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Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters

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Data on stomach contents of ten bottlenose dolphins (*Tursiops truncatus*) stranded and by-caught around Scotland (UK) between 1990 and 1999 are presented. Although the species is resident in the Moray Firth (north-east Scotland), little previous information exists on the feeding habits of the species in Scottish waters. Cod (*Gadus morhua*), saithe (*Pollachius virens*) and whiting (*Merlangius merlangus*) were found to be the main prey eaten although several other fish species were also found, including salmon (*Salmo salar*) and haddock (*Melanogrammus aeglefinus*), and also cephalopods.

INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*, Montagu 1821) have a wide distribution in temperate and tropical waters. In the north-east Atlantic, they are regularly observed off the coasts of Portugal, Spain, France and Ireland (Evans et al., 1993). In the UK, they appear to have a patchy distribution with resident populations in Cardigan Bay (Wales) and the Moray Firth (Hammond & Thompson, 1991; Wilson, 1995). However, strandings occur on the west coast of Scotland and the species is also regularly seen in the Sound of Barra (Outer Hebrides, K. Grellier, personal communication; see Figure 1). Weir et al. (2001) recorded bottlenose dolphins among the species sighted during surveys of cetaceans in the Atlantic frontier region to the north and west of Scotland. Animals from the Moray Firth population are regularly seen along the east coast of Scotland, for example around the harbour mouth in Aberdeen (K. Stockin, personal communication). Although sightings elsewhere in the North Sea were more common before 1970 (Bakker & Smeenk, 1987), few sightings are now reported from outside the range of the Moray Firth population (Wilson et al., 1999). Wilson et al. (1999) estimated a population size of 129 ±15 dolphins for the Moray Firth, pointing out that this small size and its apparent isolation make bottlenose dolphins very vulnerable.

From 1 January 1992 to 31 December 1999, a total of 32 stranded and by-caught bottlenose dolphins were recorded in Scotland (Figure 1). Stomach contents were recovered from nine, as well as from one animal stranded in 1990 (Table 1). The number of dolphins recorded per year ranged from two (in 1996, 1997) to eight (in 1999) with approximately equal numbers of males and females.

Previous studies on bottlenose dolphin diets in other parts of the world showed dolphins taking a wide variety of locally abundant prey: demersal and pelagic fish species, cephalopods and crustaceans (e.g. Norris & Prescott, 1961; Gaskin, 1982; Shane et al., 1986; Barros & Odell, 1990; Barros & Wells, 1998; Barros et al., 2000). This led some authors to consider bottlenose dolphins as opportunistic in their feeding habits. However, feeding experiments carried out by Corkeron et al. (1990) in Australia showed that although "bottlenose dolphins are catholic feeders, they demonstrate clear preferences when given a choice of food items".

In the present work, stomach contents from ten bottlenose dolphins stranded between 1990 and 1999 in Scotland were analysed, an area from which little previous information on diet was available.

MATERIALS AND METHODS

Scottish Agricultural College Veterinary Services Division, under a contract with the UK Department of Environment, Transport and the Regions, has co-ordinated and investigated marine mammal strandings in Scotland since 1 January 1992. During this period a total of 30 stranded and two by-caught bottlenose dolphins were recorded on the Scottish coast.

Full post-mortem examinations were carried out for 24 animals, of which stomach contents were recovered in nine cases (eight stranded dolphins and one animal by-caught in a salmon net, Table 1). Of the remaining animals post-mortemed, nine were less than 160 cm in length and would be expected to be suckling juveniles.

Additionally, the stomach contents of a dolphin stranded in 1990 were analysed (see Table 1).

All stomach compartments were carefully examined and the contents removed and stored in 70% ethanol or frozen. Samples were later thawed and washed through a 0.355 mm sieve. Prey remains consisted principally of otoliths and bones of fish and beaks (mandibles) of cephalopods, which were identified using reference material and published guides (Clarke, 1986; Härkönen, 1986 and Watt et al., 1997).

The minimum number of fish and cephalopods in each stomach was estimated from all identifiable hard remains. (If an odd number of otoliths was present, the number of fish represented by the otoliths was taken to be the half the number of otoliths plus one.)

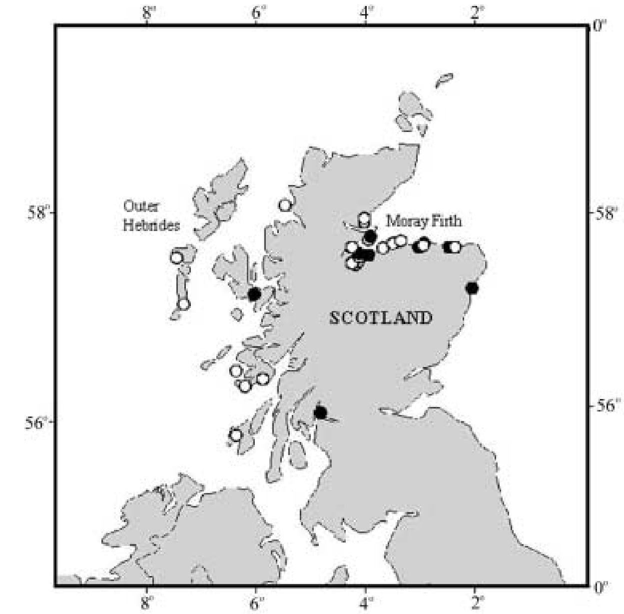

Figure 1. Map of Scotland showing the locations of bottlenose dolphin strandings and by-catches in the present study. Full circles represent animals for which stomach contents were analysed.

Fish and cephalopod sizes (lengths and weights) were estimated by measuring the otoliths and beaks respectively and applying standard regressions (Clarke, 1986; Härkönen, 1986; Bedford et al., 1986; Coull et al., 1989; Brown & Pierce, 1998: see Appendix 1). For otoliths not identifiable to species level, but identified as one of a group of species, regressions were constructed using data for all the species in that group (Pierce et al., 1991b). For salmon remains, the size of the fish ingested was estimated using a published regression of fish length on bone (premaxilla) length (Watt et al., 1997).

When reconstructing prey weights, each otolith was assumed to represent 0.5 fish, thus, when both otoliths were present, the estimated fish weight is the average of the weights estimated from the two otoliths. Complete pairs of cephalopod beaks were rarely present and in all cases weight was estimated from measurements on the lower beak. Crustacean and polychaete remains were not identified to species due to the poor state of preservation. It is often suggested that these categories are ingested secondarily, i.e. in the stomachs of the prey of marine mammals (e.g. for seals, McConnell et al., 1984).

To describe overall diet, we derived three standard indices of importance for individual prey taxa: (a) frequency of occurrence; (b) percentage of the total number of prey; and (c) percentage of total prey weight (see Hyslop, 1980; Pierce & Boyle, 1991). Since the dolphins sampled were divided evenly between 'winter' (October–March) and 'summer' samples, a preliminary comparison of winter and summer diet was attempted. The average number of prey of each category in winter and summer stomachs was compared using Kruskal–Wallis tests. We also look for evidence of differences in diet between the sexes and between east and west coast animals, although no formal statistical comparison is possible.

Table 1. *Data on stranded and by-caught in Scotland bottlenose dolphins for which stomach contents were analysed (N=10). Locations are identified using the UK national grid system.*

Code	Date of stranding	Time of year	Sex	Length (cm)	Girth (cm)	Location of stranding	Grid reference	Size range of main prey (minimum and maximum total length, mm)			
								Whiting	Cod	Saithe	Haddock
M1271/90	17/07/90	Summer	Female	310	188	Moray	NH848568	–	–	–	–
M0158/93	25/01/93	Winter	Male	312	162	Port-gordon, Moray	NJ404647	–	–	–	–
M0431/94**	01/03/94	Winter	Female	322	178	Gare Loch, Dunbarton-shire	NS255840	–	565–575 (N=2)	–	–
M1718/94	23/08/94	Summer	Female	c250	–	Rose-markie, Highland	NH744590	–	–	–	–
M2563/95	31/12/95	Winter	Male	289	–	Hilton of Cadboll, Highland	NH877773	35–125 (N=6)	–	145–335 (N=73)	–
M0774/96*	06/05/96	Summer	Male	274	156	Findochty, Grampian	NJ463682	–	–	225–255 (N=2)	–
M1049/96	17/06/96	Summer	Male	270	130	Munlochy Bay, High-land	NH685513	105 (N=1)	–	–	–
M0167/98**	25/01/98	Winter	Male	290	168	Torrin, Skye Highland	NG576199	115–255 (N=373)	525–545 (N=2)	–	115–145 (N=9)
M0591/99	26/08/99	Summer	Male	313	–	Grampian	NJ734646	–	–	–	–
M0661/99	21/12/99	Winter	Male	267	163	Grampian	NJ986195	85–165 (N=12)	95–495 (N=17)	–	55–385 (N=24)

*, indicates the by-caught animal; **, indicates strandings from the west coast.

Table 2. *Overall importance of prey species identified from bottlenose dolphins stranded and by-caught in Scotland (N=10). Importance is expressed as frequency of occurrence, percentage number and percentage weight for all stomachs combined.*

Prey species	Frequency	Number (%)	Weight (%)
All Fish	8	98.2	97.5
Sprat (*Sprattus sprattus*)	3	3.0	0.2
Salmon (*Salmo salar*)	2	0.4	5.8
Cod (*Gadus morhua*)	5	2.5	29.6
Haddock (*Melanogrammus aeglefinus*)	3	4.1	5.4
Saithe (*Pollachius virens*)	2	9.4	23.6
Whiting (*Merlangius merlangus*)	4	49.1	23.4
Trisopterus spp. (*T. esmarkii*, *T. minutus*, *T. luscus*)	3	3.3	0.7
Ling (*Molva molva*)	1	0.1	0.1
All Gadidae	7	72.1	84.1
Hake (*Merluccius merluccius*)	1	0.1	0.1
Bull-rout (*Myoxocephalus scorpius*)	2	1.0	1.0
Sea scorpion (*Taurulus bubalis*)	1	4.9	4.1
Scad (*Trachurus trachurus*)	2	0.5	0.9
Labridae	2	0.3	–
Sandeel (*Ammodytes* spp.)	3	13.8	0.8
Dragonet (*Callionymus* sp.)	2	0.3	0.1
Gobiidae	1	0.1	0.0
Plaice (*Pleuronectes platessa*)	1	0.5	0.3
Dab (*Limanda limanda*)	1	0.1	0.1
Long rough dab (*Hippoglossoides platessoides*)	1	0.3	0.1
All flatfish	4	1.1	0.5
Unidentified fish	4	1.0	–
All Cephalopoda	4	1.1	2.5
Sepiolid	2	0.5	0.0
Squid (*Loligo* sp.)	1	0.1	0.3
Squid (*Alloteuthis subulata*)	1	0.1	–
Squid (*Todarodes sagittatus*)	2	0.3	0.6
Octopus (*Eledone cirrhosa*)	2	0.3	1.6
Crustacea	2	0.3	–
Polychaeta	3	0.4	–

RESULTS

Seven out of ten dolphins for which stomach contents were examined were males, as compared to a sex ratio of 15 males: 14 females (four animals could not be sexed) among all reported strandings and by-catches of this species during 1990–1999 and 13:12 among post-mortemed animals. However, the departure from a 1:1 sex ratio is not statistically significant (χ^2 test).

Remains of at least 782 fish from 19 species and nine cephalopods from five taxa were recovered from the stomachs. Crustacean and polychaete remains were also found in a few stomachs (two and three respectively). Of the above prey, size estimates were available for 758 fish (representing an estimated total weight of 62.1 kg) and eight cephalopods (totalling 1.6 kg).

Weights were only available for 11 of the stranded and by-caught dolphins, of which only three were adults. These ranged in weight from 180 to 365 kg. The average weight of food eaten daily by a bottlenose dolphin (using the figure of 4.2% of body weight, Sergeant, 1969) is thus estimated to range from 7.6 to 15.3 kg. Food remains found in individual dolphins ranged in weight from 5 g to >21 kg, which would represent a maximum of 1.4 days' feeding.

Cod (*Gadus morhua*), saithe (*Pollachius virens*) and whiting (*Merlangius merlangus*) were the most important prey categories by weight, together comprising 77% of the estimated prey weight (Table 2). Numerically, whiting made up almost half of all prey found although only comprising 23% of prey weight.

Other fish species present in smaller numbers included sea scorpion (*Taurulus bubalis*), scad (*Trachurus trachurus*) and *Trisopterus* species. Salmon (*Salmo salar*) remains were found in two stomachs. The cephalopod species eaten were the octopus *Eledone cirrrhosa*, the squid *Todarodes sagittatus*, *Loligo* sp., *Alloteuthis subulata* and sepiolids (Table 2).

For the main prey species, the range of sizes eaten by each dolphin is summarized in Table 1. The estimated lengths of cod eaten ranged from 9.5 to 57.5 cm length, with a mode of 46.5 cm (N=27; Figure 2). Saithe eaten

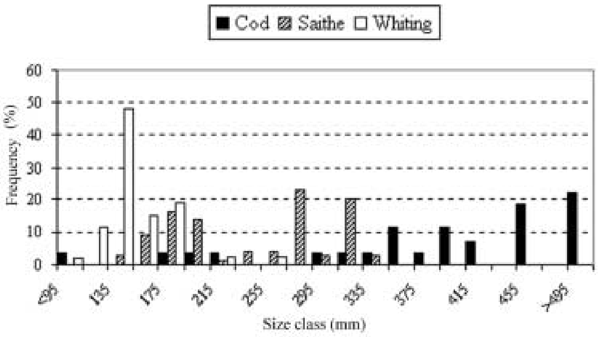

Figure 2. Frequency distribution of estimated size (standard length) of the main prey species eaten by bottlenose dolphins stranded and by-caught in Scotland. Sample sizes were $N_{cod}=27$, $N_{saithe}=74$ and $N_{whiting}=393$.

by bottlenose dolphins measured <33.5 cm with a mode of 28.5–31.5 cm (N=74; Figure 2) while whiting measured <25.5 cm with a mode of 14.5 cm (N=393; Figure 2). The shape of the histograms (polymodal for cod and saithe) suggests that more than one age class is present in the diet.

Comparisons of numbers of prey present in winter and summer stomachs are limited by the small sample size and low frequency of occurrence of most prey types. None of the individual prey taxa differed significantly in numerical importance between summer and winter (Kruskal–Wallis tests), but the average total number of gadid otoliths in the stomachs was higher in winter (Kruskal–Wallis test, $P=0.020$). Seasonal differences in the number of cod, *Trisopterus* and polychaetes all approached statistical significance ($P=0.054$, 0.054 and 0.050 respectively)—all being more numerous in winter samples.

Formal statistical comparisons of male and female diet, and of east and west coast diet, are clearly not possible. It may be noted that the three individual dolphins with large numbers of prey in their stomach were all males. Furthermore, many prey species (cod, whiting, haddock, *Trisopterus* spp., scad, wrasse (Labridae), flying squid *Todarodes sagittatus* and sepiolids) were present in stomach samples from both coasts. Hake, gobies and common squid *Loligo* sp. were only recorded in west coast animals, while a number of species, including salmon, sprat, sandeels and octopus, were only recorded in the east coast samples.

DISCUSSION

Eight out of the ten bottlenose dolphins analysed were stranded in the Moray Firth area, including one animal previously photo-identified in the resident Moray Firth population (B. Wilson, personal communication). This distribution corresponds to the geographical distribution of strandings (Figure 1), with the majority stranding in the Moray Firth—indeed only one east coast stranding occurred outside the Moray Firth. The strandings from the west coast may thus correspond to animals from a different population.

Although the number of males and females in the strandings is similar, seven out of ten animals with non-empty stomachs were males. However, since the sample size is small, this apparent bias is not statistically significant.

Wilson et al. (1997) found that bottlenose dolphin sightings in the Moray Firth were concentrated at the mouths of the inner firths, in deep, narrow channels subject to strong tidal flows. These may be feeding areas. During surveys in the Moray Firth in 1992–1994, Greenstreet et al. (1998) found sprat to be the most abundant species in winter (30% of total fish biomass), sandeel in summer (59%) and herring in autumn (27%). Haddock and whiting were also important in winter when, with sprat, they comprised ~85% of total fish biomass. Hopkins (1986) noted that exploited demersal fish species in the Moray Firth included haddock, cod, whiting, plaice and lemon sole. Other exploited species include squid (*Loligo forbesi*), scallops, crabs and lobster. It is an important nursery area for herring, and both herring and sprat have been fished in the area in the past (Hopkins, 1986). Thus, most of the common exploited fish species in the Moray Firth are also eaten by dolphins, with whiting being particularly prominent in our samples.

Whiting, sandeels, sprat and octopus are all important in the diet of harbour seals in the Moray Firth and most of the other prey species are also recorded in seal diets in the area (Pierce et al., 1991a,b; Tollit & Thompson, 1996). Whiting and sandeels also comprise the bulk of harbour porpoise diet in the Moray Firth (M.B. Santos, unpublished data).

Despite the small sample size, evidence was found for gadid fish being more important in the diet in the winter, which is consistent with known seasonal variation in diets of seals and porpoises in Scottish waters (references cited above).

The prey types found in stomachs of two bottlenose dolphins stranded on the west coast of Scotland were generally similar to those eaten by the east coast dolphins. Walker et al. (2000) showed that, in the western North Atlantic, diets of inshore populations of bottlenose dolphins mainly consist of fish, whereas animals from offshore populations consume more squid. The west coast dolphins in this study may represent a different, offshore, population but the data collected (while clearly insufficient for any formal test) provide no evidence for a greater importance of cephalopods in the diet.

An interesting point, since consumption of salmon by marine mammals (notably seals) in Scottish waters has long been a contentious issue (see Carter et al., 2001) is the presence of salmon in two of the dolphin stomachs from the Moray Firth area, including one animal found entangled in a salmon net. Captive feeding experiments on seals suggest that salmon otoliths are frequently completely digested in the stomachs of marine mammals (Boyle et al., 1990). Salmon bones are very friable (Casteel, 1976) and, consequently, evidence of feeding on salmon may not always be found in stomach contents, unless eaten very recently. Janik (2000) showed that bottlenose dolphins in the Moray Firth produce low-frequency bray calls when (based on surface observations) they are feeding on salmonids.

The present sample of only ten dolphins is too small to reach any conclusion about the amount of salmon eaten by bottlenose dolphins, although it is clear that they may follow the fish into nets and even a small number of dolphin mortalities in salmon nets could be significant in a small and isolated population (Wilson et al., 1999; Thompson et al., 2000).

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REFERENCES

Bakker, J. & Smeenk, C., 1987. Time-series analysis of *Tursiops truncatus*, *Delphinus delphis*, and *Lagenorhynchus albirostris* strandings on the Dutch coast. *ECS Newsletter*, **1**, 14–19.

Barros, N.B. & Odell, D.K., 1990. Food habits of bottlenose dolphins in the southeastern United States. In *The bottlenose dolphin* (ed. S. Leatherwood and R.R. Reeves), pp. 309–328. San Diego: Academic Press Inc.

Barros, N.B., Parsons, E.C.M. & Jefferson, T.A., 2000. Prey of offshore bottlenose dolphins from the South China Sea. *Aquatic Mammals*, **26**, 2–6.

Barros, N.B. & Wells, R.S., 1998. Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Journal of Mammalogy*, **79**, 1045–1059.

Bedford, B.C., Woolner, L.E. & Jones, B.W., 1986. Length–weight relationships for commercial fish species and conversion factors for various presentations. *Fisheries Research Data Report*, **10**, 1–41.

Boyle, P.R., Pierce, G.J. & Diack, J.S.W., 1990. Sources of evidence for salmon in the diets of seals. *Fisheries Research*, **10**, 137–150.

Brown, E.G. & Pierce, G.J., 1998. Monthly variation in the diet of harbour seals in inshore waters along the southeast Shetland (UK) coastline. *Marine Ecology Progress Series*, **167**, 275–289.

Carter, T.J., Pierce, G.J., Houseman, J.A. & Hislop, J.R.G., 2001. Predation by seals on salmonids in two Scottish estuaries. *Fisheries Management and Ecology*, **8**, 207–225.

Casteel, R.W., 1976. *Fish remains in archaeology and paleo-environmental studies*. London: Academic Press.

Clarke, M.R., ed., 1986. *A handbook for the identification of cephalopod beaks*. Oxford: Clarendon Press.

Corkeron, P.J., Bryden, M.M. & Hedstrom, K.E., 1990. Feeding by bottlenose dolphins in association with trawling operations in Moreton Bay, Australia. In *The bottlenose dolphin* (ed. S. Leatherwood and R.R. Reeves), pp. 329–336. San Diego: Academic Press Inc.

Coull, K.A., Jermyn, A.S., Newton, A.W., Henderson, G.I. & Hall, W.B., 1989. Length/weight relationships for 88 species of fish encountered in the North East Atlantic. *Scottish Fisheries Research Report*, **43**, 1–81.

Evans, P.G.H., Lewis, E.J. & Vodden, P., 1993. Cetaceans in British and Irish waters: the work of Sea Watch Foundation. In *Proceedings of the Seventh Annual Conference of the European Cetacean Society, Inverness, Scotland, 18–21 February 1993. European Research on Cetaceans*—7 (ed. P.G.H. Evans), pp. 156–160. Cambridge: European Cetacean Society.

Gaskin, D.E., 1982. *The ecology of whales and dolphins*. London: Heinemann Educational Books.

Greenstreet, S.P.R., McMillan, J.A. & Armstrong, E., 1998. Seasonal variation in the importance of pelagic fish in the diet of piscivorous fish in the Moray Firth, NE Scotland: a response to variation in prey abundance? *ICES Journal of Marine Science*, **55**, 121–133.

Hammond, P.S. & Thompson, P.M., 1991. Minimum estimate of the number of bottlenose dolphins (*Tursiops truncatus*) in the Moray Firth, NE Scotland. *Biological Conservation*, **56**, 79–87.

Härkönen, T.J., 1986. *Guide to the otoliths of the bony fishes of the Northeast Atlantic*. Hellerup: Danbui ApS.

Hopkins, P.J., 1986. Exploited fish and shellfish species in the Moray Firth. *Proceedings of the Royal Society of Edinburgh* B, **91**, 57–72.

Hyslop, E.J., 1980. Stomach contents analysis: a review of methods and their application. *Journal of Fish Biology*, **17**, 411–429.

Janik, V.M., 2000. Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society* B, **267**, 923–927.

McConnell, B.J., Prime, J.H., Hiby, A.R. & Harwood, J., 1984. Grey seal diet. In *Interactions between grey seals and UK fisheries. A report on research conducted for the Department of Agriculture and Fisheries of Scotland by the Natural Environment Research Council's Sea Mammal Research Unit 1980 to 1983*, pp. 148–183. Cambridge: SMRU, NERC.

Norris, K.S. & Prescott, J.H., 1961. Observations on Pacific cetaceans of Californian and Mexican waters. *University of California Publications in Zoology*, **63**, 291–402.

Pierce, G.J. & Boyle, P.R., 1991. A review of methods for diet analysis in piscivorous marine mammals. *Oceanography and Marine Biology. Annual Review*, **29**, 409–486.

Pierce, G.J., Miller, A., Thompson, P.M. & Hislop, J.R.G., 1991a. Prey remains in grey seal (*Halichoerus grypus*) faeces from the Moray Firth, north-east Scotland. *Journal of Zoology*, **224**, 337–341.

Pierce, G.J., Thompson, P.M., Miller, A., Diack, J.S.W., Miller, D. & Boyle, P.R., 1991b. Seasonal variation in the diet of common seals (*Phoca vitulina*) in the Moray Firth area of Scotland. *Journal of Zoology*, **223**, 641–652.

Sergeant, D.E., 1969. Feeding rates of cetacea. *Fiskeridirektoratets Skrifter, Serie Havundersøkelser*, **15**, 246–258.

Shane, S.H., Wells, R.S. & Würsig, B., 1986. Ecology, behaviour and social organization of the bottlenose dolphin: a review. *Marine Mammal Science*, **2**, 34–63.

Thompson, P.M., Wilson, B., Grellier, K. & Hammond, P.S., 2000. Combining power analysis and population viability analysis to compare traditional and precautionary approaches to conservation of coastal cetaceans. *Conservation Biology*, **14**, 1253–1263.

Tollit, D.J. & Thompson, P.M., 1996. Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. *Canadian Journal of Zoology*, **74**, 1110–1121.

Walker, J.L., Potter, C.W. & Macko, S.A., 1999. The diets of modern and historic bottlenose dolphin populations reflected through stable isotopes. *Marine Mammal Science*, **15**, 335–350.

Watt, J., Pierce, G.J. & Boyle, P.R., 1997. A guide to the premaxillae and vertebrae of North Sea fishes. *International Council for the Exploration of the Sea (Co-operative Research Report)*, no. 220, 231 pp.

Weir, C.R., Pollock, C., Cronin, C. & Taylor, S., 2001. Cetaceans of the Atlantic Frontier, north and west of Scotland. *Continental Shelf Research*, **21**, 1047–1071.

Wilson, B., Hammond, P.S. & Thompson, P.M., 1999. Estimating size and assessing local trends in a coastal bottlenose dolphin population, *Ecological Applications*, **9**, 288–300.

Wilson, B., Thompson, P.M. & Hammond, P.S., 1997. Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology*, **34**, 1365–1374.

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Appendix 1. *Regression equations used to estimate fish and cephalopod sizes from measurements of otoliths and beaks.*

Prey species	Estimated prey length (mm)	S	Estimated prey weight (g)	S
Fish				
Sprat (*Sprattus sprattus*)	L=−50.520+(OW×151.950)	P	$W=0.002236(FLcm^{3.47460})$	C
Salmon (*Salmo salar*)	$L=95.957(PML^{0.646})$	W	$W=0.243885(FLcm^{2.22101})$	H
Cod (*Gadus morhua*)	L=−141.080+(OL×44.521)	P	$W=0.020592(FLcm^{2.85710})$	C(1)
	L=−96.180+(OW×90.370)	P	$W=0.020709(FLcm^{2.85710})$	C(12)
Haddock (*Melanogrammus aeglefinus*)	L=−109.990+(OL×33.521)	H	$W=0.01798(FLcm^{2.82680})$	C(1)
	L=−130.770+(OW×94.590)	H	$W=0.01844(FLcm^{2.82680})$	C(12)
Saithe (*Pollachius virens*)	L=−125.590+(OL×43.610)	H	$W=0.02832(FLcm^{2.73740})$	C
Whiting (*Merlangius merlangus*)	L=−4.870+(OL×19.621)	P	$W=0.01130(FLcm^{2.94560})$	C(1)
	L=−88.550+(OW×85.390)	H	$W=0.010961(FLcm^{2.94560})$	C(12)
			$W=0.010057(FLcm^{2.94560})$	C(6)
Trisopterus spp. (*T. esmarkii*, *T. minutus*, *T. luscus*)	L=−37.340+(OL×27.447)*	P	$W=0.003467(OL^{4.60000})$*	P
Ling (*Molva molva*)	L=−406.000+(OL×95.731)	Ha	$W=0.004070(FLcm^{3.07000})$	B
Unidentified gadids	L=−61.590+(OL×33.304)*	P	$W=0.016042(FLcm^{2.87419})$*	P
	L=−54.350+(OW×76.582)*	P		
Hake (*Merluccius merluccius*)	L=−0.630+(OL×23.884)	Ha	$W=0.009740(FLcm^{2.91300})$	B
Bull-rout (*Myoxocephalus scorpius*)	L=−9.950+(OL×34.840)	Ha	$W=0.012600(FLcm^{3.12350})$	
Sea scorpion (*Taurulus bubalis*)	L=5.360+(OL×33.710)	Ha	$W=0.639800(OL^{2.98800})$	Ha
Scad (*Trachurus trachurus*)	L=−27.020+(OL×34.939)	Br	$W=0.003400(FLcm^{3.29430})$	C
	L=−26.110+(OW×79.010)	Br		
Sandeel (*Ammodytes* spp.)	L=8.776+(OL×51.906)	Ha	$W=0.612150(OL^{2.71000})$	Ha
Dragonet (*Callionymus* sp.)	L=−51.390+(OL×84.120)	Br	$W=0.022000(FLcm^{2.59070})$	C
Gobiidae	L=−6.460+(OW×41.770)	Ha	$W=0.232809(OW^{4.17000})$	Ha
Plaice (*Pleuronectes platessa*)	L=−3.810+(OL×47.630)	Ha	$W=0.024182(FLcm^{2.79010})$	C(12)
Dab (*Limanda limanda*)	L=−50.960+(OL×58.470)	Ha	$W=0.005450(FLcm^{3.19500})$	B
Long rough dab (*Hippoglossoides platessoides*)	L=−24.520+(OL×48.350)	Ha	$W=0.004400(FLcm^{3.20390})$	C
Unidentified flatfish	L=−29.430+(OL×52.968)*	P	$W=0.007668(FLcm^{3.08467})$*	P
Cephalopoda				
Sepiolid	L=18.540+(LHL × 1.650)*	Cl	$W=2.651170(LHL^{0.54500})$*	Cl
Squid (*Loligo sp.*)	L=−42.220+(LRL × 84.274)*	Cl	$W=6.195360(LRL^{3.24200})$*	Pi
Squid (*Alloteuthis subulata*)	L=−30.990+(LRL × 113.970)	Cl	$W=7.389060(LRL^{2.75000})$	Cl
Squid (*Todarodes sagittatus*)	L=−11.300+(LRL × 41.360)	Cl	$W=2.188030(LRL^{2.83000})$	Cl
Octopus (*Eledone cirrhosa*)	L=3.380+(LHL × 26.570)	Cl	$W=5.365600(LHL^{2.85000})$	Cl

L, total length for fish and dorsal mantle length for cephalopods; W, total weight; OL, otolith length; OW, otolith width, after Harkönen, 1986; LRL, lower rostral length; LHL, lower hood length, after Clarke, 1986. Sources (S) are as follows: B, Bedford et al. (1986); Br, Brown & Pierce (1998); C, Coull et al. (1989); H, J.R.G. Hislop (unpublished data); Ha, Harkönen (1986); Cl, Clarke (1986); P, Pierce et al. (1991b); Pi, G.J. Pierce (unpublished data). The number between parentheses indicates month of the year, i.e. C(12), regression for that species on December; *, combined data.