

1 Recent changes in the diet composition of common
2 minke whales (*Balaenoptera acutorostrata*) in Icelandic
3 waters. – Consequence of climate change?

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8
9 Abstract

10 The common minke whale (*Balaenoptera acutorostrata*) is the most abundant mammalian top
11 predator in Icelandic continental shelf waters. Although Icelandic waters are among the most
12 important feeding grounds of common minke whales in the North Atlantic, no systematic research
13 has previously been conducted on the species' feeding ecology in this area. Here, an account is
14 given on the first systematic research programme into the feeding ecology of common minke
15 whales in Icelandic waters based on analysis of minke whale stomach contents data collected in
16 Icelandic waters during 2003-2007. The results show pronounced spatial and temporal variation
17 in the diet. The temporal changes include a decrease in the proportion of sandeel in the diet over
18 the study period and a corresponding increase in herring and gadoids. The diet also differed
19 markedly from the limited previously available data from Icelandic waters. These changes in diet
20 composition are consistent with recent changes in the Icelandic continental shelf ecosystem
21 including high sea temperatures and changes in distribution of several fish species including

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22 sandeel and capelin. Although natural fluctuations cannot be ruled out at this stage, these dietary
23 changes, together with decreased abundance in coastal waters, may reflect the responses of minke
24 whales to a changed environment possibly driven by global warming.

25

26 Introduction

27 The common minke (*Balaenoptera acutorostrata*) whale is the most abundant whale
28 species in Icelandic coastal waters with mean densities up to 0.07 animals/nm.² in the
29 continental shelf area in recent decades (Pike et al. 2009). The species is generally
30 regarded as the most ichthyophagous of baleen whales and also, the most opportunistic
31 with regard to feeding habits (Tomilin 1967, Horwood 1990). Skaug et al. (1997)
32 concluded that despite being quite flexible in feeding habits, minke whales off Norway
33 show some preference for fish over krill.

34 In the Northern Hemisphere, minke whale diet varies considerably among areas and large
35 temporal variations have also been demonstrated for the species (Jonsgard 1982,
36 Horwood 1990, Klinowska 1991, Haug, Gjösæter, et al. 1995, Haug, Nilssen, et al. 1995,
37 Haug et al. 1996, Neve 2000, Tamura & Fujise 2002). Although hunting of minke whales
38 in Iceland dates back to 1914, knowledge on feeding habits of the species in Icelandic and
39 adjacent waters has been very limited. During the 20th century, only 68 minke whale
40 stomachs were examined, thereof 56 from the commercial fishery during 1977-1978, one
41 caught in 1984 and 11 stranded or by-caught animals (1988-1997). Most of these animals
42 were sampled off North Iceland in June and July. Thus, large parts of the distribution area
43 and residence period of minke whales in Icelandic waters were virtually unexamined.
44 Based on frequency of prey occurrence, this limited data indicated that approximately
45 65% of the diet consisted of fish while the remaining 35% were Euphausiid crustaceans

46 (Sigurjónsson et al. 2000). Among the identified fish species were capelin (*Mallotus*
47 *villosus*), sandeel (*Ammodytidae*), and cod (*Gadus morhua*), while the identified krill
48 species were *Thysanoessa raschii* and *Meganyctiphanes norvegica*.

49 Preliminary investigations into the ecological role of minke whales in Icelandic waters
50 have indicated that the species may have a significant effect on the long-term yield from
51 fisheries, in particular cod and capelin (Sigurjónsson & Víkingsson 1997, Stefánsson et al.
52 1997). There was however, large uncertainty associated with these estimated effects.
53 Limited knowledge on the diet of minke whales in Icelandic waters was among the most
54 important identified sources of uncertainty (Stefánsson et al. 1997). Considering the large
55 spatial and temporal variations in the diet of minke whales species observed in other
56 areas, there is clearly a need for further studies into the feeding ecology of the species in
57 Icelandic waters.

58 The Icelandic continental shelf constitutes the most important feeding ground of the
59 Central North Atlantic population of minke whales judging from the NASS series of large
60 scale sightings surveys (Gunnlaugsson & Sigurjonsson 1990, Borchers et al. 2009, Pike et
61 al. 2009). Abundance in this area has though varied considerably since systematic
62 monitoring of abundance began in 1986 with a maximum estimate of 43,633 (30,148 -
63 63,149) animals obtained in 2001 (Borchers et al. 2009) The most recent surveys (2007-
64 2009) have shown considerably lower densities (Pike, Gunnlaugsson, Elvarsson, et al.
65 2011). While the reasons for the decline are unclear, the limited minke whaling during
66 this period (a total of 207 whales taken during 2003-2007) cannot have caused a decline
67 of this magnitude (NAMMCO 2009). This sudden change in minke whale density in
68 coastal Icelandic waters seems more likely to represent a shift in distribution than a crash
69 in population size. However, due to poor coverage of offshore areas, particularly to the

70 north and west of Iceland, such a shift in distribution cannot be demonstrated from the
71 survey data and hence a real population decrease can not be excluded. A potential
72 explanation for such a shift in distribution of minke whales could be a shift in the
73 distribution of important prey species that may be related to appreciable changes in the
74 physical and biological environment observed in Icelandic waters in recent years
75 (Astthorsson et al. 2007, NAMMCO 2009). Given the euryphagous nature of the minke
76 whale, such a shift in prey species would likely be reflected in the diet of minke whales.
77 This paper presents a study on the diet composition of minke whales in Icelandic coastal
78 areas. The results are discussed in connection with the limited previously available data,
79 spatial variation and in relation to recent changes in the marine environment of Icelandic
80 coastal waters.

81 Material and methods

82 **Sampling**

83 The minke whale material used in this study was collected during 2003-2007 as a part of a
84 comprehensive research programme (Marine Research Institute 2003).

85 The whales were caught using five minke whale catching boats hired by the Marine
86 Research Institute (MRI). Cruise leaders from the MRI were in charge of the operation
87 onboard each vessel and up to four scientist in total. In most cases, dissection and
88 sampling took place onboard the vessels within three hours *post mortem*.

89 To ensure representative sampling, searching effort was distributed temporally and
90 spatially in proportion to densities of minke whales as known from previous surveys
91 (Borchers et al. 2009). The sampling was designed according to an established delineation
92 of the Icelandic continental shelf area into nine sub-areas (Fig.1), as defined by

93 (Stefansson & Palsson 1997), based on ecological and hydrographical characteristics. To
94 avoid selective sampling exhaustive attempts were made to catch the first whale sighted
95 within a given subarea and period. Whales were taken onboard immediately after death
96 for detailed dissection and sampling for the various sub-projects (Marine Research
97 Institute 2003).

98

99 **Analysis of stomach contents**

100 Based on comparison between contents of different stomach compartments, (Lindstrøm et
101 al. 1997) concluded that the fore-stomach contents are sufficient to describe the diet of
102 minke whales. Therefore this study is confined to the analysis of the fore-stomach.

103 The contents of the stomach were transferred to a special container for measuring it's total
104 volume. Preliminary identification of dominant prey species and identification of stomach
105 fill was conducted at sea by visual inspection. Then the liquid was removed by a series of
106 sieves (20mm, 5mm and 1mm) separating differently sized particles as described by Haug
107 et al. (1995a). Sub-samples were taken from stomachs with large contents of uniform prey
108 and preserved frozen (see Haug et al., 1996) while stomachs with diverse contents were
109 sampled in whole. In the laboratory, food remains were identified to the lowest possible
110 taxonomic level. For undigested fish prey, up to 50 measurements were made of length
111 and weight for each species and the age determined from growth zones in sagittal otoliths.
112 Most of the stomach contents were, however, too digested for such measurements. In
113 these cases, otoliths were used for species identification, counted and then measured
114 under a microscope using a stereo-microscope with a graticule scale in the eyepiece.

115

116 In addition to whole undigested fish, the number of fish in each stomach was calculated

117 by dividing the total number of sagittal otoliths by two or, in the case of larger otoliths, by
118 counting the number of otolith pairs. The number of cephalopods was defined as the more
119 numerous of upper or lower beaks. It was not possible to estimate the number of highly
120 digested small crustaceans. For this group, the measured volume was used to estimate its
121 contribution to the diet as done in previous studies (Tamura & Fujise 2002, Windsland et
122 al. 2007). The stomach volume and weight was analysed using generalized linear model
123 with a Gamma link function as described by Stefansson & Palsson (1997). The
124 parameters considered were area, year, month, sex and maturity. The best model was
125 selected on the basis of the Akaike Information Criterion (AIC), as discussed in Akaike
126 (1974), by stepwise removal of the above parameters.

127

128 The results are expressed as frequency of occurrence (FO) and reconstructed weight,
129 (RW) feeding indices traditionally used in analyses of stomach content (Hyslop 1980,
130 Pierce & Boyle 1991, Víkingsson et al. 2003). In addition a weighted frequency index
131 (WFO) was used for comparison with a previous Icelandic study (Sigurjónsson et al.
132 2000). Comparisons between major prey groups with respect to digestion (undigested
133 versus other digestion states) and also comparisons of whether one or more prey species
134 were found in the stomachs varied based on geography was made using a χ^2 -test.

135

136 For calculating fish size from the size of sagittal otoliths, formulae based on Icelandic
137 published (Vilhjálmsson 1994, Víkingsson et al. 2003) and unpublished measurements
138 were applied if available. In the absence of Icelandic data, formulae from other areas
139 (Härkönen 1986), were used. Otoliths that were noticeably eroded by digestion
140 ,corresponding to digestion state 3 and above as in (Recchia & Read 1989), were not used

141 in calculations of fish size. Some stomachs containing large amounts (>50) of otoliths
142 were subsampled for measurements and in few cases also for counting of prey items.
143 Further details on laboratory techniques and methods are given in Vikingsson et al.,
144 (2003)
145 Length dependant prey selection was analysed using a linear regression model for prey
146 length where prey species within individual whales were treated as a random effect. The
147 best model was selected, as in the case of stomach volume, on the basis of AIC.

148

149 Results

150 The spatial and temporal distribution of the sampling is shown in Figure 1 and Table 1
151 respectively. A total of 190 minke whales (96 males and 94 females) sampled during
152 April-September 2003-2007 were examined with respect to stomach contents.

153 **Total volume and weight of stomach contents**

154 Most (97.4 %) of the stomachs contained some food remains. The median and mean
155 volume of the unfiltered fore-stomach contents was 32 l (95% quantiles : 0 – 132.28) and
156 42 l respectively with a maximum of 200 l in a 8.1 m long female. The median and mean
157 weight of stomach contents after removal of fluid was 7.82 kg (95% quantiles : 0.03–
158 79.53) and 14.83 kg respectively with a maximum weight of 106.25 kg in a 7.85 m long
159 male.

160 The best models of stomach volume and weight, in terms of AIC, were both based on the
161 whale length and geographic area (Table 2). Other variables such as sex, month, year and
162 time of the day did not offer a significant improvement to the model. Two sampling areas,
163 2 and 10 (see Fig. 1) were significantly lower than the other 7 in terms of weight of

164 stomach contents. Whales caught in areas 2, 5, 9 and 10 had significantly lower stomach
165 volumes than those in other areas (Table 3).

166

167 **Overall diet composition**

168 In total 14 prey species were found in the stomachs including 10 species of fish and 2
169 species of euphausiids (Table 4). In addition two species of crabs (*Pagurus bernhardus*
170 and *Hyas coarctatus*) found in one stomach each were considered secondary prey (“prey
171 of prey”) and thus not included in further analyses. Most (56%) of the stomachs contained
172 only one prey species while the maximum number of species in a single stomach was six.
173 Sandeel was the most frequently encountered prey, occurring in 110 (58%) of the
174 stomachs. It was not possible to distinguish between the three species of sandeel
175 occurring in Icelandic waters. While it seems likely that the bulk of the sandeel prey is
176 *Ammodytes marinus*, the overwhelmingly dominant species in these waters (Bogason &
177 Lilliendahl 2009), the large size of some individuals shows that *Hyperoplus lanceolatus*
178 was also included to some extent. Other frequently occurring prey types include haddock
179 (*Melanogrammus aeglefinus*), herring (*Clupea haerengus*), capelin and krill found in
180 23%, 20%, 19%, 15% and 18% of the examined stomachs respectively (Table 4).

181

182 Figure 2 shows the the diet composition in terms of weighted frequency of occurrence
183 (WFO) and reconstructed weight (RW) of different prey species pooled for the research
184 period 2003-2007 compared to the previously available data (Sigurjónsson et al. (2000).
185 The two measures of diet composition (WFO and RW) show remarkably similar results
186 (Fig. 2). The diet was primarily composed of fish, with krill contributing only 8.6% in
187 terms of WFO and 8.2% in terms of RW to the diet. Sandeel was the single most

188 important prey type overall with 45% and 47% prevalence in terms of WFO and RW,
189 respectively. Other common prey species were herring, capelin, haddock and cod.
190 Together, large benthic fish (gadoids) constituted 24% and 23% of the diet respectively
191 according to these measures.

192

193 **Geographical and temporal variation**

194 Although the previous data were limited, it seems clear that significant changes have
195 occurred in the diet of minke whales in Icelandic waters between the two periods. Thus, in
196 the more recent period (2003-7), the proportion of large, benthic fish (notably cod and
197 haddock) was much higher while planktonic crustaceans accounted for much smaller
198 proportion of the diet. Overall, there were similar levels of pelagic fishes although the
199 composition of this group was quite different between the two periods with capelin
200 dominating this prey category in the earlier period and herring more prevalent in the latter
201 period.

202

203 Figure 3 shows the diet composition in terms of FO (Fig. 3a) and RW (Fig. 3b) by year
204 and area for the period 2003-2007. These two measures show generally similar results
205 although invertebrates have a somewhat higher score in terms of FO. The diet
206 composition varied considerably with geographic location. Sandeel dominated the diet in
207 the southern and western areas, while the diet was more diverse off northern and eastern
208 Iceland. The dominance of sandeel was particularly striking in the beginning (2003) when
209 it's proportion of the diet in terms of reconstructed weight amounted to 94 and 51 % in
210 the southern and northern areas respectively (Fig. 3b). This proportion decreased steadily
211 throughout the research period in both areas and was 18 and 12 % in respectively in 2007.

212 Of the pelagic fish prey capelin appeared to form a steady part of the diet in the northern
213 area throughout the observation period while being hardly detected in the southern area
214 (Fig. 3). The importance of herring in the diet however increased from being non-existent
215 in the stomachs from 2003 to constituting nearly 80% of the diet in the southern area
216 during 2007 (Fig. 3).

217 Figure 4 shows the contribution of gadoid species (and other large bony fishes) in more
218 detail. Overall, haddock and cod were the most important gadoids, contributing 9.77 and
219 7.93 % of the reconstructed weight respectively. Cod consumption was largely confined
220 to the northern area where it constituted up to 29% of the diet. Haddock was only a minor
221 component of the diet in 2003-2004, but thereafter it was an important part of the diet in
222 both areas (Fig. 4). Other gadoid species such as saithe (*Pollachius virens*), whiting
223 (*Merlangius merlangus*) and blue whiting (*Micromesistius poutassou*) appeared in the diet
224 to a lesser extent.

225

226 **Prey length and age.**

227 The reconstructed size range of fish prey for the minke whale was 1 - 93 cm in total
228 length (Fig. 5). Among the fish species taken in considerable numbers, sandeel and
229 capelin had the lowest mean length of 12.8 and 9.3 cm respectively, although individuals
230 up to 36.7 and 16.2 cm were found. All age classes (0 to 4 years) of capelin were
231 consumed by the minke whales, although a large majority was less than three years (Fig.
232 6).

233 The age of sandeel ranged between 0 and 6 years with year classes 0-3 dominating in the
234 diet.

235 The herring consumed varied from 0 to 41 cm in length and 1-14 years in age.

236 The size range for cod was 0 to 92.51 cm with a mean size of 61.99 cm. The age of cod
237 prey ranged from 0 to 14, with a mean of 6 years. The mean length of haddock was 41.63
238 cm, ranging from 2.6 to 91.78 cm, and mean age was 3.9 years, ranging from 0 to 9 years.

239 Discussion

240 **Potential sources of bias**

241 Minor sampling constraints were imposed by exclusion of whale watching areas and
242 generally worse weather in offshore areas may have caused some sampling bias.
243 However, the limited search effort that was possible in offshore areas, together with
244 information from a simultaneous sightings survey, as well as information from fishing
245 vessels further offshore indicated that the distribution of minke whales in the area was
246 indeed, very coastal during this period. Therefore, we conclude that the sampling
247 distribution was representative of the distribution of minke whales within the Icelandic
248 continental shelf area.

249 Differential digestion rates of different prey items is a potential source of error in stomach
250 contents analysis (Hyslop 1980, Pierce & Boyle 1991). For example the proportion of small
251 planktonic crustaceans in the diet may be underestimated due to higher rates of digestion (Gannon
252 1976). One way to address this problem is to compare the overall results to those of a subsample
253 of stomachs containing only virtually undigested food. Comparison of stomachs containing
254 fresh prey (n=51) with those containing digested prey (n=177) did not reveal significant
255 differences in diet composition ($\chi^2(4)=6.5967$, $p=0.1588$). This indicates that differential
256 digestion rates of prey species did not introduce any appreciable bias in the study
257 although some underrepresentation of krill cannot be ruled out. The close similarity in the
258 results using different measures (RW or WF) for diet composition also indicates absence

259 of significant bias due to differential digestion rates.

260

261 **Overall diet composition**

262 The median volume of stomach contents in this study is within the range reported off
263 Norway (Nordoy & Blix 1992) and the small proportion of empty stomachs is similar to
264 studies of minke whales from other areas (Mitchell 1974, Larsen & Kapel 1981,
265 Kasamatsu & Hata 1985, Haug, Nilssen, et al. 1995, Tamura & Fujise 2002). The
266 maximum amount of food remains retrieved from a single fore stomach (106 kg) is to our
267 knowledge the highest reported for this species.

268 Not unexpectedly, length of the whale appeared to have the largest predictive power for
269 the magnitude of stomach contents but significant geographical variation was also
270 detected. The geographical variation might however be confounded by temporal changes
271 in food availability as the sampling years were not evenly distributed on sampling areas..

272

273 This study confirms earlier findings on the euryphagous and predominantly piscivorous
274 nature of northern hemisphere minke whales (Larsen & Kapel 1981, Jonsgard 1982,
275 Tamura & Fujise 2002, Haug et al. 2002, Pierce et al. 2004, Windsland et al. 2007).

276 While the range of species taken by minke whales was large, the majority of the whales
277 (59%) had recently fed on only one prey species. This differed significantly according to a
278 north-south division ($\chi^2(1) = 15.97, p < 0.001$), where proportion of whales with only one
279 prey species was 70% in the south while 43% in the north. Low diversity of prey found in
280 individual stomachs is typical for the so called swallowing type of baleen whales (Nemoto
281 1959) feeding on swarming zooplankton and schooling fish and several variations of this
282 methods have been described for minke whales in Icelandic waters (Bertulli 2010).

283 The prey diversity reported here is somewhat higher than that reported from Norway and
284 Japan, where 69% and 90% respectively of the minke whales had only one prey species in
285 their forestomachs (Tamura & Fujise 2002, Windsland et al. 2007).

286 Sandeel was the most important prey species overall contributing nearly 50% to the diet.
287 Pelagic fish (herring and capelin) and gadoids each accounted for over 20% of the diet,
288 Although gadoids have been reported as prey of minke whales in several other areas of
289 the North Atlantic (Sergeant 1963, Larsen & Kapel 1981, Horwood 1990), their
290 contribution to the diet is usually less than that reported here, particularly off north
291 Iceland. However, comparable and even higher values for gadoids have been observed in
292 some areas off northern Norway (Jonsgard 1982, Haug & al 1995, Windsland et al. 2007).

293

294

295 According to this study, the prey of minke whales varies in size from few millimetres
296 (planktonic crustaceans and fish fry) to 92cm long gadoids. Similarly wide ranges have
297 been documented for this species from Norway (Windsland et al. 2007) where gadoids
298 upto 85cm were found in minke whale stomachs. Prey of this size contradicts the general
299 idea of baleen whales feeding primarily on planktonic crustaceans and small schooling
300 pelagic fish species and it could be argued that these large codfish are taken
301 “accidentally” together with other targeted prey. However, no evidence for this could be
302 detected in the present study. Thus in 36 % of the stomachs where gadoids were found,
303 they constituted the main prey and in 25 % the only prey group including a stomach
304 containing over 100 adult cods, mainly 5 to 7 years old. This clearly shows that these
305 large gadoids are targeted by minke whales rather than engulfed accidentally.

306

307 The absence of 0-group herring in the diet off Iceland is in contrast to results from
308 Norwegian waters where they constitute an appreciable part of the diet in some areas
309 (Haug, Gjøsæter, et al. 1995). This can be explained by the difference in spawning times
310 of the two herring stocks. Off Norway, herring spawns in late winter and spring, while in
311 Icelandic waters herring spawns in mid summer not reaching a consumable size until
312 winter.

313

314 The pronounced geographical variation in prey species composition is broadly consistent
315 with the known distribution of the prey species in Icelandic waters. Thus, sandeel is most
316 abundant off the south- and southwest coast while capelin is mostly restricted to northern
317 Icelandic waters during summer. Gadoids are distributed throughout Icelandic coastal
318 waters. Their relatively low proportion in the diet in the southern areas during the first
319 half of the period (when sandeel was abundant) could indicate a preference for sandeel
320 when both are available.

321

322 Higher diversity of the diet in the northern Icelandic areas is similar to that found for
323 harbour porpoises in Icelandic waters (Víkingsson et al. 2003). In both these cases low
324 prey diversity in the southern areas seems to be related to the cetaceans' utilization of the
325 seasonally abundant fish species capelin and sandeel.

326

327 **Temporal changes in the ecosystem**

328 The present results differ considerably from those obtained in the only previous study on
329 minke whale diet in Icelandic waters conducted during 1977-1997. The proportion of
330 capelin and krill in the diet was much higher in the earlier period. Capelin seems to have

331 been largely replaced by herring and a higher incidence of sandeel and gadoids in the
332 more recent period.

333 The difference in sampling strategies might contribute to the difference in diet
334 composition between the present study, which was designed to be representative of real
335 distribution, and the previous one (Sigurjónsson et al. 2000) which was based on
336 commercial catches upto 1985 and strandings. However, considering only comparable
337 areas, the frequency of krill in the stomachs of whales caught north of Iceland is still only
338 half of that observed in the previous study. In this area the importance of capelin was
339 similar in the two periods, while the contribution of gadoids and other large teleost fish
340 have grown from low levels to be found in roughly half of the stomachs.

341

342 Tore Haug et al. (2002) and Tamura & Fujise (2002) described temporal dietary changes
343 in minke whales off Norway and Japan, respectively which they attributed to changes in
344 the ecosystem. The sampling scheme in the present study was not designed to study inter-
345 annual variation or trends and thus, the seasonal distribution of the samples was
346 somewhat different between years. However, this is unlikely a source of bias in this
347 respect as no indications were seen from the data of within-season variability in the diet.
348 The results of this study, therefore suggest that in recent years appreciable changes have
349 occurred in the diet composition of minke whales in Icelandic coastal waters.
350 Explanations of these changes may be found in other components of the ecosystem.

351 Iceland is located at a dynamic front between warmer and saline Atlantic water masses
352 coming from the south and cold Polar water masses originating in the Arctic Ocean.
353 While the area is in general highly productive, there is also considerable variability in
354 environmental conditions particularly over the shelf north of Iceland where the Polar

355 Front separates the contrasting Atlantic and Polar water masses. During the past decade,
356 environmental conditions in Icelandic waters have been characterized by unusually high
357 temperatures and salinity (Marine Research Institute 2012a). This warming of the marine
358 environment during the last decade appears to have led to pronounced changes in
359 distribution and abundance of several fish species in Icelandic waters. Thus, southern
360 gadoids such as saithe (*Pollachius virens*), whiting (*Merlangius merlangus*) and haddock
361 as well as monkfish (*Lophius piscatorius*) have shown increase in abundance and
362 extended distribution to the waters north of Iceland (Astthorsson et al. 2007, Solmundsson
363 et al. 2010). Corresponding changes have also occurred for pelagic fish with the
364 advancement of warm water species such as mackerel (*Scomber scombrus*) and blue
365 whiting (*Micromesistius poutassou*) into Icelandic waters (Marine Research Institute
366 2012b). Haddock is noteworthy in this respect, as in addition to the northward expansion
367 of the species' distribution, the estimated biomass in Icelandic waters increased threefold
368 between 2000 and 2007 (Marine Research Institute 2012b). This increased availability of
369 haddock is clearly reflected in the diet of minke whales (Figure 4).

370 Concomitant with these environmental changes, the cold-water species capelin appears to
371 have retreated to a significant extent from Icelandic continental waters. Capelin was major
372 component of the minke whale diet according to the samples collected during 1985-1997,
373 but its contribution to the diet was much less during 2003-7. This is in accordance with
374 changes in distribution and abundance of capelin in Icelandic and adjacent waters
375 according to fish surveys in recent years (Astthorsson et al. 2007, Pálsson et al. 2009,
376 Marine Research Institute 2012b). The summer distribution has shifted away from the
377 Icelandic continental shelf towards north and to the coast of East Greenland.
378 Unfortunately, the coverage of this area in the most recent cetacean sightings survey

379 (TNASS) was very poor and insufficient to test the hypothesis whether minke whales
380 have, to some extent followed this retreat of capelin from the shelf area.

381 Sandeel was the single most important prey type overall during 2003-7. It also constituted
382 a significant proportion of the diet according to the pre-2000 data where it was probably
383 underestimated because of skewed sampling towards the northern areas. Unfortunately,
384 specific research into sandeel abundance in Icelandic waters was not initiated until 2006.
385 Indirect evidence (fish stomach samples, seabird breeding success) had then suggested a
386 decline in abundance over the previous two decades, though with large inter-annual
387 variations (Bogason & Lilliendahl 2009). The proportion of sandeel in the diet of minke
388 whales decreased markedly during the sampling period (2003-2007) as did the number of
389 sandeel detected in the stomachs of cod and haddock according to MRI's groundfish
390 surveys (Bogason & Lilliendahl 2009).

391 Available data on minke whale and sandeel abundance in Faxaflói, SW Iceland, indicate
392 that there might be a connection between the densities of the two species, although the
393 nature of the sandeel data does not allow a statistical comparison. Thus, up to around
394 2002-3, densities of both species were considerably higher than in subsequent years and
395 fluctuations in recent years appear to be synchronous. The variation in sandeel abundance,
396 has been particularly pronounced in Faxaflói Bay where the highest values have been
397 obtained. Abundance was particularly low in Faxaflói in 2007, considerably higher in
398 2008, but decreased again in 2009. . Aerial surveys conducted in Faxaflói Bay in 2007,
399 2008 and 2009 (Pike, Gunnlaugsson, & Víkingsson 2011), show similar pattern with
400 considerably higher densities of minke whales in 2008 than in 2007 and 2009. Also, the
401 decline to very low levels of sandeel abundance in Ingólfshöfði, SE Iceland, could explain
402 the drastic decline in minke whale abundance in this area in the recent surveys (2007-

403 2009).

404 The summer distribution and abundance of two species of krill in northern and eastern
405 Icelandic waters in recent years was described by (Skúladóttir et al. 2009). The
406 distribution pattern seems to reflect whale densities to some extent. In particular, high
407 abundance of humpback whales in the 1995 and 2001 surveys (Paxton et al., 2009) might
408 be explained by krill abundance in those areas. Two other predominantly krill eating
409 cetaceans have changed distribution around Iceland in recent years. A recent northward
410 shift in distribution has been observed for blue whales (*B. musculus*) in Icelandic coastal
411 waters (MRI unpublished data) and a change in distribution of fin whales (*B. physalus*)
412 has been attributed to a change in environmental conditions in the Irminger Sea
413 (Víkingsson & Valdimarsson 2006). In general, the krill densities were considerably
414 lower in 2007 than in 2001 and 1995 which may help explain its decreased importance in
415 the diet and possibly also the decreased minke whale abundance in 2007.

416

417 **Conclusion**

418 After the turn of the century, large changes have occurred in the Icelandic continental
419 shelf ecosystem. Many of these changes appear to be unfavourable to minke whales,
420 notably less abundance of important prey species such as sandeel, capelin and krill.
421 Although there is evidence of minke whales having reacted to this by switching to other
422 prey species, s.a. haddock, cod and herring, minke whale abundance has also decreased
423 significantly during this period. Detailed examinations of body condition of 190 minke
424 whales sampled during 2003-2007 have not revealed any instances of severe malnutrition.
425 Such instances would be expected if the decline in abundance was due to a real population
426 decline, as a result of food shortage. Thus, it seems more likely that the decline is the

427 result of a shift in distribution from Icelandic coastal waters as a result of declined
428 availability of preferred food types.

429

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435

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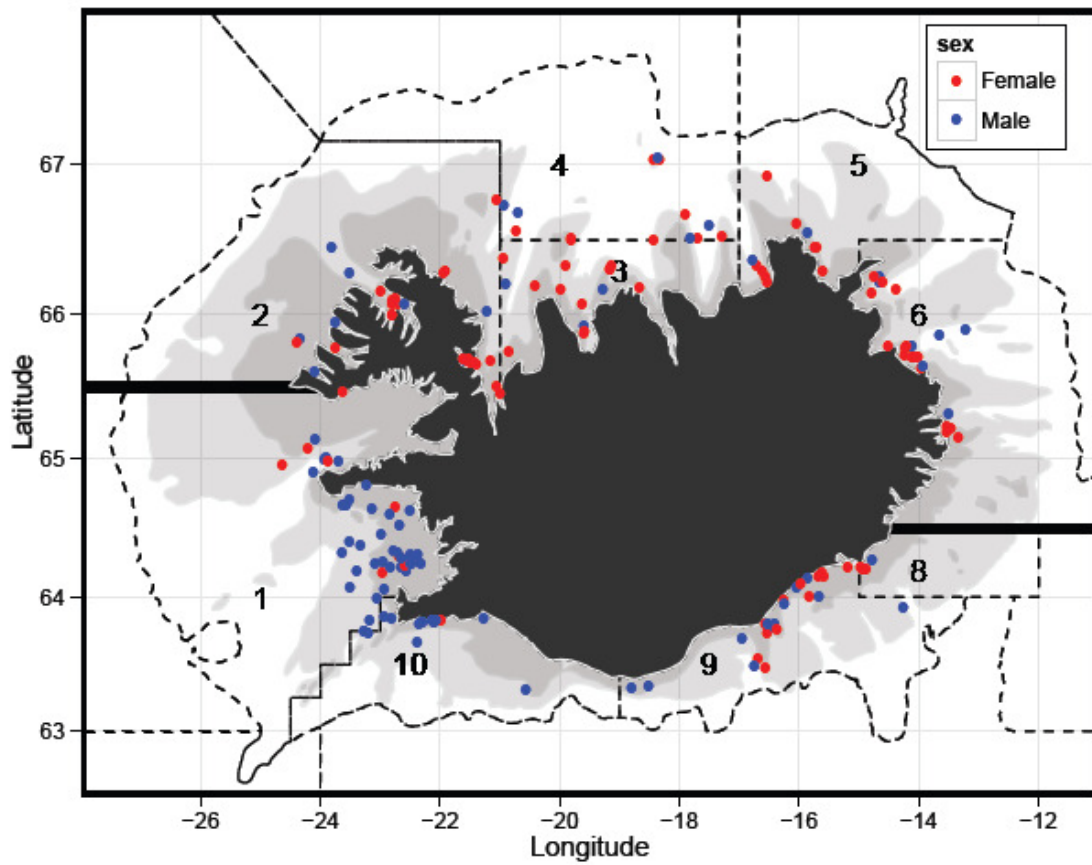
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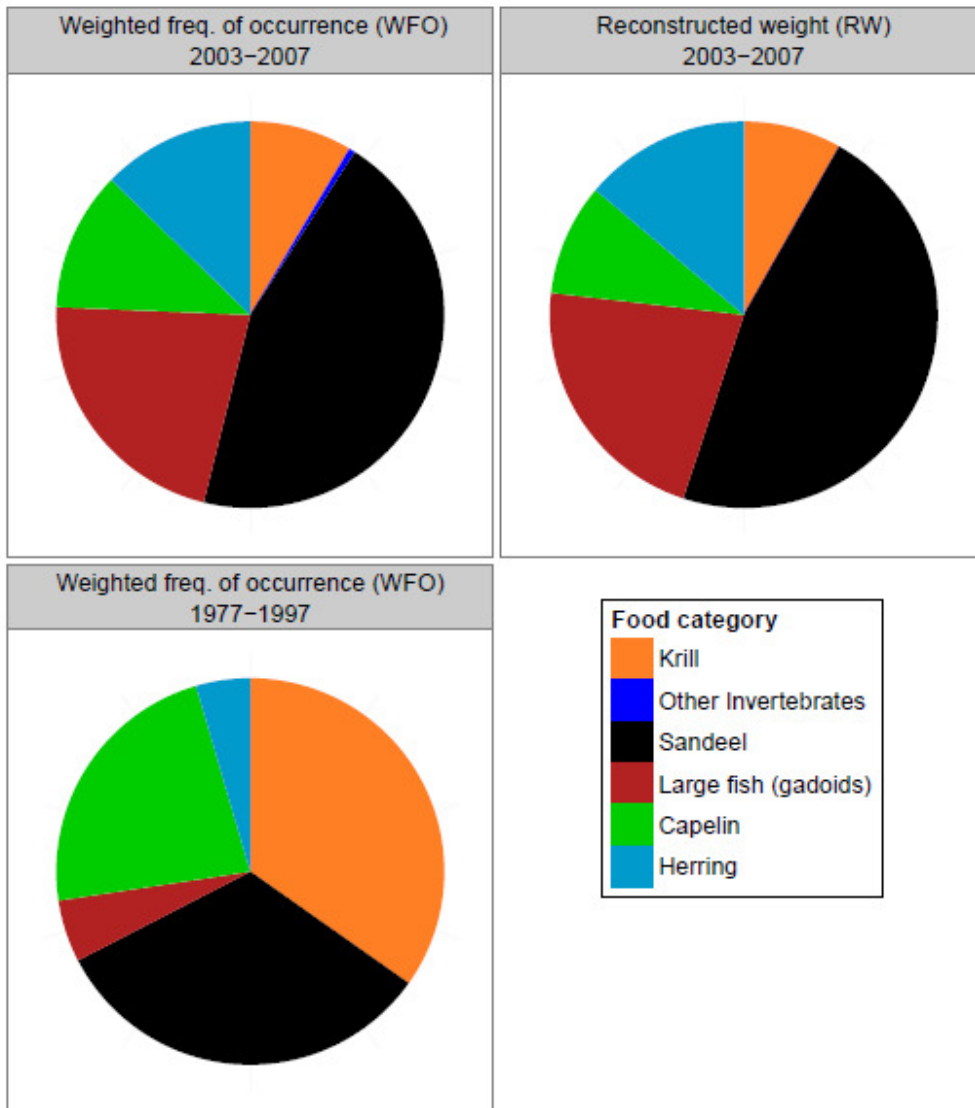
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562

563 Figure 1. Catch distribution of the minke whales caught in 2003 -2007. Numbers refer to the
 564 Boreas area division. In analysis areas 2-6 were combined to form the northern area and the
 565 remaining subareas (1, 7-10) are referred to as the southern area.
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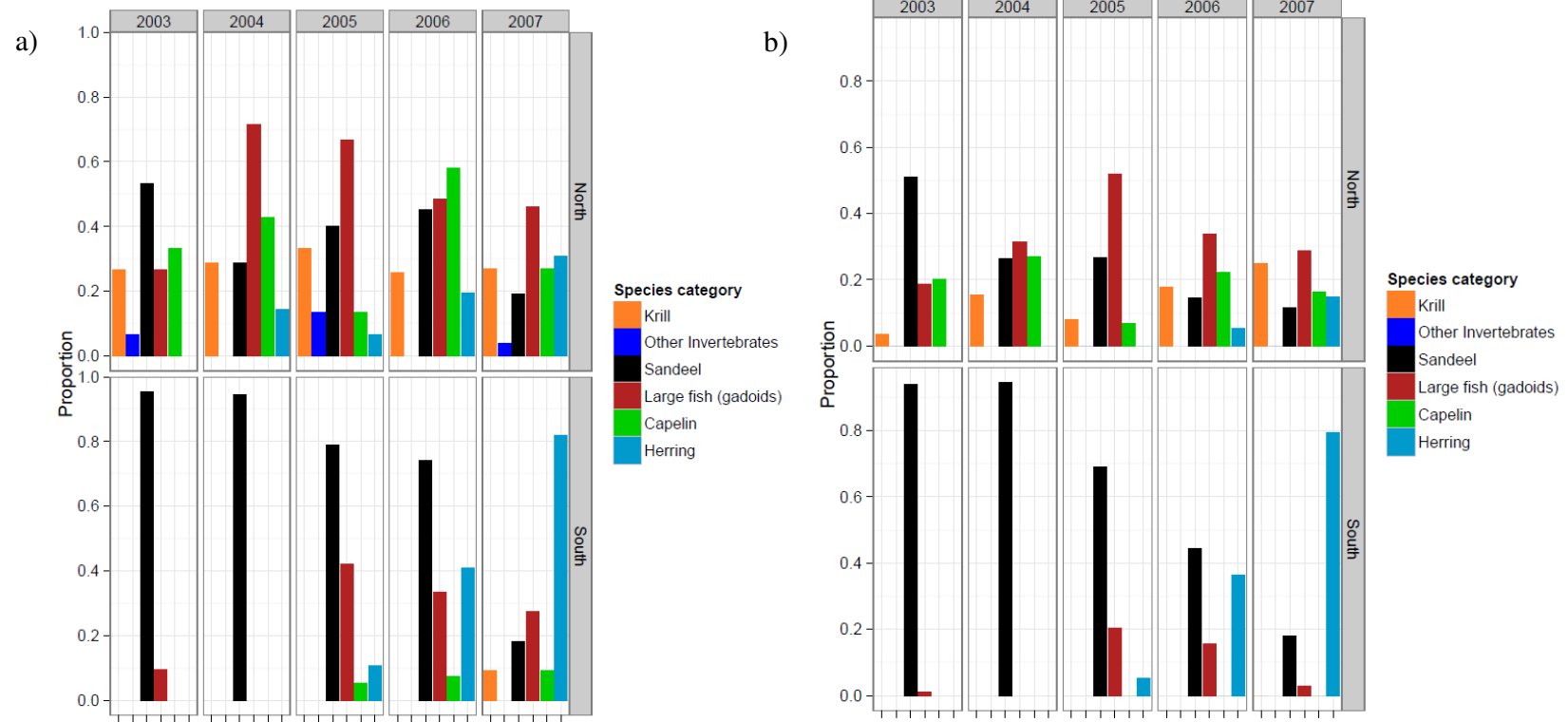
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Figure 2. Diet composition of minke whales sampled in Icelandic waters 2003-2007 shown as reconstructed weight (RW) and as weighted frequency of occurrence (WFO) for comparison with previous data (1977-1997).

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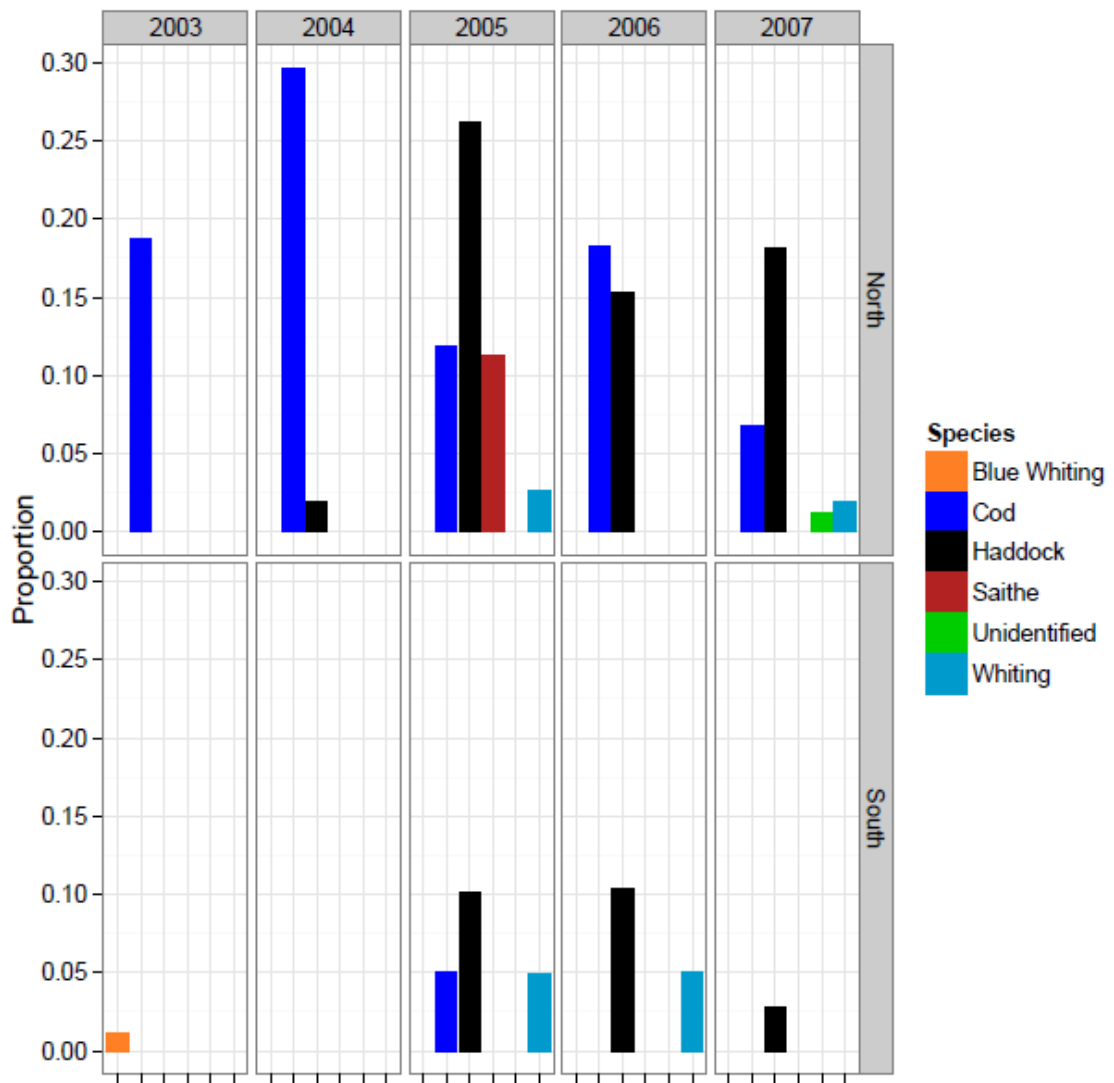
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576 Figure 3. Spatial and temporal variation in diet composition of minke whales expressed as **a)** frequency of occurrence (FO) and **b)** reconstructed weight.

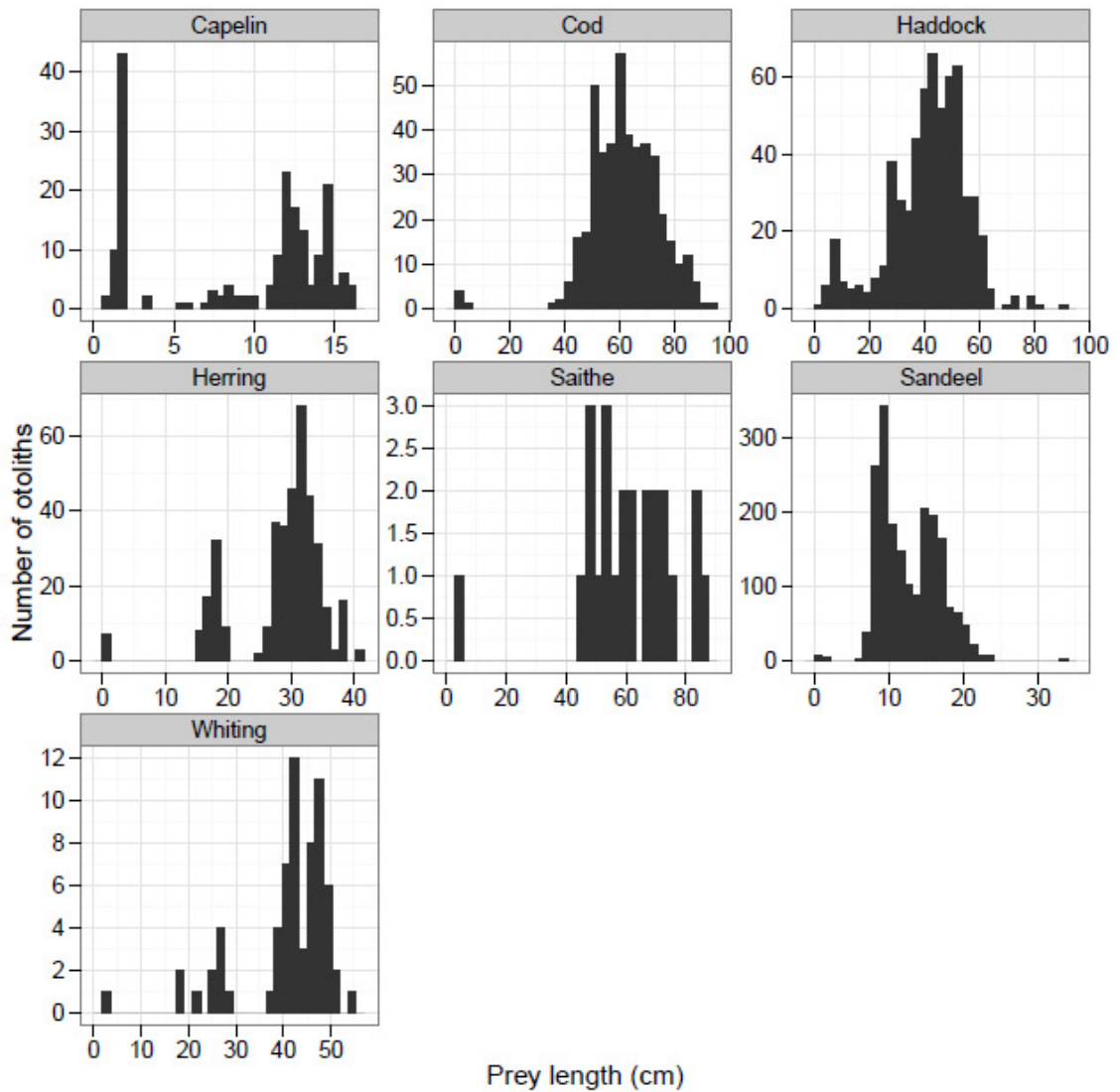
577 (RW). Area division (North-South) as in Figure 1.

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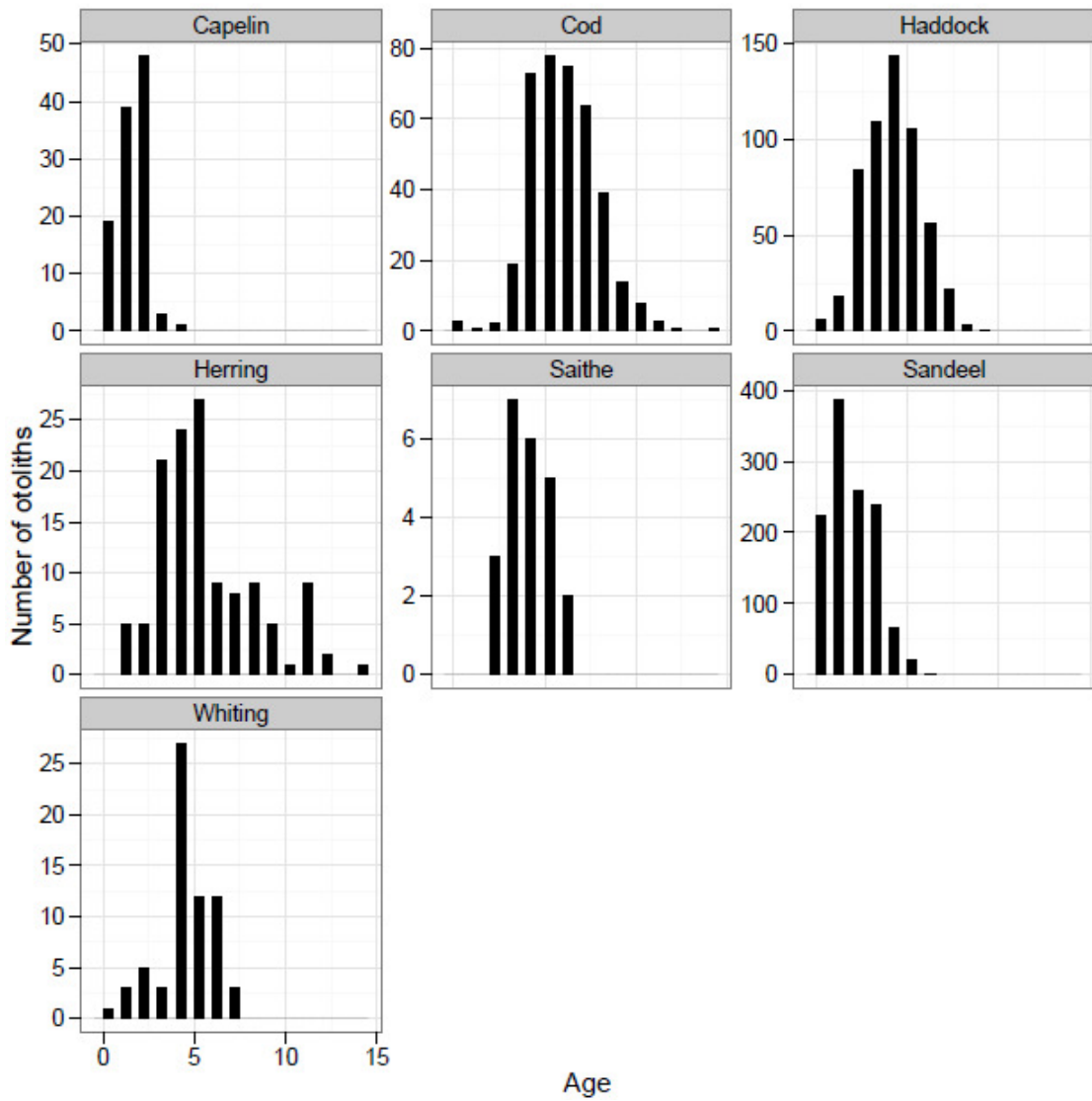
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Figure 4. Spatial and temporal variation in the contribution of the most important species of gadoids to the diet composition of minke whales (RW).



582
 583 Figure 5. Length distributions of the most common fish species identified in the forestomachs of
 584 minke whales sampled in 2003-2007 according to direct measurements (undigested fish) and
 585 calculations from otolith lengths.
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Figure 6. Age distributions of the most common fish species identified in the forestomachs of minke whales sampled in 2003-2007.

591

Table 1. Temporal distribution of the samples obtained during 2003-2007.

	April	May	June	July	August	September	Total
2003		0	0	0	18	18	36
2004		0	16	9	0	0	25
2005		0	0	18	16	0	34
2006		0	13	25	20	0	58
2007	3	7	22	0	4	1	37
2003-2007	3	7	51	52	58	19	190

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596 **Table 2.** Overview of AIC scores for the fitted GLM models for weights and volume of
 597 stomach contents. Full model includes the variables whale length, geographic area,
 598 month, year, sex and maturity. D.f.: Degrees of freedom.

	Step	D.f.	Deviance	Resid. D.f.	Resid. Dev.	AIC
Weight of stomach contents						
1	Full model			169.00	329.70	1388.87
2	- month	5.00	0.80	174.00	329.50	1379.44
3	- year	4.00	5.32	178.00	334.82	1375.21
4	- sex	1.00	0.20	179.00	335.02	1373.35
Volume of stomach contents						
1	Full model			160.00	242.40	1815.17
2	- year:month	5.00	1.39	165.00	243.80	1806.46
3	- month	5.00	1.86	170.00	245.66	1798.17
4	- year	4.00	2.17	174.00	247.84	1792.16
5	- maturity	4.00	2.38	178.00	250.22	1786.32
6	- sex	1.00	0.33	179.00	250.55	1784.62

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604 **Table 3.** Summary of the variables of the best model, in terms of AIC, for the weight and
 605 volume of stomach contents. The intercept value represents the model fit for length 0
 606 whales in Area , the t-value and the corresponding p value represent the results from a
 607 Wald's test for a single parameter difference from zero.

	Estimate	Std. Error	t value	Pr(> t)
Weight of stomach contents				
(Intercept)	0.1853	0.0741	2.50	0.0133
Length	-0.0001	0.0001	-1.38	0.1681
Location:				
Area 2	-0.0379	0.0189	-2.00	0.0466
Area 3	0.0177	0.0377	0.47	0.6389
Area 4	-0.0043	0.0314	-0.14	0.8916
Area 5	0.0099	0.0416	0.24	0.8122
Area 6	0.0404	0.0371	1.09	0.2771
Area 8	0.0566	0.0996	0.57	0.5710
Area 9	-0.0281	0.0209	-1.34	0.1813
Area 10	-0.0442	0.0200	-2.21	0.0285
Volume of stomach contents				
(Intercept)	0.1110	0.0176	6.30	0.0000
Length	-0.0001	0.0000	-4.51	0.0000
Location:				
Area 2	-0.0139	0.0045	-3.11	0.0022
Area 3	0.0002	0.0075	0.03	0.9779
Area 4	-0.0082	0.0063	-1.31	0.1928
Area 5	-0.0146	0.0061	-2.41	0.0172
Area 6	-0.0059	0.0058	-1.02	0.3113
Area 8	0.0102	0.0173	0.59	0.5554
Area 9	-0.0125	0.0048	-2.62	0.0097
Area 10	-0.0146	0.0050	-2.92	0.0039

608

609 **Table 4.** Identified prey species of minke whales and the number of stomachs in which they
 610 occurred stratified by sampling year and area. N: Northern areas S: Southern areas (see text). n:
 611 sample size.

	2003		2004		2005		2006		2007		All years	
	N	S	N	S	N	S	N	S	N	S	N	S
Area :												
Sample size:	15	21	7	18	15	19	31	27	26	11	94	96
Crustacea												
Euphausiacea												
<i>Thysanoessa raschi</i>	1		1				6		6		14	
<i>Meganyctiphanes norwegica</i>	2				1		2				5	
Krill (unidentified)	3			1	4		3		3	1	13	2
Copepoda (unidentified)	1										1	
Decapoda												
<i>Pandalus borealis</i>					1						1	
Vertebrata												
Gadidae												
<i>Gadus morhua</i>	3	1	2	2	4	1	8	3	4		21	7
<i>Melanogrammus aeglefinus</i>				1	7	4	10	8	10	3	27	16
<i>Pollachius virens</i>					2			1	1		3	1
<i>Merlangius merlangus</i>	1		1		3	1	1	3	1		7	4
<i>Micromesistius poutassou</i>	1	1			1	1	1	1			3	3
<i>Trisopterus esmarki</i>	1										1	
Unidentified. large fish	1				1	2	1		4	1	7	2
Clupeidae												
<i>Clupea harengus</i>			1		1	2	6	11	8	9	16	22
Osmeridae												
<i>Mallotus villosus</i>	4		3		2	1	17	2	7	1	33	4
Ammodytidae												
<i>Ammodytes marinus/ Hyperoplus lanceolatus</i>	9	20	2	17	6	15	13	21	5	2	35	75

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