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THE DIET OF HARBOUR PORPOISE (*PHOCOENA PHOCOENA*) IN THE NORTHEAST ATLANTIC

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Abstract The harbour porpoise (*Phocoena phocoena*) is probably the most abundant small cetacean in the northeast Atlantic and as such is an important top predator. It is also one of the most threatened species, particularly as a consequence of fishery by-catch.

Porpoises feed mainly on small shoaling fishes from both demersal and pelagic habitats. Many prey items are probably taken on, or very close to, the sea bed. Even though a wide range of species has been recorded in the diet, porpoises in any one area tend to feed primarily on two to four main species (e.g. whiting (*Merlangius merlangus*) and sandeels (Ammodytidae) in Scottish waters).

Evidence for selective predation is equivocal. Many studies provide evidence of geographic, seasonal, interannual, ontogenetic or sexual differences in prey types or prey sizes, and such differences are often (speculatively) interpreted in terms of prey availability. A few studies demonstrate trends in diet selection that are consistent with changes in prey abundance. However, lack of availability of prey abundance data at an appropriate spatial and temporal scale is often a problem.

Porpoise diets overlap extensively with diets of other piscivorous marine predators (notably seals). Many of the main prey species are also taken by commercial fisheries, although porpoises tend to take smaller fishes than those targeted by fisheries. Given their high abundance, porpoises clearly remove substantial quantities of fish.

The literature on porpoise diets in the northeast Atlantic suggests that there has been a long-term shift from predation on clupeid fish (mainly herring *Clupea harengus*) to predation on sandeels and gadoid fish, possibly related to the decline in herring stocks since the mid-1960s. Evidence from studies on seals suggests that such a shift could have adverse health consequences.

Food consumption brings porpoises into contact with two important threats – persistent organic contaminants and fishing nets, both of which have potentially serious impacts.

Introduction

The harbour or common porpoise, *Phocoena phocoena* (Linnaeus 1758), is one of the six species recognised in the family Phocoenidae (Read 1999). Its common name, porpoise, derives from the Latin *porcus piscus* (=pigfish) and was used in Ancient Rome. Linnaeus (1758) distinguished it from the common dolphin by calling it *Delphinus phocoena*, from the Greek word *phokia* (=seal), due to its lack of beak and its seal-like appearance.

Harbour porpoises, one of the most common cetaceans in European waters (Watson 1985), are small with an average adult length of 150 cm to 160 cm and an average weight of 45 kg to 60 kg (Gaskin et al. 1974). Maximum sizes of animals stranded in the UK have been reported as 163 cm and 54 kg in males and 189 cm and 81 kg in females (Lockyer 1995) although more recent work by Santos et al. (2001a) reported maximum sizes for males and females as 170 cm (55 kg) and 171 cm (55.5 kg), respectively, for porpoises stranded in Scotland. Harbour porpoises stranded in northwest Spain and Portugal seem to be larger, and several specimens have measured more than 200 cm (Donovan & Bjørge 1995, Sequeira 1996).

There is some variation in the maximum ages reported for different harbour porpoise populations: no porpoises over 17 yr of age have been found in the Bay of Fundy (eastern Canada) (Read & Gaskin 1990, Read & Hohn 1995) while animals up to 24 yr old have been reported in UK waters (Lockyer 1995) and off California (Hohn & Brownell 1990).

Harbour porpoises are widespread in coastal waters of the Northern Hemisphere; their range extends northwards from 14–15°N in the North Atlantic and from 30°N in the North Pacific (Evans 1980). They are also found in the Black Sea and some records suggest the existence of a separate population off northwestern Africa (Smeenk et al. 1992). Historically, the species was also found in the western Mediterranean but there are no confirmed records since the nineteenth century (Marchessaux 1980, Donovan & Bjørge 1995). The species is also found over offshore shallows (e.g. the Georges and Grand Banks, stretching from Newfoundland to southern New England on the edge of the North American continental shelf) and around islands such as the Faeroes and Iceland. Individuals have also been recorded considerable distances up rivers (e.g. 320 km up the river Mass in Holland, Gaskin 1984).

Intraspecific differences in morphometric and meristic skull characters have been demonstrated between the North Pacific, North Atlantic and Black Sea (Tomilin 1957, Kinze 1985, Miyazaki et al. 1987, Yurick & Gaskin 1987, Amano & Miyazaki 1992). The differences between these three areas, suggesting reproductive isolation, have been confirmed by studies on mitochondrial DNA (Rosel et al. 1995, Wang et al. 1996). Rosel et al. (1995) suggested that there are at least three subspecies: *P. phocoena phocoena* (Atlantic), *P. phocoena vomerina* (Pacific) and *P. phocoena relicta* (Black Sea). The existence of further population subdivisions within these three major areas has been proposed by several authors using a variety of methods (e.g. Yurick 1977, Gaskin 1984, Yurick & Gaskin 1987, Andersen 1993, Rosel et al. 1995, 1999, Tiedemann et al. 1996, Wang et al. 1996, Börjesson & Berggren 1997, Walton 1997, Wang & Berggren 1997, Berrow et al. 1998, Lockyer 1999, Westgate & Tolley 1999, Tolley et al. 1999, 2001, Tolley & Heldal 2002) and putative stock boundaries have been suggested by the International Whaling Commission's (IWC) Scientific Committee (Donovan & Bjørge 1995).

Historically, harbour porpoises have been taken in European waters for human consumption and for fish bait (Watson 1985). It is believed that, in some areas, the porpoise hunt goes back to the Stone Age (e.g. inner Danish waters, Möhl 1970 quoted in Kinze 1995). Porpoise meat was greatly appreciated during the Middle Ages. It was served in the English court at coronation banquets and on other important occasions (Whymper 1883). In Denmark, a harbour porpoise fishery was first mentioned in 1357 and continued until the Second World War (Kinze 1995). Kinze estimated an average catch of at least 1000 animals took place every year in Danish waters for three centuries. Along the coast of Norway, large numbers were taken as early as the eleventh century (Watson 1985). At present hunting continues, on a small scale, only in Greenland and the Faeroes (IWC 1996).

Accidental (by-catch) mortality in fishing gear is recognised as the main threat at present for harbour porpoise populations in the northeast Atlantic (ASCOBANS 1994, IWC 1994, 1996, Donovan & Bjørge 1995, Tregenza et al. 1997, Vinther 1999). The harbour porpoise suffers a high degree of by-catch mortality across its range (Read & Gaskin 1988). In northern Europe, it is the most frequently caught cetacean species in fishing nets and it is caught in a wide variety of fishing gear, mainly gill nets but also salmon drift nets, pound nets for herring and salmon and mid-water trawls (Lindroth 1962, van Utrech 1978, Andersen & Clausen 1983, Kinze 1990a, Northridge & Lankester 1992, Clausen & Kinze 1993 quoted in Lowry & Teilmann 1994, Tregenza et al. 1997, Vinther 1999). There are historical records of porpoises caught in gill nets as long ago as the sixteenth century in Europe (Belon 1551, quoted in Harmer 1927), but it is clear that increased fishing effort together with innovations in net design and use of thinner synthetic fibres (which reduces detectability) have resulted in steeply increased catch rates.

The impact of by-catches on harbour porpoise populations is, at the moment, difficult to assess but there is concern about the sustainability of these catches. In 1990 and 1991, the Scientific Committee of the IWC recommended, with the "*highest priority*", the reduction of by-catch for harbour porpoise (IWC 1991, 1992). It also noted the need to improve knowledge of stock identity and migration, and obtain reliable figures on by-catches and on abundance.

An additional cause of harbour porpoise mortality in Scotland is the bottlenose dolphin (*Tursiops truncatus*), particularly in the Moray Firth area. Post-mortem examinations of a number of porpoise carcasses (all with multiple skeletal fractures and damage to internal organs), provided the first evidence of dolphin attacks, when measurements of tooth marks present in the skin corresponded with the tooth spacing in *Tursiops* mandibles (Ross & Wilson 1996). Subsequently, bottlenose dolphins were observed attacking porpoises and repeatedly throwing them out of the water. The reasons for these interactions are unknown, but could include competition for food, play, practice-fishing or sexual behaviour (Ross & Wilson 1996).

In July 1994, a survey of Small Cetacean Abundance in the North Sea (SCANS) was carried out to estimate numbers of harbour porpoises and other small cetaceans in the North Sea and adjacent waters. To date this survey has provided the most accurate and complete information on population figures for harbour porpoises in the area. Previous ship and aerial surveys were on a smaller scale (e.g. Heide-Jørgensen et al. 1992, 1993, Bjørge & Øien 1995). The population estimates for harbour porpoise obtained from SCANS are given in Table 1. As pointed out by Hammond et al. (1995), these figures were calculated from observations that took place in only one month.

Porpoises clearly exist in large numbers in the northeast Atlantic (Hammond et al. 1995) and, as such, are likely to have a quantitatively important place in the marine food web. In addition to their ecological importance, as fish eaters they may compete with commercial fisheries. Diet has consequences for individual fitness and, ultimately, population status and it is of interest to determine whether the large-scale fluctuations in fish stocks seen in the second half of the twentieth century have influenced porpoise diet and population trends. In so far as porpoises prey on species also eaten by humans, the health consequences of diet choice (e.g. in terms of nutrition or bioaccumulation of contaminants) are of direct relevance to the human population.

The general biology of harbour porpoises is reviewed in Bjørge & Donovan (1995) and Read (1999). However, to date there has been no major review of diets of harbour porpoises

Table 1 Abundance estimates of harbour porpoise for the different blocks surveyed by the Small Cetacean Abundance in the North Sea (SCANS) survey (data from Hammond et al. 1995), CV = coefficient of variation.

Block	Area covered in the survey	CV	Porpoise abundance
A	Celtic Shelf	0.57	36 280
B	Channel and South tip North Sea	0	0
C	East coast of Britain	0.18	16 939
D	West northern North Sea (excluding J)	0.25	37 144
E	North central North Sea	0.49	31 419
F	Central North Sea (56°N–58°N)	0.25	92 340
G	South central North Sea	0.34	38 616
H	South eastern North Sea	0.29	4211
I	Kattegat	0.34	36 046
J	Waters off Shetland and Orkney	0.34	24 335
L	Coastal area S and W of Jutland	0.47	11 870
M	Off SW coast of Norway	0.27	5666
X	Bay of Kiel	0.48	588
Y	Northern Wadden Sea	0.27	5912
Total		0.14	341 366
	(95% confidence intervals)		(260 000–449 000)

and little attention has been given to their ecological role as marine top predators. The present paper reviews information on the diet of harbour porpoises in the northeast Atlantic and will try to answer the following questions:

(1) What is their feeding niche: what do harbour porpoises eat and where do they obtain their food?
(2) Are they specialist or generalist predators and is their diet related to prey abundance (opportunistic or selective)?
(3) Do porpoises compete with other top predators such as seals and other cetaceans, and do they compete with fisheries?
(4) Is there evidence of long-term trends or changes in diet composition?
(5) What are the consequences of diet composition for individual health and population status (e.g. is the diet nutritionally adequate, does diet choice play a role in fishery by-catch mortality, and are there adverse consequences of contaminant bioaccumulation)?
(6) What important questions require further research?

Study methods

Almost all published accounts of porpoise diet are based on stomach contents analysis. The largest scale studies are associated with hunting of porpoises in the Black Sea (Tsalkin 1940, quoted in Tomilin 1957) but most studies are on by-caught and stranded animals. The methodology of stomach contents analysis was reviewed by Pierce & Boyle (1991).

The present review focuses mainly on results from stomach contents analysis. However, some information on diet can also be obtained indirectly from studies on distribution and behaviour. Relatively new techniques for obtaining information on marine mammal diets such as fatty acid signature analysis of blubber and stable isotope analysis have not yet been applied to porpoises on a large scale. Fatty acids are mainly of dietary origin and stable isotope values vary geographically and, in a systematic way, with trophic level. In contrast with stomach contents analysis, these new techniques can provide information on the prey ingested over a longer period (days to months; e.g. Tiezen 1978, Hobson 1990, Iverson et al. 1995, Kirsch et al. 1998, 2000, Hooker et al. 2001). However, stable isotope analysis provides relatively coarse level data on diet, providing data mainly on the trophic level at which an animal feeds (see Pauly et al. 1998). On the other hand, fatty acid analysis has the potential to provide quantitative data on diet, although realisation of this potential requires information on the fatty acid composition of all putative prey, including data on variability, and the computing power to solve the equivalent of an extensive series of simultaneous equations. Fatty acid signature analysis is well-established as a technique for studies on seals (e.g. Iverson et al. 1997). Doubts were raised as to its applicability to cetaceans due to blubber stratification: the outer blubber layers being relatively metabolically inert while the inner layers, closer to the muscle, are metabolically active. Also, blubber from different parts of the body may show differences in fatty acid composition, as found for some cetaceans (Ackman & Lamothe 1989). Recent studies in harbour porpoise have shown that dietary fatty acids are concentrated in the inner blubber (Koopman et al. 1996, Koopman 1998) and the fatty acid composition seems to be uniform in the body with the exception of the caudal peduncle.

What do harbour porpoises eat?

The earliest published information available on the diet of harbour porpoises derives from the examination of single specimens, which were captured accidentally in fishing gear or stranded, during the nineteenth century. Dewhurst (1834) records that “porpoises live upon small fish though they will eat any offal and garbage that is thrown into the sea”. Southwell (1881) observed that “the food consists of fish and it follows the shoals of herring, etc., amongst which it commits great depredation; it has a taste for salmon (*Salmo salar*) and is sometimes taken in the salmon-nets”. Van Beneden (1889) stated that “the porpoise preys on fish, including herring, but may also eat crustaceans, cephalopods and even marine plants”.

Descriptions of porpoise diets from the late nineteenth and early twentieth centuries include records of a wide variety of fishes and, in some cases, cephalopods and crustaceans in stomachs. Scott (1903), examining the stomach contents of a porpoise caught in a salmon net in Scotland, found remains of fish (flesh and otoliths), of which the most frequent was whiting (*Merlangius merlangus*). The high numbers of otoliths found (240), in the opinion of the author, showed “how destructive these cetaceans can be when they get among a shoal of fishes”. Various small-scale studies in the northeast Atlantic from the early part of the twentieth century through to the 1970s document predation by porpoises on whiting, herring (*Clupea harengus*) and sometimes other fish species such as capelin (*Mallotus villosus*), mackerel (*Scomber scombrus*), sole (*Solea solea*), cod (*Gadus morhua*), eel (*Anguilla anguilla*), as well as shrimps and cuttlefish (Millais 1906, Stephen 1926, Harmer 1927, Freund 1932 quoted in Tomilin 1957, Fraser 1946, Darling 1947, Matthews 1952, Hardy 1959, Slijper 1962, Andersen 1965, Källquist 1975 quoted in Otterlind 1976).

Similar types of prey were recorded in other areas: for example, Pacific herring (*Clupea pallasii*), capelin, Pacific sardine (*Sardinops coerulea*) and smelt (Osmeridae) in the North Pacific (Sleptsov 1952 quoted in Tomilin 1957, Wilke & Kenyon 1952, Scheffer 1953, Fink 1959); herring, cod, mackerel (*Scomber scombrus*), hake (*Urophycis tenuis*), pollack (*Pollachius virens*), squid (*Loligo pealii*), smelt (*Osmerus mordax*), silver hake (*Merluccius bilinearis*) and redfish (*Sebastes marinus*) off eastern Canada (Sergeant & Fisher 1957, Smith & Gaskin 1974).

The most extensive published study on harbour porpoise diet was carried out in the Black Sea, where 4000 stomachs were examined by Tsalkin (1940 quoted in Tomilin 1957). The diet consisted mainly of benthic fish (several goby species, *Gobius rotan*, *G. melanostomus*, *G. syrman*, *Mesogobius batrachocephalus*; Black Sea flounder, *Pleuronectes flesus flesus*; Black Sea sole, *Solea nasuta*; bream, *Abramis brama* and Black Sea whiting, *Gadus euxinus*). Pelagic species (Black Sea silverside, *Atherina pontica*; Black Sea anchovy, *Engraulis encrasicholus*; pikeperch, *Lucioperca lucioperca*; mullet, *Mugil* sp. and Black Sea shad, *Caspialosa* sp.) were also found but were thought to be taken only when they occurred in large and dense schools.

In the northeast Atlantic, the first detailed study on harbour porpoise diet was carried out by Rae (1965). This author, concerned with the possible role of porpoises as predators of salmon, examined the stomach contents of 52 animals by-caught in different fishing gears in Scotland from 1959 to 1965. Herring and whiting were the main prey found. In a later study, from 1965 to 1971, a further 30 by-caught and 11 stranded porpoises were examined (Rae 1973). In these 41 stomachs, the main prey were clupeids (herring and sprat *Sprattus sprattus*) and small gadoids (mainly whiting). No evidence of predation on salmon was found in either study. Lindroth (1962) examined the stomach contents of 50 harbour porpoises from the Baltic Sea captured from 1960–1, again with the aim of finding out whether porpoises prey on salmon, and also found no evidence of salmon in the diet. Remains of sprat, herring, Baltic cod (*G. m. callarias*), gobies (*Aphya minuta*) and sandeels (*Ammodytes* sp.) were found.

As schemes to record and examine stranded cetaceans were set up in different countries and research programmes started collecting by-caught specimens during the 1980s and 1990s, more studies on harbour porpoise diets were carried out (see Table 2). The results of these studies demonstrated that harbour porpoises feed on both pelagic schooling fish species, for example, herring, capelin, whiting, blue whiting *Micromesistius potassou*, sardine, northern anchovy, and demersal or benthic fish, for example, hake, *Trisopterus* spp., sandeels (Ammodytidae), gobies, sole, dab *Limanda limanda*, Greenland halibut *Reinhardtius hippoglossoides* (Desportes 1985, Sekiguchi 1987, Kinze 1989, Lick 1991a,b, Aarefjord et al. 1995, Börjesson & Berggren 1996, Malinga & Kuklil 1996, Rogan & Berrow 1996, Santos 1998). Other prey species such as cephalopods (ommastrephids, sepiolids, loliginids, gonatids), other molluscs, crustaceans (e.g. euphausiids) and polychaetes (*Nereis*) were also recorded (Smith & Gaskin 1974, Desportes 1985, Sekiguchi 1987, Kinze 1989, Smith & Read 1992, Gaskin et al. 1993, Gearin et al. 1994, Rogan & Berrow 1996, Santos 1998). Plastic and other foreign objects such as nylon fishing line and a banana peel have also been recorded in the stomachs (Kastelein & Lavaleije 1992, Baird & Hooker 2000).

Table 2 Main studies on harbour porpoise diets since the 1980s (s = stranded animals, b = by-caught, m = stranded and by-caught, d = direct hunt). *No data on number of stomachs with food provided, [a]adult animals, [c]calves (from Smith & Read 1992).

Area	Stomachs analysed	Stomachs with food remains	Main Prey	Reference
NE Atlantic				
France	17 (s)	8	Blue whiting, scad, hake	Desportes 1985
Denmark, Sweden, Norway	247 (m)	179	Herring, gadids	Aarefjord et al. 1995
Germany	54 (m)	36	Sole, cod	Lick 1991a,b
	34 (m)	*	Sandeels, sole	Benke & Siebert 1996
Ireland	26 (m)	19	*Trisopterus* spp., whiting, herring	Rogan & Berrow 1996
United Kingdom	~250 (b)	100	Gadids, sandeels, gobies	Martin 1996
Scotland	72 (m)	72	Whiting, sandeels	Santos 1998
The Netherlands	62 (m)	62	Whiting	Santos 1998
Denmark	58 (m)	58	Cod, viviparous blenny, whiting	Santos 1998
NW Spain	6 (m)	6	Scad, sandeels, *Trisopterus* spp.	Santos 1998
Skagerrak and Kattegat Seas				
Sweden	171 (m)	145	Herring, sprat, whiting	Berggren 1996, Börjesson & Berggren 1996
Baltic Sea				
Germany	48 (m)	42	Cod, gobies, herring	Lick 1991a,b
	27 (m)	*	Gobies, herring, cod	Benke & Siebert 1996
Poland	16 (b)	14	Cod, gobies, herring	Malinga & Kuklik 1996
NW Atlantic				
Eastern Canada	160 (b)	127	Herring, silver hake, cod	Recchia & Read 1989
	[a]149 (b)	[a]136	Clupeids, gadids	Smith & Read 1992
	[c]31 (b)	[c]24	Euphausiids	
	138 (b)	111	Capelin, herring	Fontaine et al. 1994
	95 (b)	95	Herring, silver hake, red and white hakes	Gannon et al. 1998
Greenland	18 (d)	18	Greenland halibut, haddock	Kinze 1989
	20 (d)	20	Capelin, halibut	Kinze 1990b
Pacific Ocean				
Northern Japan	20 (b)	5	Ommastrephid squids, herring, anchovy, hake	Gaskin et al. 1993
Washington	100 (b)	94	Pacific herring, squid, smelts	Gearin et al. 1994
California	15 (m)	9	Northern anchovy	Sekiguchi 1987

Are porpoises opportunistic or selective predators?

As Dunnet (1996) pointed out, opportunism, selection and availability are "in fact shorthand for very complex biological interactions about which we know only a little in quantitative terms". Strictly applied, the term "opportunistic" predation can be taken to imply that prey are taken as encountered, with the implication that prey availability is the only criterion affecting diet choice. Following the theory of optimal diet selection (e.g. Pulliam 1974), observation of opportunistic predation (*sensu stricto*) might be taken to imply that high quality prey are relatively rarely encountered. However, the term is probably used at least as often as a catch-all phrase which indicates no more than that evidence for active selection was not found (and often was not sought).

The diversity of prey eaten and the geographical variation found in the diet have led some authors to consider the harbour porpoise to be an opportunistic feeder (e.g. Martin 1996, Teilmann & Dietz 1996), not limited to shallow waters, but able also to feed pelagically on mid-water species from deeper habitats (IWC 1996). In fact, few studies in the northeast Atlantic have been able to address this question because information on prey abundance, for all the species at an appropriate spatial and temporal scale, is rarely available. Donovan & Bjørge (1995) note that, to answer the question of whether harbour 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".

Santos (1998) compared the rank order of importance (by weight) of different fish species in harbour porpoise diets and fishery landings in Scotland, excluding species eaten by porpoises but not commercially fished, and found a positive correlation in 3 yr out of the 5 yr studied. Species that are not fished made up between 0.3% (1996) and 2.6% (1994) of the diet by weight but their absence in landings data simply reflected low (or zero) market value. Using catch statistic data as a measure of species abundance has potential risks since fishery landings are also affected by changes in market demand, fishing effort, establishment of management measures such as minimum landing size, total annual catches, area closures, etc. (Hislop 1996). Nevertheless, fishery-catch data can sometimes provide a reasonable estimate of the abundance, distribution and availability of the prey species (Evans 1975), and the correlation between the importance rankings of certain species in commercial catches and in porpoise diets (Santos 1998) remains of interest. To the extent that fisheries take species in proportion to their abundance, this result provides weak support for the notion of porpoises as an opportunistic species.

Porpoise distribution around Shetland was spatially correlated with sandeel distribution in 1992 and 1993 but there was no correlation between the seasonal patterns of porpoise numbers and prey abundance (Evans & Borges 1995).

The nature of feeding strategies can be revealed by studies of dietary variation. Against a background of varying fish abundance, piscivorous predators, especially those foraging opportunistically, might be expected to show regional, seasonal or interannual variation in diet. On the other hand, evidence of sex- or age-related variation in diet may be consistent with opportunistic predation (if there is sex- or age-related habitat segregation) or provide evidence for the role of other factors (e.g. if both sexes occupy the same habitat). Despite the existence of numerous studies on harbour porpoise diet there has been little quantitative analysis of patterns in diet in the northeast Atlantic. This is mainly due to the lack of appropriate sample sizes that would allow disentanglement of the effects of all the factors potentially affecting diet variability.

Geographical variation

Several studies on harbour porpoise diets in the northeast Atlantic have revealed geographical variation in the main prey consumed (in the UK, Martin 1996, Santos 1998; in Norway, Denmark and Sweden, Aarefjord et al. 1995, Berggren 1996; in Germany, Lick 1991a,b, Benke & Siebert 1996; in Ireland, Rogan & Berrow 1996). One caveat is that not all of these studies were contemporaneous and the confounding effect of temporal shifts in diet cannot always be ruled out.

Based on examination of prey remains from the stomachs of 100 porpoises stranded and by-caught on the British coast from 1989 to 1994, the most important prey in terms of biomass were gadoids (whiting, haddock, Norway pout *Trisopterus esmarkii* and pollack), while sandeels and gobies were by far the most frequently eaten. Differences were found between diets in different areas of the British coast, with sandeels taken in bigger numbers on the east coast, while Norway pout was taken by more than half of the porpoises from Shetland, but was not eaten elsewhere (Martin 1996). The greater dietary importance of *Trisopterus* in Shetland than elsewhere in Scotland is also supported by results in Santos (1998). Harbour porpoises from Irish waters fed mainly on *Trisopterus* spp. (Rogan & Berrow 1996).

Significant between-area differences in the diet were reported by Santos (1998), who analysed the stomach contents of 198 stranded and by-caught porpoises from Denmark, The Netherlands, Scotland and Galicia (NW Spain) mainly from 1989 to 1996. The author found various significant between-area differences in the diet. Porpoises from Scotland had eaten significantly more sandeels than had those from Denmark and Holland, also more sepiolids and fewer cod than in Denmark. Danish porpoises took significantly more gobies than did porpoises in Scotland, while viviparous blennies (*Zoarces viviparus*) were present only in the Danish diet. In Holland, porpoises had taken significantly more gobies, dragonets and squid *Loligo forbesi* than had porpoises from Scotland, and more sepiolids than porpoises from Denmark. In Galicia, despite a small sample size, a wider range of prey was recorded than in other areas, including some species found only in the Galician diet (e.g. silvery pout *Gadiculus argenteus thori*, argentine *Argentina* sp.).

Regional differences in the diet were also found by Aarefjord et al. (1995), who examined stranded and by-caught specimens from Norwegian, Danish and Swedish waters (1985–90). Overall, herring was the most important single prey species, while gadoids made up more than half of the total prey weight. However, harbour porpoises from the Danish North Sea and the Baltic took mainly cod, whiting, sandeels and gobies, while saithe, blue whiting and capelin were more frequent in porpoises from the Norwegian waters. Herring and sprat were found to be the main food of harbour porpoises stranded and by-caught during 1988–93 in the Swedish Skagerrak and Kattegat Seas (Berggren 1996).

In German waters, results from Lick (1991a,b) and Benke & Siebert (1996), from strandings and by-catches in 1985–90 and 1991–3, respectively, indicate geographic differences in the diet of harbour porpoises. In porpoises from the North Sea from 1991–3, sandeels made up almost 40% of the prey weight, with a further 30% being common sole (*Solea solea*). In contrast, in the Baltic Sea over 50% of the total prey weight was made up of gobies, while 23% was herring and 15% was cod (Benke & Siebert 1996).

Seasonal variation

Seasonal variation in harbour porpoise distribution has been described as a general inshore movement in summer and offshore movement in winter, although east–west and north–south migrations have also been proposed in different locations (e.g. Tomilin 1957, Gaskin et al. 1974, Gaskin 1977, 1984, Taylor & Dawson 1984, Gaskin & Watson 1985, Northridge et al. 1995, Read & Westgate 1997). Seasonal movements are believed to be related to prey availability or to breeding habitat (Gaskin 1977, Northridge et al. 1995, Read & Westgate 1997). Camphuysen & Leopold (1993) interpreted the higher numbers of porpoise sightings and strandings on the Dutch coast in winter than in summer as indicating a seasonal east-west movement.

Aspects of the ecology of some of the prey species may assist in interpreting seasonal differences in diet (Santos 1998). Sandeels spend most of the autumn and winter (September to March) buried in the sand, with the exception of the spawning period between December and January (Macer 1966, Reay 1970, Langham 1971, Winslade 1974, Wright 1996). This is consistent with the higher prevalence of sandeels in spring and summer diets than in autumn and winter diets of Scottish harbour porpoises (Santos 1998). Although, arguably, echolocating porpoises should be able to detect sandeels in the sand it is perhaps energetically more costly to catch them. The higher importance of whiting in the winter diet could relate to the lower availability of sandeels but is also consistent with trends in whiting abundance. Trawl survey data for the east coast of Scotland indicate that whiting, poor cod and Norway pout are more abundant in inshore waters in winter than in summer (Santos et al., unpubl. data). Seasonal variation was also documented in the diet of harbour porpoises by-caught in Swedish waters: while herring was the main prey all year round, the contribution of sprat and whiting varied seasonally (Börjesson & Berggren 1996).

Seasonal differences have also been reported in the size of prey eaten by porpoises (Santos 1998). In Scotland, smaller whiting were taken in autumn and bigger whiting were eaten in spring and summer, while bigger sandeels were taken in winter and spring than summer. In Denmark, smaller viviparous blennies and whiting were taken in spring than summer. In Holland, smaller gobies were taken in autumn than in winter and spring. Such trends may also be interpreted with reference to fish life cycles, in that small fishes are most likely to be taken when 0-group fishes move into the area used by porpoises. Thus, large numbers of 0-group sandeels become available in the summer months, when they are preyed upon by harbour porpoises and a wide variety of birds, fishes and other marine mammals (e.g. Furness & Hislop 1981, Jonsgåard 1982, Perkins et al. 1982, Furness 1987, Daan 1989, Harris & Riddiford 1989, Monaghan et al. 1989, Pierce et al. 1989, 1991a,b, Harris & Wanless 1991, Storey 1993, Thompson et al. 1991).

Seasonal differences in the diet of harbour porpoises have been reported also in studies outside the northeast Atlantic. In Atlantic Canadian and United States waters, prey diversity was higher in winter than in summer, with porpoises eating mainly herring, silver hake and pearlsides (*Maurolicus weitzmani*) in the autumn (Palka et al. 1996). Gannon et al. (1998) analysed the stomach contents of 95 harbour porpoises by-caught in autumn in the Gulf of Maine and compared the results with previous studies of harbour porpoises by-caught in summer in the Bay of Fundy (Smith & Gaskin 1974, Recchia & Read 1989, Smith & Read 1992). They noted that herring was the main prey for porpoises in both autumn and summer but was less dominant in the autumn diet than in summer. They also found that porpoises ate a wider variety of prey and of prey sizes in autumn than in summer.

Interannual variation

Interannual variation in the diet might be expected to follow variation in the availability of preferred prey. Declines in the availability of common prey could lead harbour porpoises to switch to other prey species and/or prey sizes. For some of the commercial fish species eaten by porpoises, estimates of abundance and size distributions are available. However, this is not the case for many other prey species (e.g. the smaller inshore fish such as blennies, gobies and eels).

Significant interannual differences in the average size of fishes eaten (e.g. for sandeels and whiting in Scotland, viviparous blenny and whiting in Denmark, and gobies in Holland) were described by Santos (1998). In terms of amounts eaten, significant interannual variation was found only for herring, and the significance of this variation was strongly influenced by a single porpoise killed by bottlenose dolphins in the Moray Firth in November 1994, which had eaten many small herring (<150 mm). In any case, the interannual changes were apparently unrelated to changes in herring abundance. However, it is worth noting that of the three main studies on porpoise diets in UK waters, only the earliest (Rae 1965, 1973) records herring as forming a major part of the diet and this change could reflect the decline in herring abundance in the North Sea since the 1960s. This topic is revisited in more detail below.

Outside the northeast Atlantic, Recchia & Read (1989) found some differences in the diet of harbour porpoises by-caught in groundfish gill nets in the Bay of Fundy (Canada) during two time periods (1969–72 and 1985–7). Porpoises from 1969–72 had taken mackerel and silver hake less often than porpoises from 1985 to 1987 although herring, silver hake and cod remained the main prey in the diet for both samples.

The main prey (by percentage occurrence) of harbour porpoises off northern Washington differed between the years 1988–90. In 1988 it was Pacific herring, followed by squid and smelt, while in 1989 smelt was the main prey followed by squid (*Loligo opalescens*) and gadoids. In 1990, Pacific herring was again the main prey followed by smelt and gadoids (Gearin et al. 1994).

Ontogenetic variation

Differences in diet between adult and juvenile porpoises in the northeast Atlantic have been found in several studies (Lick 1991a,b, Benke & Siebert 1996, Börjesson & Berggren 1996, Santos 1998). Juveniles cannot dive as deep as adults and could be prevented by their small size from catching and eating big prey.

Differences in the diet of young (<120 cm total length) and adult porpoises were found in a sample of 78 stomachs from porpoises stranded and by-caught in Germany. Young porpoises took more gobies, while adult porpoise took more flatfishes and gadoids and had a bigger variety of prey species in the stomach (Lick 1991a,b). Similar results were found in a sample of 61 porpoises by-caught and stranded in Germany during 1991–3 (Benke & Siebert 1996). Börjesson & Berggren (1996) also noted that gobies were important in the diet of calves (<1-yr old) from porpoises by-caught off Swedish waters. The authors concluded that the small size of gobies could make them a suitable prey for calves. Santos (1998) found that, in Scotland, adult harbour porpoises ate bigger whiting than did juveniles, while in Denmark juveniles ate bigger viviparous blenny and whiting than adults, and in Holland adults took bigger gobies and sandeels than juveniles. The author considered that it was possible that most of these differences related to adult porpoises feeding further offshore than juveniles. In addition, the analysis showed that, in Holland, smaller porpoises took fewer whiting but more gobies than did bigger porpoises.

In other studies in the northeast Atlantic, no significant differences were found between the diets of calves ($<$113 cm total length) and adult porpoises in Scandinavian waters, although gobies were the most frequent prey in the stomach of 0 and 1-yr old porpoises (Aarefjord et al. 1995), or between diets of juvenile and adult porpoises in a sample of animals stranded and by-caught in the UK (Martin 1996).

Outside the northeast Atlantic, although no differences were found between the diets of juvenile and adult porpoises in Canadian waters (Smith & Gaskin 1974), comparison of a sample of 31 calves ($<$1-yr old) and 149 adult porpoises by-caught in gill nets in the Bay of Fundy from 1985 to 1991 revealed that calves were taking euphausiids during their first summer while adult porpoises ate herring (Smith & Read 1992). The authors suggested that calves "learn" to forage on euphausiids before starting to take larger prey such as fishes. A comparison of the diets of 13 calves and 74 juvenile and adult porpoises by-caught in gill nets in the Gulf of Maine in 1989 and 1991–4 showed that calves had eaten a greater proportion of pearlsides and euphausiids than adults and had also taken smaller herring and silver hake (Gannon et al. 1998).

Diet of male and female harbour porpoises

Differences in diets of males and females might be expected if the sexes tend to inhabit different areas, as a consequence of the larger average body size in females, and if the foraging behaviour of females is affected by the presence of nursing calves.

Segregation of harbour porpoises in groups of different sex and/or age has been proposed by several authors to explain differences in by-catch figures. The predominance of mature males in the catch in the Baltic Sea was explained by Tomilin (1957) as a consequence of adult males forming separate groups that are more "mobile" than groups comprising juveniles or females with calves. Such segregation by age and sex has also been suggested as an explanation of high catches of sub-adult males in nets in offshore Canadian waters (Kinze 1994). In contrast, females accompanied by calves would tend to be associated with shallower waters (Kinze 1994). If this segregation takes place, females with calves would not only have a different distribution from males but could also be restricted in their search for food (e.g. by not being able to dive very deep or search long distances). Seasonal differences in the prey composition of adult female harbour porpoises, in a sample of 119 porpoises by-caught in the Swedish Kattegat and Skagerrak fisheries, were interpreted by Börjesson & Berggren (1996) as indicating that habitat preferences of females could be "dictated by their association with young calves". The absence of milk in the stomachs of six calves by-caught with their mothers in gill nets in the Bay of Fundy led Smith & Read (1992) to suggest calves are unable to nurse while their mothers are actively foraging. It is also possible that, rather than merely being a consequence of segregation, any differences in diet between the sexes could be a mechanism to reduce competition.

Few differences were found between the diets of male and female porpoises in Scotland, Denmark and Holland (Santos 1998). In Scotland, male porpoises ate more sepiolids and had a higher overall prey diversity than females as well as there being some difference in prey size. In Denmark, female porpoises had significantly more prey in the stomach than males. In Holland, female porpoises ate significantly more gobies than did male porpoises. This higher prey diversity in Scottish male porpoises could indicate different feeding grounds or less selectivity in the prey eaten. Female porpoises are significantly bigger and heavier than males and the higher number of prey in females' stomachs in Denmark could reflect higher energetic needs. However, this result was not found for the Scottish and Dutch porpoises. Aarefjord et al. (1995) found no significant differences in diet between seven adult females and 48 adult males, although they recognised that the number of females examined was very low. On the other hand, significant differences in the number of prey in the stomach were found between male and female porpoises of 1-yr old or less, with males eating more fish than females.

Outside the northeast Atlantic, results suggest an absence of dietary differences between the sexes. No differences in the diet between sexes were found in a sample of 81 harbour porpoises collected from eastern Canadian waters between 1969 and 1972 (Smith & Gaskin 1974) or in a sample of 100 harbour porpoises by-caught along the northern coast of Washington State (Gearin et al. 1994). Prey weight showed no significant differences between the sexes in a sample of 138 harbour porpoises by-caught in the Gulf of St Lawrence, Canada, in 1989 (Fontaine et al. 1994). Finally, no significant differences were seen in the diet of males and non-lactating females in a sample of 95 harbour porpoises by-caught in the Gulf of Maine (Gannon et al. 1998).

It should be noted that many studies do not distinguish between diets of lactating and non-lactating females and it seems that differences between diets of males and females are most likely to be seen when females are nursing calves.

Cause of death and diet variability

A basic problem with most recent studies on porpoise diets is that they are based on dead animals. Differences in stomach contents from animals dying from different causes are difficult to relate to feeding strategies. Thus, if sick animals had a diet different from healthy animals, does this difference indicate active changes in diet selection or simply a consequence of reduced mobility leading to lower prey encounter rates? Certainly, the cause of death represents a potential confounding factor and source of bias in dietary studies. If nothing else, different components of the population are represented in proportion to the frequency with which they die rather than their relative abundance in the living population. The problems arising from the use of stranded specimens in dietary analysis have been extensively discussed and reviewed elsewhere (e.g. Pierce & Boyle 1991, Sekiguchi et al. 1992). Strandings of cetaceans can be considered an "opportunistic" resource, the composition of which depends on many factors (wind and currents carrying the carcasses to the coast, accessibility of coastal locations, state of preservation, etc.). With the increase in interactions between marine mammals and fisheries, by-catches have become another source of samples for dietary studies. In contrast to strandings, which could represent injured or ill individuals, by-catches may provide samples of "healthy" animals (Kuiken et al. 1994a). However, the use of by-caught individuals is not free of potential biases, notably the possible bias of the diet towards the target species of the fishery and associated species (Waring et al. 1990) and the possible "net selection" of particular porpoise size and age classes. A disproportionately high number of juvenile porpoises amongst by-catches was reported in

Denmark (Clausen & Andersen 1988, Kinze 1994) and for the German fleet fishing in the Baltic and the North Sea (Kock & Benke 1996). It has been suggested that avoidance of nets could be related to experience, making young animals more vulnerable. Young animals could try to explore and play with the nets and become entrapped and this fact could also put females at risk if they try to rescue their calves (IWC 1994, Kinze 1994). Kinze also pointed out that the existence of age-related segregation in harbour porpoises would make some groups more vulnerable to by-catch. Gaskin & Blair (1977) found sub-adult males segregating from other groups in Canadian waters and staying closer to the coast and thus becoming more frequently entrapped in nets.

A problem with identifying by-catches, as such, arises if by-caught animals are freed from the nets (either by the fishermen or by other causes) and are found floating at sea or stranded on the coast. The diagnosis of by-catch in these animals is at present a difficult task. Carcasses are often too decomposed to allow any post-mortem study to be done and some net types do not cause net marks on the skin – perhaps the clearest indication of by-catch (Kuiken 1996). At present only a small percentage of cetaceans found stranded can be diagnosed clearly as by-catches (Siebert et al. 1996).

In Scotland, harbour porpoises killed by bottlenose dolphins is another source of samples available for analysis. However, these samples are also not free from potential biases. Ross & Wilson (1996) observed that, although there were no significant differences in the number of males and females killed, there was a bias towards porpoises of 100 cm to 140 cm, which corresponded with juvenile or prepubertal animals between 1 yr and 3 yr of age. They also noted that there is seasonal variation in the total number of strandings in the Moray Firth area, with a peak value in June, and that the "injured porpoises represented a relatively constant proportion of this number, such that within each month the number of injured porpoises was significantly correlated with the number that died of other causes".

In the northeast Atlantic, by-caught porpoises in Irish waters had eaten less clupeids and whiting than stranded porpoises but both groups had a similar proportion of gadoids in the diet (Rogan & Berrow 1996). However, the sample size in this study was small (nine and ten animals, respectively).

Santos (1998) found significant differences in the diet between porpoises killed by bottlenose dolphins and porpoises that died of other causes. Taking into consideration that the seasonal distribution of the deaths caused by bottlenose dolphins was not homogeneous, with more deaths occurring in the second and third quarters (spring and summer), the author noted that it was not surprising that porpoises killed by dolphins had taken more sandeels (since the importance of sandeels in the diet was also found to be significantly related to season with sandeels eaten mainly in spring and summer). The differences in the importance of the other species in the diet could be related not only to seasonal but also geographical differences in abundance and/or availability. The sample of harbour porpoises killed by bottlenose dolphins came mainly from the Moray Firth and the surrounding areas. A further seven came from further south, near the Firth of Forth. In all cases harbour porpoises killed by bottlenose dolphins came exclusively from the east coast of Scotland. Significant differences in the size of prey eaten, between porpoises killed by bottlenose dolphins and the remaining porpoises, could also be explained by the seasonal distribution of the deaths caused by dolphins. During the summer months, when more deaths take place, younger sandeels and bigger whiting are taken by harbour porpoises in bigger numbers.

Differences in diet between by-caught and stranded animals have been found for other cetacean species, for example, common dolphins, dusky dolphins (*Lagenorhynchus obscu-*

rus) and Heaviside's dolphins (*Cephalorhynchus heavisidii*) in South Africa (Sekiguchi et al. 1992).

Where and how do porpoises feed?

Direct information on where porpoises feed comes from studies of distribution and diving behaviour. Westgate et al. (1995) recorded diving behaviour of harbour porpoises in the Bay of Fundy by attaching time-depth recorders. Typical dives were short and shallow (mean duration 44 s and mean depth 14 m), although dives to depths of up to 226 m (the maximum water depth in the area) and durations up to 321 s were recorded. Some evidence was found that dives were less frequent, but deeper, at night. Most dives were characterised as "flat bottomed", with around one-third of the dive time being bottom time, which would be consistent with foraging at the sea bed. Pierpoint et al. (1999) recorded porpoise echolocation activity on the Welsh coast using acoustic data loggers and found that porpoise activity was highest at night and during the ebb tide.

Goodson (1994), in the context of discussing by-catches in set gill nets, comments that very little is known about the foraging strategies of harbour porpoises. However, records of by-catches themselves provide evidence about where and how porpoises feed, some information can be gleaned from records of surface observations, and relevant data are emerging from recent studies on echolocation behaviour. There is little doubt that porpoises often feed near the sea bottom, as indicated by several lines of evidence: the importance of sandeels in the diet, the presence of sepiolids in the diet, the characteristics of the sonar system and the fact that porpoises are often caught in bottom-set gill nets.

Surface observations

Harbour porpoises seem to be gregarious and schools consist normally of few animals (nine in the Bay of Fundy, Gaskin et al. 1974) although aggregations of several hundred individuals have been reported in the literature (Fink 1959, Rae 1965). However, porpoises are believed to hunt independently rather than in groups (Read 1999).

Pierpoint et al. (1994) observed porpoises in tidal races surfacing repeatedly at the same location, always orientated so as to face into the tidal stream, which they interpreted as foraging activity. The presence of gulls scavenging at the water surface supports this interpretation and, although associations between individuals were temporary, groups of up to 10 porpoises were seen. Silva et al. (1999) observed porpoises from land on the Portuguese coast during daylight hours. Numbers of sightings were highest at 09.00 and gradually declined through the day. In relation to the tidal cycle, numbers were low at both low and high tide. Maximum numbers were seen when tide height was 1 m below the height at high tide, but it is not stated whether this was during the ebb tide or flood tide.

Watson & Gaskin (1993) used surface observations to estimate dive times, which they record as being between 35 s and 4 min for feeding porpoises in the Bay of Fundy.

Echolocation in porpoises

Sturtivant et al. (1994) reviewed information on porpoise echolocation. Evans (1973) suggested that sonar in porpoises is used mainly for target detection rather than target classification owing to its monochromatic nature; Amundin et al. (1988) also noted that porpoise clicks show a narrow-band width. Hatakeyama & Soeda (1990) recorded the clicks to be mainly in the range 125–140 kHz.

Prey searching involves the use of a narrow-beam, narrow-band high-frequency sonar (with a peak frequency around 130 kHz, Kastelein et al. 1999) believed by Goodson & Sturtivant (1996) to have evolved for short-range foraging, particularly near to the sea surface or the sea bottom. Kastelein et al. (1997a) also suggest that porpoise echolocation is likely to be adapted for detecting prey on the sea bottom. Their experiments showed that porpoises could detect steel and plastic discs buried up to 7 cm deep in sand and the authors' comment that similar objects should be detectable when buried at greater depths in a muddy substratum because the substratum density would be closer to that of water.

The occurrence of very small prey such as bobtail squid (Sepiolidae, e.g. *Sepiola atlantica*, the adults of which are no more than 2 cm in length) naturally leads to questions about how they are caught. Sepiolids are sit-and-wait predators which normally remain partially buried in the substratum. They are probably detected by porpoises directing their sonar into the substratum, and it is probably the acoustic signal from the hole rather than the animal that allows them to be detected (D. Goodson, pers. comm.)

Inferences from dietary studies

Some further general inferences about feeding areas and the feeding niche can be made with reference to the ecology of the prey species. A wide variety of prey has been found in the stomachs of harbour porpoises (see previous sections), including pelagic, mesopelagic and benthic species. Prey species found in the diet of harbour porpoises are mainly small schooling fish $<$400 mm long, indeed in most cases $<$300 mm (Read 1999). It has been suggested that harbour porpoise teeth are used only to hold the prey but not to break it up into smaller pieces and, therefore, porpoises are limited as to the size of prey they can consume.

In the northeast Atlantic, a mixture of mainly demersal species (whiting, cod, sandeels, *Trisopterus* spp., gobies) has been cited as the main prey in most cases (Lick 1991a,b, Benke & Siebert 1996, Martin 1996, Rogan & Berrow 1996, Santos 1998) although in some areas a higher proportion of pelagic prey (mainly herring) has been recorded (e.g. Berggren 1996). Aarefjord et al. (1995) found a predominance of pelagic species (herring, capelin) in the diet of harbour porpoises by-caught in Norwegian waters, while benthic prey (cod, whiting, sandeels, Pleuronectidae) predominated in the stomach contents of porpoises by-caught and stranded in Sweden and Denmark. Outside the northeast Atlantic, pelagic species such as herring, capelin, smelt (Smith & Gaskin 1974, Recchia & Read 1989, Fontaine et al. 1994, Gannon et al. 1998) have been quoted as the main prey for harbour porpoises in the Bay of Fundy, the Gulf of Maine and the Gulf of St Lawrence (eastern Canada). In the North Pacific, clupeids (herring, capelin, sardine) were again recorded as the main prey for harbour porpoises (Wilke & Kenyon 1952, Scheffer 1953, Fink 1959).

In Scottish waters, the two main prey types recorded in stomach contents during the 1990s were whiting and sandeels (Santos 1998) and it may be proposed that porpoises spend a substantial amount of time in areas frequented by these species. Whiting is a demersal species living in shallow waters, usually from 39–200 m over sandy or muddy grounds. It can reach up to 70 cm standard length, although normally the size is 30–40 cm (Whitehead et al. 1989). Its distribution extends from northern Norway towards Iceland to the west and towards the northern coasts of Portugal to the south. It is also present in the Mediterranean, Aegean, Adriatic and Baltic Seas (Hislop 1972). Whiting mature at around 2 yr of age and at a modal length (for females) of 26 cm. The spawning season is extended, beginning in February in the southern North Sea and March in the northern North Sea and ending in June. Spawning normally takes place in waters less than 100 m depth (Hislop 1984). During the first year of life, whiting are found in shallow waters, concentrating in the central and southern North Sea and in Scottish coastal waters. Most of the whiting taken by Scottish, Dutch and Danish harbour porpoises in Santos (1998) were estimated to be $<$23 cm in length 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), which would explain the greater importance of whiting in Scottish and Dutch porpoise diets than in diets of porpoises from more northern areas such as Norwegian Waters.

Sandeels are a group of demersal fishes which, in the northeast Atlantic, comprise three main species with very similar otoliths, *Ammodytes marinus*, *A. tobianus* and *Gymnammodytes semisquamatus*. Two other species, *Hyperoplus immaculatus* and *H. lanceolatus* (commonly called greater sandeels) attain a bigger size, which distinguishes them from the common or lesser sandeels, and they are also less abundant. Sandeels receive their name because of their unique way of life, spending the hours of darkness and most of the winter buried in the sand (Macer 1966, Reay 1970, Langham 1971, Winslade 1974). Because of this characteristic they are considered demersal, depending on a suitable bottom substratum to burrow, but during their activity periods they lead a pelagic life (Storey 1993). Sandeels feed on plankton and move throughout the water column during the day. Of the three main species found in the Northeast Atlantic, *Ammodytes marinus* is the most common, also being one of the commonest species on the continental shelf of northwest Europe and accounting for 10–15% of the total fish biomass of the North Sea (Sparholt 1990).

Food consumption by harbour porpoises

Harbour porpoises have some unique characteristics among cetaceans. They are one of the smallest cetaceans and most of their range is in cold waters. Their life history includes a very short nursing period (usually less than 1 yr), sexual maturity is attained at around 3 yr of age and there is a very short resting period between pregnancies (usually females give birth each year), so that females are often pregnant and lactating at the same time (Read et al. 1997). Smeenk (pers. comm.) found that, in Dutch waters, most of the females do not give birth every year, perhaps due to unfavourable food conditions or impaired health. Harbour porpoise habitat and life history impose very high energetic demands. Furthermore, their small size means that they cannot store much energy and this makes them more dependent on a year-round proximity to food sources (Brodie 1995). According to Brodie, for harbour porpoise this dependence has “the consequence that its distribution and nutritive condition may more strongly reflect the distribution and energy density of its prey than for other cetaceans”.

Yasui & Gaskin (1986) estimated that the daily feeding rate of a non-lactating adult harbour porpoise would be 3.5% of its total body weight per day, considerably lower than values from previous studies based on food intake records from captive animals (e.g. 8.26% quoted by Sergeant 1969, based on data from Andersen 1965). However, more recent captive feeding studies tend to support the higher values. Kastelein et al. (1997b) recorded food consumption in captivity for the species (based on six individuals) to be between 4% and 9.5% of body weight. Lockyer et al. (2001) recorded food consumption to change seasonally from 7% to 9.5% of body weight for two harbour porpoises in captivity.

Santos (1998) used the more conservative estimate of 3.5% and population size estimates from Hammond et al. (1995) to calculate the amount of prey removed each year by harbour porpoises in Scottish, Danish and Dutch waters. Her figures indicate that porpoises could be removing significant amounts of several commercial fish species. For example, the estimated consumption of whiting by porpoises surpasses the landings of this species for human consumption in the North Sea. Thus, extrapolating from Scottish dietary data, harbour porpoises off Scotland and the east coast of England (SCANS blocks C, D and J) could consume around 14 640 t of whiting, 13 800 t of sandeels and 1000 t of herring per year. Off the Danish coast (SCANS blocks I and L), harbour porpoises could eat around 2880 t of herring, 6660 t of cod and 6230 t of viviparous blenny, while off the Dutch coast and west coast of Germany (SCANS blocks H and Y) porpoises could eat around 1800 t of whiting, 650 t of cod and 300 t of sandeels (assuming porpoises off the east coast of Germany to have a diet similar to the combined diet of Danish and Dutch porpoises). Finally, using combined dietary data for Scotland, Denmark and Holland, harbour porpoises in the central North Sea could eat around 3900 t of herring, 33 400 t of whiting and 14 000 t of sandeels.

It should be noted that confidence limits on all these estimates are wide: regardless of accuracy, the precision available is low, reflecting the level of uncertainty associated with sampling error, the regressions used to estimate size of fish prey eaten, the population size and the energy requirements (Santos 1998, see Santos et al. 2001b for a similar calculation for sperm whales).

Competition with other predators

Comparing the harbour porpoise with other predators in the northeast Atlantic, the predator with the most similar average body size is the common (or harbour) seal, which has a range in weight in UK waters of around 45–106 kg in females and 55–130 kg in males (Corbet & Harris 1991). Several studies have been carried out on the diet of common seals in the Moray Firth (e.g. Pierce et al. 1989, 1991a,b, Thompson et al. 1991, Tollit & Thompson 1996). In general, common seal diet is dominated by sandeels in summer and other species such as gadoids (whiting, cod) and clupeids (herring, sprat) in winter. Thus, in recent studies, diets of harbour porpoise and common seals are seen to follow a similar pattern, which is consistent with both types of predators exploiting the same locally abundant resources. Tollit & Thompson (1996) also found considerable interannual variation in the diet of common seals in the Moray Firth between 1989 and 1992. In the Skagerrak and Kattegat (May–September 1988), Härkönen (1988) found that the most important species in common seal diet were cod, plaice, dab, lemon sole *Microstomus kitt* and sandeels. Härkönen & Heide-Jørgensen (1991) reported the main prey of common seals in the same area in July–December 1989 to be mainly gadoids, particularly cod. Cod was also the most important species by weight in Danish harbour porpoise diets (Santos 1998), although viviparous blennies were the second most important category and very few flatfishes were eaten.

Grey seals in the Moray Firth have a similar summer diet to common seals in the same area (i.e. predominantly sandeels (Pierce et al. 1991a)). Studies elsewhere in Scotland have shown that other types of fish, particularly gadoids, dominate the winter diet (e.g. Hammond & Prime 1990, Pierce et al. 1990, Hammond et al. 1994). Again, broadly speaking, there are similarities with harbour porpoise diet.

There are few data on bottlenose dolphin diet in Scottish waters, but cod, saithe and whiting were the main prey in 10 stomachs (eight from the Moray Firth) examined by Santos et al. (2001c). It has been speculated that bottlenose dolphins kill porpoises as a result of food competition (Ross & Wilson 1996) but clearly more data are needed to test this hypothesis.

Apart from parallels with seals, the high importance of sandeel in harbour porpoise diets is shared with a large range of other predators, for example, whiting and cod (Daan 1989), pleuronectids and salmonids (Storey 1993), Arctic tern *Sterna paradisaea* (Monaghan et al. 1989), puffins *Fratercula arctica*, guillemots *Uria aalge*, razorbills *Alca torda* (Harris & Riddiford 1989), great skuas *Catharacta skua* (Furness & Hislop 1981), Arctic skuas *Stercorarius parasiticus*, kittiwakes *Rissa tridactyla* (Furness 1987), shags *Phalacrocorax aristotelis* (Harris & Wanless 1991), minke whales *Balaenoptera acutorostrata* (Jonsgåard 1982) and humpback whales *Megaptera novaengliae* (Perkins et al. 1982).

Interactions with fisheries

Interactions of marine mammals with fisheries are of two general types, operational and biological (Harwood & Greenwood 1985). The former include fishery by-catch of porpoises and the latter include predation by porpoises on fished species. Both types of interaction arguably reflect diet choice, the latter more directly.

The results of most of the studies on harbour porpoise diets in the northeast Atlantic show an overlap between the fish species consumed by porpoises and those targeted by fisheries. This potential for competition was already noted at the beginning of last century in the North Sea when direct observations of porpoises reputedly "chasing salmon" or "playing with salmon" led fishermen and naturalists to believe in the possibility of porpoises competing with local salmon fisheries (e.g. Macintyre 1934, Berry 1935). Concern over the status of the Baltic salmon stock led Svärdson (1955) to propose:

> The relation between porpoise and salmon can be and ought to be tested by an experiment. The porpoise-hunting tradition . . . must be revived and as many of the migrating porpoises as possible caught for some years, so as to see what happens to the salmon in the Baltic. If the relation is once again positive a method has been found for conserving in the Baltic a permanent salmon population more abundant than the present one.

In fact, studies from this period found no evidence of predation on salmon in porpoise stomach contents (Rae 1965, 1973, Lindroth 1962).

The North Sea and adjacent areas (waters west of Scotland and the Skagerrak/Kattegat area) have a long history of fishery exploitation. The types of fishery include pelagic and demersal fisheries for human consumption, and industrial fisheries (where the catch is used for reduction purposes). The pelagic fishery mainly targets herring, mackerel and horse mackerel, while the demersal fisheries usually catch a mixture of roundfish species (e.g. cod, haddock, whiting) and/or a mixture of flatfish species (plaice *Pleuronectes platessa* and sole) with a by-catch of roundfish. The industrial fishery mainly takes sandeels, Norway pout and sprat, although catches also include herring, haddock and whiting (Anonymous 2002a).

Whiting is the third most important species of commercial demersal fish in the North Sea. Catches of this species in the North Sea increased during the 1950s and 1960s and reached a maximum in 1969 with 200 000 t. After this date maximum landings started to decline and reached an historical low in 1998. At present the stock is considered to be outside safe biological limits (Anonymous 2002a). In recent years, a significant part of the whiting landed is taken as by-catch in the industrial fishery, mainly for Norway pout, and in addition large quantities of whiting are being discarded in favour of higher priced species.

The sandeel *Ammodytes marinus* supports the largest single-species fishery in the North Sea. Its distribution extends in the eastern North Atlantic from 74ºN to 49ºN (Channel Islands and western English Channel), including eastern Greenland, Barents Sea and the Baltic Sea (Whitehead et al. 1989). Sandeels are used for bait and food on a small scale in many areas, but the major fisheries are for the production of fishmeal with between 600 000–1 100 000 t being taken from the North Sea each year (mainly by Denmark) (Anonymous 2002a).

Santos (1998) estimated that harbour porpoises take more whiting than are landed by fisheries in the North Sea, although the whiting taken by porpoises were mainly smaller than those targeted by the fishery. In Scotland, just over 99% of the whiting consumed were below the minimum landing size established for the species (27 cm), compared with 99.5% for Denmark and 70% for Holland. However, sizes of fishes may be underestimated from measurements on otoliths because no correction was applied for otolith erosion. Wijnsma et al. (1999) carried out *in vitro* digestions of fish otoliths to estimate consequences of otoliths erosion for dietary studies on porpoises and suggested that the overall picture of diet composition for porpoises in Scottish waters was relatively robust to such errors.

Discards of smaller whiting and other species in the North Sea are at present a cause for concern because the amount of whiting discarded is estimated to be equivalent to 60% of the amount landed (Anonymous 2002a) and discards are similarly high for haddock. Discards are known to be eaten by seabirds (Hudson & Furness 1989, Berghahn & Rösner 1992, Furness et al. 1992) and it is interesting to speculate whether harbour porpoises might also take advantage of this resource. Some evidence of feeding on discards exists for other cetaceans, for example, killer whales (Couperus 1994).

Long-term trends in porpoise diet

Harbour porpoises in the northeast Atlantic may already have switched prey species following the decline in herring stocks to a diet based on sandeels, whiting and other gadoid species. The studies by Rae (1965, 1973) on harbour porpoise diet in Scotland between 1959 and 1971 showed clupeids (herring and sprat) to be the most frequent prey. Gadoids (mainly whiting) were found to be second in importance in the diet, while sandeels represented a minor proportion (being identified in less than 8% of the stomachs). Although the fact that most of the animals were obtained during the winter months could explain the lack of sandeels in the diet, the importance of herring in the stomachs of harbour porpoises analysed by Rae is clearly greater than in the diet of harbour porpoises in more recent studies.

The decline in herring stocks in the North Sea between the 1950s and 1970s is well documented (Cushing & Burd 1957, Burd 1978) and has been proposed as one of several hypothesis (together with organochlorine pollution, noise pollution produced by increasing boat traffic and by-catches in fishing gear) to explain the apparent decline in numbers of harbour porpoises in the North Sea (e.g. Verwey 1975, Otterlind 1976, Van Bree 1977, Andersen & Clausen 1983, Gaskin 1984, Kayes 1985, Smeenk 1987, IWC 1994, Kleivane et al. 1995). The collapse of the herring stocks did indeed coincide with the apparent decline in harbour porpoise numbers in the southern North Sea. However, herring was also overfished on the Scottish coasts but there is no evidence of a parallel decline in porpoise numbers (Evans 1980). Furthermore, an earlier disappearance of Zuiderzee herring (a brackish water population) in Dutch waters during the 1930s, was not accompanied by a decline in harbour porpoise numbers in the area (Smeenk 1987). On the other hand, Camphuysen (1994) noted that an increase in herring stocks in recent years had been followed by a slight increase in sightings of harbour porpoises in the southeast North Sea.

There has been speculation about the likelihood and consequences of porpoises switching to other prey species if their main prey were depleted by overfishing, because many of the prey species eaten by harbour porpoise are also commercially exploited (e.g. herring, sprat, sardine, cod, whiting, sole, sandeels) (IWC 1996).

Fish stocks have shown considerable variation in abundance and distribution in the past, some of which has been the result of over-exploitation. Well known cases include the collapse of the North Sea herring stocks (Burd 1978, Corten 1990) and the massive decrease of North Sea mackerel population in the early 1970s (Cushing 1980). Not only have pelagic species shown large fluctuations in abundance, landings from the Shetland sandeel fishery fell during the 1980s and a parallel decline in seabird breeding success followed (Monaghan et al. 1989). Changes in the structure of fish communities due to fishery exploitation have already been described for some areas (e.g. Celtic Sea, Pinnegar et al. 2002).

At present, many stocks in the North Sea are outside or close to safe biological limits, with high fishing mortality that is believed to be unsustainable in the longer term and spawning stock biomasses below safe levels or declining towards critical levels. Over-exploitation of herring for the human consumption fishery, together with considerable by-catches of juveniles in the industrial fishery in the North Sea and Skagerrak/Kattegat area, caused a rapid decline of the stock and in the 1990s emergency regulations were introduced to reduce fishing mortality. The stock is at present believed to be inside safe biological limits (Anonymous 2002b) – although reported to be outside safe biological limits in 2001 (Anonymous 2001) – but stock rebuilding has been delayed by too optimistic assessments and misreporting. The state of the sprat stock is not well known with large natural fluctuations in annual stock biomass (Anonymous 2001). The North Sea component of the mackerel stock is still severely depleted and considered to be in need of maximum protection (Anonymous 2002c).

For the species taken in the demersal fishery for human consumption, the stock of cod is considered to be outside safe biological limits and there is concern that, if the rate of fishing continues, the stock will collapse. For both haddock and whiting the North Sea stocks are also considered to be outside safe biological limits, with spawning stock biomass reaching an historical low in 1998 for whiting. The status of saithe stocks in the North Sea (including the Skagerrak area) and the West of Scotland is also causing concern, having fluctuated around safe biological limits in recent years. Of the flatfish species, plaice and North Sea sole are considered to be outside safe biological limits with the historical minimum of spawning stock biomass recorded in 1997 for plaice and in 1998 for sole (Anonymous 2002a).

Finally, for the industrial fishery, both Norway pout and sandeel stocks are considered to be inside safe biological limits but recruitment for both species appear to be highly variable and can influence the abundance of the species rapidly due to the short life-span (Anonymous 2002a).

Consequences of diet for individual health and population status

Possible causes for the decline of harbour porpoises in most European waters noted by Smeenk (1987) included the decline in herring stocks and other factors such as organochlorine pollution. Other threats to populations include fishery by-catch, habitat degradation through pollution, disturbance by ship traffic and boats and coastal development (Read et al. 1997). Of these threats, by-catch is arguably the most serious, the fishery by-catch of harbour porpoises in northeast Atlantic waters being regarded as unsustainable by the IWC (IWC 1995).

As argued above, harbour porpoises in Scottish waters have apparently already switched prey species following the decline in herring stocks to a diet based on sandeel, whiting and other gadoid species. Switching from a prey with high calorific value such as herring (Murray & Burt 1977) to one with lower calorific density could have long-term effects on survivorship and productivity. Short-term effects have been described by Dudok van Heel (1962) who 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. Evidence of physiological changes in harbour seals, related to changes in diet composition, was found by Thompson et al. (1997). Analysing haematological parameters of a harbour seal population, they found that in years when herring and sprat dominated the diet, leukocyte counts were significantly higher than in years when alternative prey dominated the diet. Evidence of widespread macrocytic anaemia was also found in years when an alternative prey dominated the diet.

Diet is the route of entry of persistent organic pollutants and toxic elements. Of all the different types of organochlorine compounds used, only two groups (especially resistant to biodegradation) have entered the marine food chain in high concentrations and are present in marine mammal tissues. These two groups are the DDTs (dichloro-diphenyl-trichloroethanes, used as pesticides in agriculture until late 1970s) and PCBs (polychlorinated biphenyls, used mainly in the electricity industry) (Aguilar & Borrell 1995).

Aguilar & Borrell (1995) found that, although levels of DDT (and other contaminants such as heavy metals) in tissues were low, levels of PCBs in harbour porpoises from the eastern North Atlantic were high enough to cause concern about their possible effects on the population. Organochlorine compounds are thought to depress reproductive performance (Subramanian et al. 1987, Addison 1989) and the immune system (Wassermann et al. 1979, Brouwer et al. 1989, Vos & Luster 1989, Swart et al. 1994, Ross et al. 1996) and have been shown in experimental studies to adversely affect mammalian reproduction (e.g. Merson & Kirkpatrick 1976, Fuller & Hobson 1986, Reijnders 1986, Boon et al. 1987, Gray et al. 1998). The harbour porpoise was the first cetacean analysed for these compounds (Holden & Marsden 1967).

Harbour porpoise, with its coastal habitat, its position at the top of the food chain and its small body size (and high metabolic rate) could be especially affected by these pollutants. Moreover, it has been suggested that the capacity of small cetaceans to metabolise certain PCB congeners is very low compared with that of birds and terrestrial mammals (Tanabe et al. 1988) and is possibly lower in harbour porpoises than in other odontocetes (Duinker et al. 1989). Jepson et al. (1999) found a significant association between elevated blubber chlorobiphenyl concentrations and mortality due to infectious diseases in harbour porpoises from England and Wales stranded and by-caught between 1990 and 1996. However, Kuiken and co-authors found blubber chlorobiphenyl concentrations to be unrelated to adrenocortical hyperplasia in porpoises stranded and by-caught in 1990 and 1991 (Kuiken et al. 1993) or mortality due to infectious diseases in porpoises stranded and by-caught between 1989 and 1992 (Kuiken et al. 1994b). At present, while the proximate origin of PCBs in porpoise blubber is clearly to be found in the prey species, it is not clear whether particular prey species (or marine habitats) are responsible for this transfer. However, it may be noted that in general the pattern of abundance of different PCB congeners in marine mammal blubber differs markedly between fish eaters (such as the harbour porpoise) and cephalopod eaters (Wells & Mckenzie 1994).

The coastal distribution of harbour porpoises makes them vulnerable to high levels of incidental fishery mortality, particularly in bottom-set gill nets but also in other fishing gear, e.g. salmon drift nets, pound nets for herring and salmon and mid-water trawls (e.g. Lindroth 1962, van Utrech 1978, Kinze 1990a, Northridge & Lankester 1992, Lowry & Teilmann 1994, Read 1999). Unlike dolphins, harbour porpoises seem likely to become entangled when the nets are on the sea bottom (Read & Gaskin 1988). However, it is unclear whether porpoises become entangled because they attempt to take fishes already caught in the nets or if they are simply foraging in the area where nets are set and fail to detect the nets (see Tregenza et al. 1997). One possibility is that, when porpoises are echolocating fishes buried in the substratum, objects in the water column (such as nets) are not detected.

Future research

Most recent results on porpoise diet derive from examination of stomach contents of stranded animals. Inevitably this leads to an incomplete and potentially biased view of diet, and makes it difficult to partition variation reliably. It is clear that there are regional, seasonal, sex- and size-related differences in diet and there may well be individual differences in food preferences. However, stomach contents of dead animals provide only a single snapshot of diet, with no possibility of repeated samples from the same animal. Furthermore, the most recent meal is not necessarily representative of the typical diet, especially if the animal was weakened by disease, but also if it was by-caught in a fishing net as a result of pursuing a particular type of fish. Last and by no means least, stomach contents analysis is complicated by the digestive erosion of prey tissues and hard parts (see review by Pierce & Boyle 1991).

In other marine mammals, notably seals (e.g. Iverson et al. 1997), analysis of fatty acid composition of the blubber has allowed inferences to be made about the average diet composition of individuals over extended periods, both overcoming some of the biases of stomach contents analysis and allowing good data to be collected from animals with empty stomachs.

There are both logistical and technical obstacles to be overcome before this method is used routinely on porpoises. Quantitative interpretation of fatty acid profiles requires extensive libraries of the fatty acid profiles of putative prey species. Calculating the most likely diet composition requires considerable computing power: the higher the number of possible prey species and the more fatty acids that are taken into account, the more possible combinations of different proportions of prey types need to be screened. Finding the relative importance of different prey in the diet is equivalent to solving a series of simultaneous equations, with data on each fatty acid expressed as a separate equation, each of which has a term for each prey species. For example, for three fatty acids and two prey species:

$$I_1 C_{a,1} + I_2 C_{a,2} = C_{a,obs}$$

$$I_1 C_{b,1} + I_2 C_{b,2} = C_{b,obs}$$

where: I_y = importance of prey type y in the diet

$C_{x,y}$ = concentration of fatty acid x in the body of prey species y

$C_{x,obs}$ = concentration of fatty acid x in porpoise blubber

In these equations, all the C terms are known and it is necessary to find the set of values for I values. Further complications are provided by variation in fatty acid profiles within prey species (e.g. in relation to the prey life cycle and reproductive cycle or variation in the prey species' own diet) and differences between the overall dietary fatty acid profile and that of the blubber (e.g. due to variation in assimilation, metabolism and *de novo* synthesis in different fatty acids). Given variation in fatty acid profiles of individual prey species, the set of simultaneous equations is unlikely to have an exact solution. The most probable solution could be calculated using computer simulations incorporating known variability in prey fatty acid profiles. The only realistic way of completely overcoming the latter problem would be to derive correction factors based on captive feeding experiments involving animals on controlled diets. However, while relatively straightforward for seals, this is unlikely to be feasible for porpoises, nor would it be ethically acceptable in some countries.

To follow the diet of an individual porpoise over its lifetime, repeated biopsy samples of blubber could be taken. Individual identification could be confirmed from DNA analysis of the tissue sample. However, fatty acids of recent dietary origin are concentrated in the lower blubber, so that complete blubber cores would be needed, potentially providing a route for infection and again raising ethical questions. Regardless of whether fatty acid analysis could or should be extended to studies on live animals, it offers the most likely method for obtaining good dietary data on this species.

For some large cetaceans, faecal analysis has proved to be viable, collecting material from behind a swimming animal using a net. It seems unlikely that this would be successfully for an animal as small (and generally shy of human contact) as a porpoise. Attachment of cameras ("crittercams") has also been successful for pinnipeds and larger cetaceans and, given a sufficiently small package, it should be possible to obtain a porpoise-eye view of its feeding activity. Other kinds of recording devices (e.g. time-depth recorders) have already been successfully attached to porpoises (e.g. Westgate et al. 1995).

Major uncertainties about the ecological importance – and indeed the status – of porpoise populations remain due to the lack of good data on population size, especially in European waters. In the North Sea, the SCANS survey – based on a single month's data collection in 1994 (Hammond et al. 1995) – still provides the most comprehensive picture of porpoise distribution and abundance. Good data on individual energy requirements are also required and could greatly affect present calculations of food consumption.

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References

Aarefjord, H., Bjørge, A., Kinze, C.C. & Lindstedt, I. 1995. Diet of the harbour porpoise, (*Phocoena phocoena*), in Scandinavian waters. In *Special Issue, 16: Biology of phocoenids*, A. Bjørge & G.P. Donovan (eds). Cambridge: International Whaling Commission, 211–222.

Ackman, R.G. & Lamothe, F. 1989. Marine mammals. In *Marine biogenic lipids, fats and oils. Vol. 2: Distribution of marine lipids*, R.G. Ackmann (ed.). Boca Raton: CRC Press, 179–381.

Addison, R.F. 1989. Organochlorines and marine mammal reproduction. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 360–368.

Aguilar, A. & Borrell, A. 1995. Pollution and harbour porpoises in the eastern North Atlantic: a review. In *Special Issue, 16: Biology of phocoenids*, A. Bjørge & G.P. Donovan (eds). Cambridge: International Whaling Commission, 231–242.

Amano, M. & Miyazaki, N. 1992. Geographic variation in skulls of the harbour porpoise, *Phocoena phocoena*. *Mammalia* **56**, 133–144.

Amundin, M., Kallin, E. & Kallin, S. 1988. The study of the sound production apparatus in the harbour porpoise, *Phocoena phocoena*, and the jacobita, *Cephalorhynchus commersoni*, by means of serial cryo-microtome sectioning and 3-D computer graphics. In *Animal sonar: processes and performance*, P. Nachtigall & P.W.G. Moore (eds). New York: Plenum Press, 61–66.

Andersen, L.W. 1993. The population structure of the harbour porpoise, *Phocoena phocoena*, in Danish waters and part of the North Atlantic. *Marine Biology* **116**, 1–7.

Andersen, S. 1965. L'alimentation du marsouin (*Phocoena phocoena* L.) en captivité. *Vie Milieu*, Series A, **16**, 799–810.

Andersen, S. & Clausen, B. 1983. Bycatches of the harbour porpoise, *Phocoena phocoena*, in Danish fisheries 1980–1981, and evidence for overexploitation. *International Whaling Commission*, SC/35/SM14.

Anonymous 2001. Report of the herring assessment working group for the area South of 62°N. *International Council for the Exploration of the Sea*, C.M. 2001/ACFM: 12, Copenhagen, Denmark.

Anonymous 2002a. Report of the working group on the assessment of demersal stocks in the North Sea and Skagerrak. *International Council for the Exploration of the Sea*, C.M. 2002/ACFM: 1, Copenhagen, Denmark.

Anonymous 2002b. Report of the herring assessment working group for the area South of 62°N. *International Council for the Exploration of the Sea*, C.M. 2002/ACFM: 12, Copenhagen, Denmark.

Anonymous 2002c. Report of the working group on the assessment of mackerel, horse mackerel, sardine and anchovy. *International Council for the Exploration of the Sea,* C.M. 2002/ACFM: 6, Copenhagen, Denmark.

ASCOBANS 1994. Agreement on the conservation of small cetaceans of the Baltic and North Seas. Report from the First Meeting of the Parties, Stockholm, 26–28 September 1994. *ASCOBANS Secretariat*, Cambridge, UK.

Baird, R.W. & Hooker, S.K. 2000. Ingestion of plastic and unusual prey by a juvenile harbour porpoise. *Marine Pollution Bulletin* **40**, 719–720.

Benke, H. & Siebert, U. 1996. The current status of harbour porpoises (*Phocoena phocoena*) in German waters. *International Whaling Commission,* SC/47/SM49, Cambridge, UK.

Berggren, P. 1996. A preliminary assessment of the status of harbour porpoises (*Phocoena phocoena*) in the Swedish Skagerrak, Kattegat and Baltic Seas. *International Whaling Commission*, SC/47/SM50, Cambridge, UK.

Berghahn, R. & Rösner, H.-U. 1992. A method to quantify feeding of seabirds on discard from the shrimp fishery in the North Sea. *Netherlands Journal of Sea Research* **28**, 347–350.

Berrow, S.D., Long, S.C., McGarry, A.T., Pollard, D., Rogan, E. & Lockyer, C. 1998. Radionuclides (^{137}Cs and ^{40}K) in harbour porpoise *Phocoena phocoena* from British and Irish coastal waters. *Marine Pollution Bulletin* **36**, 569–576.

Berry, J. 1935. British mammals and birds as enemies of the Atlantic salmon (*Salmo salar*). *Reports of the Avon Biological Research* **1934–35**, 31–64.

Bjørge, A. & Donovan, G.P. (eds) 1995. *Special Issue, 16: Biology of phocoenids*. Cambridge: International Whaling Commission, 552 pp.

Bjørge, A. & Øien, N. 1995. Distribution and abundance of harbour porpoise, *Phocoena phocoena*, in Norwegian waters. In *Special Issue, 16: Biology of phocoenids,* A. Bjørge & G.P. Donovan (eds). Cambridge: International Whaling Commission, 89–98.

Boon, J.P., Reijnders, P.J.H., Dols, J., Wensvoort, P. & Hillebrand, M.T.J. 1987. The kinetics of individual polychlorinated biphenyl congeners in female harbour seals (*Phoca vitulina*), with evidence for structure-related metabolism. *Aquatic Toxicology* **10**, 307–324.

Börjesson, P. & Berggren, P. 1996. Seasonal variation in diet of harbour porpoises (*Phocoena phocoena*) from the Kattegat and Skagerrak Seas. In *European research on cetaceans – 10,* P.G.H. Evans (ed.). Cambridge: European Cetacean Society, 261 only.

Börjesson, P. & Berggren, P. 1997. Morphometric comparisons of skulls of harbour porpoises (*Phocoena phocoena*) from the Baltic, Kattegat, and Skagerrak seas. *Canadian Journal of Zoology* **75**, 280–287.

Brodie, P.F. 1995. The Bay of Fundy/Gulf or Maine harbour porpoise (*Phocoena phocoena*): some considerations regarding species interactions, energetics, density dependence and bycatch. In *Special Issue, 16: Biology of phocoenids,* A. Bjørge & G.P. Donovan (eds). Cambridge: International Whaling Commission, 181–187.

Brouwer, A., Reijnders, P.J.H. & Koeman, J.H. 1989. Polychlorinated biphenyl (PCB)-contaminated fish induces vitamin A and thyroid hormone deficiency in the common seal (*Phoca vitulina*). *Aquatic Toxicology* **15**, 99–106.

Burd, A.C. 1978. Long-term changes in North Sea herring stocks. *Rapports et Procès-verbaux des Réunions, Conseil International pour l'Exploration de la Mer* **172**, 137–153.

Camphuysen, C.J. 1994. The harbour porpoise, *Phocoena phocoena* in the southern North Sea. II: A come-back in Dutch coastal waters? *Lutra* **37**, 54–61.

Camphuysen, C.J. & Leopold, M.F. 1993. The harbour porpoise, *Phocoena phocoena* in the southern North Sea, particularly the Dutch sector. *Lutra* **36**, 1–24.

Clausen, B. & Andersen, S. 1988. Evaluation of bycatch and health status of the harbour porpoise (*Phocoena phocoena*) in Danish waters. *Danish Review of Game Biology* **13**, 1–20.

Corbet, G.B. & Harris, S. (eds) 1991. *The handbook of British mammals.* London: Blackwell, 3rd edn.

Corten, A. 1990. Long-term trends in pelagic fish stocks of the North Sea and adjacent waters and their possible connection to hydrographic changes. *Netherlands Journal of Sea Research* **25**, 227–235.

Couperus, A.S. 1994. Killer whales (*Orcinus orca*) scavenging on discards of freezer trawlers north east of the Shetland islands. *Aquatic Mammals* **20**, 47–51.
Cushing, D.H. 1980. The decline of the herring stocks and the gadoid outburst. *Journal du Conseil pour l'Exploration Internationale de la Mer* **39**, 70–81.
Cushing, D.H. & Burd, A.C. 1957. On the herring of the southern North Sea. *Fishery Investigations, London, Series 2* **20**, 1–31.
Daan, N. (ed.) 1989. Data base report of the stomach sampling project 1981. ICES Cooperative Research Report, No. 164, Copenhagen, Denmark.
Darling, F.F. 1947. *Natural history in the Highlands and Islands*. London: Collins.
Desportes, G. 1985. *La nutrition des odontocetes en Atlantique nord-est (cotes Francaises – iles Feroe)*. PhD thesis, Université de Poitiers, France.
Dewhurst, H.W. 1834. *The natural history of the order Cetacea*. London: Dewhurst.
Donovan, G.P. & Bjørge, A. 1995. Harbour porpoises in the North Atlantic: edited extract from the Report of the IWC Scientific Committee, Dublin 1995. In *Special Issue, 16: Biology of phocoenids*, A. Bjørge & G.P. Donovan (eds). Cambridge: International Whaling Commission, 3–25.
Dudok van Heel, W.H. 1962. Experiments with *Phocoena phocoena* L. *Netherlands Journal of Sea Research* **1**, 427–458.
Duinker, J.C., Hillebrand, M.T.J., Zeinstra, T. & Boon, J.P. 1989. Individual chlorinated biphenyls and pesticides in tissues of some cetaceans species from the North Sea and the Atlantic Ocean; tissue distribution and biotransformation. *Aquatic Mammals* **15**, 95–124.
Dunnet, G.M. 1996. Aquatic predators and their prey: the take-home messages. In *Aquatic predators and their prey*, S.P.R. Greenstreet & M.L. Tasker (eds). Oxford: Fishing News Books, Blackwell Science, 184–186.
Evans, P.G.H. 1980. Cetaceans in British waters. *Mammal Review* **10**, 1–52.
Evans, P.G.H. & Borges, L. 1995. Associations between porpoises, seabirds, and their prey in south-east Shetland, N. Scotland. In *European research on cetaceans – 9*, P.G.H. Evans (ed.). Cambridge: European Cetacean Society, 173–178.
Evans, W.E. 1973. Echolocation by marine delphinids and one species of freshwater dolphin. *Journal of the Acoustical Society of America* **54**, 191–199.
Evans, W.E. 1975. *Distribution, differentiation of populations, and other aspects of the natural history of* Delphinus delphis *Linnaeus in the northeast Pacific Ocean*. PhD thesis, University of California, Los Angeles, California.
Fink, B.D. 1959. Observations of porpoise predation on a school of Pacific sardines. *California Fish and Game* **45**, 216–217.
Fontaine, P.M., Hammill, P.O., Barrette, C. & Kingsley, M.C. 1994. Summer diet of the harbour porpoise *(Phocoena phocoena*) in the estuary and the northern Gulf of St Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 172–178.
Fraser, F.C. 1946. Report on Cetacea stranded on the British coasts from 1933 to 1937. British Museum (Natural History) No. 12, London.
Fuller, G.B. & Hobson, W.C. 1986. Effects of PCBs on reproduction in mammals. In *Vol. 2: PCBs and the environment*. Florida: CRC Press, 101–125.
Furness, R.W. 1987. *The skuas*. Calton: T. & A.D. Poyser.
Furness, R.W., Ensor, K. & Hudson, A.V. 1992. The use of fishery waste by gull populations around the British Isles. *Ardea* **80**, 105–113.
Furness, R.W. & Hislop, J.R.G. 1981. Diets and feeding ecology of great skuas *Catharacta skua* during the breeding season in Shetland. *Journal of Zoology, London* **195**, 1–23.
Gannon, D.P., Craddock, J.E. & Read, A.J. 1998. Autumn food habits of harbour porpoises, *Phocoena phocoena*, in the Gulf of Maine. *Fishery Bulletin* **96**, 428–437.
Gaskin, D.E. 1977. Harbour porpoise *Phocoena phocoena* (L.) in the western approaches to the Bay of Fundy 1969–75. *Reports of the International Whaling Commission* **27**, 487–492.
Gaskin, D.E. 1984. The harbour porpoise, *Phocoena phocoena* (L.): regional populations, status, and

information on direct and indirect catches. *Reports of the International Whaling Commission* **34**, 569–586.

Gaskin, D.E., Arnold, P.W. & Blair, B.A. 1974. *Phocoena phocoena*. *Mammalian Species* **42**, 1–8.

Gaskin, D.E. & Blair, B.A. 1977. Age determination of harbour porpoise, *Phocoena phocoena* (L.), in the western North Atlantic. *Canadian Journal of Zoology* **55**, 18–30.

Gaskin, D.E. & Watson, A.P. 1985. The harbor porpoise, *Phocoena phocoena*, in Fish Harbor, New Brunswick, Canada: occupancy, distribution, and movements. *Fishery Bulletin* **83**, 427–442.

Gaskin, D.E., Yumamoto, S. & Kawamura, A. 1993. Harbour porpoise, *Phocoena phocoena* (L.), in the coastal waters of northern Japan. *Fishery Bulletin* **91**, 440–454.

Gearin, P.J., Melin, S.R., DeLong, R.L., Kajimura, H. & Johnson, M.A. 1994. Harbour porpoise interactions with a Chinook salmon set-net fishery in Washington State. In *Special Issue, 15: Gillnets and cetaceans*, W.F. Perrin et al. (eds). Cambridge: International Whaling Commission, 427–438.

Goodson, A.D. 1994. Bottom-set gillnets: problems of perception for dolphins and porpoises. In *European research on cetaceans – 8*, P.G.H. Evans (ed.). Cambridge: European Cetacean Society, 54–57.

Goodson, A.D. & Sturtivant, C.R. 1996. Sonar characteristics of the harbour porpoise (*Phocoena phocoena*): source levels and spectrum. *ICES Journal of Marine Science* **53**, 465–472.

Gray, L.E., Ostby, J., Wolf, C., Lambright, C. & Kelce, W.R. 1998. The value of mechanistic studies in laboratory animals for the prediction of reproductive effects in wild life. *Environmental Toxicology and Chemistry* **17**, 109–118.

Hammond, P.S., Benke, H., Berggren, P., Borchers, D.L., Buckland, S.T., Collet, A., Heide-Jørgensen, M.-P., Heimlich-Boran, S., Hiby, A.R., Leopold, M.F. & Øien, N. 1995. Distribution and abundance of the harbour porpoise and other small cetaceans in the North Sea and adjacent waters. Final Report to the EU, Life 92-2/UK/027.

Hammond, P.S., Hall, A.J. & Prime, J.H. 1994. The diet of grey seals around Orkney and other island and mainland sites in north-eastern Scotland. *Journal of Applied Ecology* **31**, 340–350.

Hammond, P.S. & Prime, J.H. 1990. The diet of British grey seals (*Halichoerus grypus*). *Canadian Bulletin of Fisheries and Aquatic Sciences* **222**, 243–254.

Hardy, A.C. 1959. *The open sea: II. Fish and fisheries*. London: Collins.

Härkönen, T.J. 1988. Food-habitat relationships of harbour seals and black cormorants in the Skagerrak and Kattegat. *Journal of Zoology, London* **214**, 673–681.

Härkönen, T.J. & Heide-Jørgensen, M.-P. 1991. The harbour seal *Phoca vitulina* as a predator in the Skagerrak. *Ophelia* **3**, 191–207.

Harmer, S.F. 1927. Report on Cetacea stranded on the British coasts from 1913 to 1926. British Museum (Natural History) No. 10, London.

Harris, M.P. & Riddiford, N.J. 1989. The food of some young seabirds on Fair Isle in 1986–1988. *Scottish Birds* **15**, 119–125.

Harris, M.P. & Wanless, S. 1991. The importance of the lesser sandeel *Ammodytes marinus* in the diet of the shag *Phalacrocorax aristotelis*. *Ornis Scandinavica* **22**, 375–382.

Harwood, J. & Greenwood, J.J.D. 1985. Competition between British grey seals and fisheries. In *Marine mammals and fisheries*, J.R. Beddington et al. (eds). London: George Allen & Unwin, 153–169.

Hatakeyama, Y. & Soeda, H. 1990. Studies on echolocation of porpoises taken in salmon gillnet fisheries. In *Sensory abilities of cetaceans, laboratory and field evidence*, J.A. Thomas & R.A. Kastelein (eds). New York: Plenum Press, 269–281.

Heide-Jørgensen, M.-P., Mosbech, A., Teilmann, J., Benke, H. & Schultz, W. 1992. Harbour porpoise (*Phocoena phocoena*) densities obtained from aerial surveys north of Fyn in the bay of Kiel. *Ophelia* **35**, 133–146.

Heide-Jørgensen, M.-P., Teilmann, J., Benke, H. & Wulf, J. 1993. Abundance and distribution of harbour porpoises *Phocoena phocoena* in selected areas of the western Baltic and the North Sea. *Helgoländer Meeresuntersuchungen* **47**, 335–346.

Hislop, J.R.G. 1972. *Some aspects of the biology of whiting,* Merlangius merlangus *(L.)*. PhD thesis, University of Aberdeen, Aberdeen, Scotland.

Hislop, J.R.G. 1984. A comparison of the reproductive tactics and strategies of cod, haddock, whiting and Norway pout in the North Sea. In *Fish reproduction: strategies and tactics,* G.W. Potts & R.J. Wootton (eds). London: Academic Press, 311–329.

Hislop, J.R.G. 1996. Changes in North Sea gadoid stocks. *ICES Journal of Marine Science* **53**, 1146–1156.

Hobson, K.A. 1990. Stable isotope analysis of marbled murrelets: evidence for freshwater feeding and determination of trophic level. *Condor* **92**, 897–903.

Hohn, A.A. & Brownell, R.L. 1990. Harbour porpoise in central Californian waters: life history and incidental catches. *International Whaling Commission*, SC/42/SM47, Cambridge, UK.

Holden, A.V. & Marsden, K. 1967. Organochlorine pesticides in seals and porpoises. *Nature* **216**, 1274–1276.

Hooker, S.K., Iverson, S.J., Ostrom, P. & Smith, S.C. 2001. Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. *Canadian Journal of Zoology* **79**, 1442–1454.

Hudson, A.V. & Furness, R.W. 1989. The behaviour of seabirds foraging at fishing boats around Shetland. *Ibis* **131**, 225–237.

Iverson, S.J., Frost, K.J. & Lowry, L.F. 1997. Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. *Marine Ecology Progress Series* **151**, 255–271.

Iverson, S.J., Oftedal, O.T., Bowen, W.D., Boness, D.J. & Sampugna, J. 1995. Prenatal and postnatal transfer of fatty acids from mother to pup in the hooded seal. *Journal of Comparative Physiology, B* **165**, 1–12.

IWC 1991. Report of the scientific committee. Annex G. Report of the sub-committee on small cetaceans. *Reports of the International Whaling Commission* **41**, 172–188.

IWC 1992. Report of the scientific committee. Annex G. Report of the sub-committee on small cetaceans. *Reports of the International Whaling Commission* **42**, 178–234.

IWC 1994. Report of the workshop on mortality of cetaceans in passive fishing nets and traps. In *Special Issue, 15: Gillnets and cetaceans*, W.F. Perrin et al. (eds). Cambridge: International Whaling Commission, 1–71.

IWC 1995. Report of the scientific committee. Annex G. Report of the sub-committee on small cetaceans. *Reports of the International Whaling Commission* **45**, 165–186.

IWC 1996. Report of the scientific committee. Annex H. Report of the sub-committee on small cetaceans. *Reports of the International Whaling Commission* **46**, 160–179.

Jepson, P.D., Bennett, P.M., Allchin, C.R., Law, R.J., Kuiken, T., Baker, J.R., Rogan, E. & Kirkwood, J.K. 1999. Investigating potential associations between chronic exposure to polychlorinated biphenyls and infectious disease mortality in harbour porpoises from England and Wales. *The Science of the Total Environment* **243/244**, 339–348.

Jonsgåard, A. 1982. The food of minke whales (*Balaenoptera acutorostrata*) in the northern North Atlantic waters. *Reports of the International Whaling Commission* **32**, 259–262.

Kastelein, R.A., Au, W.W.L., Rippe, H.T. & Schooneman, N.M. 1999. Target detection by an echolocating harbour porpoise (*Phocoena phocoena*). *Journal of the Acoustical Society of America* **105**, 2493–2498.

Kastelein, R.A., Hardeman, J. & Boer, H. 1997b. Food consumption and body weight of harbour porpoises (*Phocoena phocoena*). In *The biology of harbour porpoise*, A.J. Read et al. (eds). Woerden, The Netherlands: De Spil Publishers, 217–233.

Kastelein, R.A. & Lavaleije, M.S.S. 1992. Foreign bodies in the stomachs of a female harbour porpoise (*Phocoena phocoena*) from the North Sea. *Aquatic Mammals* **18**, 40–46.

Kastelein, R.A., Schooneman, N.M., Au, W.W.L., Verboom, W.C. & Vaughan, N. 1997a. The ability of a harbour porpoise (*Phocoena phocoena*) to discriminate between objects buried in the sand. In *The biology of harbour porpoise*, A.J. Read et al. (eds). Woerden, The Netherlands: De Spil Publishers, 329–342.

Kayes, R.J. 1985. The decline of porpoises and dolphins in the southern North Sea: a current status report. Greenpeace International, Political Ecology Research Group, Oxford.

Kinze, C.C. 1985. Intraspecific variation in Baltic and North Sea harbour porpoises (*Phocoena phocoena* (L., 1758)). *Videnskabelige Meddelelser fra Dansk Naturhistorie Forening,* **146**, 63–74.

Kinze, C.C. 1989. On the reproduction, diet and parasitic burden of harbour porpoise (*Phocoena phocoena*) in the west Greenland waters. In *European research on cetaceans – 3*, P.G.H. Evans (ed.). Cambridge: European Cetacean Society, 91–95.

Kinze, C.C. 1990a. Cetacean mortality in passive fishing nets and traps in the Baltic Sea: a review. *International Whaling Commission*, SC/O90/G25, Cambridge, UK.

Kinze, C.C. 1990b. Marsvineundersøgelser 1989, afsluttende rapport. *Zoologisk Museum,* Copenhagen, Denmark.

Kinze, C.C. 1994. Incidental catch of harbour porpoises (*Phocoena phocoena*) in Danish waters, 1986–1989. In *Special Issue, 15: Gillnets and cetaceans*, W.F. Perrin et al. (eds). Cambridge: International Whaling Commission, 183–187.

Kinze, C.C. 1995. Exploitation of harbour porpoises (*Phocoena phocoena*) in Danish waters: a historical review. In *Special Issue, 16: Biology of phocoenids*, A. Bjørge & G.P. Donovan (eds). Cambridge: International Whaling Commission, 141–153.

Kirsch, P.E., Iverson, S.J. & Bowen, W.D. 2000. Effects of diet on body composition and blubber fatty acids in captive harp seals (*Phoca groenlandica*). *Physiological and Biochemical Zoology* **73**, 45–59.

Kirsch, P.E., Iverson, S.J., Bowen, W.D., Kerr, S.R. & Ackman, R.G. 1998. Dietary effects on the fatty acid signature of whole Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1378–1386.

Kleivane, L., Skaare, J.U., Bjorke, A., Ruiter, E. de & Reijnders, P.J.H. 1995. Organochlorine pesticide residue and PCBs in harbour porpoise (*Phocoena phocoena*) incidentally caught in Scandinavian waters. *Environmental Pollution* **89**, 137–146.

Kock, K.H. & Benke, H. 1996. On the by-catch of harbour porpoise (*Phocoena phocoena*) in German fisheries in the Baltic and the North Sea. *Archives of Fishery and Marine Research* **44**, 95–114.

Koopman, H.N. 1998. Topographical distribution of the blubber of harbour porpoises (*Phocoena phocoena*). *Journal of Mammalogy* **79**, 260–270.

Koopman, H.N., Iverson, S.J. & Gaskin, D.E. 1996. Stratification and age-related differences in blubber fatty acids of the male harbour porpoise (*Phocoena phocoena*). *Journal of Comparative Physiology, B* **165**, 628–639.

Kuiken, T. 1996. Review of the criteria for the diagnosis of by-catch in cetaceans. In *Newsletter 26 (Special Issue): Diagnosis of by-catch in cetaceans, Proceedings of the Second ECS Workshop on Cetacean Pathology*, T. Kuiken (ed.). Saskatoon, Canada: European Cetacean Society, 38–43.

Kuiken, T., Bennett, P.M., Allchin, C.R., Kirkwood, J.K., Baker, J.R., Lockyer, C.H., Walton, M.J. & Sheldrick, M.C. 1994b. PCBs, cause of death and body condition in harbour porpoises (*Phocoena phocoena*) from British waters. *Aquatic Toxicology* **28**, 13–28.

Kuiken, T., Hoefle, U., Bennett, P.M., Allchin, C.R., Kirkwood, J.K., Baker, J.R., Appleby, E.C., Lockyer, C.H., Walton, M.J. & Sheldrick, M.C. 1993. Adrenocortical hyperplasia, disease and chlorinated hydrocarbons in the harbour porpoise (*Phocoena phocoena*). *Marine Pollution Bulletin* **26**, 440–446.

Kuiken, T., Simpson, V.R., Allchin, C.R., Bennett, P.M., Codd, G.A., Harris, E.A., Howes, G.J., Kennedy, S., Kirkwood, J.K., Law, R.J., Merrett, N.R. & Phillips, S. 1994a. Mass mortality of common dolphins (*Delphinus delphis*) in south west England due to incidental capture in fishing gear. *Veterinary Record* **134**, 81–89.

Langham, L.P.E. 1971. The distribution and abundance of larval sand-eels (Ammodytidae) in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom* **51**, 697–707.

Lick, R. R. 1991a. *Untersuchungen zu Lebenszyklus (Krebse – Fische – marine Säuger) und Gefrierresistentz anisakider Nematoden in Nord- und Ostsee [Investigations concerning the life cycle (crustaceans – fish – marine mammals) and freezing tolerance of anisakine nematodes in the North Sea and the Baltic Sea]*. PhD thesis, University of Kiel, Kiel, Germany.

Lick, R. R. 1991b. Parasites from the digestive tract and food analysis of harbour porpoise (*Phocoena phocoena*) from German waters. In *European research on cetaceans – 5*, P. G. H. Evans (ed.). Cambridge: European Cetacean Society, 65–68.

Lindroth, A. 1962. Baltic salmon fluctuations 2: porpoise and salmon. *Reports of the Institute of Freshwater Research of Drottningholm* **44**, 105–112.

Lockyer, C. 1995. Investigation of aspects of the life history of the harbour porpoise, *Phocoena phocoena*, in British waters. In *Special Issue, 16: Biology of phocoenids*, A. Bjørge & G. P. Donovan (eds). Cambridge: International Whaling Commission, 189–197.

Lockyer, C. 1999. Application of a new method to investigate population structure in the harbour porpoise, *Phocoena phocoena*, with special reference to the North and Baltic Seas. *Journal of Cetacean Research and Management* **1**, 297–304.

Lockyer, C., Desportes, G., Anderson, K., Labberté, S. & Siebert, U. 2001. Monitoring growth of harbour porpoise (*Phocoena phocoena*) in human care. International Council for the Exploration of the Sea, C. M. 2001/J:29, Copenhagen, Denmark.

Lowry, N. & Teilmann, J. 1994. Bycatch and bycatch reduction of the harbour porpoise (*Phocoena phocoena*) in Danish waters. In *Special Issue, 15: Gillnets and cetaceans*, W. F. Perrin et al. (eds). Cambridge: International Whaling Commission, 203–209.

Macer, C. T. 1966. Sandeels (Ammodytidae) in the southwestern North Sea: their biology and fishery. *Fishery Investigations, London, Series 2* **24**, 1–55.

Macintyre, D. 1934. Sea enemies of salmon. *Salmon and Trout Magazine* **74**, 38–42.

Malinga, M. & Kuklik, I. 1996. Food consumption of harbour porpoises (*Phocoena phocoena*) in Polish waters of the Baltic Sea. In *European research on cetaceans – 10*, P. G. H. Evans (ed.). Cambridge: European Cetacean Society, 260 only.

Marchessaux, D. 1980. A review of the current knowledge of the cetaceans in the eastern Mediterranean Sea. *Vie Marina* **2**, 59–64.

Martin, A. R. 1996. The diet of harbour porpoises (*Phocoena phocoena*) in British waters. International Whaling Commission, SC/47/SM48, Cambridge, UK.

Matthews, L. H. 1952. *British mammals*. London: Collins.

Merson, M. H. & Kirkpatrick, R. L. 1976. Reproductive performance of captive white-footed mice fed a PCB. *Bulletin of Environmental Contamination and Toxicology* **16**, 392–398.

Millais, J. G. 1906. *Mammals of Great Britain and Ireland*. London: Longmans Green.

Miyazaki, N., Amano, M. & Fujise, Y. 1987. Growth and skull morphology of the harbour porpoises in the Japanese waters. *Memoirs of the Natural Science Museum of Tokyo* **20**, 137–146.

Monaghan, P., Uttley, J. D., Burns, M. D., Thaine, C. & Blackwood, J. 1989. The relationship between food supply, reproductive effort and breeding success in Arctic terns *Sterna paradisaea*. *Journal of Animal Ecology* **58**, 261–274.

Murray, J. & Burt, J. R. 1977. *The composition of fish*. Torry Advisory Note No. 38, MAFF, Aberdeen.

Northridge, S. P. & Lankester, K. 1992. Sightings of the harbour porpoise in the North Sea and some notes on interactions with the fisheries. International Whaling Commission, SC/42/SM46, Cambridge, UK.

Northridge, S. P., Tasker, M. L., Webb, A. & Williams, J. M. 1995. Distribution and relative abundance of harbour porpoises (*Phocoena phocoena* L.), white-beaked dolphins (*Lagenorhynchus albirostris* Gray) and minke whales (*Balaenoptera acutorostrata* Lacepède) around the British Isles. *ICES Journal of Marine Science* **52**, 55–66.

Otterlind, G. 1976. The harbour porpoise (*Phocoena phocoena*) endangered in Swedish waters. International Council for the Exploration of the Sea, C. M. 1976/N:16, Copenhagen, Denmark.

Palka, D. L., Read, A. J., Westgate, A. J. & Johnston, D. W. 1996. Summary of current knowledge of harbour porpoises in US and Canadian Atlantic waters. *Reports of the International Whaling Commission* **46**, 559–565.

Pauly, D., Trites, A.W., Capuli, E. & Christensen, V. 1998. Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science* **55**, 467–481.

Perkins, J.S., Bryant, P.J., Nichols, G. & Patten, D.R. 1982. Humpback whales (*Megaptera novaeangliae*) off the west coast of Greenland. *Canadian Journal of Zoology* **60**, 2921–2930.

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

Pierce, G.J., Boyle, P.R., Diack., J.S.W. & Clark, I. 1990. Sandeels in the diets of seals: application of novel and conventional methods of analysis to faeces from seals in the Moray Firth area of Scotland. *Journal of the Marine Biological Association of the United Kingdom* **70**, 829–840.

Pierce, G.J., Diak, J.S.W. & Boyle, P.R. 1989. Digestive tract contents of seals in the Moray Firth area of Scotland. *Journal of Fish Biology* **35** (Suppl. A), 341–343.

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, London* **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, London* **223**, 641–652.

Pierpoint, C., Earl, S. & Baines, M. 1994. Observations of harbour porpoise in West Wales, 1993. In *European research on cetaceans – 8*, P.G.H. Evans (ed.). Cambridge: European Cetacean Society, 75–78.

Pierpoint, C.J.L., Baines, M.E., Earl, S.J., Harris, R. & Tregenza, N. 1999. Night-life of harbour porpoise. In *European research on cetaceans – 13*, P.G.H. Evans et al. (eds). Cambridge: European Cetacean Society, 70–71.

Pinnegar, J.K., Jennings, S., O'Brien, C.M. & Polunin, N.V.C. 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market place distribution. *Journal of Applied Ecology* **39**, 377–390.

Pulliam, H.R. 1974. On the theory of optimal diets. *American Naturalist* **108**, 59–74.

Rae, B.B. 1965. The food of the common porpoise (*Phocoena phocoena*). *Journal of Zoology, London* **146**, 114–122.

Rae, B.B. 1973. Additional notes on the food of the common porpoise (*Phocoena phocoena*). *Journal of Zoology, London* **169**, 127–131.

Read, A.J. 1999. The harbour porpoise – *Phocoena phocoena* (Linnaeus, 1758). In *Handbook of marine mammals Vol. 6: The second book of dolphins and the porpoises*, S.H. Ridgway & R. Harrison (eds). London: Academic Press, 323–355.

Read, A.J. & Gaskin, D.E. 1988. Incidental catch of harbour porpoises by gill nets. *Journal of Wildlife Management* **52**, 517–523.

Read, A.J. & Gaskin, D.E. 1990. Changes in growth and reproduction of harbour porpoises, *Phocoena phocoena*, from the Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 2158–2163.

Read, A.J. & Hohn, A.A. 1995. Life in the fast lane: the life history of harbour porpoises from the Gulf of Maine. *Marine Mammal Science* **11**, 423–440.

Read, A.J. & Westgate, A.J. 1997. Monitoring the movements of harbour porpoises (*Phocoena phocoena*) with satellite telemetry. *Marine Biology* **130**, 315–322.

Read, A.J., Wiepkema, P.R. & Nachtigall, P.E. 1997. The harbour porpoise (*Phocoena phocoena*). In *The biology of the harbour porpoise*, A.J. Read et al. (eds). Woerden, The Netherlands: De Spil Publishers, 3–6.

Reay, P.J. 1970. Synopsis of biological data on north Atlantic sandeels of the genus *Ammodytes* (*A. tobianus*, *A. dubius*, *A. americanus* and *A. marinus*). *FAO Fisheries Synopsis* **82**.

Recchia, C.A. & Read, A.J. 1989. Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. *Canadian Journal of Zoology* **67**, 2140–2146.

Reijnders, P.J.H. 1986. Reproductive failure in common seals feeding on fish from polluted coastal waters. *Nature* **324**, 456–457.

Rogan, E. & Berrow, S.D. 1996. A review of harbour porpoises, *Phocoena phocoena*, in Irish waters. *Reports of the International Whaling Commission* **46**, 595–605.

Rosel, P.E., Dizon, A.E. & Haygood, M.G. 1995. Variability of the mitochondrial control region in populations of the harbour porpoise, *Phocoena phocoena*, on interoceanic and regional scales. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1210–1219.

Rosel, P.E., France, S.C., Wang, J.Y. & Kocher, T.D. 1999. Genetic structure of harbour porpoise *Phocoena phocoena* populations in the northwest Atlantic based on mitochondrial and nuclear markers. *Molecular Ecology* **8**, S41–S54.

Ross, G.J.B. 1984. The smaller cetaceans of the south east coast of southern Africa. *Annals of the Cape Provincial Museums (Natural History)* **15**, 173–410.

Ross, H.M. & Wilson, B. 1996. Violent interactions between bottlenose dolphins and harbour porpoises. *Proceedings of the Royal Society of London, B* **263**, 283–286.

Ross, P.S., De Swart, R.L., Timmerman, H.H., Reijnders, P.J.H., Vos, J.G., Van Loveren, H. & Osterhaus, A.D.M.E. 1996. Suppression of natural killer cell activity in harbour seals (*Phoca vitulina*) fed Baltic Sea herring. *Aquatic Toxicology* **34**, 71–84.

Santos, M.B. 1998. *Feeding ecology of harbour porpoises, common and bottlenose dolphins and sperm whales in the northeast Atlantic.* PhD thesis, University of Aberdeen, Aberdeen, Scotland.

Santos, M.B., Clarke, M.R. & Pierce, G.J. 2001b. Assessing the importance of cephalopods in the diets of marine mammals and other top predators. *Fisheries Research*, **52**, 121–139.

Santos, M.B., Pierce, G.J., Reid, R.J., Patterson, I.A.P., Ross, H.M. & Mente, E. 2001c. Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom* **81**, 873–878.

Santos, M.B., Spencer, N., Pierce, G.J., Lockyer, C., Reid, R.J., Patterson, I.A.P. & Edwards, W. 2001a. Life history parameters of harbour porpoise (*Phocoena phocoena*) in Scottish waters. 15th Annual Conference of the European Cetacean Society, Rome, Italy.

Scheffer, V.B. 1953. Measurements and stomachs contents of 11 delphinids from the northeast Pacific. *Murrelet* **34**, 27–30.

Scott, T. 1903. Some further observations on the food of fishes, with a note on the food observed in the stomach of a common porpoise. *Report of the Fishery Board for Scotland* **21**, 218–227.

Sekiguchi, K. 1987. *Occurrence and behaviour of harbour porpoises (*Phocoena phocoena*) at Pajaro Dunes, Monterey Bay, California*. MSc thesis, San Jose State University, California.

Sekiguchi, K., Klages, N.T.W. & Best, P.B. 1992. Comparative analysis of the diets of smaller odontocete cetaceans along the coast of Southern Africa. *South African Journal of Marine Science* **12**, 843–861.

Sequeira, M. 1996. Harbour porpoises, *Phocoena phocoena*, in Portuguese waters. *Reports of the International Whaling Commission* **46**, 583–586.

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

Sergeant, D.E. & Fisher, H.D. 1957. The smaller Cetacea of eastern Canadian waters. *Journal of the Fisheries Research Board of Canada* **14**, 83–115.

Siebert, U., Benke, H., Frese, K., Pirro, F. & Lick, R. 1996. Postmortem examination of by-catches from German fisheries and of suspected by-catches found on the coast of Germany. In *Newsletter 26 (Special Issue): Diagnosis of by-catch in cetaceans, Proceedings of the Second ECS Workshop on Cetacean Pathology*, T. Kuiken (ed.). Saskatoon, Canada: European Cetacean Society, 27–30.

Silva, M.A., Sequeira, M., Prieto, R. and Alexandre, B. 1999. Observations of harbour porpoises (*Phocoena phocoena*) on the northern coast of Portugal. In *European research on cetaceans – 13*, P.G.H. Evans et al. (eds). Cambridge: European Cetacean Society, 267–269.

Slijper, E.J. 1962. *Whales*. London: Hutchinson.

Smeenk, C. 1987. The harbour porpoise *Phocoena phocoena* (L., 1758) in the Netherlands: stranding records and decline. *Lutra* **30**, 77–90.

Smeenk, C., Leopold, M.F. & Addink, M.J. 1992. Note on the harbour porpoise *Phocoena phocoena* in Mauritania, West Africa. *Lutra* **35**, 98–104.
Smith, G.J.D. & Gaskin, D.E. 1974. The diet of harbour porpoises (*Phocoena phocoena* (L.)) in coastal waters of Eastern Canada, with special reference to the Bay of Fundy. *Canadian Journal of Zoology* **52**, 777–782.
Smith, R.J. & Read, A.J. 1992. Consumption of euphausiids by harbour porpoises (*Phocoena phocoena*) calves in the Bay of Fundy. *Canadian Journal of Zoology* **70**, 1629–1632.
Southwell, T. 1881. *The seals and whales of the British seas*. London: Jarrold.
Sparholt, H. 1990. An estimate of the total biomass of fish in the North Sea. *ICES Journal of Marine Science* **46**, 200–210.
Stephen, A.C. 1926. Common porpoise stranded at Granton. *Scottish Naturalist* **1926**, 46.
Storey, G. 1993. *The trophic ecology of the sandeel* Ammodytes tobianus *(L.), and other planktivorous fish species from Aberdeen Bay*. PhD thesis, University of Aberdeen, Aberdeen.
Sturtivant, C.R., Datta, S. & Goodson, D.S. 1994. A review of echolocation research on the harbour porpoise *Phocoena phocoena* and the common dolphin *Delphinus delphis*. In *European research on cetaceans – 8*, P.G.H. Evans (ed.). Cambridge: European Cetacean Society, 164–168.
Subramanian, A.N., Tanabe, S., Tatsukawa, R., Saito, S. & Miyazaki, N. 1987. Reduction in the testosterone levels by PCBs and DDE in Dall's porpoises of northwestern North Pacific. *Marine Pollution Bulletin* **18**, 643–646.
Svärdson, G. 1955. Salmon stock fluctuations in the Baltic Sea. *Reports of the Institute of Freshwater Research of Drottningholm* **36**, 226–262.
Swart, R. de L., Ross, P.S., Vedder, L.J., Timmerman, H.H., Heisterkamp, S., Loveren, H.V., Vos, J.G., Reijnders, P.J.H. & Osterhaus, A.D.M.E. 1994. Impairment of immune function in harbour seals (*Phoca vitulina*) feeding on fish from polluted waters. *Ambio* **23**, 155–159.
Tanabe, S., Watanabe, S., Kan, H. & Tatsukawa, R. 1988. Capacity and mode of PCB metabolism in small cetaceans. *Marine Mammal Science* **4**, 103–124.
Taylor, B.L. & Dawson, P.K. 1984. Seasonal changes in density and behaviour of harbour porpoise (*Phocoena phocoena*) affecting census methodology in Glacier Bay National Park, Alaska. *Reports of the International Whaling Commission* **34**, 479–483.
Teilmann, J. & Dietz, R. 1996. Status of the harbour porpoises (*Phocoena phocoena*) in Greenland. International Whaling Commission, SC/47/SM44, Cambridge, UK.
Thompson, P.M., Pierce, G.J., Hislop, J.R.G., Miller, D. & Diack, J.S.W. 1991. Winter foraging by common seals (*Phoca vitulina*) in relation to food availability in the inner Moray Firth, N.E. Scotland. *Journal of Animal Ecology* **60**, 283–294.
Thompson, P.M., Tollit, D.J., Corpe, H.M., Reid, R.J. & Ross, H.M. 1997. Changes in haematological parameters in relation to prey switching in a wild population of harbour seals. *Functional Ecology* **11**, 743–750.
Tiedemann, R., Harder, J., Gmeiner, C. & Haase, E. 1996. Mitochondrial DNA sequence patterns of harbour porpoises (*Phocoena phocoena*) from the North and the Baltic Sea. *Zeitschrift für Säugetierkunde* **61**, 104–111.
Tiezen, L.L. 1978. Carbon isotope fractionation in biological material. *Nature* **276**, 97–98.
Tolley, K.A. & Heldal, H.E. 2002. Inferring ecological separation from regional differences in radioactive caesium in harbour porpoises (*Phocoena phocoena*). *Marine Ecology Progress Series* **228**, 301–309.
Tolley, K.A., Rosel, P.E., Walton, M., Bjørge, A. & Øien, N. 1999. Genetic population structure of harbour porpoises (*Phocoena phocoena*) in the North Sea and Norwegian waters. *Journal of Cetacean Research and Management* **1**, 265–274.
Tolley, K.A., Víkingsson, G.A. & Rosel, P.E. 2001. Mitochondrial DNA sequence variation and phylogeographic patterns in harbour porpoises *Phocoena phocoena* from the North Atlantic. *Conservation Genetics* **2**, 349–361.
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.

Tomilin, A.G. 1957. Vol. IX: Cetacea. In *Mammals of the U.S.S.R. and adjacent countries*, V.G. Geptner (ed.). Moscow: Izdat. Akad. Nauk SSSR. (English Translation, 1967, Jerusalem: Israel Program for Scientific Translations).

Tregenza, N.J.C., Berrow, S.D., Leaper, R. & Hammond, P.S. 1997. Harbour porpoise, *Phocoena phocoena* L., by-catch in set gill nets in the Celtic Sea. *ICES Journal of Marine Science* **54**, 896–904.

van Beneden, P.J. 1889. Histoire naturelle des delphinides des mers d'Europe. *Mémoirs du Course de l'Academie Royal Belge* **43**, 1–253.

van Bree, P.J.H. 1977. On former and recent strandings of cetaceans on the coast of the Netherlands. *Zeitschrift fur Saugetierkunde* **42**, 101–107.

van Utrech, W.L. 1978. Age and growth in *Phocoena phocoena* Linnaeus, 1758 (Cetacea, Odontoceti) from the North Sea. *Bijdragen tot de Dierkunde* **48**, 16–28.

Verwey, J. 1975. The cetaceans *Phocoena phocoena* and *Tursiops truncatus* in the Marsdiep area (Dutch Wadden Sea) in the years 1931–1973. *Nederlands Instituut voor Onderzoek der Zee, Publicaties en verslagen, 1975* **17**, 1–153.

Vinther, M. 1999. Bycatches of harbour porpoises (*Phocoena phocoena* L.) in Danish set-net fisheries. *Journal of Cetacean Research and Management* **1**, 123–135.

Vos, J.G. & Luster, M.I. 1989. Immune alterations. In *Halogenated biphenyls, terphenyls, naphthalenes, dibenzodioxins and related products*, R.D. Kimbrough & A.A. Jensen (eds). Amsterdam: Elsevier, 295–322.

Walton, M.J. 1997. The population structure of harbour porpoises *Phocoena phocoena* in the seas around the UK and adjacent waters. *Proceedings of the Royal Society of London, B* **264**, 89–94.

Wang, J.Y., Gaskin, D.E. & White, B.N. 1996. Mitochondrial DNA analysis of harbour porpoise, *Phocoena phocoena*, subpopulations in North American waters. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 1632–1645.

Wang, J.Y. & Berggren, P. 1997. Mitochondrial DNA analysis of harbour porpoises (*Phocoena phocoena*) in the Baltic Sea, the Kattegat–Skagerrak Seas and off the west coast of Norway. *Marine Biology* **127**, 531–537.

Wang, J.Y., Gaskin, D.E. & White, B.N. 1996. Mitochondrial DNA analysis of harbour porpoise, *Phocoena phoconea*, subpopulations in North American waters. *Canadian Journal of Fisheries and Aquatic Sciences* **5**, 1632–1645.

Waring, G.T., Gerrior, P., Payne, P.M., Parry, B.L. & Nicolas, J.R. 1990. Incidental take of marine mammals in foreign fishery activities off the northeast United States, 1977–88. *Fishery Bulletin* **88**, 347–360.

Wassermann, M., Wassermann, D., Gershon, Z. & Zellermayer, L. 1979. Effects of organochlorine insecticides on body defense systems. In *Biological effects of pesticides in mammalian systems*, H.F. Kraybill (ed.). New York: Annals of the New York Academy of Sciences, 393–401.

Watson, A.P. & Gaskin, D.E. 1983. Observations on the ventilation cycle of the harbour porpoise *Phocoena phocoena* in coastal waters of the Bay of Fundy. *Canadian Journal of Zoology* **61**, 126–132.

Watson, L. 1985. *Whales of the world*. London: Hutchinson.

Wells, D.E. & McKenzie, C. 1994. Techniques for pattern recognition of organochlorine residues in sea mammals from Scottish coastal waters. *International Council for the Exploration of the Sea*, C.M. 1994/E + N:10, Copenhagen, Denmark.

Westgate, A.J., Read, A.J., Berggren, P., Koopman, H.N. & Gaskin, D.E. 1995. Diving behaviour of harbour porpoises, *Phocoena phocoena*. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1064–1073.

Westgate, A.J. & Tolley, K.A. 1999. Geographical differences in organochlorine contaminants in harbour porpoises *Phocoena phocoena* from the western North Atlantic. *Marine Ecology Progress Series* **177**, 255–268.

Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J. & Tortonese, E. (eds) 1989. *Fishes of the north-eastern Atlantic and the Mediterranean*. UNESCO, Paris.

Whymper, F. 1883. *The fisheries of the world. An illustrated and descriptive record of the international fisheries exhibition*. London: Cassell.
Wijnsma, G., Pierce, G.J. & Santos, M.B. 1999. Assessment of errors in cetacean diet analysis: *in vitro* digestion of otoliths. *Journal of the Marine Biological Association of the United Kingdom* **79**, 573–575.
Wilke, F. & Kenyon, K.W. 1952. Notes on the food of fur seal, sea-lion, and harbour porpoise. *Journal of Wildlife Management* **16**, 396–397.
Winslade, P. 1974. Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt). II. The effect of light intensity on activity. *Journal of Fish Biology* **6**, 577–586.
Wright, P.J. 1996. Is there a conflict between sandeel fisheries and seabirds? A case study at Shetland. In *Aquatic predators and their prey*, S.P.R. Greenstreet & M.L. Tasker (eds). Oxford: Fishing News Books, Blackwell Science, 154–165.
Yasui, W.C. & Gaskin, D.E. 1986. Energy budget of a small cetacean, the harbour porpoise, *Phocoena phocoena* (L.). *Ophelia* **25**, 183–197.
Yurick, D.B. 1977. *Populations, subpopulations and zoogeography of the harbour porpoise,* Phocoena phocoena *(L.)*. MSc thesis, University of Guelph, Guelph, Ontario.
Yurick, D.B. & Gaskin, D.E. 1987. Morphometric and meristic comparisons of skulls of harbour porpoise *Phocoena phocoena* (L.) from the North Atlantic and North Pacific. *Ophelia* **27**, 53–75.