 1987 to 1.8 million tons in 2007. During the past 3-4 decades the ecological role of humpback whales has thus changed dramatically from being a rarely occurring species to being one of the most important marine mammal predator in Icelandic continental shelf area.

The effects of continued warming on the distribution of cetaceans in Icelandic and adjacent waters are hard to predict. The potential effects on ice-dependent marine mammals in the Arctic have been discussed by several authors e.g. (Anderson et al., 2013; Laidre et al., 2008; MacLeod *et al.* 2004, 2009; Moore, 2008; Moore and Laidre, 2006; Moore and Huntington, 2008). These effects are likely to differ between truly Arctic species, sub-arctic species and those that are dependent on the arctic only for part of their life cycle, e.g. the migratory baleen whales. For example subarctic or temperate cetacean species may benefit from the retreat of sea ice as the ice coverage represents a barrier for their distribution (Kovacs et al., 2011; Laidre et al., 2008; Moore and Laidre, 2006). Such an expansion of sub-arctic species can increase the negative effects of the warming on the truly arctic species by increased competition, increased risk of predation by killer whales and increased disease and parasite risks.

The research presented in this thesis indicates that effects of warming are already evident in Icelandic and adjacent waters (Papers 5, 6 and 12). The NASS series has revealed appreciable changes in distribution of several cetacean species and studies into feeding ecology and energetics provide possible explanations for these changes. While it is premature to conclude whether these changes are following the predictions outlined above for subarctic and/or migratory cetaceans, they do not contradict these predictions. The potential benefits of global warming to subarctic species through increased size of suitable habitat (Kovacs et al., 2011; Laidre et al., 2008; Moore and Huntington, 2008; Moore and Laidre, 2006; MacLeod *et al.* 2009) might, however be partly offset by increased competition from the further south, i.e. expansion of temperate species into sub-arctic waters. The “invasion” of the Northeast Atlantic mackerel stock into Icelandic waters, starting around 2006 is likely to have had appreciable impact on the ecosystem. Total consumption by mackerel in Icelandic waters during summer was estimated as 2.2.-3.4 million tons in each of the years 2010 and 2011 (Óskarsson et al., 2012) and the abundance of mackerel in the area has increased since (Marine Research Institute, 2015). Limted studies on the diet composition of mackerel in Icelandic waters indicate calanoid zooplankton as the most important prey species while Euphausiids and fish species, including sand eel and capelin are aslo included in the diet (Óskarsson et al., 2012).

Continued monitoring of the distribution and abundance of cetaceans as well as further studies into their feeding ecology are essential for better understanding of the recent and ongoing changes documented here. With decreased direct exploitation of whales in recent decades there may be less incentive for governments to monitor distribution and abundance of cetaceans by expensive surveys. However, the value of such monitoring is not limited to conservation and management of the whale stocks. As top predators, cetaceans, and other marine mammals are well suited to serve as indicators of climate change (e.g. Moore 2008) and should be included in future comprehensive schemes for monitoring the effects of climate change.

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