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**FEEDING STUDIES ON THE HARBOUR PORPOISE (*Phocoena phocoena*)
IN ICELANDIC COASTAL WATERS**

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ABSTRACT

Harbour porpoise (*Phocoena phocoena*) is one of the most abundant cetacean species in coastal Icelandic waters. Until recently very limited research had been conducted on the species in these waters. As a part of its multi-species research efforts, the Marine Research Institute (MRI), Reykjavik initiated in 1991 an organized sampling scheme for harbour porpoises incidentally caught in gillnets. The present paper reports on some preliminary findings on food and feeding of the species in Icelandic waters during 1991-1995.

Most of the samples were obtained from two areas southwest (SW) and southeast (SE) of Iceland and the majority were taken in March-April. The sex ratio was skewed in "favour" of males (m/f: 1.87). The sex ratio and mean lengths of both sexes were higher in the SE area than in the SW area. More than 95% of all examined stomachs had identifiable food remains. Overall capelin (*Mallotus villosus*) comprised the predominant prey, followed by sandeel (*Ammodytidae sp.*) and then gadoids and cephalopods, while other prey groups were of less importance. There was considerable seasonal variation in prey frequency, where capelin appears to be dominant in late winter and spring and sand-eel in the summer through early winter. This coincides with the spawning migration of capelin from northern waters along the east, south and west coasts of Iceland. The length distribution of the capelin consumed by the porpoises shows predominance of 2-4 year old fish according to analysis of otoliths. The length distribution of sandeel shows somewhat smaller modal length.

The diet of the harbour porpoise seems less diverse in the present study than in some other areas that have been investigated. However, the apparent opportunistic feeding habits of the species, and the non-random nature of the sampling may have contributed to this homogeneity.

INTRODUCTION

The harbour porpoise (*Phocoena phocoena*) is one of the most common small cetacean in coastal Icelandic waters (Sæmundsson 1932, Sigurjónsson and Víkingsson 1995, Sigurjónsson 1993). The global distribution of the species is limited to temperate and subarctic waters of the N-hemisphere (Klinowska 1991). The species shows some seasonality in movements probably as a result of seasonal variations in local prey availability (Tomilin 1957, Gaskin 1992, Berggren and Arrhenius 1995). The feeding ecology of the harbour porpoise has been studied in numerous studies in different parts of its distribution area (Tomilin 1957, Rae 1964, 1973, Smith and Gaskin 1974, Gaskin *et al.* 1974, Recchia and Read 1989, Smith and Read 1992, Fontaine *et al.* 1994, Aarefjord *et al.* 1995). These studies have shown considerable spatial and temporal variation in the diet of the species.

Until recently, no systematic studies had been undertaken on the biology and ecology of the harbour porpoise in Icelandic waters. The distribution of the species overlaps with the operational area of the coastal fisheries which may cause conflicts of interests (competition, bycatch etc.). Calculations, based on rough approximations of stock size and food analysis from other areas in the N-Atlantic, have indicated that the total consumption of harbour porpoises in Icelandic waters may be in the range of 48,000 tonnes, the bulk of which consists of fish (Sigurjónsson and Víkingsson 1992).

As a part of the Marine Research Institute's (MRI) multispecies research programme a special study on feeding ecology and life history of the harbour porpoise and white-beaked dolphin (*Lagenorhynchus albirostris*) was conducted in 1992-1995. The present paper gives some preliminary results on the feeding habits of harbour porpoises while further analysis of the data is underway.

MATERIAL AND METHODS

The study is based solely on the examination of animals caught incidentally in the gillnet fishery in nearshore Icelandic waters in 1991-1995. The porpoises were collected either through contacts at fish markets or directly from the fishermen by MRI staff and cooperating individuals throughout the country.

The seasonal distribution of the sample is shown in Figure 1 and the geographical distribution in Figure 2. The sampling is uneven both in time and space. While porpoises were sampled in all months except July and August, the overwhelming majority of the samples were taken in March and April. Similarly, most of the animals were sampled in two main sampling areas: off southwestern (SW) and southeastern (SE) Iceland. In the analysis below distinction is made between 5 areas: the SW- and SE-areas, Breiðafjörður (W) area, Ísafjörður (NW) area and northeastern (NE) area, the last two containing only 3 and 20 animals, respectively.

In most cases whole carcasses were received for autopsy by MRI staff members, but in some cases samples were taken by coworkers along the coast. The carcasses were usually kept frozen until dissection at the laboratory. During dissection the fullness of the forestomach was visually assessed (empty, 1/4, 1/2 etc.) before the stomach was refrozen until further laboratory analysis.

In the laboratory the weight of the stomach content was estimated by weighing the stomach before and after the contents had been removed. The state of digestion was assessed using a five stage scale ranging from fresh newly ingested food (stage 1) to otoliths or other hard parts being the only food remains (stage 5). The stomach content was washed through sieves with a mesh size of 0.3mm and then separated into prey groups before final species identification and measurements. Relatively undigested prey was identified to species as far as possible and weighed. However, in most of the stomachs the only identifiable remains were hard parts, otoliths, bones, cephalopod beaks, etc. The otoliths and cephalopod beaks were identified and measured using published identification guides (Clarke 1986, Härkönen 1986) and the MRI's reference collection.

Two methods were used for measuring the otoliths. A part of the sample was measured using a stereo-microscope with a graticule scale in the eyepiece. As this is a very time consuming method, experiments were made using an image analyzer (Leica Quantimet 500+) for these measurements. Comparison between the two methods revealed no significant difference (t-test $t=0.1701$, $df=19$, $p=0.8667$).

For calculating fish size from otolith size the formulae of Härkönen (1986) were used except for capelin (*Mallotus villosus*) where a new formula was created (see below). It was not considered feasible to distinguish between the otoliths of the three species of sandeel (*Ammodytidae* sp.) found off Iceland and therefore Härkönen's formula for greater sandeel (*Ammodytes marinus*) was used to calculate fish length in this group. No attempt was made to correct for digestion of otoliths so the calculated sizes of fish may be underestimated.

As all measurements of food remains have not been completed, at this stage the different prey species/groups have been arbitrarily classified as primary, secondary, etc. prey in each stomach. This classification was primarily based on relative numbers of individuals of each prey species found in the stomach. Calculations of original (reconstructed) weight of stomach content from otolith size were made on a subsample of stomachs from the SW and SE areas containing capelin and sandeel.

During dissection of the porpoises various measurements were made and samples taken for related studies such as morphometrics, age and reproductive parameters, parasites, genetics and energetic studies. These studies are not completed and cannot be incorporated into the present analysis of the feeding data at this stage.

RESULTS

The length and sex distributions of the porpoises sampled in SW and SE subareas is shown in Figure 3. Almost twice as many males as females were sampled, resulting in an overall sex ratio (SR : males/females) of 1.87. The inequality of the sex proportions was more pronounced in the SE area (SR=2.33) than in the SW area (SR= 1.54). Harbour porpoises of both sexes were significantly larger in the SE area ($135.9\text{cm}\pm 0.62$ s.e. and $137.1\text{cm}\pm 1.10$ SE for males and females, respectively) than in the SW area (129.3 ± 0.63 s.e. and 134.2 ± 0.88 s.e.; t-test : $t=6.48$, $p=0.000$ for males and $t=2.07$, $df=317$, $p=0.039$ for females).

Most of the examined stomachs contained some food remains. Figure 4 shows frequencies of the five visually assessed degrees of stomach fullness. Although 16 % of the stomachs were assessed empty by this method, most of these stomachs contained some food remains upon closer examination.

Frequencies of the different prey species present in stomachs are shown in Figure 5, separately for the different geographical areas. Overall, capelin is clearly the dominant prey species, occurring in 86% of the stomachs examined. sandeel was the second most frequent prey, occurring in 29% of all stomachs, followed by cephalopods and gadoids with 12 and 10% frequency of occurrence, respectively.

There were some differences between areas in frequency of prey species. In the SE area capelin was the overwhelming dominant species occurring in 99% of the examined stomachs, while sandeel, the second most frequent prey was found in only 13% and gadoids in 1% of the stomachs. In the SW area the diet was more variable, capelin occurring in 71% of the stomachs, sandeel in 47% and gadoids in 20%. The Breiðafjörður area appears to be somewhat more diverse with respect to food selection of harbour porpoises, with capelin found in 76% of the examined stomachs, sandeel in 44% and gadoids in 41%. It is, however noticeable that cephalopods were not observed in stomachs from this area (Figure 5). The small sample size in this area ($n = 60$) must, however, be borne in mind.

The dominance of capelin as a prey species in the total sample is even more clear when the assessed relative importance of prey species is considered. In 96% of all stomachs containing capelin, it was the primary prey species, while sandeel, gadoids and cephalopods were considered primary prey in respectively 38, 25 and 10% of the cases when they were found in stomachs.

Figure 6 shows the seasonal variation in relative frequency of primary prey species/groups for the SW and SE areas. Although the sample size is very small in the SW area during June-September and December-February seasonal variation is evident from the data. Capelin increases in frequency during February to April, decreasing thereafter sharply in May, and is absent as a primary prey species in June. For the rest of the year, capelin was found only in four stomachs as a primary prey species. From the latter part of May the role of capelin seems to be taken over by sandeel, and to a lesser degree gadoids and other fish species.

As indicated above, the diet in the SE area is overwhelmingly dominated by capelin. However, the sampling period in this area was limited to the months March-May. The apparent difference in prey composition between the SW and SE areas in May (Figure 6) is probably caused by the fact that no samples were taken in the SE area after 7 May.

A preliminary investigation revealed no significant differences in prey composition between sexes nor with respect to sexual maturity. However, the relationship between diet on one side and age and reproductive status on the other awaits further analysis.

Calculations of original weight of stomach content from the size of hard food remains have not been completed. Preliminary calculations of length distribution of capelin using Härkönen's (1986) relationship between otolith length (OL) and fish contradicted MRI's research on capelin from the same year and area (H. Vilhjálmsson pers.commn.). The relationship between otolith length and fish length was therefore investigated in a sample of capelin from Icelandic waters in 1995. The results are shown in Figure 7. The Icelandic capelin clearly has a higher fish-length/otolith-length ratio than the sample used by Härkönen.

The calculated length distribution of capelin, using the new formula (Figure 7) is shown in Figure 8. No significant difference was observed between the two main sampling areas. The peak length class was 14-15cm in both areas, corresponding to capelin of ages 2 and older (Vilhjálmsson 1994). All available length classes of capelin during spring were, however, represented to some degree in the porpoise's stomach.

Figure 9 shows the length distribution of sandeel (*Ammodytidae sp.*) as calculated from otolith lengths using Härkönen's formula for *Ammodytes marinus*. The total size range (approximately 5-20cm) is similar to the size range of capelin found in the stomachs, but the mean length is considerably smaller (t-test $p < 0.05$). There was no significant difference in the length of sandeel, found in porpoise stomachs in the SW and SE areas.

Figure 10 shows the frequency distribution of the reconstructed weight of stomach content in animals from the SW and SE areas containing sandeel and/or capelin. There was no significant difference in total weight of stomach content between the two areas: There was wide variation in the calculated stomach content although most animals contained less than 1kg. In stomachs containing capelin the calculated weight of that species ranged from 0.6g to 4,431g (mean=690g, n: 290, SD: 723) while the corresponding figures for sand eel were 0.3g-6,146g (mean=600g, n: 120, SD: 1,306).

DISCUSSION

The uneven distribution of the sampling in time and space probably reflects both the sampling effort (i.e. the distribution of the gillnet fishery in Icelandic waters), the spawning migration of capelin and possible inshore/offshore migrations of harbour porpoises. The peak of the gillnet season is in March-April and is most concentrated off SW and SE Iceland. The main target species of the gillnet fishery are cod (*Gadus morhua*), saithe (*Pollachius virens*) and haddock (*Melanogrammus aeglefinus*). This fishery coincides in time and space with the spawning migration route of capelin. The

main spawning grounds are off south and west Iceland, the first migrations generally arriving in the coastal waters off southeast Iceland in February and continuing westward along the south coast (Vilhjálmsón 1994). The spawning takes place mostly in March-April. No systematic studies have been undertaken on the seasonal distribution of harbour porpoises around Iceland, but Sæmundsson (1932) described the harbour porpoise in Icelandic waters as migratory, arriving in coastal areas in March, seemingly following the capelin.

The high proportion of males in the sample and the difference in length distributions between areas (Figure 3) may indicate some kind of temporal and/or spatial segregation in the stock. Further analysis of the distribution with respect to age and reproductive status is underway.

The present study agrees with most earlier studies that the harbour porpoise feeds predominantly on fish although cephalopods, crustaceans and other invertebrates have been identified as minor components of the diet (Tomilin 1957, Rae 1973, Smith and Gaskin 1974, Recchia and Read 1989, Smith and Read 1992, Palka and Read 1995, Aarefjord *et al.* 1995, Teilmann and Dietz 1995, Santos *et al.* 1994, 1995). According to these studies the harbour porpoise feeds on wide variety of fish species in the N-Atlantic. Although herring seems to be the most important prey species on both sides of the N-Atlantic (Smith and Gaskin 1974, Aarefjord *et al.* 1995, Recchia and Read 1989) capelin has been identified as an important component off N-Norway (Aarefjord *et al.* 1995), Greenland (Teilmann and Dietz 1995) and Canada (Fontaine *et al.* 1994). Other important prey groups in the N-Atlantic include hake (*Merluccius sp.*) (Recchia and Read 1989, Smith and Read 1992, Aarefjord *et al.* 1995, Teilmann 1995), sandeel (Santos *et al.* 1995, Aarefjord *et al.* 1995) and members of the cod family (*Gadidae*) (Rae 1973, Aarefjord *et al.* 1995, Santos *et al.* 1994).

Overall, capelin was the predominant prey species in the present study (Figure 5). The consumption of capelin seems, however, to be mostly limited to few months of the year, and the seasonal distribution of prey frequencies (Figure 6) indicates that sandeel and to a lesser degree gadoids are more important components of the annual food consumption than indicated by the pooled sample. However, during the capelin spawning period porpoise feeding activity seems to be intense, judging from the high proportion of investigated stomachs with identifiable food remains compared to most other studies (Smith and Gaskin 1974, Recchia and Read 1989, Fontaine *et al.* 1994, Aarefjord *et al.* 1995). This may reflect the seasonal and geographical nature of the present sample, coinciding with the abundant food supply of the capelin spawning migration. Seasonal changes in diet have also been found in other areas (Tomilin 1957, Smith and Read 1992, Palka and Read 1995, Santos *et al.* 1995). An assessment of the relative importance of different prey species on an annual basis using reconstructed weight of stomach contents is underway. Energetic studies may also indicate possible seasonal variation in feeding rates related to the capelin migration.

The apparent similarity of food composition between sexes and length classes of porpoises in the present study is in agreement with studies from Canada (Smith and Gaskin 1974) and Scandinavia (Aarefjord *et al.* 1995).

The use of image analyzer greatly enhanced the efficiency in otolith measurements as upto 50 otoliths can be measured at a time. The technique also has other potentials, such as species identification as various aspects of shape (length, width, area, roundness, etc.) can be automatically measured at the same time.

The calculated size range of capelin and sandeel taken by the porpoises (Figures 8-9) is within the size range of fish prey reported from other areas (Fontaine, *et al.* 1994, Santos *et al.*, 1994).

Although analysis of the present material is not completed, the preliminary results confirm the primarily ichthyophagous feeding habits of harbour porpoises. Off Iceland, capelin and sandeel appear to be the most important prey species, and there is great seasonal variation in the relative importance of these two key species. During the spawning migration of capelin into coastal waters during late winter/spring it is clearly the overwhelming dominant prey species of the harbour porpoise in the areas covered in this study. Whether this applies to the stock in general remains unresolved until further sampling from other areas. Further analysis of the available data will include assessment of the relative importance of different prey items based on calculated weight (Pierce and Boyle 1991), analysis of the stomach content with respect to age, sex, reproductive status, energetic condition and calculations of annual consumption rates of different prey species.

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Figure 1. Seasonal distribution of stomach samples in the four geographical areas (see Fig. 2)

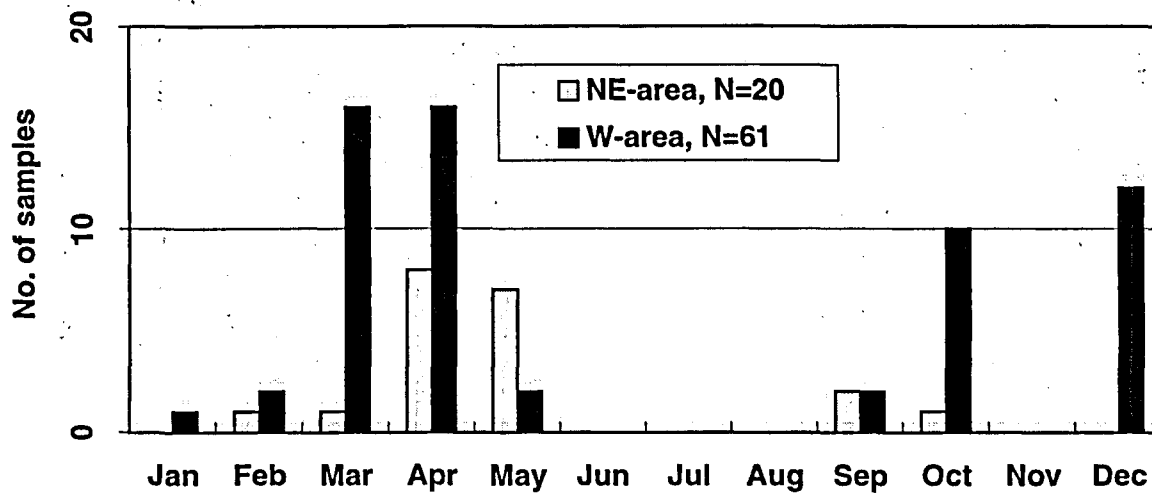
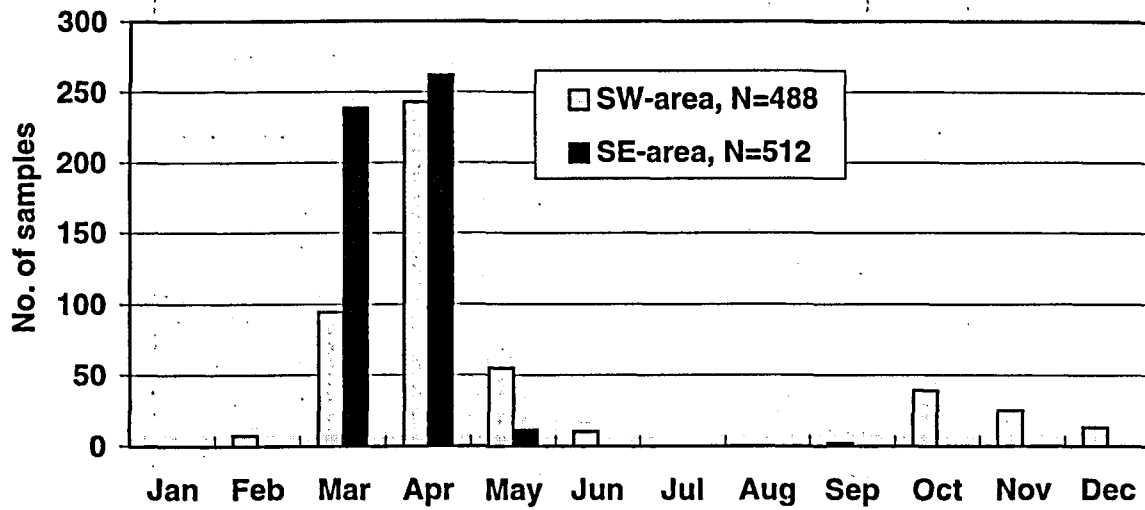


Figure 2. Harbour porpoise – Sampling distribution off Iceland.
The number of animals sampled in subsquares. Letters indicate the 5 sampling areas.

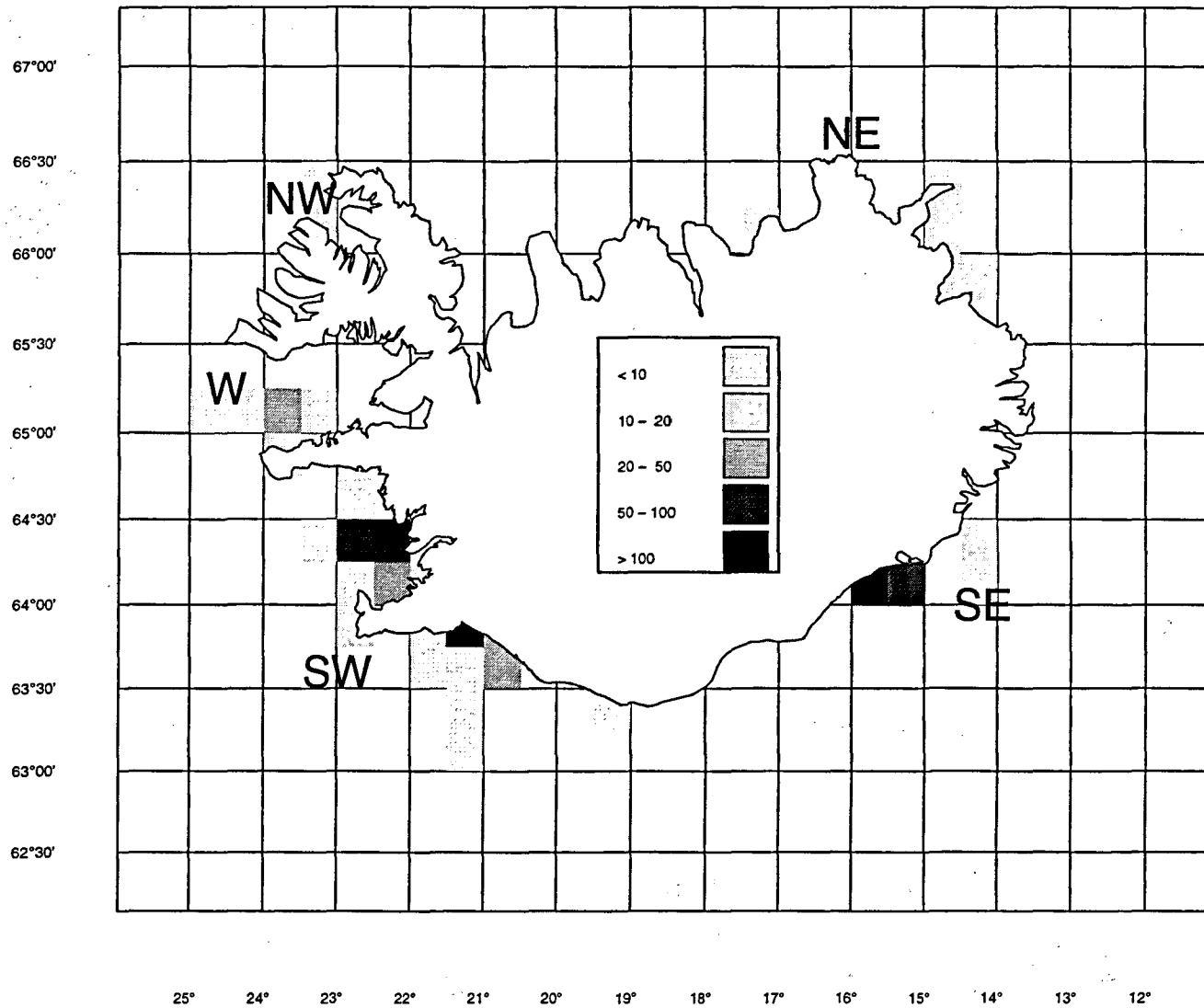


Figure 3. Length distribution of harbour porpoises sampled SW and SE off Iceland.

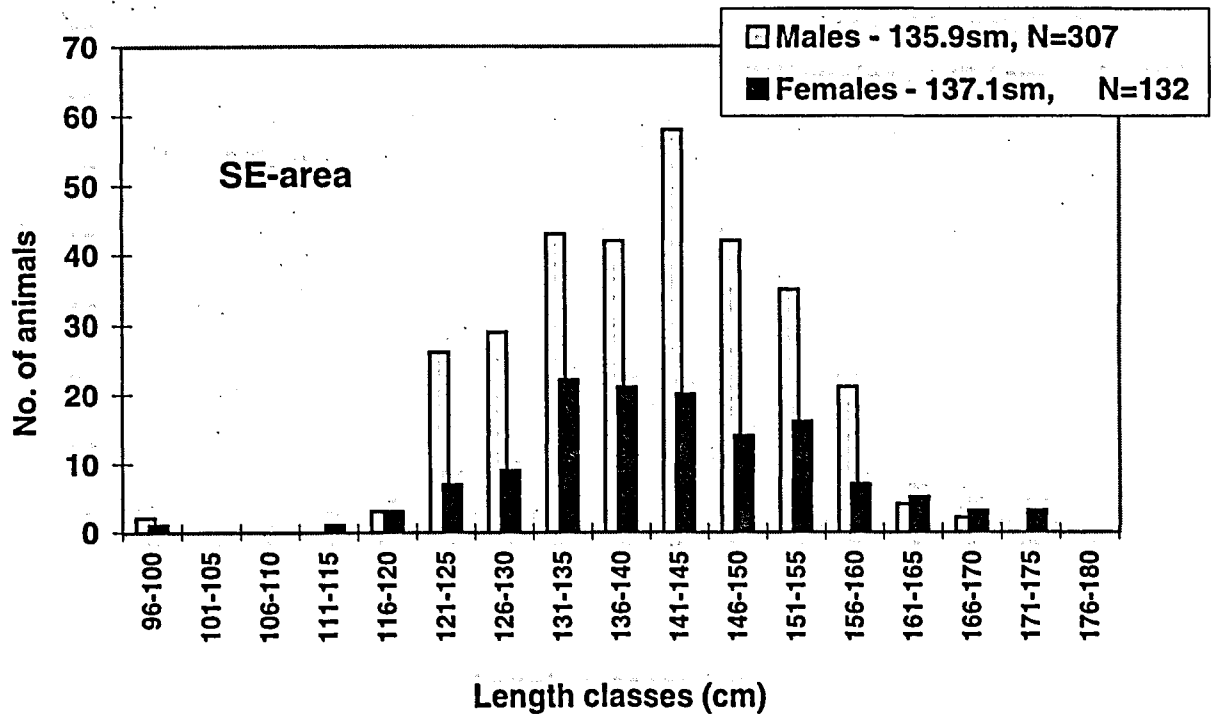
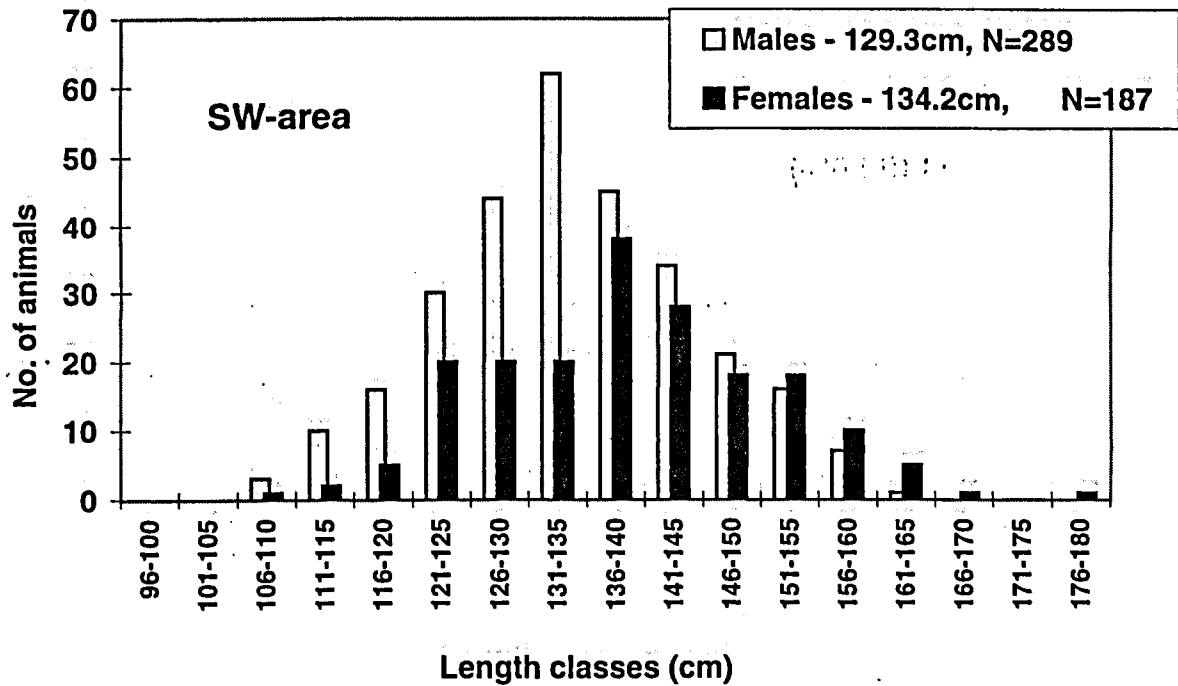


Figure 4. Visual assessment of stomach fullness

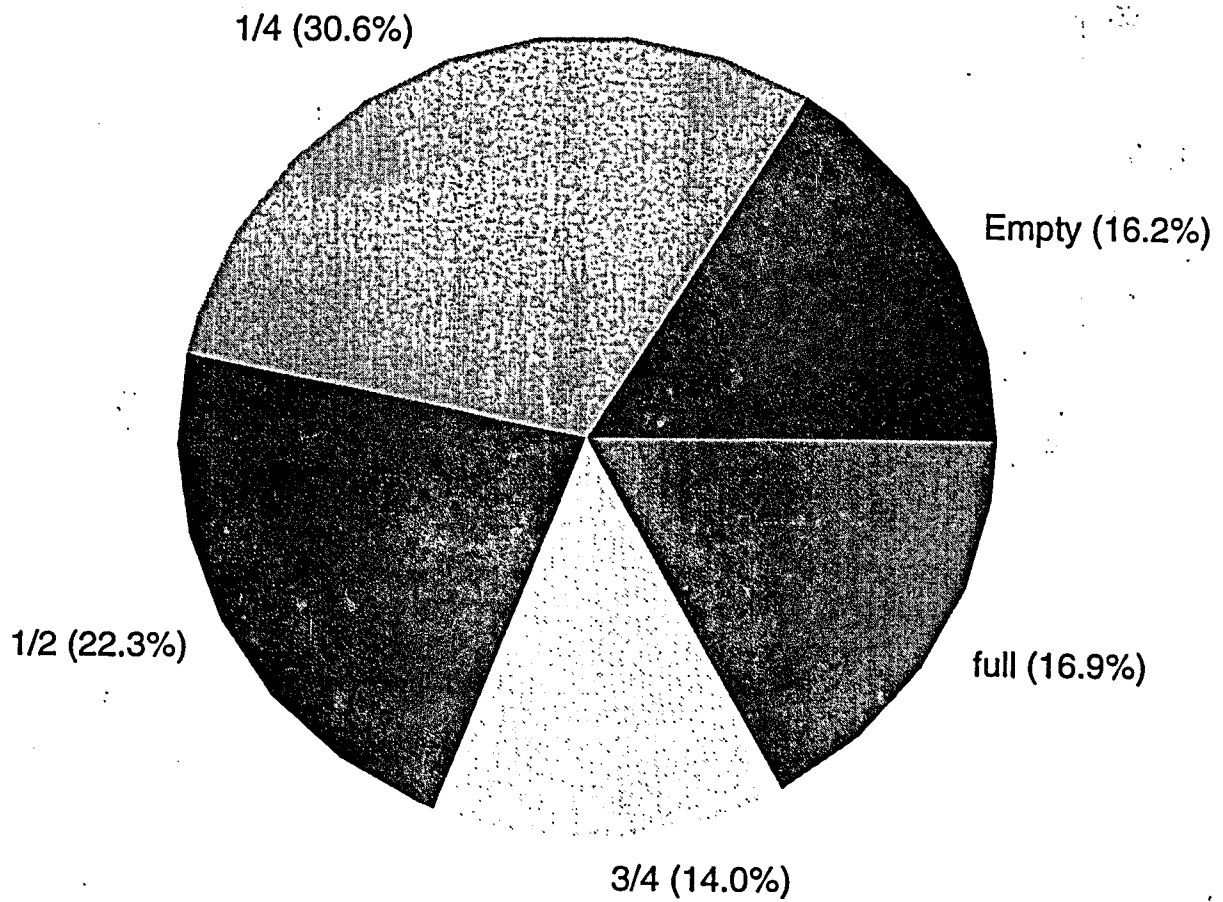


Figure 5. Frequency of prey groups in three geographical areas off Iceland.

Prey groups are classified as primary (1°), secondary (2°) etc. according to estimated relative importance.

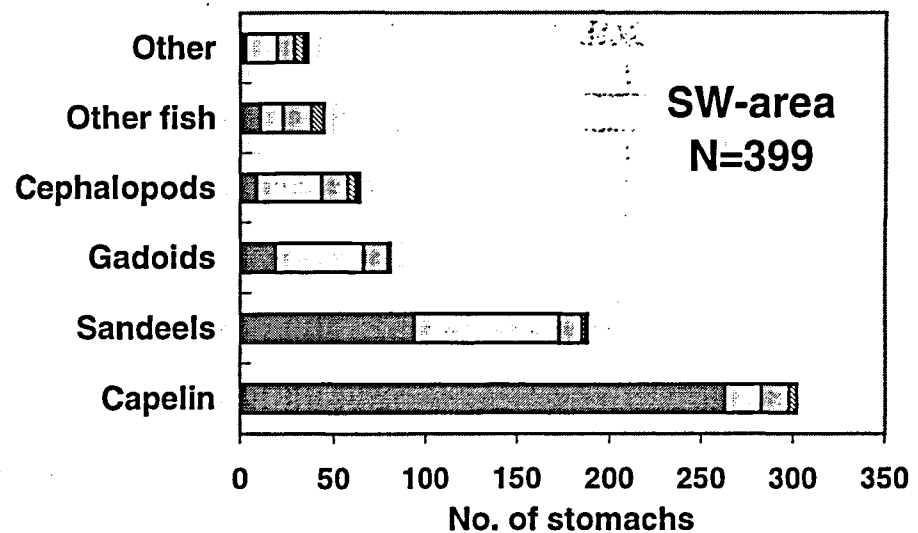
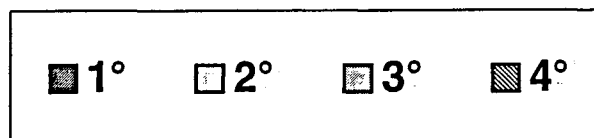
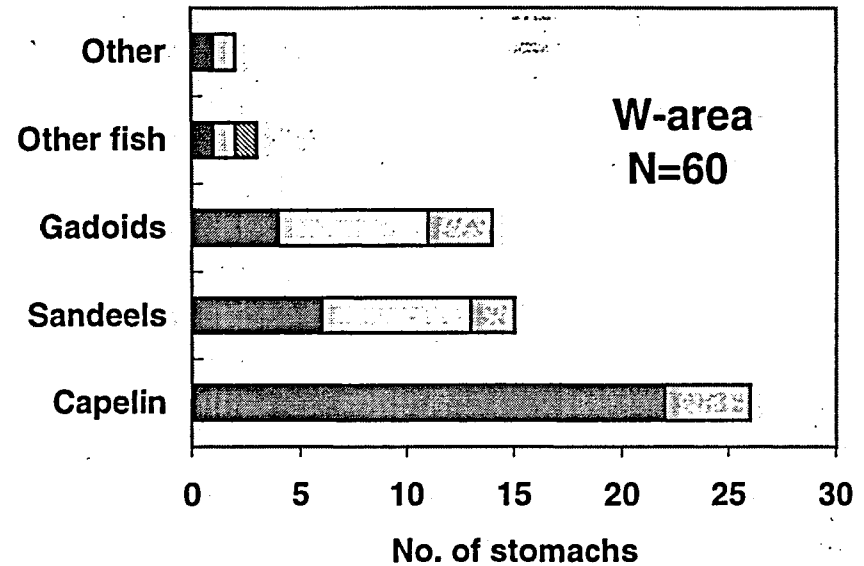
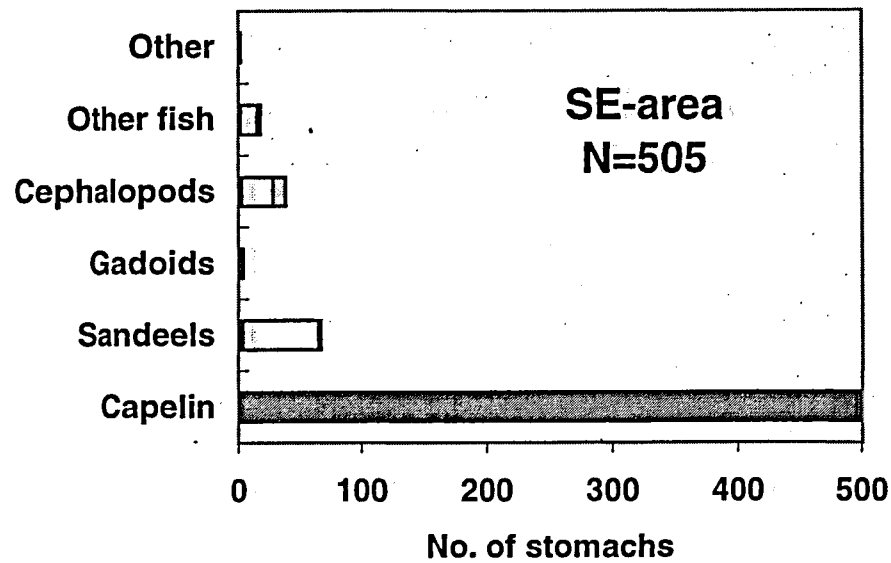


Figure 6. Primary prey species: relative seasonal variation in frequency.

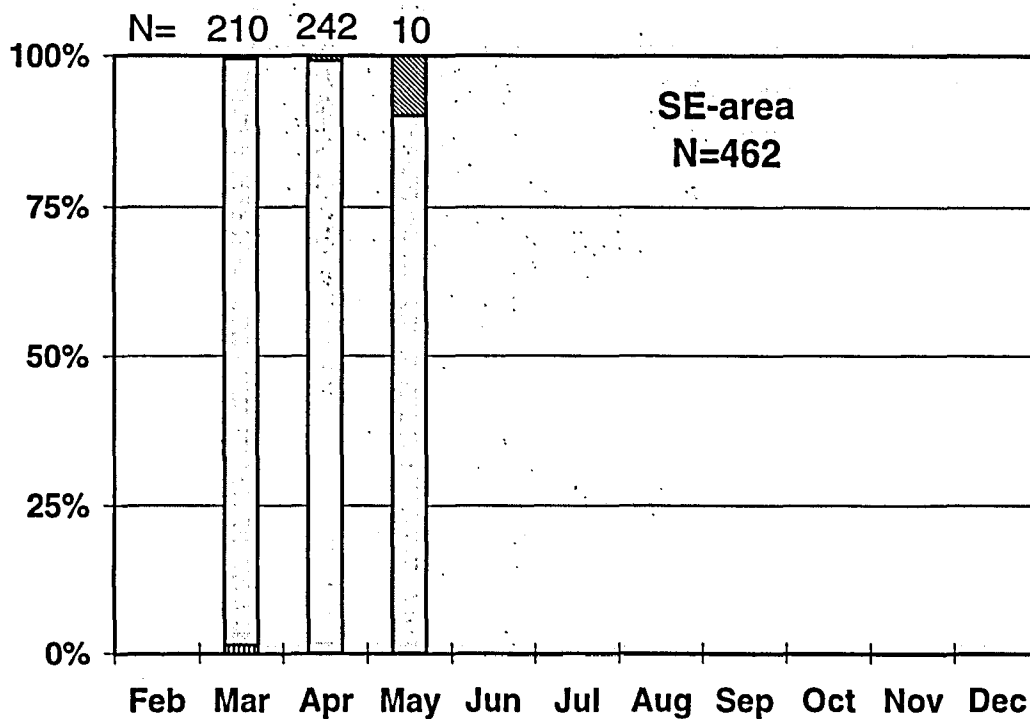
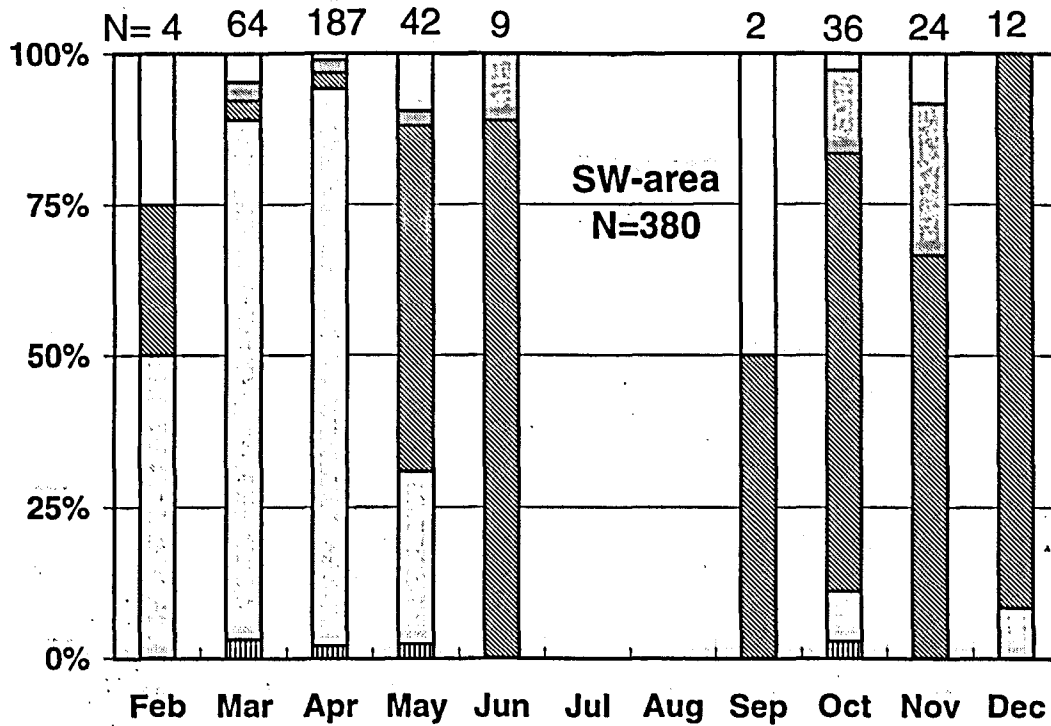


Figure 7. Capelin – relationship between otolith length (OL) and fish length (FL).
The solid line shows the regression line for the Icelandic data while the dotted line shows the relationship given by Harkönen (1986)

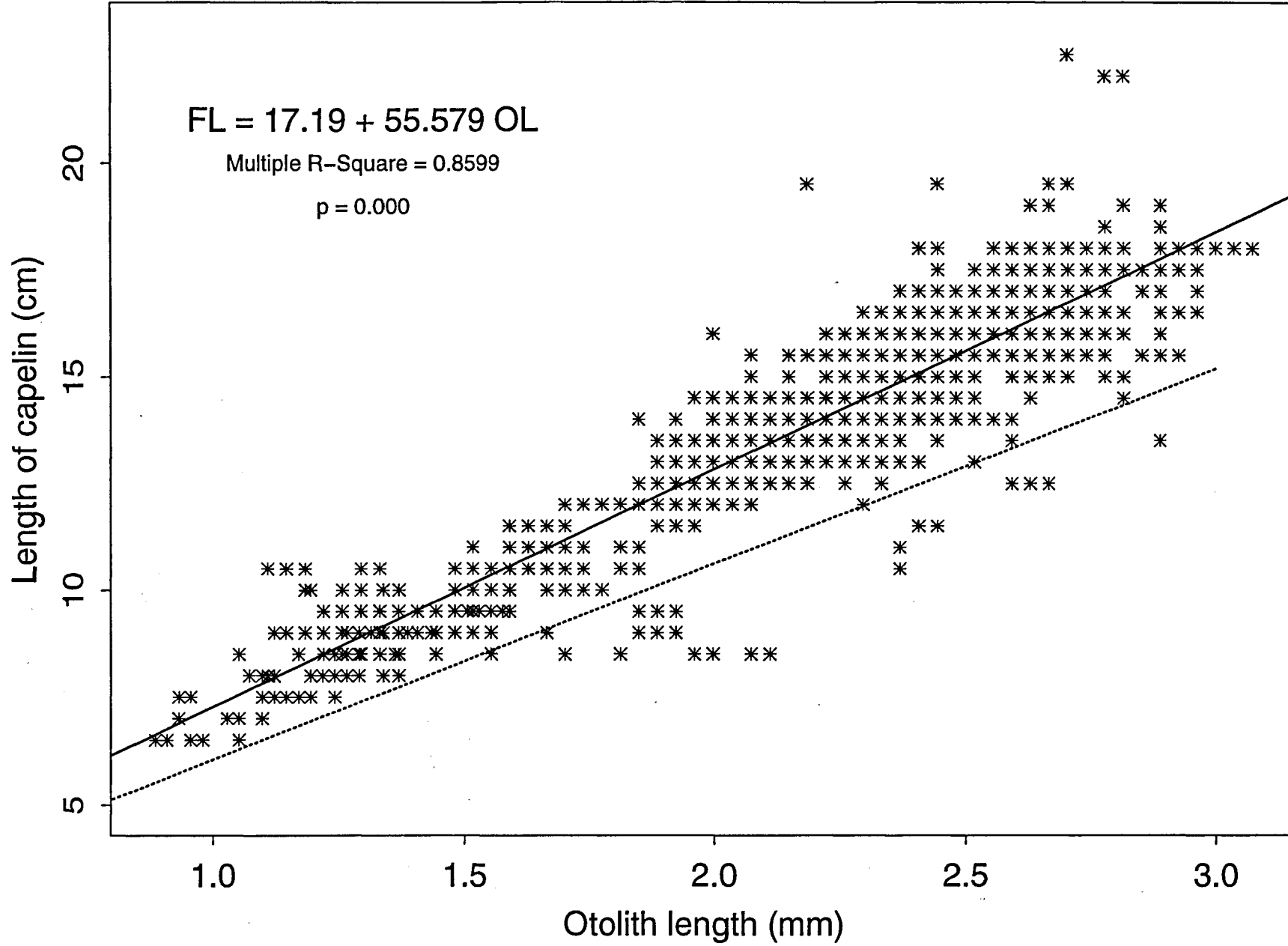


Figure 8. Length distribution of capelin consumed by harbour porpoises, as calculated from otolith lengths

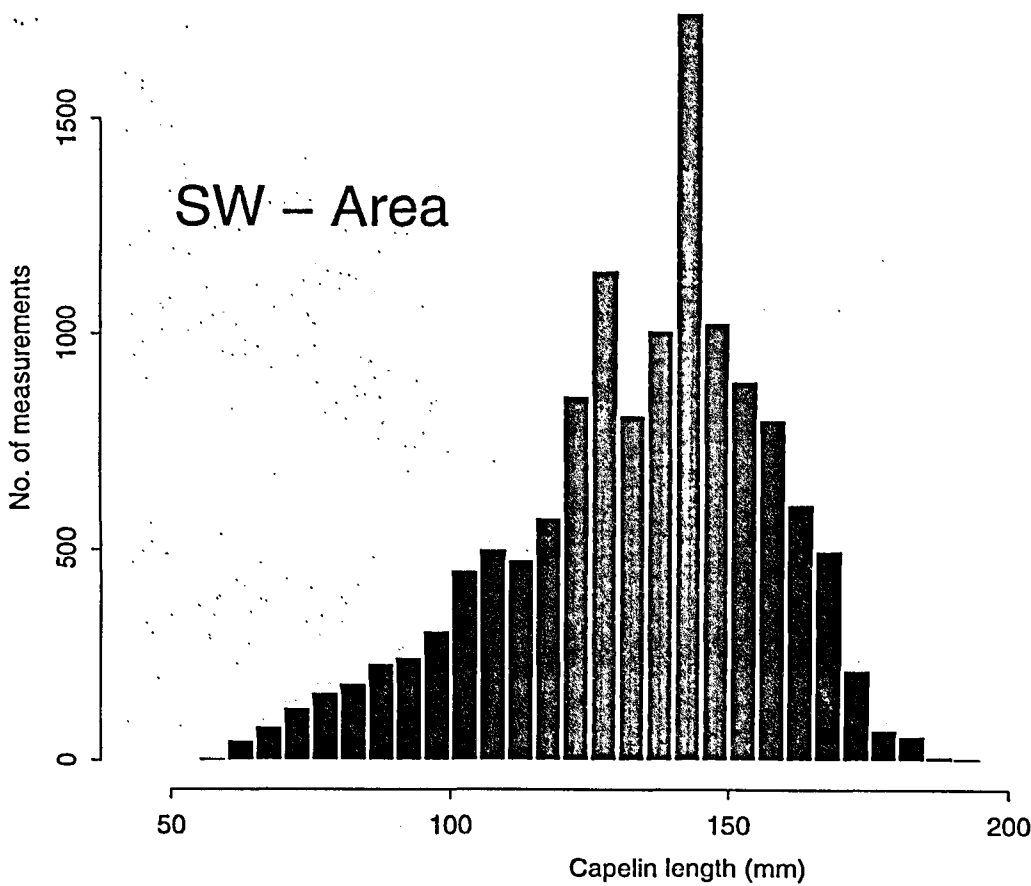
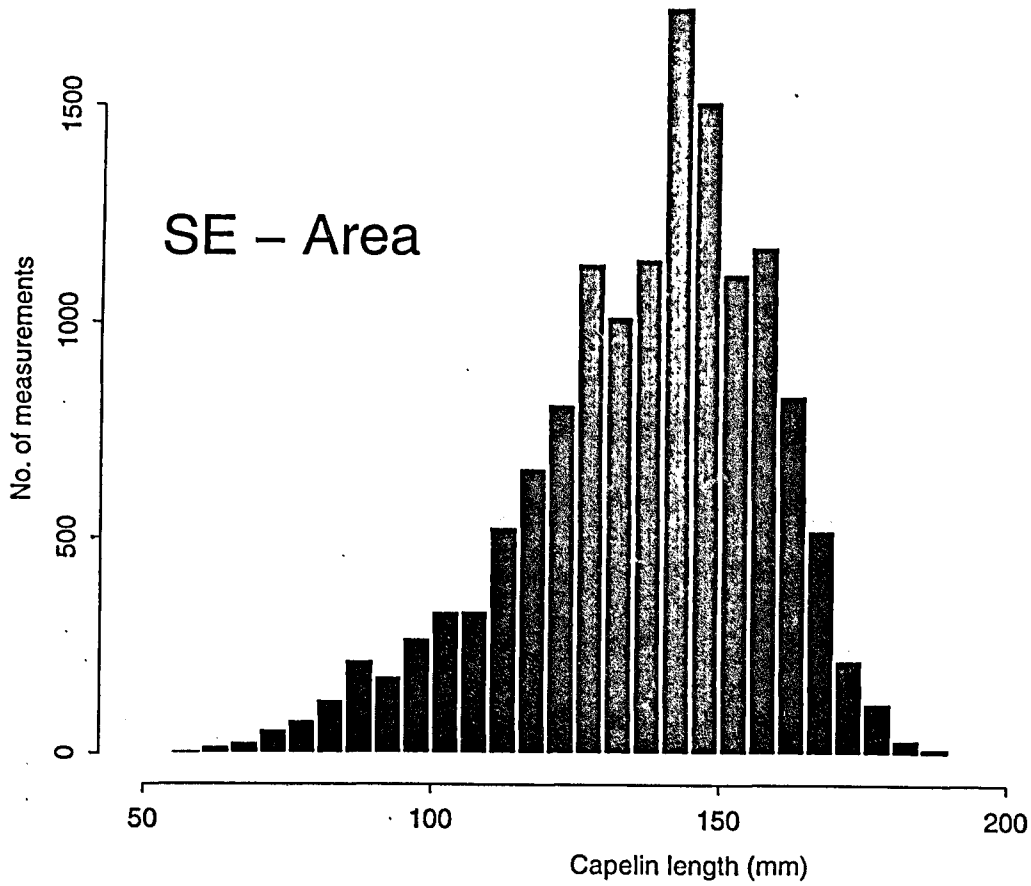


Figure 9. Length distribution of sand eel consumed by harbour porpoises as calculated from otolith lengths

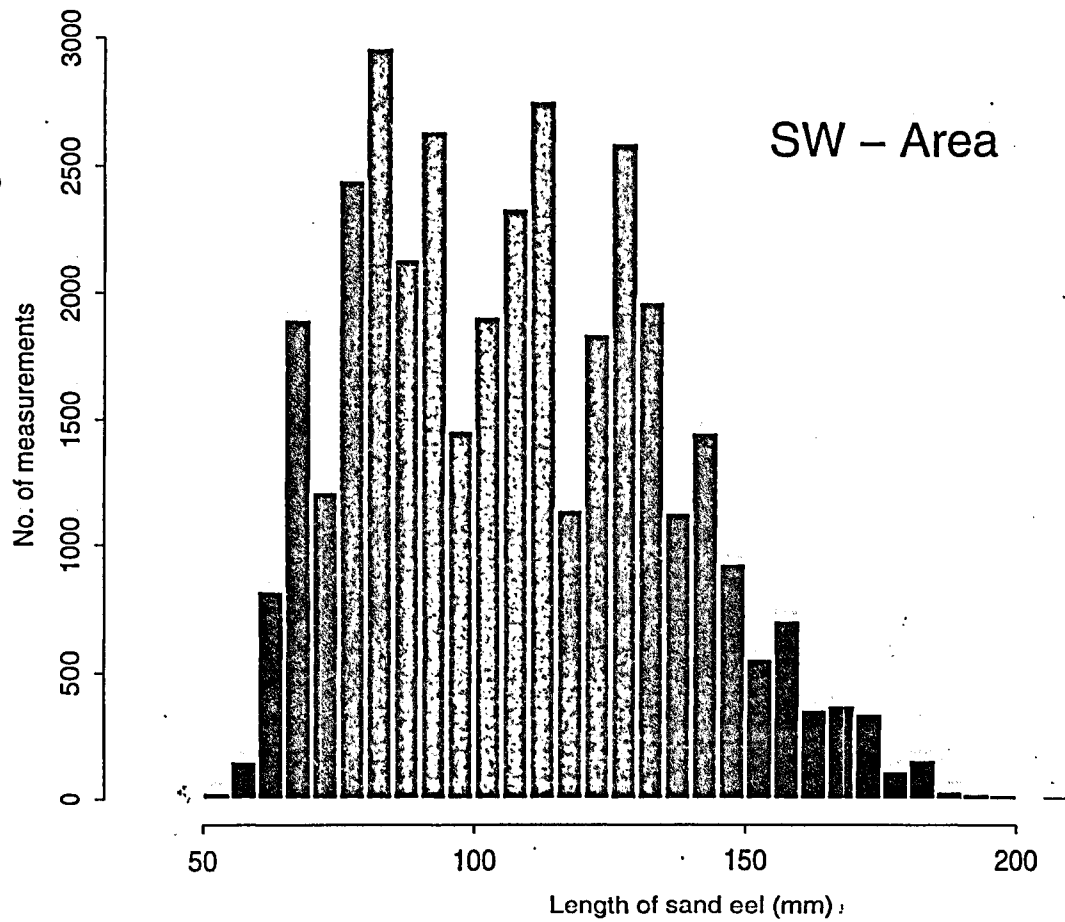
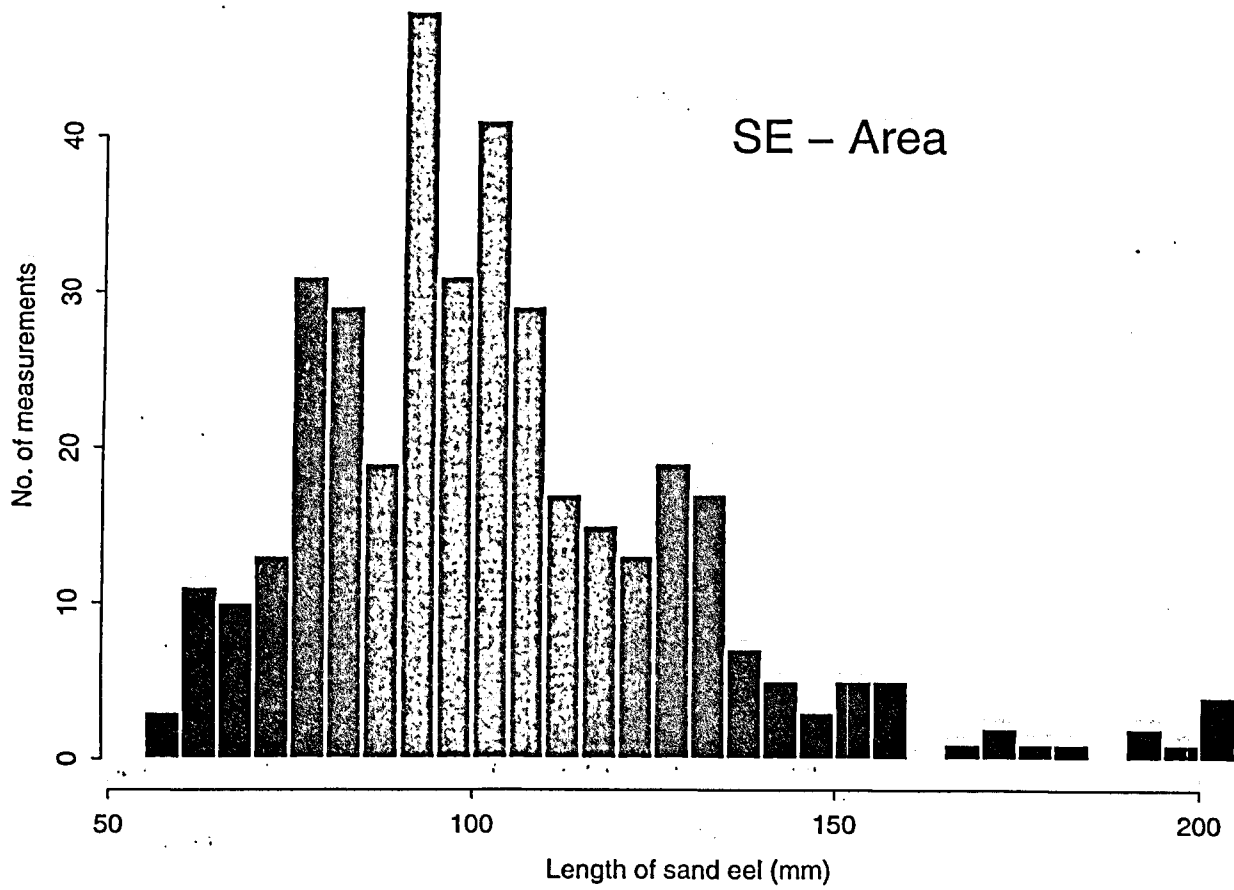


Figure 10. Reconstructed weight of stomach content as calculated from the size and numbers of capelin and/or sand eel otoliths

