Phuket mar. biol. Cent. Res. Bull. **66:** 291–298 (2005)

A NOTE ON NICHE OVERLAP IN TEUTHOPHAGOUS WHALES IN THE NORTHERN NORTHEAST ATLANTIC

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ABSTRACT: Sperm whale (*Physeter macrocephalus*), Northern bottlenose whale (*Hyperoodon ampullatus*) and Cuvier's beaked whale (*Ziphius cavirostris*) are oceanic cetaceans occurring in the northern Northeast Atlantic and feeding mainly on deep-water cephalopods. The present paper uses previously published stomach contents data from strandings to examine niche overlap and niche breadth and test the hypothesis that northern bottlenose whale and Cuvier's beaked whale, both being considerably smaller than sperm whales, would take smaller squid.

Samples consisted of stomach contents of 24 sperm whales, 6 northern bottlenose whales and 4 Cuvier's beaked whales stranded in various parts of the North Sea and elsewhere in the northern Northeast Atlantic. The oceanic squid *Gonatus* sp. (probably *G. fabricii*) was the main prey of both sperm and northern bottlenose whale, whereas *Gonatus* sp. and another oceanic squid *Teuthowenia megalops* were the most frequent prey of Cuvier's beaked whale. Stomach contents of sperm whales and northern bottlenose whales overlap almost completely in the North Sea and the diets of northern bottlenose and Cuvier's whales overlap considerably elsewhere in the northern Northeast Atlantic. The latter species has a slightly broader diet.

Comparing the sizes of *Gonatus* eaten, sperm whales had eaten almost exclusively large, probably mature, squid (with some evidence that larger individual whales took larger squid). The stomachs of bottlenose whales contained mainly smaller, including post-juvenile, squid. Cuvier's beaked whale took the widest range of sizes of *Gonatus*, including all size classes taken by the other two whale species.

INTRODUCTION

Sperm whale (*Physeter macrocephalus*), Northern bottlenose whale (*Hyperoodon ampullatus*) and Cuvier's beaked whale (*Ziphius cavirostris*) are oceanic cetaceans known to feed mainly on deep-water cephalopods.

The sperm whale occurs throughout Northeast Atlantic waters, the northern bottlenose whale occurs as far south as the Azores while Cuvier's beaked whale generally occurs as far north as the northern coast of Ireland (*e.g.* Rice, 1989; Gowans, 2002). However, the distribution of all three species overlaps on the west coast of Britain and there appears to be the potential for competition between the three species.

Since these whales coexist in the northern Northeast Atlantic it is of interest to determine the extent to which their feeding niches overlap or whether there is resource partitioning. Recent data on feeding derive almost exclusively from strandings. In the North Sea - considered to be a "sperm whale trap" by Smeenk (1997) - most strandings of large whales are probably due to navigation errors.

We analysed previously published data on stomach contents of the three species from the North Sea and elsewhere in the northern Northeast Atlantic to quantify feeding niche overlap between the three species, as well as evaluating dietary breadth, and the size composition of prey eaten. We test the hypothesis that the northern bottlenose whale and Cuvier's beaked whale, both being considerably smaller than sperm whales, would take smaller squid. We also ask whether larger sperm whales take larger squid.

METHODS

The data analysed arise from stomach contents of sperm whales, northern bottlenose whales and

Cuvier's beaked whales stranded in Scotland, Denmark, The Netherlands, Ireland and NW Spain, mainly during the 1990s (see Table 1, Figure 1). Results on diet composition for the individual cetacean species were previously published by Santos *et al.* (1999, 2001a,b, 2002). These data and unpublished data on the stomach contents of three more recently stranded individuals (2 northern bottlenose and 1 Cuvier's beaked whale) were used in the present analysis. In total, the sample comprised 24 sperm whales, 6 northern bottlenose whales and 4 Cuvier's beaked whales.

Diet composition for each animal was calculated as percentage by reconstructed weight of the stomach contents. Overall diets for each species-area-season combination were derived by pooling prey remains from all samples in the relevant category. To calculate indices of niche overlap and diet breadth, since in some cases prey could not be identified to species level but to genus level only, prey were categorised into families, ensuring consistent treatment of the data.

Comparisons of diet composition between whale species, areas and seasons made use of Pianka's index of niche overlap (Pianka, 1973) to provide a measure of the overall similarity of the diets (*i.e.* prey species were grouped into families):

$$O_{j,k} = \frac{\sum P_{i,j} \times P_{i,k}}{\left(\sum P_{i,j}^2 \times \sum P_{i,k}^2\right)^{\frac{1}{2}}}$$

where $O_{j,k}$ is the measure of niche overlap between predators j and k

$P_{i,j}$ is the proportion by weight of prey type i in relation to the total amount of prey consumed by predator species j.

This index varies between 0 (no overlap) and 1 (complete overlap), with values above 0.6 being regarded as "biologically significant" (Wallace, 1981). Niche breadth was calculated using Levin's standardised index (Krebs, 1989) to provide a measure of how specialised a species is (again prey species were grouped into families):

$$B_j = \frac{1}{n-1}\left[\frac{1}{\sum P_{i,j}^2} - 1\right]$$

where B_j is the measure of niche breadth of predator j.

n is the number of prey categories.

Index values vary from 0 to 1 with a value of 0 indicating a specialist predator and 1 a generalist diet. Where many prey types have similar importance in the diet, the value of the index tends towards 1.

Table 1. Strandings data, tabulated by species and area.

Species	N	Strandings information	Biological information
Sperm whale	22	North Sea, Nov-Mar (1937-1998)	Males, 12-16 m length, 20-25 years old
Sperm whale	2	W. Ireland, Mar 96, N. Scotland, Aug 98	Males
Northern bottlenose whale	4	North Sea, Feb 97, Aug 56/93, Nov 1885	2 males, 2 females
Northern bottlenose whale	2	W. Ireland, Aug 01 W. Scotland, Sep 01	Females
Cuvier's beaked whale	1	W. Scotland, Feb 99	Female, 5.9 m length
Cuvier's beaked whale	3	NW Spain, Feb 90/95 Nov 00	2 males, 1 female, 4.9 – 5.1 m length

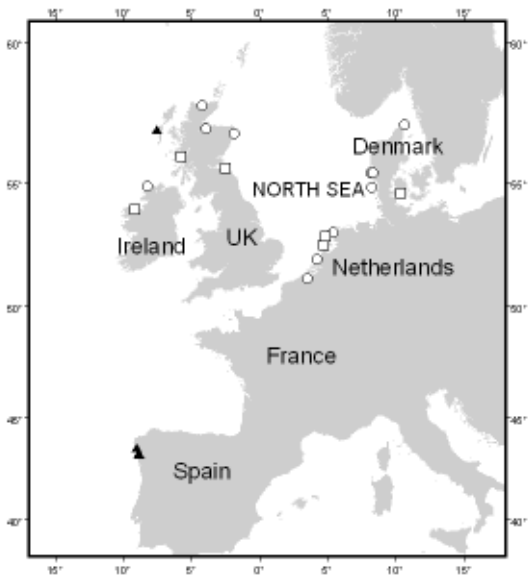


Figure 1. Location of strandings: ○ sperm whales, □ northern bottlenose whales, ▲ Cuvier's beaked whales.

For sperm whales, the species for which the data set is largest, we were able to test whether larger whales tended to eat larger *Gonatus*.

RESULTS

Species present in stomach contents

None of the whales had any fresh prey in the stomachs. Remains consisted mainly of cephalopod beaks along with some fish bones and eye lenses. In all three whale species, oceanic squid species were the main prey.

Gonatus sp. (probably *G. fabricii*) was the main prey of sperm whales, with *Histioteuthis bonnellii* and *Teuthowenia megalops* also being important. Two of the sperm whales did not fit the general pattern and their stomach contents may be indicative of regional and seasonal variation in diet (see Table 3). One sperm whale stranded in northern Scotland in August 1998 contained relatively few *Gonatus* and may have migrated south early. A sperm whale stranded on the west coast of Ireland in March 1996 also contained few *Gonatus* and the most important prey species was *Haliphron atlanticus*. This whale may have migrated southwards from a different area to that utilized by whales ultimately stranding in the North Sea or could have been travelling northwards.

In Northern bottlenose whales, *Gonatus* sp. was the main prey, with *Taonius pavo*, *Teuthowenia megalops* and *Histioteuthis* spp. also important. One of the Danish animals (see Table 1), stranded in February 1997, contained relatively few *Gonatus*. This animal may have stranded during the northward migration and suggests seasonal variation in diet.

As with sperm whales, strandings from the west of the British Isles offer a somewhat different view of the diet – in two northern bottlenose whales from the west of Ireland (August 2001) and west of Scotland (September 2001), the stomach contents comprised mainly beaks of *Teuthowenia megalops* and *Taonius pavo*, with relatively few *Gonatus*. Since the timing is consistent with southward migration, these animals provide evidence of regional differences in diet.

Teuthowenia megalops was the most frequently recorded prey in the stomach contents of Cuvier's beaked whales, with *Gonatus* sp., *Mastigoteuthis*, and *Histioteuthis* spp. also important. *Gonatus* appeared in the stomach contents of two of the Galician animals but in this case is probably *G. steenstrupi*, which has a more southerly distribution than *G. fabricii.*

Prey families eaten: niche overlap and niche breadth

Overall, there is substantial overlap in the families of prey eaten by the sperm whale and northern bottlenose whale (Table 2). Looking in more detail, sperm whale and bottlenose whale stomach contents were essentially identical in the North Sea but both species ate different prey in the northern Northeast Atlantic (*i.e.* north and west Scotland, Ireland). Northern bottlenose whales and Cuvier's beaked whales diets also contained the same families of prey.

Niche breadth calculations indicate sperm whales and bottlenose whales have quite specialised diets (although with wider niche breadth outside the North Sea. A small niche

breadth figure indicates that a predator is very selective, specialising on particular prey species, whereas a high figure indicates that a predator has a more generalist diet, exploiting a range of prey species). Cuvier's beaked whale has a more varied diet than the other two species (Table 3). Note that, although the number of different prey families recorded in *Ziphius* stomachs is only slightly higher than for the other two whale species, there is less tendency for any one prey type to dominate.

Prey size

The maximum size of *Gonatus* eaten by the three species of whale was similar, perhaps reflecting the maximum available. However, while sperm whales had eaten almost exclusively large (probably mature) squid, the stomachs of bottlenose whales contained mainly smaller (post-juvenile) individuals.

Cuvier's beaked whale took the widest range of sizes of *Gonatus* sp., including both adults and juveniles (Figure 2a).

Examining data from the North Sea separately, some overlap is seen in the size classes of squid eaten by sperm whales and northern bottlenose whales (Figure 2b) but a clearer separation in the size of squid eaten is seen in data from the northern Northeast Atlantic (Figure 2c).

Using data on *Gonatus* beak sizes (lower beak rostral length) in stomach contents of 16 sperm whales for which individual length measurements were available, the correlation between sperm whale body length and beak size is 0.116 (N= 7187, P<0.001). Using mean beak length from each whale (*i.e.* avoiding pseudo-replication), the correlation is 0.493 (N=16, P=0.052; see Figure 3). Thus there is weak (but inconclusive) evidence that larger sperm whales eat larger *Gonatus*.

Table 2. Niche overlap values

(a) Between species, data for all seasons

	All areas	*North Sea*	*Northern Northeast Atlantic**
Physeter v Hyperoodon	*0.90*	*1.00*	*0.04*
Physeter v Ziphius	*0.49*	-	*0.04*
Hyperoodon v Ziphius	*0.77*	-	*0.86*

* Northern Northeast Atlantic = west and north Scotland, Ireland, Galicia

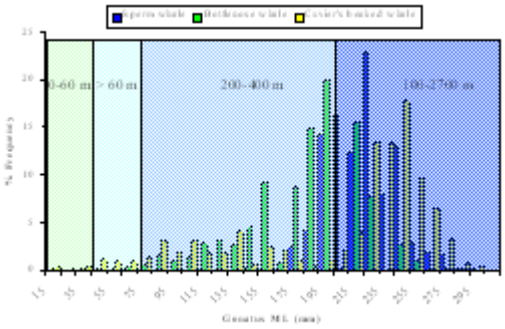
(b) Between areas and seasons, within species

	Physeter	*Hyperoodon*	*Ziphius*
N Sea v Northern NE Atlantic	0.05	0.19	-
Summer v Winter	0.17	0.99	-

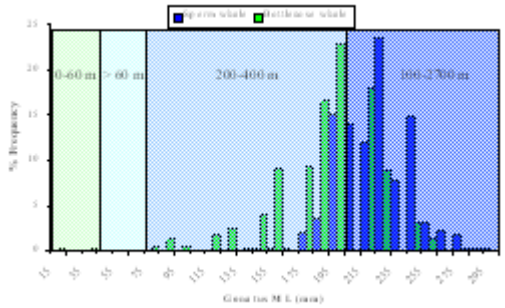
Table 3. Niche breadth values (and numbers of different prey categories recorded).

	All areas	*North Sea*	*Northern NE Atlantic**
Physeter	*0.04 (12)*	*0.02 (8)*	*0.14 (8)*
Hyperoodon	*0.07 (12)*	*0.01 (11)*	*0.15 (10)*
Ziphius	*0.28 (13)*	-	*0.28 (13)*

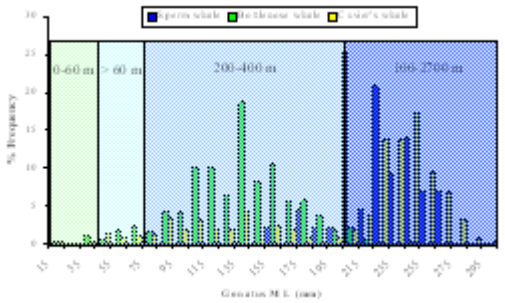
* Northern NE Atlantic = west and north Scotland, Ireland, Galicia



(a) Northern Northeast Atlantic and North Sea data combined (sperm whale - 20318 beaks, northern bottlenose whale - 2940 beaks, Cuvier's beaked whale - 999 beaks). The background colouring indicates the depth range in which squid of a given size category are normally found.



(b) North Sea only (sperm whale - 16565 beaks, northern bottlenose whale - 2546 beaks)



(c) Northern Northeast Atlantic data (i.e. excluding North Sea) (sperm whale - 43 beaks, northern bottlenose whale - 395 beaks, Cuvier's beaked whale - 945 beaks). The background colouring indicates the depth range in which squid of a given size category are normally found.

Figure 2. Size distribution of *Gonatus* in stomachs of whales. Different depths at which different size ranges of squid had been found are also distinguished (data from Wiborg *et al.* 1982, 1984; Bjørke, 1995).

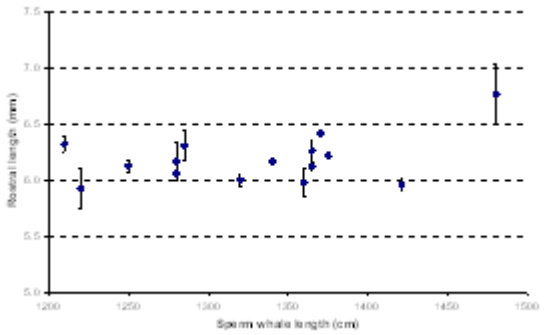


Figure 3. Size of *Gonatus* (mean±1 standard deviation) eaten by sperm whales in relation to sperm whale body length.

DISCUSSION

Niche overlap

The range of all three teuthophagous whale species studied overlaps to the west of the UK, although Cuvier's beaked whale generally has a more southerly distribution. Thus the potential for feeding competition is present.

Niche overlap data clearly indicate strong similarities in the suite of prey types eaten by sperm whales and northern bottlenose whales in the North Sea, and in prey of northern bottlenose and Cuvier's beaked whales elsewhere in the northern Northeast Atlantic.

Data on prey size indicate that sperm whales and northern bottlenose whales tend to eat different sized squid. The difference in sizes of *Gonatus* eaten by sperm whales and northern bottlenose whales is consistent with the former feeding at greater depths. Juvenile *Gonatus* (mantle length de 50 mm) are found near the surface whereas post-juvenile (and mature) individuals are found in deeper waters (Bjørke, 1995). Squids of 80 to 250 mm mantle length have been found at depths of 200–550 m with deep pelagic and bottom trawls (Wiborg *et al.* 1982, 1984). A difference in size of squid eaten might also be expected from the considerable difference in body size of sperm whales and northern bottlenose whales (adult sizes 12–15 m and 6–7 m respectively, Leatherwood and Reeves, 1983).

Cuvier's beaked whale appears to be somewhat more of a generalist teuthophage, feeding at a range of depths. Although it is a considerably smaller animal than the sperm whale and slightly smaller than the northern bottlenose whale (typical adult size 5.5–6 m, Leatherwood and Reeves, 1983), it feeds on size classes of squid also taken by the other two whale species. It may thus use other means to avoid food competition. Studies in the Bay of Biscay suggest that the two species of beaked whales tend to be present at different times (A. Williams, per. comm.) and analysis of strandings data for the UK coastline also suggests some temporal segregation (MacLeod *et al.*, In Press).

The almost universal occurrence of gonatid squid in stomachs of teuthophagous whales stranded in the North Sea does not imply that this squid species is resident. It is however present off Norway where the whales were presumably feeding before entering the North Sea (see Santos *et al.*, 1999; Bjorke, 2001).

Representativeness of sampling

A possible cause for concern in estimating niche overlap and breadth is that small sample sizes do not adequately represent the range of prey eaten. Some reassurance on this point may be obtained from comparisons with other studies in the area. For example, for sperm whales, the stomach contents of two animals stranded in the North Sea (in Germany and the Netherlands in 1994) analysed by Lick *et al.* (1995) and Clarke (1997) show the same predominance of *Gonatus* sp. In a further 10 stomachs of sperm whales stranded in Denmark in 1991, 1997 and 2001, *Gonatus fabricii* was the main prey species (more than 99% of the beaks identified belonged to this species) (Simon *et al.*, 2003). Nevertheless, the extent to which the sampled sperm whales are representative of the wider population may be questioned. All the sperm whales examined in the present study and those mentioned above were males, either solitary or "bachelor" groups (pubertal males, sexually mature but not necessarily socially mature; Rice, 1989), stranded while travelling south from feeding grounds in Arctic waters and Subarctic waters off Norway.

Data on sperm whale diets elsewhere in the northern Northeast Atlantic are more scarce. A small sperm whale stranded in Galicia (NW Spain) had few beaks in the stomach (González *et al.*, 1994). Sperm whales taken by whaling off Galicia in 1966 (N=1) and 1974 (N=2) had few prey remains in the stomachs - and *Gonatus* was not recorded (Clarke and Macleod, 1974; Xampeny and Filella, 1976). Dietary data are also available from whaling off Iceland and between Iceland and Greenland (*e.g.* Roe, 1969; Clarke and MacLeod, 1976; Martin and Clarke, 1986) but we have not considered this as part of our study area.

The northern bottlenose whales examined in the present study were stranded in the North Sea mainly in August and September. Other individuals stranded at this time of year (in the Faroes in 1897, Denmark in 1978 and Germany in 1993) have also been found to have mainly *Gonatus* in the stomachs (Clarke and Kristensen, 1980; Lick and Piatkowski, 1998). *Gonatus* was the only cephalopod recorded in stomachs of 46 northern bottlenose whales taken by whalers off Iceland in the summer of 1967 and fish remains were recorded in four of the whales (Benjaminsen and Christensen, 1979). Seven out of eight northern bottlenose whales taken by Faroese whalers in August/September between 1982 and 1993 had *Gonatus* in their stomachs, although *Taonius* sp. and *Teuthowenia* were also recorded (Bloch *et al.*, 1996).

Data on the diet of Cuvier's beaked whale are scarce. Desportes (1985) examined stomachs of eight whales stranded in France between 1979 and 1985 (including 1 stranded on the Mediterranean coast), of which only five had food remains in the stomach. Although the results given are not fully quantitative, squid of the family Gonatidae were recorded amongst the prey.

An additional possible cause of concern when analysing stomach contents of stranded animals is whether results are biased, since sick and/or injured animals are in theory more likely to strand. There have been very few pathological studies on the whales stranded in the northern NE Atlantic. Some of the sperm whales stranded on North Sea coasts showed evidence of ill-health, but it was not thought to have directly contributed to the

stranding – and the animals examined were ones with no food remains in their stomachs (Jauniaux and Coignoul 1996, Jauniaux *et al*., 1996, 1998). As mentioned above, stranding of large whales in the North Sea at least probably relates more frequently to navigational errors than to ill health.

Stomach contents present only a snapshot of diet. Cephalopod beaks are believed to accumulate in the stomachs of teuthophagous whales until they are regurgitated or excreted but there have been no studies on how long beaks might remain in the stomach of a whale. Clarke (1980) estimated that a beak could remain in the stomach of a male sperm whale for 1.2. to 1.6 days and slightly longer for a female.

ACKNOWLEDGEMENTS

We would like to thank the following people for their assistance at various stages of the work reported here: Marjan Addink, Julie Andersen, Peter Boyle, Malcolm Clarke, Gareth Duguid, Manuel García Hartmann, Jerry Herman, Sascha Hooker, Carl Kinze, Thijs Kuiken, Alfredo López, Colin MacLeod, Tony Patterson, Bob Reid, Harry Ross, Chris Smeenk, Jianjun Wang

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