Geographical, and seasonal variation in the diet of harbour porpoises (*Phocoena phocoena*) in Icelandic coastal waters

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ABSTRACT

The stomach contents of 1,047 harbour porpoises (*Phocoena phocoena*) bycaught in gillnets off Iceland were analysed. Most of the samples were obtained southwest (SW) and southeast (SE) of Iceland and the majority were taken in March and April. The sex ratio was biased towards males (63% males), particularly in the SE area (76%). The proportion of sexually mature porpoises was 35% and was higher in the northern part of the study area. Most examined stomachs contained identifiable food remains (97%). More than 40 fish and invertebrate prey taxa were identified. Overall capelin (*Mallotus villosus*) comprised the predominant prey, followed by sandeel (*Ammodytidae* sp.), then gadids, cephalopods and redfish (*Sebastes marinus*), while other taxa were of less importance. Differences were detected in diet composition among 5 areas around Iceland with redfish and gadids more prominent in the northern areas. Off SW Iceland there was considerable seasonal variation in the porpoise diet, where capelin appeared to be dominant in late winter and spring and sandeel in the summer through early winter. Predominance of capelin in the diet coincided with the spawning migration of capelin from northern waters along the east, south and west coasts of Iceland. Mature females appeared to have a more diverse diet than other reproductive classes. The length distributions of fish consumed by the porpoises ranged from 1 to 51 cm although most fish prey were less than 30 cm.

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INTRODUCTION

The harbour porpoise (*Phocoena phocoena*) is among the most common small cetaceans in temperate and subarctic coastal waters of the Northern Hemisphere (Klinowska 1991). The species is believed to show some seasonality in movements, probably as a result of seasonal variations in local prey availability (Tomilin 1957, Gaskin 1992, Berggren and Arrhenius 1995, Read and Westgate 1997). During summer, harbour porpoises are distributed throughout most of the Icelandic continental shelf area (Gunnlaugsson *et al.* 1988, Donovan and Gunnlaugsson 1989, NAMMCO 1998) while the distribution is poorly documented at other times of the year. A minimum summer abundance estimate of around 27,000 animals was derived from a sightings survey primarily designed for large baleen whales (Sigurjónsson and Víkingsson 1997). Sæmundsson (1932, 1939) stated that harbour porpoises approach the south and southwest coasts of Iceland in great numbers in spring, spend the summer in bays and fjords, and retreat to the open sea at the onset of winter. He considered harbour porpoises to be the most common of all cetaceans in Icelandic waters.

The feeding ecology of the harbour porpoise has been the subject of numerous studies in different parts of its distribution area (Tomilin 1957, Rae 1965, 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, Gannon *et al.* 1998). These studies have shown primarily piscivorous feeding habits, and indicated considerable spatial and temporal variation in the diet of the species.

In recent years, the study of species interactions in the marine ecosystem has received increased attention in connection with development of multispecies models for management purposes. Several of these studies have addressed the role of cetaceans in the marine ecosystem (see for example Overholtz *et al.* 1991, Kenney *et al.* 1997, Stefánsson *et al.* 1997, Bogstad *et al.* 2000, Schweder *et al.* 2000). Although studies have been conducted on food composition and feeding rates of some cetaceans in Icelandic waters (Rørvik *et al.* 1976, Martin and Clarke 1986, Sigurjónsson *et al.* 1993, 2000, Víkingsson 1995, 1997, Sigurjónsson and Víkingsson 1997), the feeding ecology of cetaceans is poorly known for most species in this area.

Prior to 1990, no systematic research had been undertaken on the biology and ecology of the harbour porpoise in Icelandic waters. However, Sæmundsson (1939) indicated that the porpoises pursued large spawning schools of capelin (*Mallotus villosus*) during their spring inshore movements, while later in the summer they moved into bays and fjords to feed on herring (*Clupea harengus*). The sources of this information were, however, not given.

The distribution of the harbour porpoise overlaps largely with the operational area of the Icelandic coastal fisheries, which may cause conflicts, for example bycatch of porpoises and competition for fish species. Rough calculations, based on the above stock size, that was probably severely underestimated, and information on food composition from other areas in the North Atlantic, indicate that minimum annual consumption of fish by harbour porpoises in Icelandic waters may be around 48,000 tons (Sigurjónsson and Víkingsson 1997).

The present study is a part of a large research programme, conducted by the MRI, on the feeding ecology of a wide variety of fishes and other marine organisms in Icelandic waters for the purpose of studying multispecies interactions in the marine ecosystem (Stefánsson *et al.* 1997, Stefánsson and Pálsson 1998). It comprises the first systematic study on the feeding ecology of the harbour porpoise in Icelandic waters, and presents the diet composition in relation to locality, season and reproductive status. Aspects of the stomach contents analysis relating to feeding rates will be considered in connection with energetic studies. The animals collected for this study were also utilised for a wide variety of other studies such as growth and reproductive biology (Ólafsdóttir *et al.* 2003), parasitology, genetics (Tolley *et al.* 2001) histology, fatty acid composition and energetics.

MATERIALS AND METHODS

This investigation is based on examination of harbour porpoises caught incidentally in nearshore Icelandic waters during 1991-1997. The animals were collected either through contacts at fish markets or obtained directly from fishermen by MRI staff and co-operating individuals throughout the country. Most of the animals were caught in bottom set gillnets that were generally soaked for around 24 hours. The main target species of the Icelandic gillnet fishery is cod (*Gadus morhua*), but saithe (*Pollachius virens*) and haddock (*Melanogrammus aeglefinus*) often constitute significant portions of the catch.

Most of the carcasses were autopsied by MRI staff members, but sometimes (mostly in the southeastern area) samples were taken and measurements made by contracted co-workers along the coast. The majority of the intact carcasses were kept frozen until dissection at the MRI laboratory, while in some cases fresh carcasses were dissected and sampled shortly after landing. While all stomach compartments were routinely investigated, identifiable food remains were only found in the forestomach. The weight of the stomach content was measured by weighing the stomach before and after the contents were removed. The stomach contents were washed through sieves with a mesh size of 0.3 mm and then separated into prey groups before final species identification and measurements were made. 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: sagittal otoliths, bones, cephalopod beaks, *etc.* The otoliths and cephalopod beaks were identified according to published identification guides (Clarke 1986, Härkönen 1986) and a reference collection held at the MRI.

The number of fish in each stomach was calculated by dividing the total number of sagittal otoliths by 2 or, in the case of larger otoliths, by counting the number of otolith pairs. The number of cephalopods was defined as the more numerous of upper or lower beaks. It was not possible to estimate the number of highly digested small crustaceans (euphausiids, amphipods *etc.*).

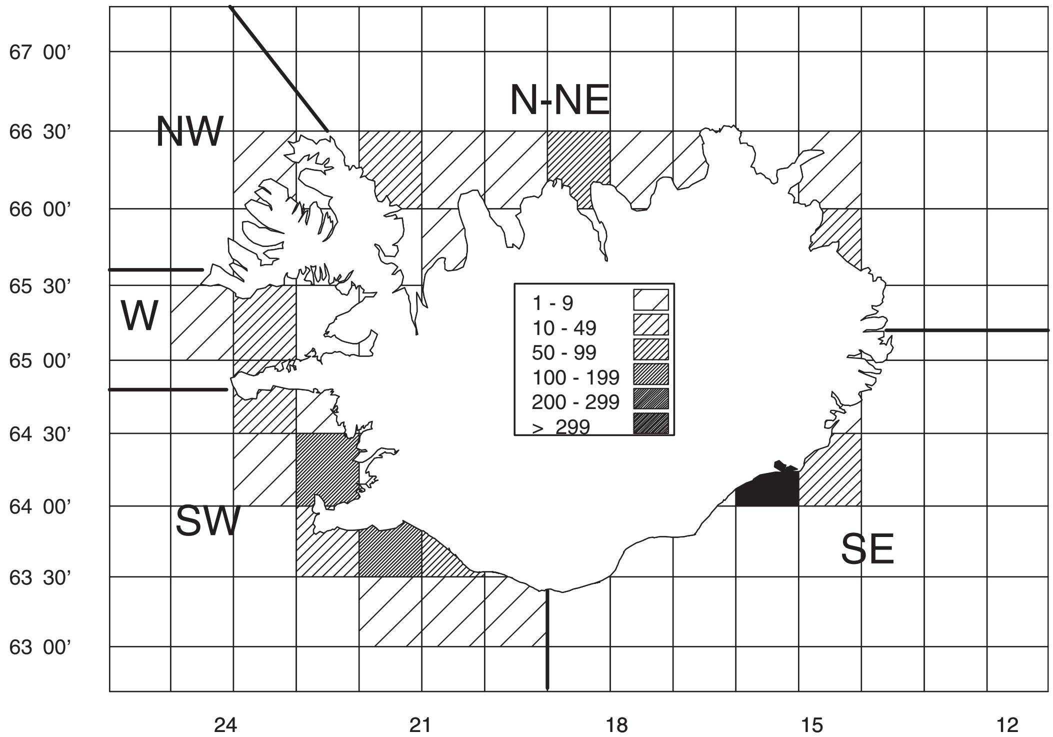
Otolith length was measured using a stereomicroscope with a graticule scale in the eyepiece or by using an image analyzer (Leica Quantimet 500+). Comparison between the 2 methods revealed no significant difference (t-test: $P = 0.8667$).

For calculating fish size from the size of sagittal otoliths, formulae based on Icelandic published (Vilhjálmsson 1994) and unpublished measurements were applied if available. In the absence of Icelandic data, formulae from other areas (Härkönen 1986) were used. The equations used for calculating fish size (total fish length and/or fish weight) from otoliths are given in the Appendix. For capelin and sandeel, different equations were applied for different times of the year to account for seasonal variability in the length/weight relationship (Vilhjálmsson 1994). While most fish could be identified to the species level it was not considered feasible to distinguish between the otoliths of the 3 species of sandeel (*Ammodytes marinus, A. tobianus* and *Hyperoplus lanceolatus.*) found in Icelandic waters. As the greater sandeel (*A. marinus*) is believed to be the most common in Icelandic waters, Härkönen's formula for greater sandeel was used to calculate fish length for the sandeel group. For similar reasons, formulae for the cod (*Gadus morhua*) and the American plaice (*Hippoglossoides platessoides*) were used for unidentified gadids and flatfish respectively. Calculation of fish size from otolith dimensions was not possible for 3 fish species: snake blenny (*Lumpenus lampretaeformis*), spotted snake blenny (*Leptoclinus maculatus*) and lumpfish (*Cyclopterus lumpus*). For these species, mean weights derived from a database held at the MRI, of 20 g, 2 g and 314 g respectively, were used, assuming similar size selection by harbour porpoises and the database sampling procedure for these prey species.

Otoliths that were noticeably eroded by digestion (corresponding to digestion state 3 and above in Recchia and Read (1989)) were not used in calculations of fish size and some stomachs containing large amounts (>50) of otoliths were subsampled for measurements and in a few cases also for counting of prey items. The length distribution of otoliths that were not measured was assumed to be the same as that of the measured part for each prey species within a given stomach. Thus, when estimating the length distribution of the total sample within a given stomach, the number of fish in each length interval (resulting from the measured subsample) was multiplied with a correction factor (total number of otoliths/number of measured otoliths). In cases where all otoliths within a given stomach were considered too eroded for length measurements, reconstruction of stomach content was done by assigning a mean weight, for the particular prey species, area and season, to the number of otoliths in the stomach. These data were excluded from studies of length distribution of prey.

The weight of cephalopods was calculated from relationships between beak size and body weight (see Appendix) given by Clarke (1986). Clarke's (1986) equation for *Rossia macrosoma* was used for *Rossia* spp. as there are no other available equations for this genus. For *Sepiola atlantica* and *Gonatus fabriciii* Clarke's (1986) equations for *Sepiola* spp. and *Gonatus* spp. were applied. The weight of other invertebrates was taken as the mean weight of the respective species in a database held at the MRI, again assuming similar size selection by the porpoises and the sampling procedure.

Fig. 1. *Distribution of samples used to study food habits of harbour porpoises in Icelandic coastal waters 1991-1997 and delineation of the study area into subareas. Numbers refer to sample sizes in geographical squares.*



The relative importance of different food items was estimated using the following measures: 1) *Frequency of occurrence*, the percentage of non-empty stomachs in which a particular prey was found; 2) *Numerical occurrence*, the total number of individuals of a prey species or prey group as a percentage of the total number of all prey individuals in the pooled sample; and 3) *Proportion by weight* as reconstructed from measurements of otoliths or other hard food remains.

Age determination was performed by reading growth layers in stained tooth sections (Ólafsdóttir *et al.* 2003). Reproductive condition of females was assessed by Ólafsdóttir *et al.* (2003) according to the presence of follicles and corpora in the ovaries and classified as follows: immature (solely primordial follicles), pubertal (secondary or third stage follicles), or mature (at least 1 *corpus luteum* or *corpus albicans*). Mature females were further classified as pregnant, lactating or resting. Males were classified as immature, pubertal or mature based on microscopic examination of testes tissue (Halldórsson and Víkingsson 2003).

In analysing geographical variation distinction was made between 5 areas (Fig. 1): the southwestern (SW) and southeastern (SE) areas, Breiðafjörður (W) area, Ísafjörður (NW) area and northern/northeastern (N-NE) area. This delineation is basically in accordance with that used by researchers on multispecies modelling in Icelandic waters (Stefánsson and Pálsson 1998), based on a combination of biogeographical and hydrographical features. However, due to the heterogenous nature of the porpoise sampling, some modifications, including merging of subareas, were made.

RESULTS

Sampling distribution

A total of 1,047 harbour porpoise stomachs were sampled during 1991-1997. The geographical and spatial distribution of the sample is shown in Figs 1 and 2. The sampling was uneven both in time and space. While some samples were obtained in all months except July and August, the overwhelming majority of the samples were taken in March and April (Fig. 2). Similarly, although samples were obtained in most parts of Icelandic nearshore waters, most of the animals were taken in 2 main sampling areas: off

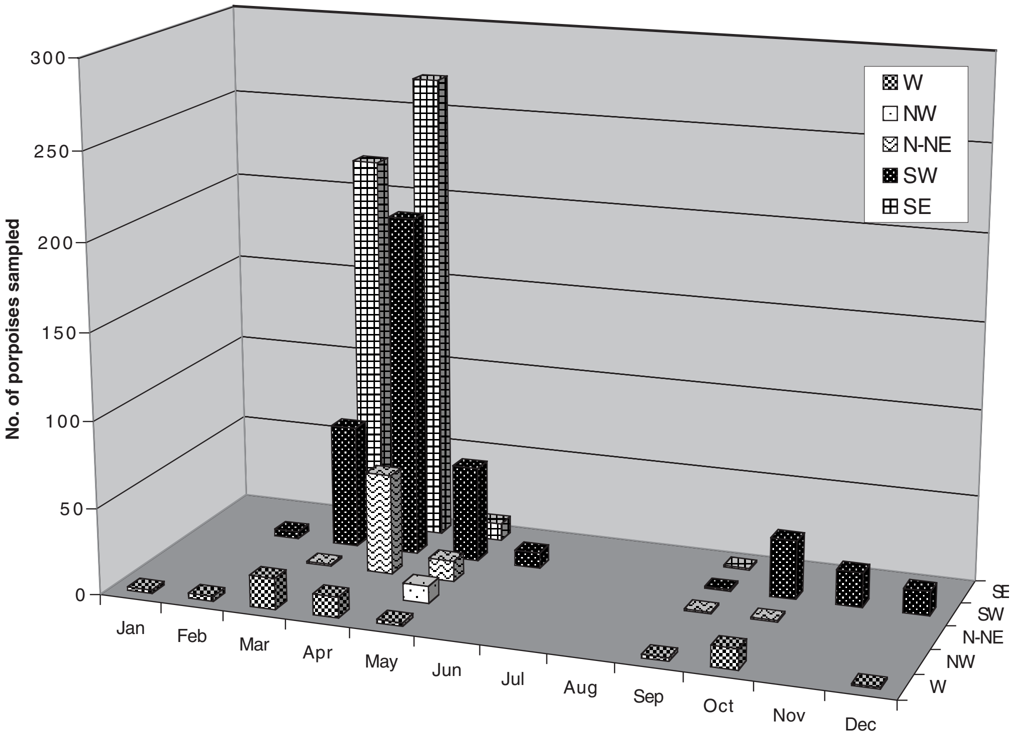


Fig. 2. *Seasonal and geographical distribution of harbour porpoises sampled to study food habits. Subareas correspond to those in Fig. 1.*

southwestern and southeastern Iceland (Fig. 1). Thus, 73% of the total sample was obtained from these 2 areas during the months of March and April. Only 10 animals were sampled from the NW area (all in May) and 56 and 73 animals were obtained from the western and northern areas respectively. The majority of samples taken during autumn were obtained from the SW area. Within the defined subareas, samples were also unevenly spread. Most of the bycatch occurred in nearshore areas (<100 m depth) although some porpoises were obtained further offshore (Fig.1).

The sample was also skewed with respect to the geographical distribution of reproductive classes (Fig. 3). Males constituted 63% of the total sample. This uneven sex ratio was largely caused by overwhelming male dominance (76%) in the southeastern sample. The sex ratio was closer to unity in the other areas, except for the small ($n = 9$) northwestern sample where only 1 male was taken. Most of the sampled animals were immature: only 35% of the examined porpoises had reached full sexual maturity. The proportion of mature animals was highest in the northern areas (Fig. 3). Only 8 of the females were found to be actively lactating. These were all pregnant as well, and sampled in the SW area during October-December.

Overall diet composition

Thirty-five (3.3%) of the stomachs were empty, of those only 7 belonged to females. Of the stomachs 15% were considered full. The mean weight of food remains (including digestive fluid) recovered from the stomachs was 298 g (S.E. = 8.4 g; range 0-1,822 g). In most cases the contents of the stomach were very digested, consisting primarily of hard food remains such as otoliths, fish bones and cephalopod jaws in addition to unidentifiable dissolved flesh. Only 2 porpoises contained virtually undigested prey, which could be measured and weighed directly. From here on, only stomachs containing prey remains are referred to.

The stomach contents included a wide range of fish and invertebrate species and more than 40 taxa were identified. Seaweeds were found in 11 stomachs (Table 1).

Of the 14 species of invertebrates which could be identified, cephalopods were the most com-

Table 1. Prey taxa found in the stomachs of harbour porpoises in different subareas (see Fig. 1) of Icelandic coastal waters. No. of prey: Total number of prey individuals found. No. of porp: Number of harbour porpoises in which the particular prey was found. Numbers of non-empty stomachs examined from each area are shown in parenthesis.

		West (54)		South West (393)		North West (9)		North-North East (69)		South East (483)	
Prey group		No.of prey	No.of porp	No.of prey	No.of porp	No.of prey	No.of porp	No.of prey	No.of porp	No.of prey	No.of porp
Seaweed	Algae				9		1				1
Mollusca											
Rossia	*Rossia sp.*			507	60					128	38
Sepiola	*Sepiola atlantica*			4	3			1	1	1	1
Gonatus	*Gonatus fabricii*	3	3	10	2	2	2	108	6	4	3
Sepiola/Rossia	*Sepiola sp. / Rossia sp.*			79	8					6	5
Unidentified squid	*Cephalopoda*			32	9					8	7
Bivalves	*Bivalvia*					5	2	1	1		
Gastropods	*Gastropoda*							1	1		
Other molluscs	*Mollusca*			4	2			1	1		
Arthropoda											
Pholychaetes	*Polychaeta*	1	1	20	6			1	1	2	2
Amphipod	*Gammarellus homari*				1						
Unidentified amphipods	*Amphipoda*				1		2		2		3
Euphausiids	*Euphausiacea*		4		5				4		
Sand shrimp	*Cragnon allmani*				1						
Crabs	*Decapoda*			1	1	4	1	1	1		
Barnacles	*Cirripedia*					1	1				
Unidentified crustaceans	*Crustacea*						1		1		
Bryozoa											
Sea mats	*Bryozoa*					1	1			1	1
Echinodermata											
Sea urchins	*Echinoidea*					1	1				
Chordata											
Herring	*Clupea harengus*	6	1	44	12			9	2	16	5

Table 1. (con´d)

Prey group		West (54)		South West (393)		North West (9)		North-North East (69)		South East (483)	
		No.of prey	No.of porp	No.of prey	No.of porp	No.of prey	No.of porp	No.of prey	No.of porp	No.of prey	No.of porp
Atlantic argentine	*Argentina silus*			70	9			1	1		
Capelin	*Mallotus villosus*	1,995	33	16,457	297	2	2	2,721	57	33,329	477
Lanternfishes	*Myctophidae*									8	4
Cod	*Gadus morhua*	32	7	41	20	27	5	89	25	1	1
Arctic cod	*Boreogadus saida*							1	1		
Haddock	*Melanogrammus aeglefinus*	1	1	14	9	4	2	5	4	1	1
Whiting	*Merlangius merlangus*	26	6	1,430	28			1	1		
Blue whiting	*Micromesistius poutassou*			8	4			1	1		
Saithe	*Pollachius virens*			11	3						
Norway pout	*Trisopterus esmarki*			1,025	17						
Fourbeard rockling	*Rhinonemus cimbrius*			1	1						
Silver rockling	*Onogadus argentatus*					1	1				
European ling	*Molva molva*			1	1						
Other gadids	*Gadidae*	22	5	1,898	32	3	3	80	10	5	3
Sandeel	*Ammodytes sp.*	5,388	32	36,018	172	393	3	491	23	492	85
Atlantic catfish	*Anarhichas lupus*							3	1		
Snake blenny	*Lumpenus lampretaeformis*			1	1	1	1	3	2	1	1
Spotted snake blenny	*Leptoclinus maculatus*					1	1	6	4		
Vahl's eelpout	*Lycodes vahli*	1	1	3	1	1	1	1	1		
Redfish	*Sebastes marinus*	25	4	53	22	101	7	137	14	6	5
Lumpfish	*Cyclopterus lumpus*			2	1					1	1
Norwegian topknot	*Phrynorhombus norvegicus*	10	1								
European plaice	*Pleuronectes platessa*			1	1						
American plaice	*Hippoglossoides platessoides*	1	1	5	3			4	1	1	1
Lemon dab	*Microstomus kitt*	3	1								
Other flatfish	*Pleuronectiformes*			4	2	1	1				

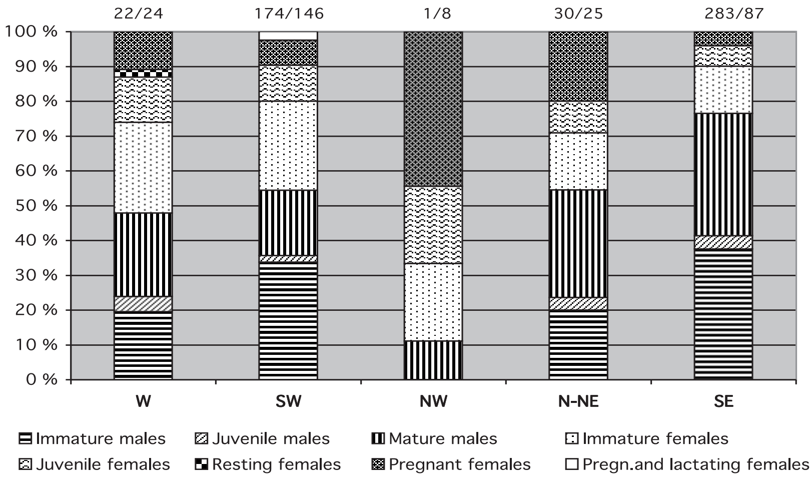


Fig. 3. *Demographic composition of the harbour porpoise sample by area. Numbers at top: Sample size of males/females assigned to a reproductive class.*

mon, found in 15% (n=147) of the non-empty stomachs. Although up to 88 cephalopods were found in a single stomach, most contained only few individuals. Thus 81% of stomachs with cephalopods contained 5 or fewer individuals while 13% of the stomachs contained more than 10 cephalopods. Two species of cephalopods were identified, *Sepiola atlantica* and *Gonatus fabricii*, but the most common type could be determined only at the genus level (*Rossia* sp.). The mean weight of the cephalopods as calculated from beak measurements was around 2 g.

Euphausiids were identified in stomachs from 13 porpoises (1.3% of non-empty stomachs). Nine of these porpoises were age-determined, 5 of them belonging to the age classes 0 and 1 and the oldest one being 4 years. In the age group 0-4 years, there was no significant difference in age between porpoises containing euphausiids (mean age 1.67 years) and those not containing euphausiids (mean age 2.72 years) in their stomachs (t-test P=0.18). Three porpoises (0-4 years) contained only euphausiids, while the remaining 10 animals had 1-6 additional prey species in their stomachs. Other crustaceans were found in 15 (1.5%) of the stomachs examined representing porpoises of all reproductive classes and a wide age range (0-13 years). Although most of these crustaceans were too digested for identification of species and the number of individuals, 2 species, the sand shrimp, *Cragnon almani* and the amphipod *Gammarellus homari*, could be identified.

Otoliths allowed the identification of 23 species of fish and in addition 3 families where species identification was not possible (Table 1). Eight

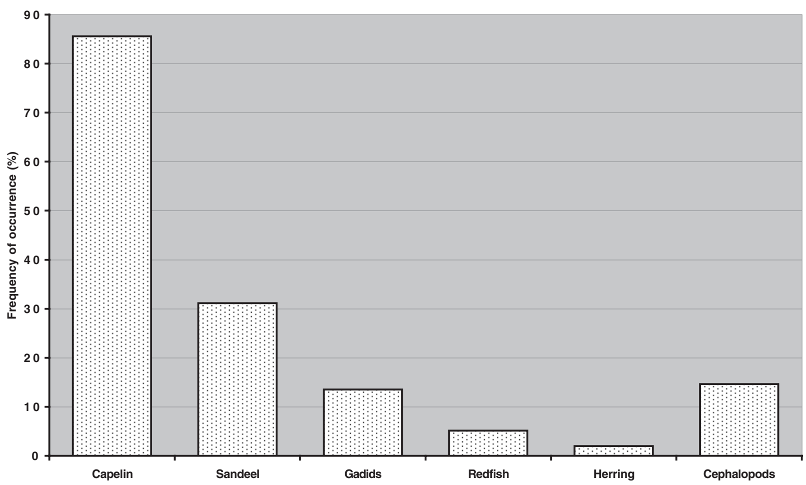


Fig. 4. *Frequency of occurrence (%) of the prey taxa most commonly found in the stomachs of harbour porpoises from Iceland.*

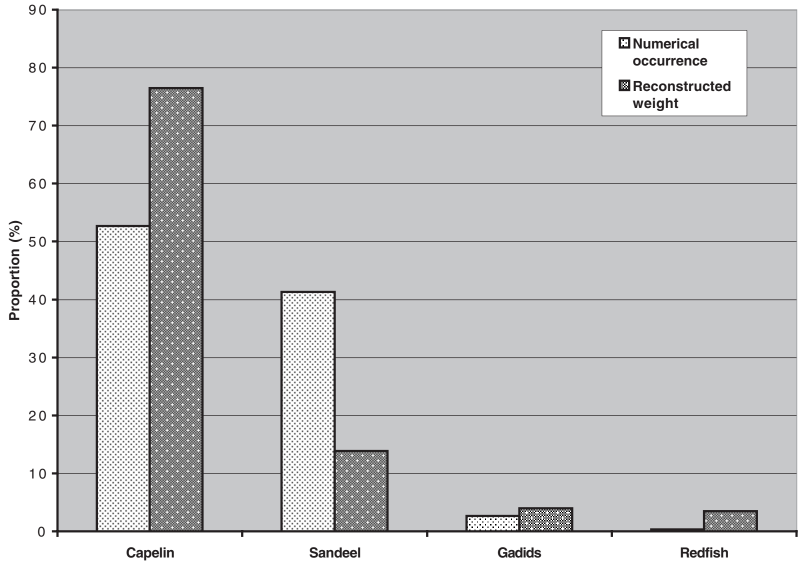


Fig. 5.
Relative importance of the most common prey taxa as assessed by numerical occurrence and reconstructed weight. All measures are given as percentages of the total sample.

of these 23 species were found in only 1 porpoise stomach, thereof 5 as a single prey item. Ten species of gadids were identified as porpoise prey, while the remaining taxa varied widely and belonged to 12 different families.

Figure 4 shows the frequency of occurrence for different prey species or groups. Capelin (*Mallotus villosus*) had by far the highest rate of occurrence and was found in 85% of all non-empty stomachs. Sandeel (*Ammodytes* sp.) occurred in 31% of the stomachs, gadids and cephalopods in around 15% each, redfish (*Sebastes marinus*) in 5% and "other fish" species were found in around 10% of the stomachs. Other prey groups had considerably lower rates of occurrence. Within the gadid prey group, cod (*Gadus morhua*) was the most commonly detected species (5.7% occurrence) followed by whiting (*Merlangius merlangus*), (3.4%), haddock (*Melanogrammus aeglefinus*), (1.7%) and Norway pout (*Trisopterus esmarki*), (1.7%).

The importance of capelin in the diet was not as pronounced when numerical occurrence of prey species was considered (Fig. 5). Capelin was, however, still the most numerous prey species, representing more than half of all identified prey items. Over 40% were sandeels, so numerically these 2 species accounted for 94% of all prey items identified in this study (Fig. 5). Ninety nine percent of the total prey numbers identified were fish species while invertebrates (excluding crustaceans) were 1%. The mean number of individual fish remains in single stomachs was 63 (S.E. 2.53, range: 1-1,050) for capelin and 136 (S.E. 21.17, range: 1-3,200) for sandeel.

Considering the proportional reconstructed weight of different prey species the dominance of capelin was even more pronounced. The contribution of redfish to the diet increased markedly as compared to using numerical occurrence (Fig. 5), while the importance of sandeel decreased. The contribution of cephalopods was 15%, 0.9% and 0.2% using the measures frequency of occurrence, numerical occurrence and reconstructed weight, respectively.

Geographical variation

The diet composition (% weight) in 5 different sub-areas in Icelandic coastal waters is given in Figure 6. In the southeastern (SE) area 99% of the diet consisted of capelin although at least 16 other prey species were found in small amounts. The proportion of capelin was considerably lower (61%) off the southwestern coast (SW). In this area sandeel comprised 33% of the prey weight and the remaining 6% were divided among more than 20 species, mostly fish. In the Breiðafjörður bay (W-area) similarly high proportions of capelin (66%) were found as in the SW area whereas the proportion of sandeel in the diet was lower (18%). In this area redfish and various gadids constituted a

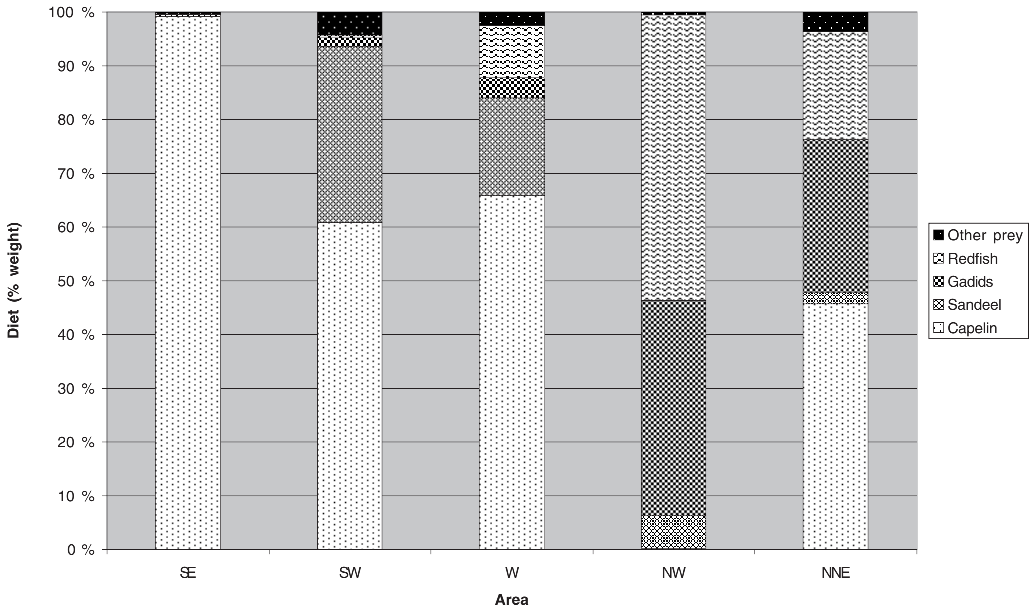


Fig. 6. Diet composition (% weight) of harbour porpoises in the 5 sub-areas within the main study area in Icelandic coastal waters.

larger proportion of the diet than in the more southerly areas (SW and SE). The prey composition is quite different in the NW area (Fig. 6) where sample size was, however, very small (*n*=10). Here redfish accounted for more than half (53%) of the diet and gadids (mainly cod) comprised another 40% of the prey weight. Capelin was almost absent from this sample (0.2%) and sandeel accounted for 6% of prey weight. One porpoise in the NW area contained at least 11 prey species in its stomach, the maximum detected in this study. In the northeastern area (N-NE) nearly half (46%) of the diet consisted of capelin while 27% were cod (1% other gadids) and 20% redfish. The remaining 6% were composed of at least 11 other fish species and 9 invertebrate species/groups.

Seasonal variation

The clumped temporal and spatial distribution of the sample (Fig. 2) prevented analysis of seasonal variation of prey composition within areas,

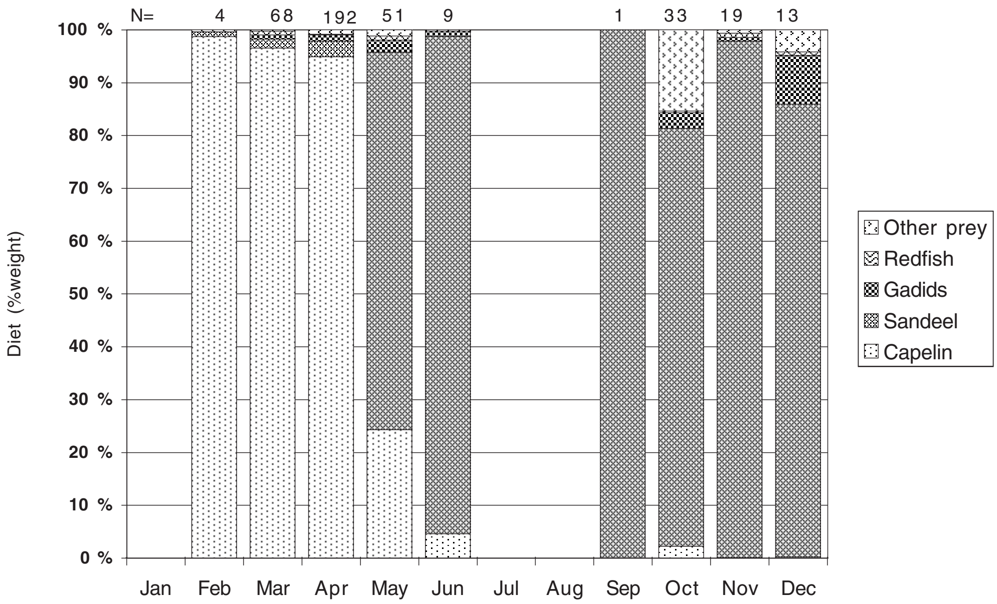


Fig. 7. Seasonal variation in the diet of harbour porpoises (%weight) from the SW area of Iceland. N= number of harbour porpoises examined.

except for the SW area (Fig. 7). Although no samples were obtained in this area during January, July or August, and sample sizes were very small in some months, there appeared to be a clear pattern of seasonal shift in diet throughout the year. Capelin was totally dominant in the stomach contents from February through April accounting for 95% or more of the reconstructed weight of stomach contents in each of the months. In May the proportion of capelin fell to 24% while the proportion of sandeel increased from 3% in April to 71% in May. In June the contributions of sandeel and capelin were 94% and 5% respectively. During the autumn sandeel remained the predominant prey species accounting for more than 80% of the diet during September-December. In October Atlantic argentine (*Argentina silus*) constituted 15% of the stomach contents.

Differences among reproductive classes

Figure 8 shows the diet composition (% weight) by reproductive class. The diet composition was similar for all 3 reproductive classes of male porpoises. Capelin amounted to 82-85% of the diet and sandeel 12-15% in all classes (Fig 8a). The food composition of immature and pubertal females was similar to that of males although capelin constituted slightly less part of the diet (Fig. 8b). The pregnant but non-lactating females had a more diverse food composition, as capelin (34%) and sandeel (14.5%) together contributed less than half of the diet, while redfish and gadids accounted for 28% and 18% respectively. Sandeel was the dominant prey species in the small sample of simultaneously lactating and pregnant females, while 6 other fish species and at least 2 invertebrate species were also among the stomach contents.

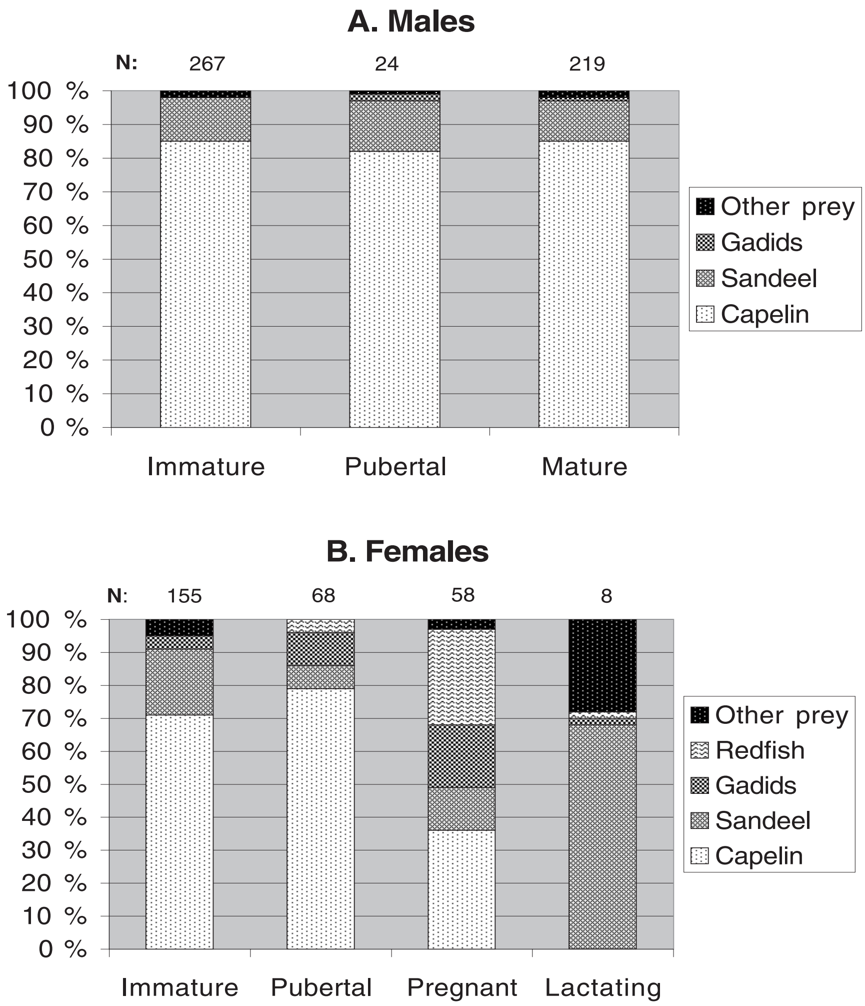
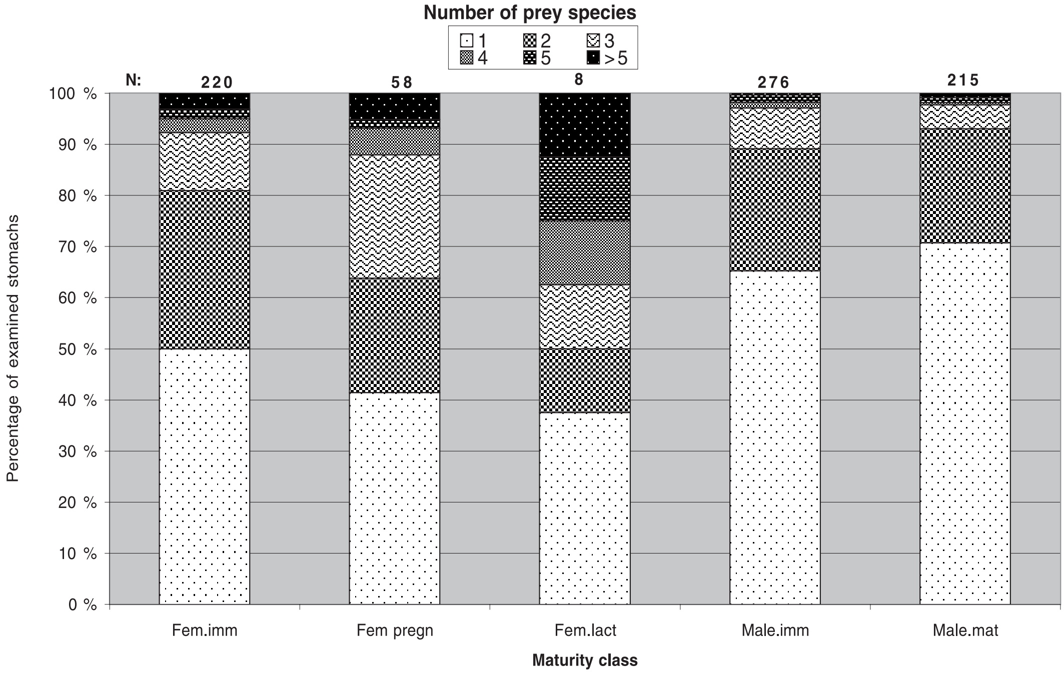


Fig. 8. *Diet composition (%weight) of 7 reproductive classes of harbour porpoises. All lactating females were simultaneously pregnant, while the category "pregnant" refers to non-lactating pregnant females.*

Fig. 9. Diversity in prey composition by sex and maturity expressed as percentage of porpoises containing different numbers of prey taxa (1,2,3,4,5,>5) in their stomachs. The immature male category includes pubertal animals.



Females also appear to show greater diversity in feeding habits when the number of prey taxa retrieved from individual stomachs is considered (Fig. 9). Thus 71% and 65% of mature and immature males respectively contained only 1 prey species while the corresponding values for females were 41% and 50%. The difference between males and females in proportions of animals with more than 1 prey species was significant (λ^2= 28.00, d.f.=1 P<0.001). At the other end 5% and 3% of mature and immature females respectively contained more than 5 prey species while the corresponding figures were 0.9% and 0.4% for mature and immature males (Fig. 9). The proportion of animals containing more than 2 prey species was significantly higher in mature females (36%) than in immature females (20%) (λ^2= 6.37, d.f.=1 P=0.012). Within the mature female class, lactating animals seemed to have the most diverse diet, but the sample size was too small (8) for a meaningful statistical comparison.

Prey size

The calculated size range of fish prey in the harbour porpoise stomachs was 1-51 cm in total length. The overwhelming majority of ingested fish had lengths less than 30 cm. Among the species taken in considerable numbers, whiting and Norway pout had the lowest calculated mean lengths (Figs. 10f and 10g), although individuals up to 35 and 21 cm long, respectively were found. The size of capelin ranged from 3.5-30 cm, although most were between 10 and 17 cm (Fig. 10a). The sandeel were considerably smaller, the majority being less than 10 cm long (Fig. 10b). Redfish prey ranged from 4.5 to 36.7 cm in length (Fig. 10c), the mean value being 20 cm. The mean length of cod was 22.4 cm, including the largest food item identified in the present investigation, corresponding to a length of 51 cm and a weight of 1,257 g. This large cod was taken by a 159 cm pregnant female. The next largest food item, a 46 cm (907 g) cod, was eaten by a female of unknown length and reproductive status. The length distribution of cod appears to have 2 peaks at 5-13 cm and 25-35 cm respectively (Fig. 10d). The length of Atlantic argentine taken by porpoises ranged from 20-28 cm (Fig. 10e). Most of the whiting identified in the stomachs were 3-6 cm in length, although fish up to more than 30 cm, were taken (Fig. 10f) and the Norway pout had similar distribution (mean: 3.8 cm, range 1-21 cm; Fig. 10g). The lengths of herring taken by the porpoises were quite evenly spread between 8 and 28 cm (Fig. 10h).

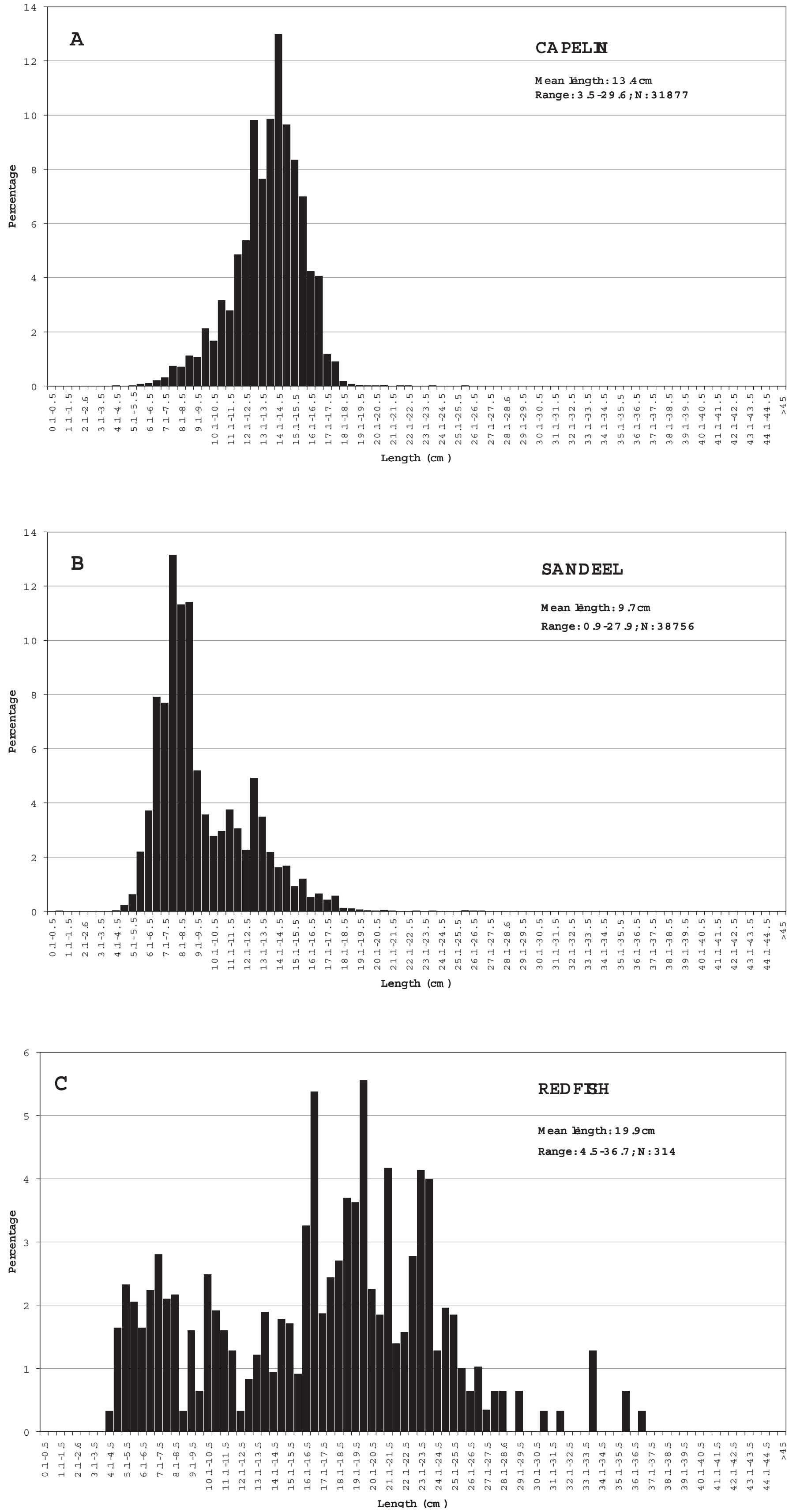
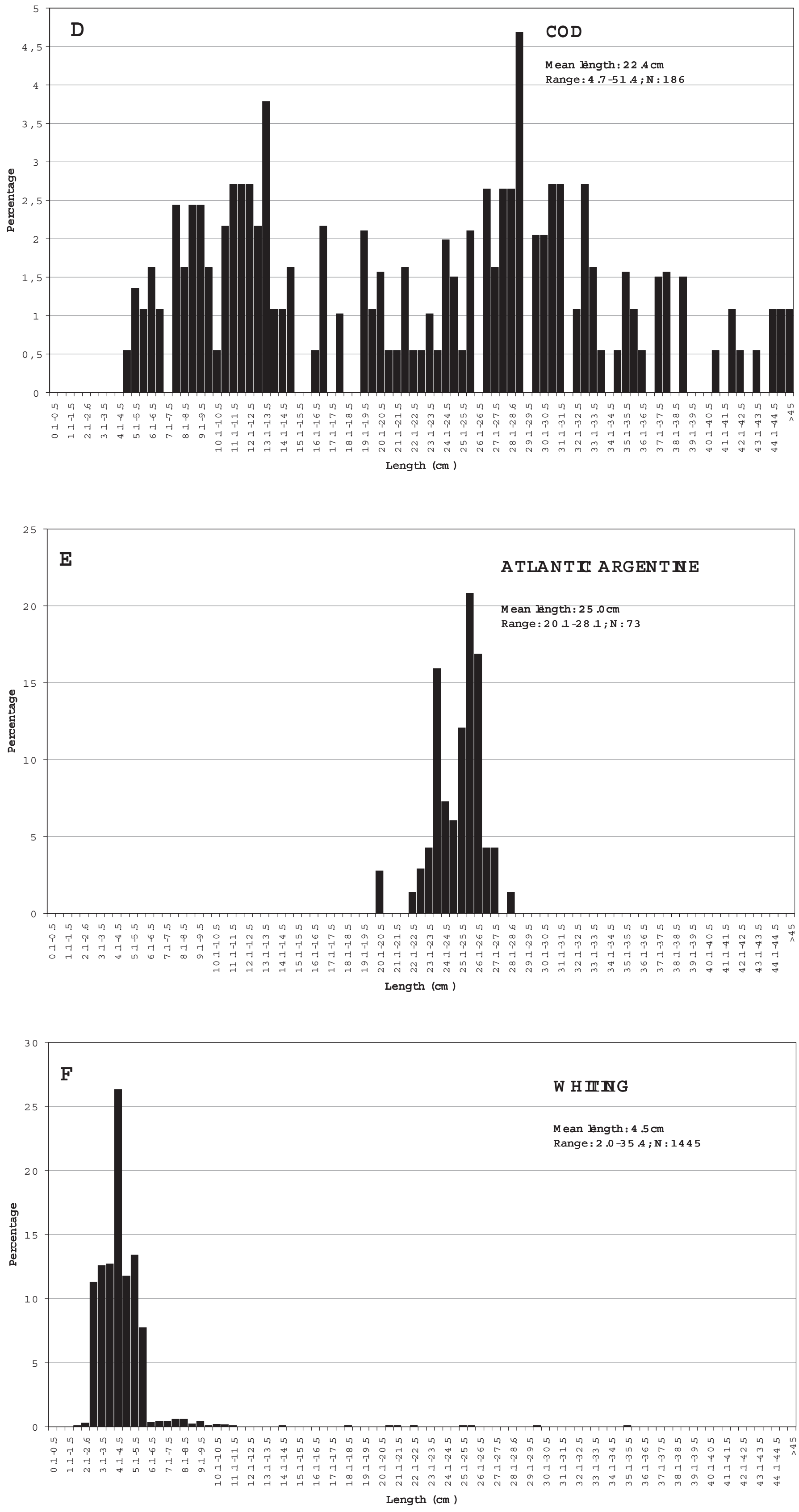


Fig. 10.
Length distributions of the most common fish species identified in the stomachs of harbour porpoises as calculated from otolith lengths. (The graphs include the calculated lengths of fishes where a portion of the otoliths was not measured (because of subsampling and/or digestive erosion of otoliths). In these cases the number of fish in each length interval was multiplied with a correction factor (total number of otoliths/number of measured otoliths) assuming the same length distribution of measured and unmeasured otoliths within each stomach sample. This often resulted in the estimated number of fish in a given length interval not being whole numbers. Data from stomachs where all otoliths of a particular species were too eroded for measurements are excluded.)

Fig 10.
(con´d)


D
COD
Mean length: 22.4 cm
Range: 4.7-51.4; N: 186
Percentage
Length (cm)
E
ATLANTIC ARGENTINE
Mean length: 25.0 cm
Range: 20.1-28.1; N: 73
Percentage
Length (cm)
F
WHITING
Mean length: 4.5 cm
Range: 2.0-35.4; N: 1445
Percentage
Length (cm)

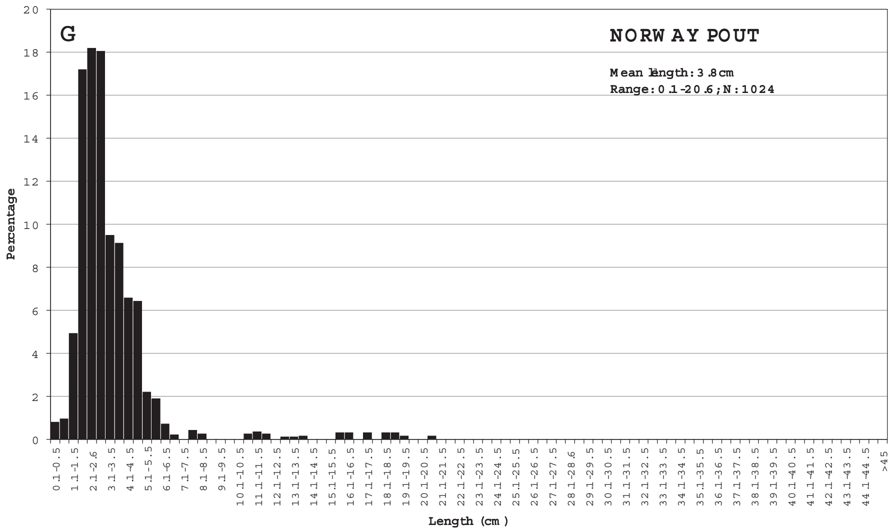
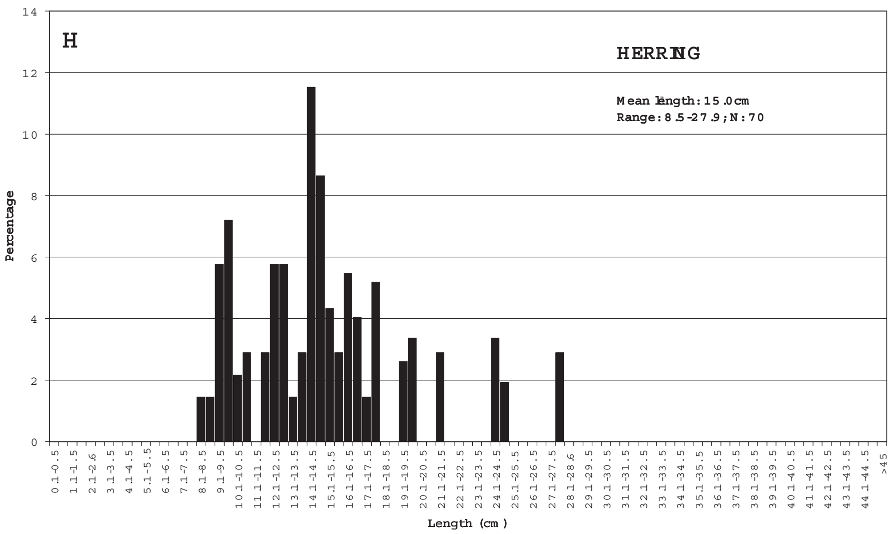


Fig 10.
(con´d)



For cod, redfish (Fig. 11) and Norway pout, linear regression analysis revealed a significant (P<0.001) positive relationship between the calculated length of fish prey and the length of the porpoise predators:

Cod:
L = -43.15 + 0.459*PL, R^2=0.278)

Redfish:
L= -15.86 + 0.213*PL, R^2=0.210)

Norway pout:
L= -17.33 + 0.152*PL, R^2=0.111)

where L is length of fish prey and PL is the length of harbour porpoise, both in cm. As indicated by the relatively low R^2 there was, however, a large variation in prey size for a given porpoise length. For other prey species R^2 was less than 0.01.

DISCUSSION

Although the total sample size in this study is large there are several factors that may affect the results with regard to the objective of giving a balanced picture of feeding ecology of harbour porpoises in Icelandic waters. Some of these are common to most diet studies based on analysis of stomach contents, including differ-

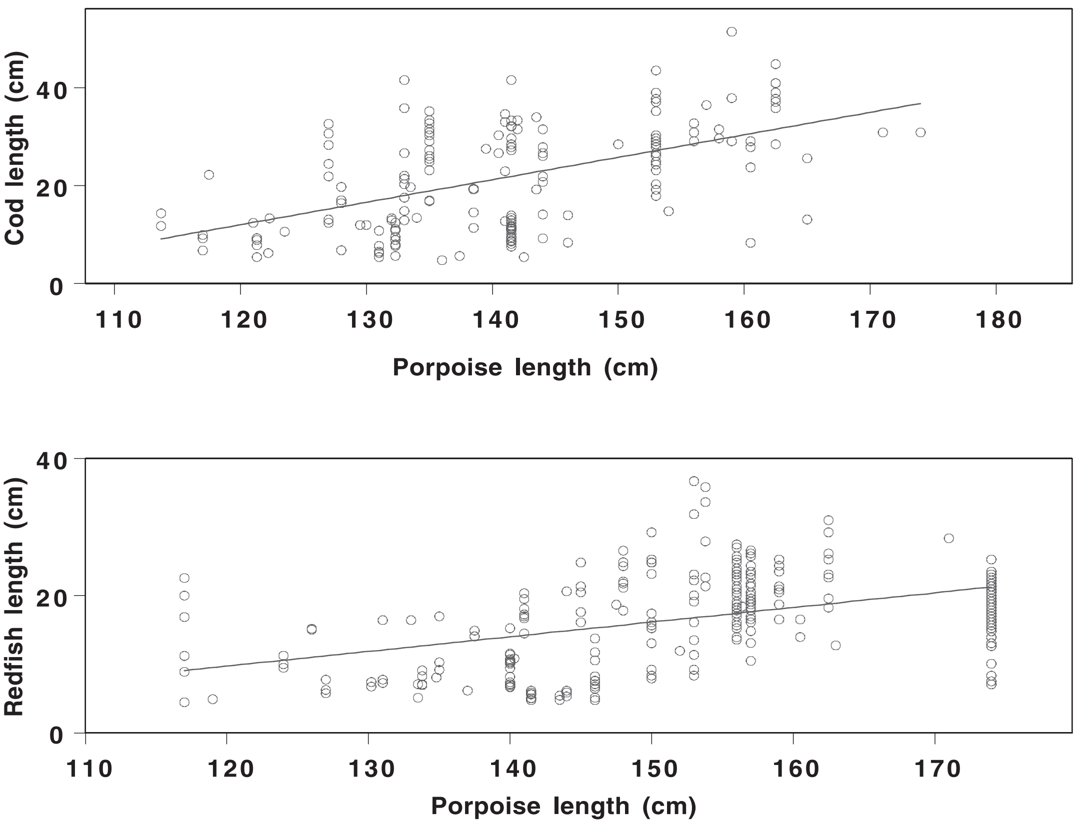


Fig 11. *Relationship between the lengths of porpoises and the lengths of cod and redfish prey.*

ential digestion rates of prey species and distinction between prey consumed by the porpoises and prey consumed by the porpoise prey. Other potential biasing factors are associated with the sampling procedure in the present study and need special consideration here.

Representativeness of the sample

Although efforts were made to obtain samples from porpoises all around Iceland and throughout the year, the resulting numbers of samples were very unevenly spread in time and space. The uneven distribution of the sampling may reflect both the distribution of harbour porpoises and the sampling effort (*i.e.* the distribution of the gillnet fishery in Icelandic waters). Information on seasonal variability in abundance of harbour porpoises in Icelandic waters is very limited. The relatively few samples obtained during summer cannot be considered indicative of low density, as recent sightings surveys have demonstrated that harbour porpoises are abundant in coastal waters all around Iceland during summer (Gunnlaugsson *et al.* 1988, Donovan and Gunnlaugsson 1989, NAMMCO 1998).

The peak of the gillnet season is in March-April and the fishery is most concentrated off SW and SE Iceland. The gillnet fishery overlaps largely in time and space with both the spawning grounds of cod, the primary target species of this fishery, and the spawning migration route of capelin. Capelin is considered a keystone species in the marine ecosystem around Iceland, and an important food source for many species of fish (in particular cod), seabirds and marine mammals (Pálsson 1994, Stefánsson *et al.* 1997, Lilliendahl and Sólmundsson 1997, Anonymous 1997). During summer, capelin distribution is mostly confined to offshore areas north and northeast of Iceland (Vilhjálmsson 1994). The first spawning migrations generally arrive in the coastal waters off southeast Iceland in February and continue westward along the south coast

(Vilhjálmsson 1994). Spawning takes place mostly during March-April in shallow waters off south and west Iceland, after which most of the mature animals are believed to die. The temporal and spatial overlap between the seasonal gillnet fishery and the large influx of biomass associated with the capelin migration must therefore be considered a potential source of sampling bias in this study.

The sampling distribution in this study may seem to support Sæmundsson's (1932, 1939) theory that harbour porpoises enter southern- and southwestern Icelandic coastal waters from offshore areas in March pursuing the capelin spawning migration and migrate to offshore areas at the onset of winter. However, the fact that harbour porpoise bycatches occur in most months, despite low fishing effort in many months, indicates the presence of the species in coastal Icelandic waters throughout most of the year.

While it seems clear that large numbers of harbour porpoise are found along the southern coast of Iceland during the capelin migration, abundance remains high throughout summer, and at least some harbour porpoises overwinter in Icelandic coastal waters, so that the relative seasonal abundance of the species remains unclear. It is thus not possible, from the available data, to draw firm conclusions about seasonal movements of the species in this area and possible links to seasonal variability in the availability of capelin or other prey species.

Another possible source of bias is the sampling gear itself, as bottom set gillnets may bias the results towards benthic prey species in general (Recchia and Read 1989), and the target species of the fishery in particular (see discussion below).

The high proportion of male harbour porpoises in the total sample and the geographical variation in proportions of reproductive classes seems to indicate some kind of temporal and/or spatial segregation within the stock. Thus, the SE sample was heavily dominated (>75%) by males, about half of which were immature. Immature males were also more than 30% of the SW sample although the overall sex ratio was close to unity in that area. The proportion of mature animals was highest in the 2 northern areas (N-NE and NW). Segregation by sex and maturity has been suggested as a possible causal factor for biased sample distribution in harbour porpoises bycaught in Danish waters (Lockyer and Kinze 2003) and this may also apply for this study.

Although previous information is rather sparse on seasonal variation in distribution and abundance of harbour porpoises in Icelandic waters, and on population structure (including segregation of sex/age classes), the observed composition of the present sample is clearly affected by the nature of the sampling method. Therefore, without further information on the above, the sample cannot, as a whole, be considered representative of the population.

Possible bias in diet reconstruction

Various sources of potential bias are associated with reconstruction of diet from stomach contents (Härkönen 1986, Pierce and Boyle 1991). Differential digestion rates of prey species may affect the assessment of the relative importance of prey species (Pierce and Boyle 1991). The contribution of some invertebrates may thus be somewhat underestimated as weight percentage in the present study. However, judging from the frequency of occurrence, a measure which tends to overestimate the importance of small food items (Hyslop 1980), it seems evident that these groups, with the possible exception of cephalopods (see below), play a minor role in the overall diet of the harbour porpoise in Icelandic waters.

The prey species for which mean weights had to be assumed had low frequency of occurrence and were found in low numbers in the harbour porpoise stomachs. Thus, the assumption that no size selectivity occurred for these species should not have affected the estimation of their relative importance in the diet to any considerable degree.

Emphasis was placed on using otolith length/fish length relationships based on data from Icelandic waters when available to account for possible geographical variation in these relationships (Härkönen 1986). This was, however, not possible for all species (Appendix). Another potential source of bias in reconstructing stomach contents occurs if the size range of otoliths in the stomach contents is wider than the size range of otoliths upon which the relationship is built. In the present study, estimates for whiting and Norway pout are most vulnerable to this kind of bias, as most of the otoliths were below the size range given for the formulae (Härkönen 1986). Although most capelin otoliths were within the "formula range", the calculated length of some individuals exceeded the maximum size recorded for this species (Winters 1970). Given the large number of capelin otoliths measured, such overestimation of few individuals is to be expected as a result of the natural variability in the relationship between otolith length and fish length.

Overall diet composition

The proportion of empty stomachs was low, and the number of prey items found in the stomachs relatively high compared to most other studies based on bycatch data (Rae 1973, Smith and Gaskin 1974, Recchia and Read 1989, Smith and Read 1992, Fontaine *et al.* 1994, Aarefjord *et al.* 1995). This might indicate that the porpoises were well fed at the time of sampling. Further analysis of body condition (blubber thickness, girths *etc*.) and seasonal variation in feeding rates is, however, needed to evaluate this further, since the energetic content of the different prey is an influential factor in addition to quantities ingested.

The present study agrees with most earlier studies that the harbour porpoise feeds predominantly on fish, although cephalopods, crustaceans and other invertebrates have also been identified, most often as minor components of the diet (Tomilin 1957, Rae 1973, Smith and Gaskin 1974, Recchia and Read 1989, Kinze MS 1989, Smith and Read 1992, Gonzaléz *et al.* 1994, Aarefjord *et al.* 1995, Santos *et al.* MS 1994, MS 1995, Martin MS 1995, Gannon *et al.* 1998).

Invertebrate prey and miscellaneous items

Small crustacea were found in only 27 of the non-empty stomachs (2.7%) and, although digested, appeared to be in small quantities. Cephalopods on the other hand occurred in 15% of the non-empty stomachs and sometimes in large numbers.

Because of their small size, cephalopods do not appear to contribute significantly by weight to the overall diet. The weight percentage of cephalopods is unlikely to be underestimated by the method used here, and may in fact be overestimated, as cephalopod beaks are believed to be retained in the stomach for a longer time than otoliths (Pierce and Boyle 1991). This underlines the small contribution by cephalopods and other invertebrates to the overall diet.

Some of the rarely occurring invertebrate prey such as bryozoans, sea urchins, barnacles, bivalves and gastropods may have ended up in the stomachs as artefacts, either as stomach contents of other prey species, or items taken unintentionally when foraging on other prey. These taxa were always found together with fish prey. The pieces of seaweed, occurring in 11 stomachs are also likely to fall into the last category. In fact, the occurrence of seaweed in the stomachs indicates that these porpoises may have been feeding on dead post-spawning capelin on the sea floor among the seaweed. All but 2 of these "vegetarian" porpoises had been feeding primarily on capelin in the main spawning area (SW-SE) during, or shortly after, the peak of the capelin spawning season. Harbour porpoises are also known from captive and field studies to forage at the bottom in a vertical position, in the so-called “bottom grubbing behaviour”, poking with the snout in the sand or among stones and seaweeds (Desportes *et al.* MS 2001, MS 2002). The occurrence of this foraging behaviour in Icelandic waters would explain the occurrence of non-food benthic items and is supported by the relative importance of benthic fish (see also under **Feeding behaviour**).

Fish prey

According to earlier studies the harbour porpoise feeds on wide variety of fish species in the North Atlantic including herring, capelin, hake (*Merluccius* sp.), sandeel, gobies and a large number of gadids (Rae 1965, Rae 1973, Recchia and Read 1989, Lick 1991, Smith and Read 1992, Santos *et al.* MS 1994, MS 1995, Aarefjord *et al.* 1995, Addink *et al.* MS 1995, Gannon *et al.* 1998).

Capelin has been identified as a major component of harbour porpoise diet off northern Norway (Aarefjord *et al.* 1995), Greenland (Kinze MS 1989) and Canada (Fontaine *et al.* 1994). In the overall Icelandic sample capelin is the overwhelmingly dominant prey species. However, the food composition of the pooled sample is almost certainly not a reflection of the diet on an annual basis. For example in the southeastern area, where the diet was completely dominated by capelin, samples were mostly confined to the period March-April, *i.e.* during the capelin spawning migration in this area. The geographical and seasonal variation in diet indicates that the prevalence of capelin is probably not as pronounced as indicated by the total pooled sample. Thus, sandeel appears to be the dominant prey species in the southwestern area during May-June and September-December (no samples in July-August), although sample sizes were small for most of these months. Sandeel were only a minor component of the diet in areas other than SW and W, which is in accordance with the distribution and abundance of the 3 species of sandeels around Iceland (Jónsson 1992). Sandeel are also important prey species of harbour porpoises off Britain (Santos *et al.* MS 1995, Martin MS 1995) and in the North Sea (Benke *et al.* 1998, Lockyer and Kinze 2003). For other prey species the geographical variation in diet is also in accordance with their distribution in Icelandic coastal waters. Redfish, cod and other gadids of the size range taken by harbour porpoises are most abundant in shallow waters off the northern part of Iceland. This area constitutes the main nursery grounds for these species and is the area where these fish species are the most prominent parts of the diet.

Herring has been identified as the most important prey species for harbour porpoises in studies on both sides of the North Atlantic (Smith and Gaskin 1974, Aarefjord *et al.* 1995, Recchia and Read 1989, Gannon *et al.* 1998), and Sæmundsson (1939) indicated that herring was an important prey species in Icelandic coastal waters during summer. In the present study herring was found in only 20 stomachs, 70 fish in total, and all during the period October-May. Because of the very low sample size during summer, it cannot be concluded from the present study whether Sæmundsson's (1939) statement holds true today. It seems clear, however, that herring is not among the most important components of the harbour porpoise diet in Icelandic coastal waters during October-May, and the species was not found among food remains in the few stomachs collected in June and September. From the present material, and the lack of earlier data supporting Sæmundsson's (1939) statement, it is not possible to evaluate whether a decreased availability of herring resulting from the collapse in the 1960's of the large Atlanto-Scandian stock of herring (Jakobsson and Østvedt 1999) has resulted in changes of diet composition of harbour porpoises in Icelandic waters. This herring stock spawns during spring in Norwegian waters and, prior to the collapse, migrated to the feeding grounds in north Icelandic waters. The proportion of herring in the present study seems, however, to be lower than might be expected from the size of the summer spawning stock of herring residing in Icelandic waters year round.

The following 7 fish species have to our knowledge not previously been identified as prey of harbour porpoises: snake blenny, spotted snake blenny, Vahl's eelpout (*Lycodes vahli*), Norwegian topknot (*Phrynorhombus norvegicus*), lemon dab (*Microstomus kitt*), Atlantic catfish (*Anarhichas lupus*) and silver rockling (*Onogadus argentatus*).

Feeding behaviour

Most (91%) of the identified fish prey species are benthic, at least partly (*i.e.* during juvenile stages or vertically migrating). The most commonly identified cephalopods in the stomach contents were benthic cuttlefish (*Rossia* sp.). The overall dominant prey species, capelin, is pelagic. However, this species was mostly eaten by porpoises during its spawning, which takes place at the sea bottom in shallow waters (Vilhjálmsson 1994), and even possibly after spawning (*i.e.*, postmortem). These indications of benthic feeding habits of harbour porpoises in Icelandic coastal waters may, however, be affected by the nature of the sampling (*i.e.* bottom set gill nets). Benthic feeding habits may, at the same time, be one of the main reasons for the relatively high bycatch rates in this type of fishing gear in Iceland as elsewhere, for example in the North Sea (Vinther 1999).

Geographical and seasonal variation in diet

The large number of prey taxa taken by harbour porpoises in Icelandic coastal waters is in accordance with numerous studies in other areas (Smith and Gaskin 1974, Kinze MS 1989, Recchia and Read 1989, Fontaine *et al.* 1994, Martin MS 1995, Aarefjord et al 1995, Gannon *et al.* 1998, Lockyer *et al.* 2003). Although more than 40 prey species were identified in this study the harbour porpoise appears to feed mostly on 1 or few prey species within any given area. Hence, 1-3 prey account for 90% or more of the diet in each of the subareas. Overwhelming predominance of 1-3 prey within small areas has also been demonstrated for harbour porpoises in other areas and seems to be particularly common where pelagic species such as capelin and herring are abundant. (Recchia and Read 1989, Fontaine *et al.* 1994, Aarefjord *et al.* 1995, Lockyer *et al.* 2003).

Prey diversity in the stomachs seems to be somewhat higher in the northern areas (NW and N-NE) than in the more southern areas (SE, SW and W) where capelin and sandeel dominated the diet to a greater extent. While harbour porpoises may exhibit some prey preferences, this pattern is consistent with the large biomass of capelin and sandeel in southern Icelandic waters during the time of sampling and could just as well be a reflection of prey availability.

The low diversity in stomach contents at any given time is well demonstrated in the SW area, the only area where sampling distribution allowed seasonal stratification of the data. The shift in diet from capelin to sandeel during spring was abrupt so that within any month a single prey species accounted for 3/4 or more of the diet. Santos *et al.* (MS 1995) found similar seasonal variation in diet of harbour porpoises off Scotland. In their study sandeel was the dominant prey species during summer while in winter the diet composition changed to gadids and herring. Seasonal changes in diet have also been found in other areas (Tomilin 1957, Recchia and Read 1989, Smith and Read 1992, Gannon *et al.* 1998).

Changes in diet according to age and reproductive status

Smith and Read (1992) found a pronounced difference in diet composition of harbour porpoise calves (<1 year old) and adults (>1 year old) in Canada, the former preying mostly on euphausiids while the diet of adults was mostly composed of clupeid and gadid fishes. Similar differences have been detected in German and Dutch waters where young (<120 cm) porpoises feed almost exclusively on gobies while older animals have a more diverse diet (Lick 1991, Addink *et al.* MS 1995). In the present study more than half of the porpoises feeding on euphausiids were less than 2 years of age. However, euphausiids were still only a minor part of the diet in these age classes, as in older porpoises, and fish species such as capelin and sandeel appear to be much more important. The sample sizes of small calves during the first 6-8 months after birth, which occurs in summer (Ólafsdóttir *et al.* 2003), is, however, small in the present study. The age and length composition of porpoises feeding on other crustaceans was not different from the rest of the sample. In the present study the overall diet composition of males (all classes) and subadult females was similar, while adult females differed considerably from these, having a much lower proportion of capelin, which was supplemented mostly by redfish and gadids. Mature females appear to have more diverse diet than males and subadult females, although this is obviously influenced by differences in geographical distribution of reproductive classes. Indications of difference in composition and/or diversity in diet among noncalf sex and maturity groups have been detected in some earlier studies (Smith and Gaskin 1983, Aarefjord *et al.* 1995, Gannon *et al.* 1998) while no such differences were detected in other studies (Smith and Gaskin 1974, Recchia and Read 1989, Martin MS 1995). Sample sizes were however too small for this to be conclusive in most of these studies.

Prey size

Prey size varied widely, from tiny crustaceans to a cod estimated to be 51 cm and 1,257 g taken by a large pregnant female. The 2 peaks in the length distribution of cod prey correspond to the length of age classes 1 and 2 during spring, the period of most intensive sampling (Jónsson 1992). Three-year old cod are around 50 cm long, or near the apparent prey size limit for harbour porpoises. Most of the capelin taken were between 12 and 17 cm in length although the range covered the total spectrum of capelin length distribution. In Icelandic waters most capelin spawn at ages 3 and 4, corresponding to lengths 14-17 cm, although a minor part of the capelin stock matures and spawns at age 2 (12-14 cm) or older than 4 years (Vilhjálmsson 1994). The calculated length distribution of capelin found in porpoise stomachs therefore appears to reflect broadly the composition of the spawning stock and there is no evidence of size selection in the data. Sandeel were on average considerably smaller than capelin although the total range was similar for the 2 species. Most of the sandeel were 7-10 cm long while there seemed to be another small peak at 12-14 cm length which may correspond to age classes 1 and 2 respectively (Jónsson 1992). The majority of redfish ranged 16-26 cm in length although the distribution was relatively even throughout the length range (5-37 cm). Although whiting and Norway pout, up to a length of 30 and 20 cm respectively, were taken by the porpoises, most of the otoliths found in the stomachs correspond to fish less than 6 cm long, which again corresponds to less than 1 year old fish (0 group) (Jónsson 1992, Pálsson 2001). Most of these 2-6 cm whiting and Norway pout were found in stomachs of porpoises caught during autumn, which is in agreement with the fact that these species spawn in late winter/early spring. Herring ranged from 8-28 cm in length corresponding to 1-3 years of age (Jónsson 1992). There was no clear peak in the length distribution of herring found in the stomachs.

The length distributions of fish prey is generally in agreement with earlier studies on prey size of harbour porpoises for those prey species where such data is available (Recchia and Read 1989, Fontaine *et al.* 1994, Aarefjord *et al.* 1995, Martin MS 1995, Benke *et al.* 1998, Gannon *et al.* 1998). The maximum prey size (51 cm cod) reported here is however slightly larger than those previously published for harbour porpoises which were a 48.5 cm cod (Aarefjord *et al.* 1995) and a 40 cm mackerel (Fontaine *et al.* 1994).

Although there was considerable variation in prey size found in individual porpoise stomachs there was a positive correlation between the length of porpoises and some of their prey species (cod, redfish and Norway pout). Santos *et al.* (MS 1994) found a significant relationship between porpoise length and the length of whiting as prey, but this was not evident in the present study.

CONCLUSIONS

The present study supports indications from other studies that the harbour porpoise, as a species, is flexible and opportunistic in its feeding habits. There appears to be considerable variation in diet according to location, season and possibly also sex and maturity. Heterogenous sampling and the apparent temporal and spatial segregation by sex and maturity preclude quantitative assessment of the importance of each of these parameters separately. The seasonal variation in the SW area is clearly associated with availability of prey, as capelin is very abundant when the large spawning schools enter the area in February/March, whereas the species is virtually nonexistent in the area during autumn. While a quantitative assessment of the importance of this seasonal feeding of spawning capelin for the annual energy budget of the porpoises is beyond the scope of the present paper, is seems clear that the species makes significant use of this food source during late winter. There are, however, indications that mature females do not utilize capelin to the same degree as other reproductive classes, at least not in relative terms. Ongoing studies on body condition and estimated feeding rates may help clarify such potential differences among reproductive classes in terms of annual feeding/energy budget.

Although the sample size in this study was large, the sample was highly non-random and significant gaps remain in our knowledge of the feeding ecology of harbour porpoises in Icelandic waters. In order to evaluate the relative importance of the different prey species on an annual basis, further sampling is required from areas and months where sample sizes are low or nonexistent. More information is also needed on the spatial and temporal variation in harbour porpoise distribution in Icelandic waters and on possible seasonal variation in feeding rates. Whether or not differential feeding preferences among sex and age classes are the driving force behind the apparent segregation indicated by the present study, a possible sample bias caused by such a segregation would have to be taken into consideration in any quantitative assessment of consumption by harbour porpoises on an annual basis.

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APPENDIX

Equations used to calculate fish size from otolith size, and size of cephalopods from beak size for harbour porpoises in Icelandic waters. L= total fish length (mm), O=otolith length (mm), W=prey weight (g), F=total fish length (cm), R=lower beak rostral length, H=hood length, "Applied to": The portion of the sample to which the equation was applied. For capelin weight was calculated from fish length as the average of the results for male and females. NA: data not available.

Species	Regression		Applied to	Source
	Equation	Statistics (R^2; otolith size range)		
Fish				
Herring	$L = 106.63 * O^{0.701}$	$R^2 = 0.859$; 2-5mm	All	Erlingur Hauksson and Valur Bogason unpubl.
Herring	$W = 8.871 * O^{2.217}$	$R^2 = 0.856$; 2-5mm	All	Erlingur Hauksson and Valur Bogason unpubl.
Atlantic argentine	$L = 10.466 + 40.03 * O$	$R^2 = 0.993$; 2-11mm	All	Härkönen 1986
Atlantic argentine	$W = 0.559 * O^{3.173}$	$R^2 = 0.986$; 2-11mm	All	Härkönen 1986
Capelin	$L = 17.19 + 55.579 * O$	$R^2 = 0.859$; 1-3mm	All	Present study
Capelin	$W = 0.0009 * F^{3.632}$	NA	December-February females	Vilhjálmsson 1994
Capelin	$W = 0.0007 * F^{3.7}$	NA	December-February males	Vilhjálmsson 1994
Capelin	$W = 0.0026 * F^{3.103}$	NA	March-May females	Vilhjálmsson 1994
Capelin	$W = 0.0018 * F^{3.382}$	NA	March-May males	Vilhjálmsson 1994
Capelin	$W = 0.0017 * F^{3.380}$	NA	June-August females	Vilhjálmsson 1994
Capelin	$W = 0.0007 * F^{3.742}$	NA	June-August males	Vilhjálmsson 1994

Capelin	$W = 0.0007 * F^{3.698}$	NA	September-November females	Vilhjálmsson 1994
Capelin	$W = 0.0004 * F^{3.913}$	NA	September-November females	Vilhjálmsson 1994
Cod	$L = 1.800 * O^{1,247}$	$R^2 = 0.95$; 1-23mm	Otolith length <15mm	Erlingur Hauksson and Valur Bogason unpubl.
Cod	$W = 0.049 * O^{3.780}$	$R^2 = 0.943$; 1-23mm	Otolith length <15 mm	Erlingur Hauksson and Valur Bogason unpubl.
Cod	$L = 0.585 * O^{1.658}$	$R^2 = 0.93$; 5-23mm	Otolith length >15 mm	Erlingur Hauksson and Valur Bogason unpubl.
Cod	$W = 0.001 * O^{5.182}$	$R^2 = 0.93$; 5-23mm	Otolith length >15 mm	Erlingur Hauksson and Valur Bogason unpubl.
Arctic cod	$L = 25.457 * O^{0.9816}$	$R^2 = 0.921$; 5-11mm	All	Erlingur Hauksson and Valur Bogason unpubl
Arctic cod	$W = 0.1486 * O^{2.822}$	$R^2 = 0.909$; 5-11mm	All	Erlingur Hauksson and Valur Bogason unpubl
Haddock	$L = 10.265 * O^{1.341}$	$R^2 = 0.92$; 7-23mm	All	Erlingur Hauksson and Valur Bogason unpubl
Haddock	$W = 0.0042 * O^{4.321}$	$R^2 = 0.928$; 7-23mm	All	Erlingur Hauksson and Valur Bogason unpubl
Whiting	$L = -11.936 + 19.7 * O$	$R^2 = 0.981$; 4-24mm	All	Härkönen 1986
Whiting	$W = 0.0127 * O^{3.535}$	$R^2 = 0.976$; 4-24mm	All	Härkönen 1986
Blue whiting	$L = -40.94 + 25.39 * O$	$R^2 = 0.981$; 8-18mm	All	Härkönen 1986
Blue whiting	$W = 0.0067 * O^{3.892}$	$R^2 = 0.975$; 8-18mm	All	Härkönen 1986
Saithe	$L = 8.097 * O^{1.57}$	$R^2 = 0.925$; 5-21 mm	All	Erlingur Hauksson and Valur Bogason unpubl
Saithe	$W = 0.0077 * O^{4.530}$	$R^2 = 0.913$; 5-21 mm	All	Erlingur Hauksson and Valur Bogason unpubl
Norway pout	$L = -42.6 + 29.52 * O$	$R^2 = 0.904$; 5-8.5 mm	All	Härkönen 1986
Norway pout	$W = 0.0028 * O^{4.729}$	$R^2 = 0.920$; 5-8.5 mm	All	Härkönen 1986
Fourbeard rockling	$L = -28.8 + 70.344 * O$	$R^2 = 0.762$; 3-5 mm	All	Härkönen 1986
Fourbeard rockling	$W = 0.1752 * O^{3.482}$	$R^2 = 0.724$; 3-5 mm	All	Härkönen 1986
European ling	$L = -406 + 95.73 * O$	$R^2 = 0.784$; 9-13 mm	All	Härkönen 1986
European ling	$W = 0.0077 * O^{4.996}$	$R^2 = 0.709$; 9-13 mm	All	Härkönen 1986

Sandeel	$L = 5.131 * O^{1.134}$	$R^2 = 0.931$; 0.9-3.8 mm	June-December	Erlingur Hauksson and Valur Bogason unpubl.
Sandeel	$W = 0.275 * O^{3.944}$	$R^2 = 0.920$; 0.9-3.8 mm	June-December	Erlingur Hauksson and Valur Bogason unpubl.
Sandeel	$L = 4.394 * O^{1.236}$	$R^2 = 0.919$; 1.4-3.5 mm	January-May	Erlingur Hauksson and Valur Bogason unpubl.
Sandeel	$W = 0.171 * O^{3.916}$	$R^2 = 0.885$; 1.4-3.5 mm	January-May	Erlingur Hauksson and Valur Bogason unpubl.
Atlantic catfish	$L = 6.414 * O^{1.625}$	$R^2 = 0.946$; 1-5.5 mm	All	Erlingur Hauksson and Valur Bogason unpubl
Atlantic catfish	$W = 0.653 * O^{5.07}$	$R^2 = 0.944$; 1-5.5 mm	All	Erlingur Hauksson and Valur Bogason unpubl
Vahl's eelpout	$L = 21.19 + 37.74 * O$	$R^2 = 0.612$; 3-4.6 mm	All	Härkönen 1986
Vahl's eelpout	$W = 1.002 * O^{1.993}$	$R^2 = 0.408$; 3-4.6 mm	All	Härkönen 1986
Redfish	$L = 2.6357 * O^{1.022}$	$R^2 = 0.713$	All	Erlingur Hauksson and Valur Bogason unpubl
Redfish	$W = 0.373 * O^{2.887}$	$R^2 = 0.723$	All	Erlingur Hauksson and Valur Bogason unpubl
European plaice	$L = 4.110 * O^{1.099}$	$R^2 = 0.849$; 3-9 mm	All	Erlingur Hauksson and Valur Bogason unpubl
European plaice	$W = 1.2193 * O^{3.036}$	$R^2 = 0.828$; 3-9 mm	All	Erlingur Hauksson and Valur Bogason unpubl
American plaice	$L = 4.255 * O^{1.045}$	$R^2 = 0.915$; 2-9 mm	All	Erlingur Hauksson and Valur Bogason unpubl
American plaice	$W = 0.2994 * O^{3.560}$	$R^2 = 0.905$; 2-9 mm	All	Erlingur Hauksson and Valur Bogason unpubl
Lemon dab	$L = 10.93 + 88.46 * O$	$R^2 = 0.727$; 1.5-4 mm	All	Härkönen 1986
Lemon dab	$W = 0.489 * O^{3.45}$	$R^2 = 0.697$; 1.6-4.2 mm	All	Härkönen 1986
Cephalopods				
Gonatus spp.	$\ln(W) = -0.655 + 3.33 * \ln(R)$	NA	All	Clarke 1986
Rossia macrosoma	$\ln(W) = 2.18 + 1.65 * \ln(H)$	NA	All	Clarke 1986
Sepiola spp.	$\ln(W) = 0.4 + 0.35 * \ln(H)$	NA	All	Clarke 1986