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VARIABILITY IN THE DIET OF HARBOR PORPOISES (*PHOCOENA PHOCOENA*) IN SCOTTISH WATERS 1992–2003

M. B. Santos
G. J. Pierce
J. A. Learmonth
Department of Zoology,
University of Aberdeen, Tillydrone Avenue,
Aberdeen, AB24 2TZ, United Kingdom
E-mail: m.b.santos@abdn.ac.uk

R. J. Reid
H. M. Ross
I. A. P. Patterson
SAC Veterinary Science Division,
Drummondhill,
Stratherrick Road,
Inverness, IV24JZ, United Kingdom

D. G. Reid
D. Beare
Fisheries Research Services Marine Laboratory, Aberdeen,
P. O. Box 101,
Victoria Road,
Aberdeen, AB11 9DB, United Kingdom

Abstract

Interannual, seasonal, and regional variation in the diet of porpoises, *Phocoena phocoena*, in Scottish (UK) waters was studied using stomach contents of animals stranded between 1992 and 2003. Most samples came from the east coast (including many porpoises killed by bottlenose dolphins), with smaller numbers from the west coast and from Shetland. The most important prey types, in terms of contribution by number and mass, were whiting (*Merlangius merlangus*) and sand eels (Ammodytidae). Multivariate analysis confirmed the existence of regional, seasonal, and interannual variation in diet, as well as differences (*i.e.*, biases) related to cause of death. These differences were further explored using univariate analyses. Sand eels were more important in the summer months (quarters 2 and 3) and on the east coast, whereas gadids were more important in winter and in the Shetland area. Some, but not all, observed trends in the numerical importance and size of prey taken were consistent with trends in abundance and size of fish taken during research trawl surveys. There was some evidence that porpoises <1 yr old took more gobies (Gobiidae) and shrimps than did older porpoises. Clupeids (herring *Clupea harengus* and sprat *Sprattus sprattus*) formed a relatively small proportion of the diet, but their importance varied from year to year. Although possible methodological biases prevent firm conclusions, it appears that the importance of clupeids in porpoise diet may have decreased since the 1960s, mirroring the decline in North Sea herring abundance. The recovery of the North Sea herring stock in recent years is not as yet reflected in porpoise diet.

Key words: harbor porpoise, *Phocoena phocoena*, cetaceans, dietary variability, northeast Atlantic.

The harbor porpoise (*Phocoena phocoena*) is the most frequently sighted and stranded cetacean in British waters (Evans 1980). In July 1994, numbers of harbor porpoises and other small cetaceans in the North Sea and adjacent waters were estimated during the SCANS (Small Cetacean Abundance in the North Sea) survey, the estimated total porpoise numbers being around 340,000 (Hammond *et al.* 2002). The first detailed studies on harbor porpoise diet in the eastern North Atlantic were carried out by Rae (1965, 1973*a*), who found herring (*Clupea harengus*), sprat (*Sprattus sprattus*), and whiting (*Merlangius merlangus*) to be the main prey in Scotland during 1959–1971. Martin (1996) found that gadids (Gadidae), sand eels (Ammodytidae), and gobies (Gobiidae) were the most important prey in porpoises in UK waters.[1] These published data suggest that porpoise diets have changed over the last four decades. There has been speculation about the likelihood and consequences of porpoises switching to other prey species if their main prey were depleted by overfishing (IWC 1996). Indeed, Smeenk (1987) suggested that the decline in herring stocks might have caused the (apparent) decline of harbor porpoises in most European waters. However, to date there has been no detailed analysis of patterns of variation in porpoise diet. Such an analysis should help to indicate whether porpoises are specialist or generalist predators. Of course, it is difficult to interpret observed variation in diet without information on prey availability. Fishery data can provide an indication of broad trends in abundance, but not necessarily at an appropriate spatial and temporal scale. In the North Sea regular research trawl surveys provide an alternative source of data on fish abundance.

Currently, dead porpoises found stranded provide the main source of information on diet. Records of stranded harbor porpoises in the UK go back to 1913 (Harmer 1914). Stranded animals may have died due to various causes. In northern Europe the porpoise is the most frequently caught cetacean species in fishing nets (IWC 1996). On the east coast of Scotland, particularly in the Moray Firth (UK) (Fig. 1), many porpoise deaths are due to violent interaction with bottlenose dolphins (*Tursiops truncatus*). The reasons for these interactions are unknown, but could include competition for food and/or space (Ross and Wilson 1996).

Use of stranded animals for dietary analysis has evident drawbacks, *e.g.*, concerning the representativeness of the sample. Sample size is also necessarily limited and a "balanced" experimental design difficult to achieve. Thus some caution is needed in interpreting the results. In the present study, we describe the diets of stranded and by-caught harbor porpoises from Scotland during 1992–2003, analyze

[1] Martin, A. R. 1996. The diet of harbour porpoises (*Phocoena phocoena*) in British waters. International Whaling Commission Working Paper SC/47/SM48, 6 pp.

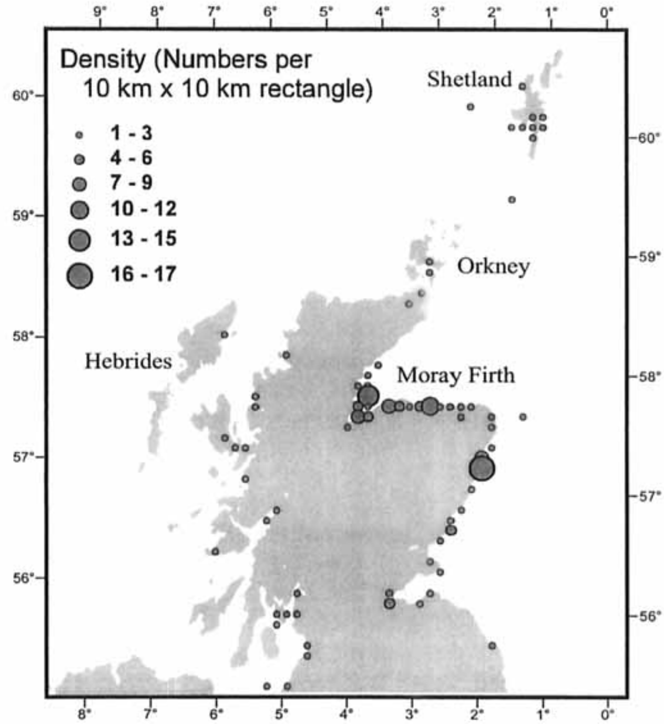

Figure 1. Map of the study area, showing locations of strandings (and bycatches) of porpoises from which stomach contents were obtained. The main island groups (Hebrides, Orkney, and Shetland) are shown and the location of the Moray Firth is indicated. Data are displayed as densities on a 10 × 10 km grid. Not all bycatch locations are shown (for some only the landing port is known and for others the location data were too imprecise).

variation in diet in relation to area, season, cause of death, size, sex, and year, and ask whether dietary variation can be related to prey abundance.

Methods

Sample Collection

Non-empty stomachs were recovered from 188 stranded porpoises collected between 1992 and 2003. When the condition of the animal permitted, full post-mortem examinations were carried out to try to establish the cause of death. In the early days of the recording program, post-mortem reports did not always indicate whether milk was present in the stomach of young animals. Review of post-mortem reports for 2000–2003 indicated that only three animals had milk in their stomach, none of which had any other food remains present. Unless an animal dies within around 2 h of suckling, it is unlikely that there will be milk present in the stomach (RJR, personal observation). Therefore, the present analysis is restricted to those animals with remains of solid food in the stomach.

Standard measurements, including body length, were taken. Since data on age and reproductive status are not available for all the animals studied, we use body length as a proxy for age and maturity. We include a brief analysis of mortality patterns in relation to area, season, year, sex and size, based on chi-squared tests.

Prey Identification and Estimation of Prey Size

Hard remains of fish and cephalopods were identified using reference material and published guides (Clarke 1986, Härkönen 1986, Watt *et al.* 1997). The minimum number of fish and cephalopods in each stomach was estimated from hard remains. The majority of identifications for fish were based on otoliths, but vertebrae and jawbones were also routinely used. Not all prey could be identified to species, and some composite categories were therefore used. Thus, for statistical analysis of numerical importance, herring and sprat were grouped as Clupeidae since they could not always be distinguished from each other (*e.g.*, when identified from vertebrae). Similarly, haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), and pollack (*P. pollachius*) have very similar otoliths and were therefore grouped for statistical analysis, although some haddock were identifiable either from otoliths or bones (*e.g.*, the post-temporal of haddock is quite distinctive).

Sizes of prey were estimated from standard regressions relating prey body length and weight to otolith and beak dimensions (Bedford *et al.* 1986, Clarke 1986, Härkönen 1986, Coull *et al.* 1989, Brown and Pierce 1998). Fish size estimates were generally based on otolith length, but width was used for otoliths with broken tips and for all otoliths of clupeids and gobies (Härkönen 1986). For cephalopods, measurements were normally made on the lower beak: rostral length for squid and hood length for octopus and sepiolids (Clarke 1986). For stomachs in which one category of fish or cephalopod was represented by >30 otoliths (or beaks), a random sample of 30–60 (from that category) was measured. For otoliths identifiable to one of a group of species, regressions based on combined data from all the species in the group were used. Each otolith was assumed to represent 0.5 fishes. Complete pairs of cephalopod beaks were rarely present and in all cases size was estimated from either the upper or the lower beak. Few crustacean remains were present in the samples but these were identified to species when possible. Their small size was such that their contribution to total prey weight was negligible. The presence of other animal material (*e.g.*, polychaete jaws) was also recorded.

Note that no corrections were made for loss or reduction of size of prey remains due to digestion. Cephalopod beaks are relatively robust to mammalian digestive processes (Tollit *et al.*, 1997), but otoliths are subject to digestive erosion. Although it is theoretically possible to apply correction factors to take account of size reduction (see Wijnsma *et al.*, 1999), it is not straightforward to determine what degree of correction is appropriate. Some authors recommend quantification only of freshly ingested prey remains in marine mammal stomachs. This is not really an option when the sample consists mainly of stranded animals. In any case, the majority of the statistical analysis concerns variation in numbers of prey (rather than estimated size) and focuses on variation *within* prey species rather than across prey species. Thus, although we recognize that there are errors and biases associated with estimating the size of ingested fish, much of the analysis is robust to such problems.

Assessment of the Importance of Individual Prey Categories

Overall importance of each prey type in the diet of porpoises was assessed using (1) frequency of occurrence, (2) proportion of the total number of prey, and (3) proportion of total prey wet mass. Although prey mass provides the best proxy for the energetic importance of each prey type to porpoises, not all prey remains could be used to estimate prey size and the mass data are thus slightly less complete than data on prey numbers or presence (see results). To evaluate the effect of this on estimated overall diet composition, corrections were made for prey that could be identified (*e.g.*, from bone fragments), but for which size could not be estimated, it is assumed that they had the same size distribution as the prey measured. In several cases bones could be identified to family level but not species. In these cases they were assigned *pro rata* to the species (from that family) already identified. This adjustment was not possible at the individual (porpoise) level. No explicit "weighting" was applied to individual stomach samples. Thus, when calculating the overall diet, the contribution of each stomach is proportional to the total estimated reconstructed mass of the prey contained therein.

We analyzed dietary variation related to area, season (quarter), cause of death, porpoise size, sex, and year. Three porpoise length classes were defined: $\leq$118 cm, 119–140 cm, >140 cm. This division serves to separate first year animals ($\leq$118 cm, Lockyer 1995) from yearlings and older animals, as well as giving a reasonably even division of the data. Three geographical areas were defined, east coast (mainland, east of 4°W, and the Orkney Islands), Shetland, and west coast (mainland, west of 4°W, and the Hebridean islands). There were three main cause-of-death categories: *Tursiops* attack, fishery bycatch, and infection/parasitism, and analysis focused on these. The homogeneity of sample composition in relation the various factors (area, season, *etc.*) was analyzed using chi-squared tests and logistic regression.

Multivariate Analysis

To examine multivariate patterns in diet and to identify which "environmental" factors (in this case season, sex, and body size) best explained these patterns we used PRIMER 5 software (Primer-E Ltd). PRIMER routines were used as follows:

"MDS" (multidimensional scaling) was used to visualize patterns in the dietary data. For this analysis, the complete set of dietary data could be used. All prey categories except "unidentified" were included in this analysis, although haddock was merged with "haddock/saithe/pollack." Dietary data were fourth root transformed prior to calculating similarity matrices based on Euclidean distance.

The "RELATE" routine was used to test the null hypothesis that there was no multivariate relationship between dietary and environmental data. The categorical and ordinal "environmental" variables area, quarter, year, sex, length class, and cause of death were recoded into dummy variables, each of which took a value of 0 or 1. For example, area was re-coded into two dummy variables, "east coast" (0 or 1) and "west coast" (0 or 1), such that east coast samples scored [1,0], west coast samples scored [0,1], and Shetland samples scored [0,0]. Similarity matrices were based on Euclidean distance. RELATE was used for three subsets of "environmental" variables:

(1) Area, quarter, year, sex, length class. Animals with missing data for length or sex were excluded. "Cause of death" was excluded due to the many missing values.
(2) Area, quarter, year, sex, length class, cause of death. The analysis was based on the subset of animals for which cause of death was one of the three main categories. Cause of death was then coded into two dummy variables, "*Tursiops*" and "bycatch."
(3) Latitude, longitude, and body length. These three interval variables were treated separately.

The "BIOENV" and "BVSTEP" routines were used to select the set of environmental variables best explaining patterns in the dietary data. Both compute rank correlations between dietary and environmental similarity matrices using different permutations of the environmental variables. The former compares different combinations of a specified number of environmental variables; the latter uses a stepwise procedure to identify the best subset of variables. Note that the set of environmental variables selected is not necessarily the set of variables that, individually, correlate most highly with dietary variation. If two environmental variables are strongly correlated with each other, once the first has been selected as a predictor the second will add little to predictive power and is unlikely to be selected.

Univariate Analyses

To examine the effects on diet of each factor in more detail, univariate analyses were used. Diets of different groups of porpoises were compared in terms of numbers and average (median) size for each prey type in individual porpoise stomachs. For illustration of prey size spectra we reconstructed the overall size distributions, for each prey category, for each group of porpoises. However, since different individual fish of the same species from a single stomach are not independent samples, for statistical comparisons we used median prey lengths for each prey category for each porpoise. This avoids the problem of pseudoreplication.

Because the statistical distributions of dietary parameters were generally non-normal, we relied primarily on non-parametric tests, particularly the Kruskal-Wallis test. Where significant variation was detected using Kruskal-Wallis tests, each pair of samples was compared using Mann-Whitney tests to identify which groups differed significantly from others. We also used correlation analysis to quantify the relationship between body size and porpoise diet.

Power Analysis

To investigate the sample size necessary to detect statistically significant differences during univariate analyses, we ran some simple simulations. It is assumed that a prey type is present in the diet of all porpoise groups, but may differ between groups both in frequency of occurrence and numerical abundance.

We first investigated the extreme case in which a prey type is important in only one group of porpoises and the 188 porpoises are divided into 2, 3, 4, or 12 equally sized groups (mimicking comparisons of sexes, areas, quarters, and years, respectively). The frequency of occurrence of the prey type is set to 1 (*i.e.*, presence in one stomach), and its numerical importance is set to 1.0 in all but one group. In the last group its frequency varies from 1 up to the number of porpoises in the group and its numerical importance when present is always 2.0.

Obviously the less clear-cut the difference, the smaller the chance that the difference will be detected. A slightly more conservative scenario assumes equal frequency of occurrence in all porpoise groups but a consistent numerical difference between one group and all the rest. Equivalent simulations were run using this scenario.

Comparisons with Fish Abundance

We used trawl survey catch rates (number of fish caught per hour) in northern UK waters, 1992–2003. This was compiled from surveys by FRS Marine

Laboratory's research vessel *Scotia*. The unit of data is the survey trawl haul, typically based on a tow of 0.5 or 1 h. The surveys provide data on abundance of a range of fish species. Sand eels were generally poorly represented in trawl catches. They may not be caught due to being buried in the seabed substrate and, if caught, due to their small size and elongated body form, they can readily pass through the mesh. Lesser sand eel (*Ammodytes tobianus*) was recorded in only one out of 2,923 hauls. However, Raitt's sand eel (*A. marinus*) was caught with sufficient regularity to be included in the analysis.

Analysis was restricted to an area bounded by 54.5°N, 10°W, and 5°E. The most northerly data points were at 62°N. The boundaries serve to exclude (1) trawling south of the Scottish border, (2) trawling in the eastern North Sea, closer to the coast of the Netherlands and Denmark than the UK, and (3) trawling at Rockall Bank. On the west coast of Scotland, almost all trawls fall within the 200-m isobath. Porpoises are known to occur throughout the selected survey area, although sightings between the Outer Hebridean islands and the shelf edge are very sparse (see Evans and Wang 2002). The selected data set comprises catch data from between 212 and 284 hauls annually. Frequency distributions of catch rates are invariably skewed, with modes at or near zero.

Within the selected survey area, hauls taken west of 4°W are defined as "west coast." Within the remaining data set, hauls north of 59.5°N were designated as "Shetland" and hauls south of this line as "east coast." This matches the division of strandings as closely as possible.

We treated survey trawl catch rates from each haul as independent observations. Since we cannot say with any certainty where individual animals had been feeding, analysis was confined to checking whether observed seasonal, interannual, and area differences in diet corresponded to differences in average catch rates and fish sizes in survey hauls. Since the data were clearly non-normal, and mean catch rates were strongly influenced by extreme high values, we used median values in analysis.

For any of the main prey species that showed significant interannual variation in importance in porpoise diet, the correlation between dietary importance and estimated stock abundance (spawning stock size, SSB) (Anonymous 2002) was examined.

Results

Composition of the Sample of Porpoises

Numbers of stomachs examined each year, tabulated by area, season, sex, size and cause of death, are summarized in Table 1. The majority of samples were from the east coast (n = 138), particularly the Moray Firth. Thirty-four stomach samples were from the west coast and 16 from Shetland. Almost half of the animals sampled were mortalities due to interactions with bottlenose dolphins (Table 2). The other main causes of death were infection/parasitism and fishery bycatch. For 11 animals, other causes were recorded, including six cases of starvation and three of trauma. Cause of death could not be diagnosed in 34 animals.

Chi-squared tests indicate that the distribution of samples by area, quarter, size class, and cause of death varied between years, although there was no significant interannual variation in sex ratio. The geographical distribution of causes of death in the studied sample was significantly non-random ($\chi^2 = 75.2$, df = 4, $P < 0.001$), with all mortalities due to interaction with *Tursiops* being found on the east coast. Correspondingly, the size distribution varied between areas ($\chi^2 = 22.6$, df = 4,

Table 1. Summary of sampled porpoises in each year, by (1) area, (2) season (quarter), (3) sex, (4) size class, (5) cause of death. Areas are (W) west coast, (Sh) Shetland, and (E) east coast. Size classes are (S) ≤118 cm, (M) 119–140 cm, (L) >140 cm. Causes of death are (T) killed by *Tursiops*, (B) fishery bycatch, (I) infection or parasitism, (O) other or undiagnosed. (Note: four animals had no length measurements, sex was not determined in one case.)

		By area			By quarter				By sex		By size			By cause of death			
Year	*n*	E	Sh	W	Q1	Q2	Q3	Q4	F	M	S	M	L	T	B	I	O
1992	16	13	2	1	0	5	6	5	10	6	2	9	5	8	3	0	5
1993	18	13	2	3	1	13	2	2	10	8	2	7	8	12	0	0	6
1994	18	18	0	0	8	2	4	4	9	9	6	9	3	11	0	0	7
1995	10	9	1	0	1	2	2	5	5	5	2	6	2	6	0	2	2
1996	21	18	1	2	7	9	2	3	6	15	11	5	4	14	1	1	5
1997	13	9	1	3	3	6	2	2	4	8	5	3	4	6	5	0	2
1998	10	7	1	2	7	2	1	0	5	5	2	3	5	3	2	4	1
1999	17	6	2	9	7	5	3	2	6	11	1	6	10	2	6	5	4
2000	14	12	1	1	2	7	4	1	5	9	7	3	4	7	1	4	2
2001	24	17	1	6	7	10	6	1	12	12	11	9	3	13	1	6	4
2002	17	9	4	4	2	9	3	3	8	9	6	2	9	6	3	5	3
2003[a]	10	7	0	3	9	1	0	0	4	6	6	2	2	2	0	4	4
Total	188	138	16	34	54	71	35	28	84	103	61	64	59	90	22	31	45

[a] Data collection terminated on 3 April 2003.

$P < 0.001$), with the highest proportion of small animals in the east coast sample. There was no significant difference in the seasonal patterns of strandings or sex ratios between the three areas. There was no significant seasonal variation in sex ratio, size distribution, or cause of death. The size distribution was similar in males and females, but the relative frequency of different causes of death differed significantly between sexes, with a bias towards males in the fishery bycatches ($\chi^2 = 8.1$, df = 2, $P = 0.015$). There was a highly significant interaction between size class and cause of death ($\chi^2 = 30.0$, df = 4, $P < 0.001$), with *Tursiops* kills being recorded mainly among the smaller porpoises, and mortality due to infection/parasitism and bycatch being seen more often among the largest porpoises. The size-area, size-cause of death, and area-cause of death relationships are clearly all related. Using ordinal logistic regression, with size class as the dependent variable and all other factors as independent variables, only cause of death is a significant predictor of size class ($Z = -3.68$, $P < 0.001$).

Overall Diet Composition

Remains of at least 15,499 fish from 15 taxa, 1,443 cephalopods from five taxa and 129 crustaceans from four taxa were recovered from the stomachs. Of these prey, size could be estimated for 15,252 fish (representing an estimated total weight of 103.2 kg) and 1,423 cephalopods (totalling 3.8 kg). Polychaete and non-cephalopod mollusc remains were also found in 17 and one stomach, respectively. One animal had only unidentified (digested food) material in the stomach and was not used in subsequent analyses.

Whiting and sand eels were the most important prey categories both numerically and by wet mass, together comprising around 80% of the diet (Table 3). The sand eels included a small proportion of greater sand eels (*Hyperoplus* spp.), but otherwise

Table 2. Cross-tabulations of sampled animals in relation to cause of death, area, size class, season, and sex.

		By area			Size class			Quarter				Sex	
Cause of death	*n*	E	Sh	W	S	M	L	Q1	Q2	Q3	Q4	F	M
T	90	90	0	0	42	32	15	18	42	18	12	39	51
B	22	6	5	11	4	7	11	7	6	6	3	4	18
I	31	14	5	12	6	4	21	13	8	6	4	18	13
O	45	28	6	11	18	7	17	16	15	5	9	23	21
Total	188	138	16	34	70	50	64	54	71	35	28	84	103

		Size class			Quarter				Sex	
Area	*n*	S	M	L	Q1	Q2	Q3	Q4	F	M
E	138	49	53	32	33	56	27	22	62	75
Sh	16	1	2	13	7	5	2	2	9	7
W	34	11	9	13	14	10	6	4	13	21
Total	188	61	64	58	54	71	35	28	84	103

		Quarter				Sex	
Size class	*n*	Q1	Q2	Q3	Q4	F	M
S	70	23	30	10	7	24	37
M	50	12	17	10	11	32	32
L	64	18	21	15	10	25	34
Total	184	53	68	35	28	81	103

		Sex	
Quarter	*n*	F	M
Q1	54	25	29
Q2	71	34	36
Q3	35	18	17
Q4	28	7	21
Total	188	84	103

could not be identified to genus or species. The next most important prey categories were the gadid groups haddock/saithe/pollack and *Trisopterus* spp. (Norway pout *T. esmarkii* and poor-cod *T. minutus*). Other gadids present in smaller numbers included cod (*Gadus morhua*), ling (*Molva molva*), blue whiting (*Micromesistius poutassou*), and four-bearded rockling (*Rhinonemus cimbrius*). Unidentified Gadidae was the fifth most important prey category, comprising fish identified to family level primarily from small or eroded otoliths and vertebrae: it is likely that they consisted mostly of the species previously mentioned. Other fish identified included herring and sprat (Clupeidae), gobies (Gobiidae), mackerel (*Scomber scombrus*), and

Table 3. Overall diet composition. Importance of the main fish and cephalopod prey categories identified in the 188 harbour porpoise stomachs. The first estimate (%F) indicates the percentage of stomachs containing each prey category. The estimates for total number of individuals are based on (N_1) otoliths and beaks only and (N_2) all prey remains. Measurements on otoliths and beaks were used to derive the first estimate of total prey weight (W_1, g), while the second estimate (W_2, g) is adjusted to take account of fish and cephalopods identified from other remains. All four latter estimates are also expressed as percentages. All prey categories used here are mutually exclusive, although some were grouped for further analysis.

Prey type	%F	N_1	N_2	W_1	W_2	$\%N_1$	$\%N_2$	$\%W_1$	$\%W_2$
Sand eels	48.9	11,469	11,555	27,399	27,604	68.72	67.61	25.60	24.79
Whiting	51.1	2,259	2,294	56,719	57,598	13.54	13.42	53.00	51.73
Trisopterus spp.	13.3	751	755	4,085	4,107	4.50	4.42	3.82	3.69
Blue whiting	1.6	19	20	229	241	0.11	0.12	0.21	0.22
Cod	2.7	31	34	603	661	0.19	0.20	0.56	0.59
Haddock	4.8	34	36	1,428	1,512	0.20	0.21	1.33	1.36
Haddock/saithe/ pollack	6.4	27	31	5,947	6,828	0.16	0.18	5.56	6.13
Rocklings	1.6	3	3	23	23	0.02	0.02	0.02	0.02
Other Gadidae	0.5	1	7	143	1,001	0.01	0.04	0.13	0.90
Unid. Gadidae	21.3	336	350	3,598	3,748	2.01	2.05	3.36	3.37
Herring	9.0	64	74	1,370	1,584	0.38	0.43	1.28	1.42
Sprat	1.8	114	124	363	395	0.68	0.73	0.34	0.35
Unid. Clupeidae	5.3	1	40	12	480	0.01	0.23	0.01	0.43
Gobiidae	9.0	136	140	36	37	0.81	0.82	0.03	0.03
Mackerel	2.1	6	8	1,251	1,668	0.04	0.05	1.17	1.50
Scad	1.1	1	2	8	16	0.01	0.01	0.01	0.01
Unid. fish	12.2	12	26	–	0	0.07	0.15	–	–
Sepiolidae	33.5	1,378	1,390	3,623	3,655	8.26	8.13	3.39	3.28
Alloteuthis spp.	4.3	44	44	173	173	0.26	0.26	0.16	0.16
Other cephalopods	4.8	1	2	4	8	0.01	0.01	0	0.01
Unid. cephalopods	3.7	1	7	–	–	0.01	0.04	–	–
Other molluscs	0.5	–	1	–	–	–	0.01	–	–
Brown shrimp	3.7	–	24	–	–	–	0.14	–	–
Crabs	0.5	–	85	–	–	–	0.50	–	–
Isopods	1.1	–	4	–	–	–	0.02	–	–
Amphipods	0.5	–	1	–	–	–	0.01	–	–
Unid. crustaceans	4.3	–	15	–	–	–	0.90	–	–
Polychaetes	9.0	–	18	–	–	–	0.11	–	–
Total		16,688	17,090	107,014	111,339	100	100	100	100

scad (*Trachurus trachurus*) (Table 3). In 5% of stomachs, fish remains consisted only of unidentifiable bone fragments and/or eye lenses.

The main consequence of correcting diet composition estimates, to take account of fish identified from hard parts other than otoliths, is the increased importance of clupeid and gadid fish not identifiable to species. Despite this, the general picture of diet composition changes very little (Table 3): the importance (by mass) of the Clupeidae rose from 1.6% to 2.2% when correcting for individuals identified only from bones.

Most of the cephalopods eaten were bobtail squids (Sepiolidae), including *Sepiola* spp., *Sepietta* spp. and *Rossia* spp. All are small-bodied, and they contributed little to total prey mass. The only other cephalopods identified were the small loliginid squid *Alloteuthis* spp., the octopus *Eledone cirrhosa*, and a squid of the Ommastrephidae family (Table 3).

The brown shrimp (*Crangon crangon*) was the most frequently occurring crustacean prey, being found in seven porpoise stomachs. Individual shrimps were around 35 mm or less in body length. Other crustaceans were not identified to species but included small crabs, isopods, and amphipods. All 85 crabs were found in a single stomach, the largest having a carapace width of 9 mm although the majority were 2–3 mm wide (Table 3).

Whiting eaten by porpoises ranged up to 35.5 cm with a mode at 12–13 cm (Fig. 2). The shape of the histogram suggests that several age classes are present in the diet. The estimated lengths of sand eels eaten ranged up to 23 cm, with a modal size of 7 cm (Fig. 3). *Trisopterus* eaten ranged up to 18 cm in length, with a modal size of 7 cm and, again, it is probable that several age classes are present. The estimated size of herring eaten ranged up to 29 cm, with a modal size of 11 cm. The estimated mantle lengths of sepiolids eaten ranged from 1.5 to 4.1 cm, individuals identified as *Sepiola atlantica* being uniformly 1.5–1.6 cm in length.

Fish Abundance

The most numerically abundant species in trawl survey catches were haddock (median catch 542 fish per hour), whiting (352), Norway pout (291), and herring (59). Of other species that were eaten by porpoises, the median catches were all low or zero: cod (4), poor cod (0), sprat (0), saithe (0), and Raitt's sand eel (0). All the main fish species in the trawls showed significant between-area, between-season, and between-year variation in median catch rates (Kruskal-Wallis tests). Similarly, all the main species showed significant variation in size in relations to area, season, and year (except for Raitt's sand eel in relation to area). These results are summarized in Table 4 (results for interannual variation not shown).

Multivariate Analysis of Overall Variation in Diet

Visual examination of MDS plots indicated some separation of data points (which relate to numbers of prey) in relation to area, quarter, and cause of death. No obvious patterns could be seen in relation to length-class, sex, or year.

To quantify the correlation of dietary and "environmental" similarity matrices and to identify the best environmental predictors, we initially excluded cause of death data for which there were many missing values. In those animals with complete data for the remaining variables ($n = 183$), the overall correlation between the dietary and environmental similarity matrices was positive, but not statistically significant (rho = 0.039, $P = 0.066$). Correlation was greatest (rho = 0.136) using six of the dummy environmental variables. These variables (indicating correlations when used individually) were: "east coast" (rho = 0.055), "west coast" (rho = 0.021), "quarter 1" (rho = 0.065), "1992" (rho = 0.023), "2001" (rho = 0.069), and "2002" (rho = 0.076). Thus area, quarter, and year all contributed significantly to overall dietary variation.

Removing one further animal from the analysis (due to missing data on precise location of capture), the similarity matrix for an "environmental" matrix comprising latitude, longitude, and body length was uncorrelated with the dietary

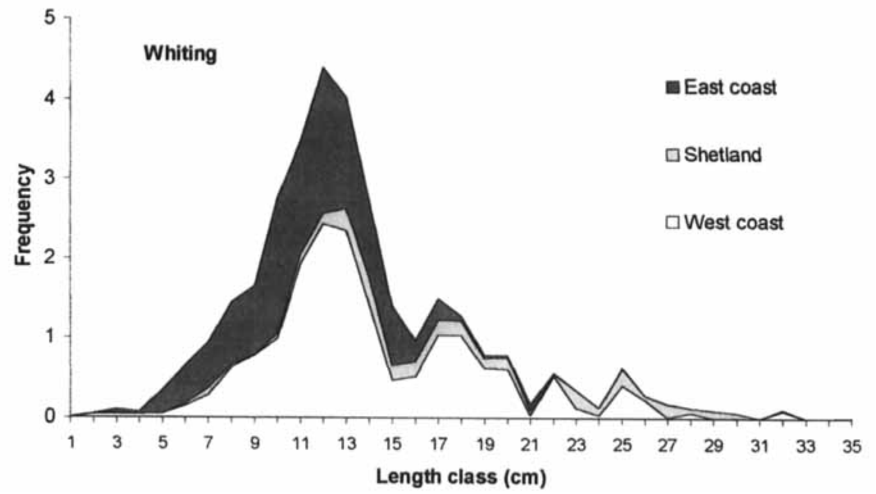

Figure 2. Frequency distributions of estimated size of whiting eaten by porpoises, using combined data for 1992–2003. Frequencies are shown, cumulatively, for average porpoises from each of the three areas.

similarity matrix (rho = 0.007, $P = 0.41$). The best prediction of diet from these three variables uses latitude and longitude (rho = 0.079). If the three interval variables were added to the previously used set of categorical environmental variables, none of the interval variables was among the best predictors of diet.

Further reduction of the dataset ($n = 141$) allowed inclusion of cause of death amongst the categorical "environmental" variables. The overall correlation between the dietary and environmental similarity matrices was significant and positive (rho = 0.086, $P = 0.008$). Correlation was maximized (rho = 0.177) using seven of the dummy environmental variables, namely "bycatch" (rho = 0.087), "east coast" (rho = 0.108), "quarter 1" (rho = 0.074), "1995" (rho = 0.006), "1998" (rho = 0.045), "2001" (rho = 0.077), and "2002" (rho = 0.082). This result supports the previous analysis in that area, quarter, and year are seen to have significant effects, but also indicates that cause of death also has a significant effect.

Power Analysis for Univariate Analyses

In the first simulation (variable occurrence and numerical importance of prey types), for the 2-group and 3-group cases (*e.g.*, comparisons of sexes or areas, respectively) a significant difference was detected when the prey type occurred in as few as eight stomachs. For the 3-group case, the prey type must have occurred in at least nine stomachs before a significant difference was detected. For the 12-group case, the prey type must have occurred in at least 18 stomachs before a difference in importance was detectable. In the second simulation (constant occurrence, variable numerical importance of prey types), for the 2-group case, the prey must have been present in 72 stomachs before a significant difference was detected. In the 3- and 4-group cases, this rises to 84 and 96, respectively. For 12 groups, the prey type must have been present in 144 stomachs.

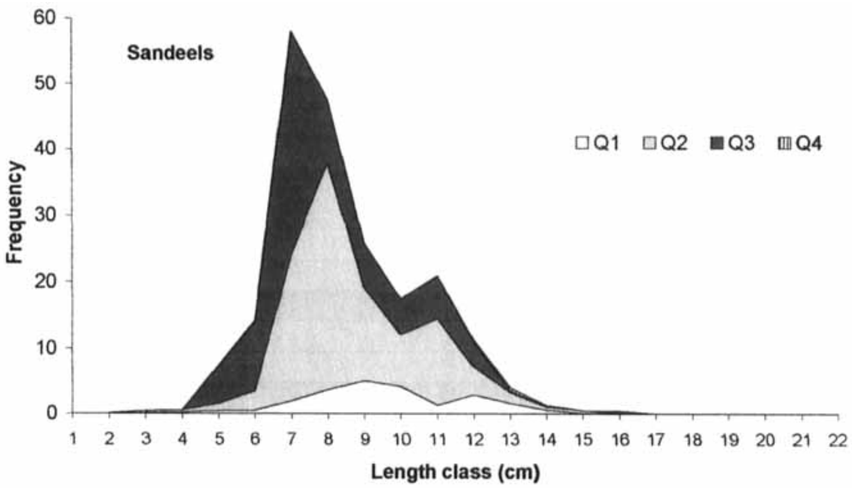

Figure 3. Frequency distributions of estimated size of sandeels eaten by porpoises, using combined data for 1992–2003. Frequencies are shown, cumulatively, for average porpoises in each season.

These simulations do not map precisely onto the present data set since the real group sizes are unequal. However, it is clear that differences in diets between groups should be detectable even for relatively rare prey types. However, if prey types have similar frequency of occurrence across groups, differing only in numerical importance, differences are likely to be detectable only for the most common prey types.

It should be noted that comparisons of median fish size in samples are inevitably less likely to detect significant differences than comparisons of numbers of otoliths—data on median size being available only for samples in which a prey category is present.

Geographical Variation in Diet

Analysis of the average number of prey items in stomachs revealed among-area differences for three of the eight main prey categories (Table 5). Sand eels were least important in the west coast diet (median = 0), while the difference in importance of sand eels between the east coast (median = 2) and Shetland (median = 0) was non-significant. Survey catch rates for Raitt's sand eel were highest on the east coast (Table 4). *Trisopterus* spp. were least numerous in the east coast diet. Survey abundance was highest in Shetland, but the difference in abundance between east and west coasts was not significant. Haddock/saithe/pollack were more numerous in the Shetland diet than in the east coast diet (Table 5). Equivalent trends were also apparent in survey abundance of haddock and saithe, although survey abundances of these species differed significantly between all three areas (Table 4). Significant between-area differences in abundance of other fish species (*e.g.*, whiting, herring, sprat; see Table 4) were not reflected in differences in diet.

Comparisons of median sizes of whiting eaten by individual porpoises (Table 6) indicated significant between-area variation, with the smallest fish being taken on

Table 4. Variation in fish catch and median size in survey hauls: Kruskal-Wallis test results (the test statistic H, the probability *P*, and the direction of any significant difference) for comparisons of the average number and size of fish caught per hour in 2,741 survey hauls (1992–2003), in relation to: (1) area (E = east coast, Sh = Shetland, W = west coast), and (2) season (1 = quarter 1, *etc.*). Fish species are listed in reverse order of abundance (overall median number of caught fish per hour is given in parentheses).

Fish species (median catch rate)	Abundance area	Abundance season	Median size area	Median size season
Haddock (542)	269.47; 0. 000 Sh > E > W	135.99; 0.000 3 > 1,2 > 4	56.26; 0.000 W > E, Sh	63.83; 0.000 4 > 1,2,3; 1 > 3
Whiting (352)	151.90; 0.000 E > W, Sh	43.70; 0.000 1,2,3 > 4; 2 > 4	339.12; 0.000 Sh > W > E	118.45; 0.000 4 > 2,3 > 1
Norway pout (291)	132.68; 0.000 Sh > E, W	20.21; 0.000 1,4 > 3; 1 > 2	77.32; 0.000 Sh > E, W	134.00; 0.000 3 > 2 > 1 > 4
Herring (59)	40.34; 0.000 E > W > Sh	102.10; 0.000 2 > 1 > 3 > 4	524.84; 0.000 Sh > W > E	152.50; 0.000 4 > 3 > 1,2
Cod (4)	390.82; 0.000 Sh > E > W	273.82; 0.000 2,3 > 1 > 4	578.60; 0.000 W > Sh > E	164.22; 0.000 4 > 1,2 > 3
Poor cod (0)	783.73; 0.000 W > Sh > E	855.84; 0.000 4 > 1 > 2 > 3	83.30; 0.000 E, Sh > W	162.95; 0.000 2 > 3 > 1 > 4
Sprat (0)	216.79; 0.000 E, W > Sh	224.51; 0.000 1,2 > 3,4	14.62; 0.001 E, Sh > W	50.43; 0.000 3 > 1,2,4; 4 > 1
Saithe (0)	425.06; 0.000 Sh > W > E	81.52; 0.000 2,3 > 1,4; 1 > 4	11.76; 0.003 E > Sh, W	41.48; 0.000 2 > 1,3 > 4
Raitt's sand eel (0)	16.65; 0.004 E > Sh, W	113.88; 0.000 2 > 1 > 3 > 4	2.25; 0.325	33.48; 0.000 2,4 > 1,3

Table 5. Variation in diet: Kruskal-Wallis test results (the statistic H, the probability P, and the direction of any significant differences) for comparisons, of the number of prey in stomachs, between groups of porpoises defined by the following factors: (1) area (E = east coast, Sh = Shetland, W = west coast), (2) season (1 = quarter 1, *etc.*), (3) size (L = large, M = medium, S = small), (4) cause of death (T = killed by *Tursiops*, I = infection or parasites, B = fishery bycatch, (5) year, (6) sex. The last column contains correlation results, giving values for r and P. Significant values for test statistics are shown in bold face. Also shown are the number of porpoises for which data on factor levels were available (n) and the number of stomachs in which each category of prey was recorded (*i.e.*, frequency of occurrence, F).

Prey type	Area (n = 187)	Season (n = 187)	Size class (n = 183)	Cause of death (n = 142)	Year (n = 187)	Sex (n = 186)	Size (correlation) (n = 187)
Whiting (F = 95)	2.21; 0.332	**15.52; 0.001** 1,4 > 2,3	0.78; 0.679	1.86; 0.394	11.99; 0.365	0.16; 0.687	−0.020; 0.784
Sand eels (F = 92)	**25.38; <0.001** E, Sh > W	**31.96; <0.001** 2,3 > 1,4	1.02, 0.599	**24.41; <0.001** T > B,I	16.12; 0.137	0.46; 0.499	0.046; 0.535
Sepiolidae (F = 48)	0.32; 0.852	**14.29; 0.003** 4 > 2,3; 1 > 3	0.43; 0.807	0.70; 0.704	8.61; 0.657	2.10; 0.147	−0.095; 0.202
Clupeidae (F = 41)	3.25; 0.197	4.23; 0.238	**8.15; 0.017** M > L	2.99; 0.224	**26.96; 0.005** 94,95,02 > 92; 94,95 > 97[b]	2.28; 0.131	−0.045; 0.545
Unid. Gadidae (F = 40)	5.65; 0.059	**11.87; 0.008** 1,4 > 2	5.18; 0.075	4.02; 0.134	13.46; 0.264	0.21; 0.643	0.009; 0.908
Trisopterus sp. (F = 25)	**27.82; <0.001** Sh, W > E	14.39; 0.002 1,4 > 2	3.55; 0.169	**20.70; <0.001** B, I > T	10.88; 0.453	1.14; 0.286	0.088; 0.237
Had/Sai/Pol[a] (F = 21)	**10.59; 0.005** Sh > E	4.59; 0.205	4.38; 0.112	**13.85; 0.001** I > T, B	10.38; 0.497	2.60; 0.107	**0.173; 0.020**
Gobiidae (F = 17)	1.81; 0.404	4.83; 0.185	**12.52; 0.002** S > M, L	0.32; 0.852	18.77; 0.065	0.63; 0.428	**−0.188; 0.011**

[a] The category "Had/Sai/Pol" comprises haddock, saithe, and pollack and includes fish identified to species.
[b] No clupeids were eaten in two years 1993 and 2000. Data for these years could not therefore be used in Mann-Whitney U tests.

Table 6. Variation in diet: Kruskal-Wallis test results (the test statistic H, the probability P, and the direction of any significant differences) for comparisons, of the size of prey in stomachs, between groups of propoises defined by (1) area [E = east coast, Sh = Shetland, W = west], (2) season (1 = quarter 1, *etc.*), (3) size (L = large, M = medium, S = small, (4) cause of death (T = killed by *Tursiops*, I = infection or parasites, B = fishery bycatch, (5) year, (6) sex. The last column contains correlation results, giving values for r and P. Significant values for test statistics are shown in bold face; borderline significance is indicated by italics. Also shown are the number of stomachs in which each category of prey was recorded and prey size was known (F).

Prey type	Area	Season	Size class	Cause of death	Year	Sex	Size (correlation)
Whiting (F = 93)	**14.17; 0.001** Sh, W > E	3.70; 0.296	0.87; 0.649	**7.42; 0.024** B > T, I	8.18; 0.697	1.78; 0.182	0.133, 0.207
Sand eels (F = 88)	**6.68; 0.035** Sh > E	**10.49; 0.015** 1,2 > 3	**6.92; 0.031** L > M, S	4.26; 0.372	13.72; 0.249	**6.66; 0.010** M > F	*0.199, 0.068*
Sepiolidae (F = 47)	**6.97; 0.031** W > E	0.85; 0.837	3.81; 0.149	1.86; 0.394	9.40; 0.585	0.47; 0.493	0.177; 0.239
Clupeidae (F = 33)	0.86; 0.649	1.21; 0.751	1.53; 0.466	1.68; 0.432	9.37; 0.312	0.12; 0.730	0.218; 0.223
Trisopterus sp. (F = 25)	4.25; 0.120	1.27; 0.735	0.63; 0.731	**8.58; 0.014** B > I	9.45; 0.490	0.76; 0.382	0.020; 0.925
Had/Sai/Pol[a] (F = 21)	*5.88; 0.053* W > E	2.38; 0.496	*6.01; 0.050* L > S	4.43; 0.109	7.74; 0.654	0.05; 0.828	*0.436; 0.062*
Gobiidae (F = 17)	1.61; 0.205	2.82; 0.420	4.20; 0.123	0.73; 0.695	6.79; 0.341	0.00; 1.000	0.151; 0.562

[a] the category "Had/Sai/Pol" comprises haddock, saithe, and pollack and includes fish identified to species.

the east coast (Fig. 2). The median size of whiting taken in survey catches was also smallest on the east coast (Table 4). Survey data also show bigger whiting to be available in Shetland than on the west coast, a trend that is suggested by the dietary data, but not quite statistically significant (Mann-Whitney U test, $P = 0.057$), reflecting the small sample size for Shetland ($n = 5$).

Larger sand eels were taken by porpoises in Shetland than on the east coast (Table 6). This trend was not evident in the trawl survey data, although it should noted that only 145 hauls in the study area took Raitt's sand eels and most catches were in single figures. Larger sepiolids were taken by porpoises on the west coast than on the east coast (Table 6). No survey abundance data were available for sepiolids.

Overall between-area variation in the estimated size of haddock/saithe/pollack in stomach contents was not quite statistically significant, but bigger fish were taken on the west coast than on the east coast (Table 6). Haddock in survey catches were also bigger on the west coast than on the east coast (Table 4), although for the much less abundant saithe, the biggest fish were caught on the east coast. Several other fish species taken in survey hauls showed regional differences in median size that were not reflected in porpoise diets.

Seasonal Variation in Diet

There were seasonal differences in numerical importance for five of the eight main prey categories (Table 5). Sand eels were more numerous in the diet during quarters 2 and 3 than in quarters 1 and 4. This trend was not replicated in survey catches of Raitt's sand eel, although catches were highest in quarter 2 and lowest in quarter 4 (Table 4).

Whiting was more important in the diet in quarters 1 and 4 than in quarters 2 and 3 (Table 5). However, average survey catch rates tended to decrease from quarters 1 through to 4 (Table 4). *Trisopterus* spp. and unidentified Gadidae were more important in quarters 1 and 4 than in quarter 2 (Table 5). Similar differences are apparent in survey abundance of poor-cod. Survey abundance of Norway pout was higher in quarter 1 than in quarters 2 and 3, and higher in quarter 4 than in quarter 3 (Table 4). Sepiolids were more important in the diet in quarters 4 than in quarters 2 and 3. Significant seasonal differences in survey abundance of other fish species (*e.g.*, haddock, saithe, herring, and sprat; Table 4) were not reflected in dietary differences.

The only statistically significant seasonal variation in prey size was for sand eels, which were larger in quarters 1 and 2 than in quarter 3 (Table 6, see also Fig. 3). The average size of Raitt's sand eel in survey catches was higher in quarters 2 and 4 than in quarters 1 and 3. As noted above, significant seasonal differences for median sizes of fish in survey hauls were seen for all the other main species present in the survey catches.

Body Length and Diet

Numerical importance varied significantly between porpoise length classes for two prey categories (Table 5). Clupeids were more important in the diet of medium-sized porpoises than in the diet of large porpoises, while gobies were most numerous in the diet of the smallest length class of porpoises ($\leq$118 cm).

The numerical importance of haddock/saithe/pollack in the diet was positively correlated with porpoise length, while there was a significant negative correlation between porpoise length and the importance of gobies (Table 5). There were non-significant trends for *Trisopterus* and unidentified Gadidae to be more numerous in the stomachs of larger porpoises (Table 5), and for the crustacean *Crangon crangon* to be more numerous in the stomachs of the smallest porpoises (Kruskal-Wallis H = 5.82, $P = 0.054$).

The largest size classes of porpoises tended to eat the largest sand eels, although the overall correlation between median sand eel size and porpoise length was not statistically significant ($P = 0.068$; see Table 6). Larger porpoises also tended to eat larger haddock/saithe/pollack. For all other prey categories, there was no significant variation in median prey size between different size classes of porpoise (Table 6).

Diet and Cause of Death

Differences in importance of prey, among porpoises in the three cause-of-death categories, were apparent for three of the main types of prey (Table 5). Sand eels were most important, and *Trisopterus* spp. were least important, in the diets of porpoises killed by *Tursiops*. Haddock/saithe/pollack were most important in the diets of porpoises that had died from infection or parasitism. The average size of whiting eaten was largest in bycaught porpoises (Table 6, Fig. 4). Similarly, by-caught porpoises had eaten larger *Trisopterus* spp. than had porpoises dying from infection or parasitism (Table 6).

Interannual Variation in Diet

Although all the main species in survey hauls showed significant interannual variation in abundance and average size (Table 4), of all the prey categories recorded, only Clupeidae showed significant interannual variation in importance in porpoise diet (Table 5). There were no significant interannual differences in average prey size (Table 6).

Annual mean numbers of clupeids in stomach contents were positively correlated with annual median survey catch rates for herring ($r = 0.623$, $P = 0.040$), but not with annual median survey catch rates for sprat ($r = 0.507$, $P = 0.111$). Dietary importance of clupeids was not correlated with spawning stock biomass of herring in the North Sea or on the west coast of Scotland ($P > 0.9$ in both cases). No SSB data were available for sprat but dietary importance of clupeids was positively correlated with annual landings of sprat from the northern North Sea ($r = 0.635$, $P = 0.036$). These trends are illustrated in Figure 5. It should be noted that clupeids occurred in a relatively small proportion of porpoise stomachs (Table 3) and the median number of clupeid fish in the stomachs exceeded zero only in 1995. Median survey catch rate of sprat exceeded zero only in 1994 and 1995.

Differences in Diet of Male and Female Harbor Porpoises

There were no significant differences between males and female porpoise diets with respect to the numerical importance of prey but the average size of sand eels eaten was larger in male porpoises (Table 5, 6).

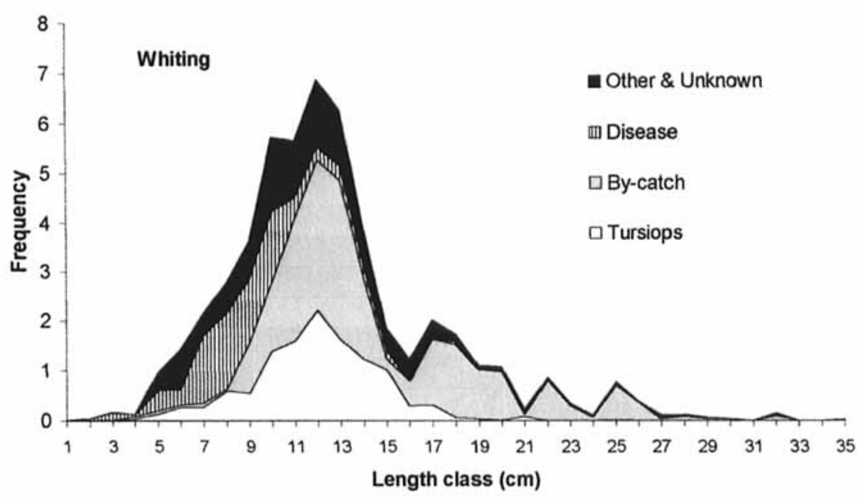

Figure 4. Frequency distributions of estimated size of whiting eaten by porpoises, using combined data for 1992–2003. Frequencies are shown, cumulatively, for porpoises dying from different causes (bycatch, *Tursiops* kills, disease, or parasites).

DISCUSSION

Sampling Issues

Sampling from stranded animals is inevitably opportunistic and sample composition depends on many factors (Pierce and Boyle 1991, Sekiguchi *et al.* 1992). Diagnosis of fishery bycatch is difficult, and it is likely that many bycatches are undetected (Siebert *et al.* 1996). Unlike animals dying from disease, fishery bycatches will tend to provide samples of "healthy" individuals (Kuiken *et al.* 1994), although stomach contents may be biased towards the target species of the fishery and associated species (Waring *et al.* 1990). Almost half of the porpoises from which stomach contents were obtained in the present study had been killed by bottlenose dolphins, and these were mainly small porpoises. Ross and Wilson (1996) found that the majority of porpoises killed by bottlenose dolphins were 100–140 cm in length, which corresponds to juvenile or prepubertal animals of 1–3 yr of age.

Another issue is that some fish sizes may be underestimated due to otolith erosion. Many different factors may affect the amount of time otoliths are exposed to acid digestion in the stomach (see, *e.g.*, Murie and Lavigne 1985) and the possible effects of otolith erosion on estimates of porpoise diet are explored in Wijnsma *et al.* (1999). In the present study, since analysis of fish size is restricted to within-species comparisons of the average size eaten by different groups of porpoises, our conclusions should be relatively robust to this kind of bias.

The information available for prey abundance was limited to data on the most common commercially important fish species. For these common species a standardized sampling program of trawling is carried out every year in Scottish waters. Although the resulting abundance indices can be used for comparisons of single species abundance between years, areas, and seasons, it cannot be inferred that trawl survey abundance is the same as availability to porpoises. Different fish species show different "catchability" and nets will in any case not retain all the smallest fish. Trawling may also take fish larger than the maximum size eaten by porpoises.

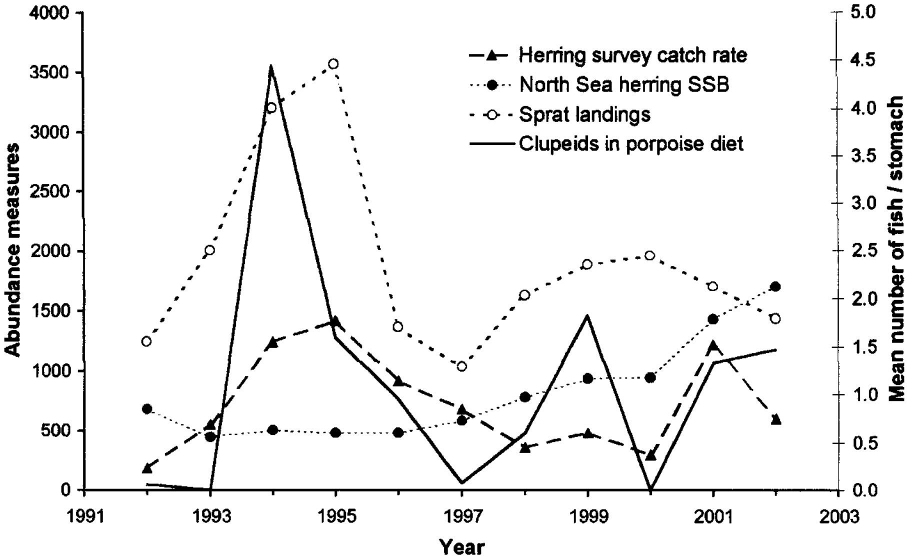

Figure 5. Interannual trends in importance of clupeids in the diet of harbor porpoises (mean number of clupeid fish per stomach) shown alongside interannual trends in North Sea herring spawning stock biomass (thousands of tonnes), median survey catch rates (fish per hour, ×10), and sprat landings from the northern North Sea (hundreds of tonnes).

Although sand eels were taken in the trawls, it is probable that few of the sand eels caught were retained in the net due to their body form and small size. Thus, while catches can provide a relative abundance index for Raitt's sand eel (the most frequently caught sand eel species), nothing can be said about the abundance of sand eels relative to, say, whiting. Another point to note is that, although the stranding (or bycatch) location and date is known for all sampled porpoises, it is not feasible to precisely match abundance measures to individual porpoises.

Overall Diet Composition

Over the sampling period the diet of porpoises was apparently dominated by just four prey categories, whiting, sand eels, haddock/saithe/pollack, and *Trisopterus* spp. (Norway pout and poor cod). Of these, the gadid species, particularly whiting, Norway pout, and haddock are among the most numerous fish in survey hauls. To this extent it may be inferred that porpoises tend to feed on abundant prey, as expected for an opportunist predator. On the other hand, the bulk of the diet comprises a very limited range of prey species, suggesting some degree of feeding specialization. Some authors consider harbor porpoises to be opportunistic feeders (*e.g.*, Martin 1996). However, the idea that the importance of each type of prey in the diet is related to its availability has rarely, if ever, been tested.

Porpoise diet in Scotland during 1959–1971, based on analysis of the contents of stomachs of 82 by-caught and 11 stranded animals, consisted mainly of herring, sprat, and whiting (Rae 1965, 1973*a*). Based on examination of stomachs of around 100 bycaught porpoises, mainly off England from 1989 to 1994, Martin (1996) found gadoids (whiting, haddock, Norway pout, and pollack) were the main prey by percentage weight, while sand eels and gobies were by far the most frequently eaten prey. Given the different provenance of the three sets of samples, some caution is needed in reaching conclusions. Nevertheless, whiting figures prominently in porpoise diet in all three UK studies, whereas clupeids have apparently become less important and sand eels more important with time. The apparent importance of sand eels in gray seal (*Halichoerus grypus*) diet increased markedly between studies in the 1950s and 1960s (Rae 1973*b*) and the 1980s (*e.g.*, Hammond *et al.* 1994). However, as for the studies on porpoises, effects of methodological biases cannot be ruled out: Rae's studies were based mainly on stomach contents of animals killed in and around salmon nets on the northeast coast of Scotland, whereas studies in the 1980s were based on fecal analysis and no samples were collected from the northeast coast of Scotland.

A reduction in the importance of herring in porpoise diet since the 1960s might be expected given that herring stocks in the North Sea declined between the mid-1960s and the mid-1970s, recovering to around half the peak spawning stock biomass (SSB) in 1989, but then fell again until 1996. However, the last three years have seen a marked recovery in the North Sea stock, with the projected SSB for 2003 being slightly higher than the 1960s peak (Anonymous 2002). This recovery in herring is not evident in the recent porpoise dietary data. Available estimates of sand eel stock size go back to 1975 and, although spawning stock biomass in the 1990s was generally higher than in the late 1970s (Anonymous 2002), we do not have estimates contemporaneous with Rae's studies.

In the present study the main prey of porpoises in summer were sand eels. Among the five northeast Atlantic species, Raitt's sand eel is the most abundant and is, indeed, one of the commonest fish species on the continental shelf of northwest Europe, accounting for 10%–15% of the total fish biomass of the North Sea (Sparholt 1990). It is of considerable ecological importance as prey for many marine predators (*e.g.*, Jonsgåard 1982, Daan 1989, Harris and Wanless 1991, Pierce *et al.* 1991, Hammond *et al.* 1994). Goodson and Sturtivant (1996) suggest that porpoises search for prey using a narrow-beam, narrow-band, high-frequency sonar, consistent with foraging close to either the sea surface or the bottom, where sand eels would be expected to occur.

Whiting is among the most important species of commercial demersal fish in the North Sea, living in shallow waters, usually from 39 to 200 m, over sandy or muddy grounds. Most of the whiting taken by porpoises in this study were smaller than 23 cm and were, therefore, probably younger than 2 yr old (Hislop, 1984). Concentrations of 1-yr-olds are found mainly in Scottish coastal waters and in the central and southern North Sea (Hislop 1984, Zheng *et al.* 2001). The spawning stock biomass of whiting reached an all-time low in 1998 and the stock is considered to be outside safe biological limits (Anonymous 2002). Given that over half of the porpoise diet by weight comprised whiting, the downward trend in whiting abundance could pose a threat to porpoises.

Studies on porpoise diet elsewhere in the northeast Atlantic indicate a similar range of prey species, although also revealing geographic variation in species importance. Aarefjord *et al.* (1995) found herring to be the most important prey in Scandinavian waters, with other important prey differing between Norwegian waters (saithe, blue whiting *Micromesistius poutassou*, and capelin *Mallotus villosus*) and the Danish North Sea and Baltic (cod, whiting, sand eels, and gobies). Börjesson *et al.* (2003) found herring to be the main prey in the Swedish Skagerrak and Kattegat Seas. In German North Sea waters, sand eels and common sole (*Solea*

solea) were the most important prey, whereas in German Baltic waters, the main species eaten were gobies, herring, and cod (Benke *et al.* 1998). In Ireland harbor porpoises were found to have taken mainly *Trisopterus* spp. (Rogan and Berrow 1996).

Sources of Variation in Diet

Given the relatively small sample size, it is difficult to disentangle the effects of the various possible factors influencing porpoise diet (in this case: year, quarter, area, cause of death, sex, and size). Probably the biggest difficulty is in separating possible "sampling bias," due to using data from animals in different cause-of-death categories, from real geographical differences in diet. This relates to the restriction of mortality caused by bottlenose dolphins to the east coast of Scotland. However, multivariate analysis indicated that area, quarter, year, and cause of death all contributed significantly to variability in diet. This gives us some confidence that the main trends identified by the univariate analyses are real and not simply a consequence of interactions between explanatory variables. The power analyses carried out indicate that, for the sample size available, differences in diet between different subsets of the sample are potentially detectable using Kruskal-Wallis tests.

Geographical Variation in Diet

The general picture arising is of porpoises on the east coast eating most sand eels, whereas those from Shetland take more gadids (notably *Trisopterus* spp. and haddock/saithe/pollack). Whiting is an important component of the diet in all three areas, although smaller whiting were taken on the east coast. The directions of the differences seen were mostly consistent with survey abundance differences. The survey data revealed abundance and size differences not apparent in dietary data. However, this may simply be a consequence of the low statistical power available for detecting differences for the less commonly eaten prey species. Our results support those of Martin (1996), who found that sand eels were taken in bigger numbers by porpoises on the east coast than on the west coast, and recorded Norway pout only in porpoises from Shetland, where it occurred in more than half of the porpoises examined.

Seasonal Variation in Diet

Diets of porpoises in Scotland showed a clear change from mainly sand eels in quarters 2 and 3 ("summer") to mainly gadids, especially whiting, in quarters 1 and 4 ("winter"). The size of sand eels eaten by porpoises was smallest in the quarter 3, when big numbers of 0-group sand eels become available.

Trawl survey data for the east coast of Scotland confirmed that whiting were more abundant in winter than in summer. Sand eels are generally thought to be more available to predators in summer than in winter, due to their remaining buried in the substrate in winter. Trawl data do not indicate a consistent difference in sand eel abundance between winter and summer but sand eels were probably the species least effectively sampled by trawling. Although echolocating porpoises should be able to detect sand eels buried in the substrate, it is possible that it is more costly energywise to forage for sand eels in winter. Tollit and Thompson (1996) found that consumption of sand eels by harbor seals in the Moray Firth was high in the winters of years in which local clupeid abundance was low, suggesting that sand eels were available but were taken only when more profitable food was unavailable.

Some of the results of the present study thus point to seasonal changes in diet being related to prey availability. In other studies harbor porpoises show a general inshore movement in summer and offshore movement in winter, presumed to be related to prey availability or to breeding habitat (Gaskin 1977, Northridge *et al.* 1995). Indirect evidence that the seasonal variation in diet of porpoises relates to changes in prey availability comes from observations of similar changes in diets of other predators. Harbor seals in the Moray Firth changed from a diet of mainly sand eels in quarters 2 and 3 to other species (including gadids and clupeids) in quarters 1 and 4 (Pierce *et al.* 1991, Tollit and Thompson 1996).

Börjesson and Berggren (1996) found that herring was the main prey of harbor porpoises in Swedish waters all year round, but the contribution of sprat and whiting to the diet varied seasonally. Gannon *et al.* (1998) reported that herring was the main prey of harbor porpoises in the Gulf of Maine in both summer and autumn, but was more important in the summer diet while silver, red, and white hakes and pearlsides were more important in the autumn diet. In Atlantic Canadian and United States waters, a higher diversity of prey was seen in winter than in summer (Palka *et al.* 1996).

Interannual Variation in Diet

Against a background of varying fish abundance, piscivorous predators, especially those foraging opportunistically, might be expected to show interannual variation in diet. In the present study only the interannual differences in dietary importance of clupeids were statistically significant. This variation was correlated with the trend in survey catches of herring (and with landings of sprat).

Other fish species present in the diet showed significant interannual variation in survey abundance which was not reflected in dietary importance. There are, however, problems of scale in such analyses. Donovan and Bjørge (1995) note that, to answer the question of whether harbor porpoise feeding patterns follow prey availability, it would be necessary to study "the distribution of prey and target species on a very small spatial scale, much smaller than presently documented in fishery literature." Nevertheless, trawl survey data are probably the best abundance data available.

Recchia and Read (1989) found that harbor porpoises bycaught in groundfish gill nets in the Bay of Fundy (Canada) during 1969 to 1972 had taken mackerel and hake less often than porpoises from 1985 to 1987, although herring, silver hake (*Merluccius bilinearis*), and cod remained the main prey in the diet in both periods. Gearin *et al.* (1994) reported that the main prey of harbor porpoises off northern Washington in 1988 and 1990 was Pacific herring (*Clupea pallasii*), while in 1989 smelts (Osmeridae) were the main prey.

Cause of Death and Diet: A Possible Source of Bias

Other studies have shown dietary differences between by-caught and stranded porpoises (*e.g.*, Lick 1991, Aarefjord *et al.* 1995, Benke *et al.* 1998). Rogan and Berrow (1996) found that, in Ireland, bycaught porpoises had eaten less clupeids and whiting than had stranded porpoises.

The cause of death could not be diagnosed in all sampled animals. Furthermore, the increased frequency with which death due to disease or parasites was diagnosed in the latter years of the study probably reflects, at least in part, improving diagnostic procedures. Nevertheless, diets differed by cause of death even when regional, seasonal, and interannual variation had been taken into account. However, the most obvious trends, *e.g.*, the high importance of sand eels in the stomach contents of porpoises killed by bottlenose dolphins, were consistent with regional differences in diet. Mortality caused by bottlenose dolphins was restricted to the east coast, where the importance of sand eels in the diet appears to be high.

Ontogenetic Variation in Diet

We found no evidence of significant variation in diet related to body size in the multivariate analysis. However, univariate analyses identified differences which could be interpreted as indicative of ontogenetic shifts in diet. The importance of gobies as food was highest in the smallest length class of porpoises (animals probably <1 yr old) and there was a suggestion (statistically non-significant) that the decapod crustacean *Crangon crangon* was also most important in the diet of young porpoises. Unpublished observations on harbor porpoise diet in Dutch waters also point to the importance of gobies as "baby food."[2] In the Bay of Fundy (Canada) porpoise calves took euphausiids while adult porpoises ate mainly herring (Smith and Read 1992). However, Martin (1996) found no significant differences in the diet between juvenile and adult porpoises in UK waters and Smith and Gaskin (1974) found no differences in the diet of juvenile and adult porpoises in Canadian waters.

Conclusion

Harbor porpoises are one of the smallest cetaceans and most of their range is in cold waters. Their habitat and life history impose very high energy demands. Furthermore, their small size means that they cannot store much energy and this makes them more dependent on all-year-round proximity to food sources. This dependence has "the consequence that [porpoise] distribution and nutritive condition may more strongly reflect the distribution and energy density of its prey than for other cetaceans" (Brodie 1995). Northeast Atlantic harbor porpoise populations are also threatened by fishery bycatch (IWC 1996). Changes in the nutritional quality of the diet could have consequences for population status. Dudok van Heel (1962) observed that captive porpoises fed on young cod lost weight, but this weight loss was halted when the diet was changed to the same amount of herring. Thus we suggest that continued monitoring of harbor porpoise diet composition is necessary.

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[2] Personal communication from Marjan Addink, National Museum of Natural History, Darwinweg 2, 2300 RA, Leiden, The Netherlands.

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