The diet and feeding ecology of the short-beaked common dolphin (*Delphinus delphis)* in the northeast Atlantic

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ABSTRACT

Stomach contents from 129 individuals were used to examine the variation in the diet of short-beaked common dolphins (*Delphinus delphis*) in the northeast Atlantic. Samples were obtained from dolphins found stranded along the Irish coast (*n*=76) between 1990 and 2004, representing neritic foraging, and individuals incidentally captured in the Irish albacore tuna (*Thunnus alalunga*) driftnet fishery (*n*=58) between 1996 and 1999, representing offshore foraging. A total of 46 prey species were recorded consisting of 31 fish species and 15 cephalopods. The remains of a total of 15,283 prey items were recovered from the stomachs of offshore dolphins. Teleost fish were numerically the most important prey group (95% prey numbers), with cephalopods comprising only 5%. A small number of crustaceans were also recorded. Fish representing at least six families and 16 species were identified. Myctophids dominated the fish component accounting for 54% of the fish recovered. Despite the dominance of myctophids, at a species level the carangid *Trachurus trachurus* was the most commonly recorded, followed by the myctophids *Myctophum punctatum* and *Notoscopelus kroyeri;* combined the three species comprised 92% of fish prey. Fish (97%) also formed the dominant portion of the stomach contents of dolphins from the neritic area. Gadidae comprised 59% of the fish component of the neritic dolphin diet, and the most commonly occurring fish were *Trisopterus* spp. (45%) and Gobiidae (28%). In both groups, the foraging strategy appears to involve targeting relatively small-sized shoaling fish. The offshore dolphins were found to feed nocturnally when the migrating deep scattering layer species approaches the surface. In neritic areas, aggregations of small, pelagic fish are preyed upon. For the offshore group, a positive relationship was found between dolphin body length and total prey numbers and between body length and prey species number, but not between dolphin body length and proportion of cephalopods in the diet. No significant difference for these variables was found between different age-sex maturity groups. For the inshore group, no correlation was found between dolphin body length and total prey numbers, prey species number or proportion of cephalopod in the diet. The stomachs of stranded females contained a significantly higher number of prey items than stranded males, but there were no other significant differences between age-sex maturity groups for fish species number of proportion of cephalopod in the diet. Nine dolphins from the offshore group had only milk in their stomachs (aged 0-3 months), while three (aged 3-6 months) had both milk and solid food suggesting that weaning occurs between 3 and 6 months.

ATLANTIC OCEAN, COMMMON DOLPHIN, FEEDING, FOOD/PREY, INCIDENTIAL CATCHES, MOVEMENTS

INTRODUCTION

With fisheries and cetaceans often exploiting the same fish resources, or at least present in the same areas, interactions between the two inevitably occur. These interactions can vary from feeding associations to depredation on target species and damage to gear, as well as incidental cetacean mortality. Nearly all cetacean species around the world have been reported as bycaught in the course of commercial or artisanal fishing operations (IWC, 1994) and the short-beaked common dolphin (*Delphinus delphis)* is no exception. The common dolphin has been reported as feeding in association with, and incidentally captured in, fishing operations world-wide (Fertl and Leatherwood, 1997).

In the northeast Atlantic, short-beaked common dolphins have been incidentally caught in the Dutch pelagic trawl fishery for mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*) (Couperus, 1997). Dietary studies carried out on these bycaught animals showed that mackerel and horse mackerel made up almost half of the fresh prey remains found, suggesting that the dolphins were feeding on the target species of the fishery; the remainder of the prey consisted of hake (*Merluccius merluccius*) and blue whiting (*Micromesistius poutassou*) (Couperus, 1997). In contrast, dolphins have been incidentally captured in pelagic trawls in the western English Channel targeting sea bass *Dicentrarchus labrax*, a species not thought to be consumed by the common dolphin (Northridge *et al*., 2006).

Morizur *et al*. (1999) also reported incidences of incidental capture of short-beaked common dolphins in a number of other trawl fisheries in the northeast Atlantic, including the French hake, albacore tuna (*Thunnus alalunga*) and sea bass fisheries. In Irish waters, gillnets, whether drift, static or tangle, were responsible for all short-beaked common dolphin bycatch incidences reviewed by Berrow and Rogan (1999). The association between tuna and short-beaked common dolphins inevitably leads to interactions between tuna fisheries and common dolphins. These interactions have varying degrees of importance, with the pole-and-line fishery in the

Azores resulting in no incidental mortality of common dolphins (Silva *et al*., 2002), while during the 1990s, the Irish, French and (of lesser importance) UK albacore tuna drift-net fisheries in the northeast Atlantic resulted in considerable bycatch of marine mammals, with an estimated peak reported in 1999 of 2,101 short-beaked common dolphins (Hassani *et al*., 1997; Rogan and Mackey 2007). Since 2001, with the ban on driftnets and the introduction of pelagic trawl fishing, bycatch rates have been reduced, though not eliminated. An estimated 128 individuals were incidentally captured by Irish and French tuna-pelagic trawl fisheries in both 2003 and 2004 (Northridge *et al.*, 2006).

Data available on the diet of common dolphins globally have increased greatly over the last two decades, with dietary studies carried out on both stranded and incidentally captured individuals, including: northeast Atlantic (Pascoe, 1986; Hassani *et al*., 1997; Silva, 1999; Pusineri *et al*., 2007), Mid-Atlantic Bight (Overholtz and Waring, 1991), southern African coast (Sekiguchi *et al*., 1992; Young and Cockcroft, 1994), northern Pacific (Chou *et al*., 1995) and New Zealand (Meynier *et al*., 2008). Using a different approach (sightings and fisheries data), Doksæter *et al*. (2008) ascertained that common dolphins feed on mesopelagics fish, in particular *Lampanyctus macdonaldi*, *Stomias boa ferox* and *Chauliodus sloani*, along the Mid-Atlantic Ridge. Short-beaked common dolphins appear to be opportunistic feeders, focusing on locally abundant species, which results in the diet varying with abundance and availability of prey (Young and Cockcroft, 1994; Silva, 1999). This dietary variation therefore exists on both temporal and spatial scales. In coastal or neritic waters, the short-beaked common dolphin has been shown to feed on epipelagic shoaling fish and squid (Sekiguchi *et al*., 1992; Young and Cockcroft, 1994; Silva, 1999; Meynier, 2004), while in oceanic waters individuals exploit organisms of the deep scattering layer (DSL), dominated by meso- and bathypelagic species such as myctophid fish and, to a lesser extent, squid (Chou *et al*., 1995; Hassani *et al*., 1997; Pusineri *et al*., 2007).

Genetic and cranial morphometric data suggest that only one common dolphin population exists in the northeast Atlantic, ranging from waters off Scotland to Portugal (Murphy *et al.*, 2006, SC/61/SM27), though separate populations exist in the Northwest Atlantic and Mediterranean Sea (Mirimin *et al*., 2009, Natoli *et al*., 2008). As genetic and skull samples were obtained from western European continental shelf and slope waters, and oceanic waters of the Bay of Biscay, the full distributional range of the northeast Atlantic population is not known - though analysis of sightings data suggests that the distributional range extends to the Mid-Atlantic ridge, and this species may even be distributed across the whole North Atlantic (see Murphy *et al*., 2009, and ref. therein).

Within the northeast Atlantic, in recent years, seasonal changes in sighting patterns of short-beaked common dolphins have been identified. In wintertime (November-April), sightings rates declined in surveyed areas off the shelf and the Bay of Biscay, and increased considerably on the Celtic shelf, in the western English Channel and off Brittany, France (WGMME, 2005). Using sightings data obtained opportunistically onboard ferries, Brereton *et al*. (2005) reported a 10-fold increase in the density of common dolphins in the western English Channel during the wintertime, and Macleod *et al.* (2009) reported a 5-fold increase in occupancy in this region. It is not known if short-beaked common dolphins follow migratory patterns of their preferred prey, however winter inshore movements of short-beaked common dolphins into the Celtic Sea and western English Channel have been attributed to feeding opportunities (WGMME, 2005). During the summertime, Kiszka *et al.* (2007) found aggregations to be larger in the northern Bay of Biscay than in the western English Channel, using sightings data also obtained opportunistically onboard ferries, operating predominately between July and October. It has been suggested that the increased abundance of short-beaked common dolphins at the shelf edge may be related to the concentration of its main prey species in this area, *Sardina pilchardus* and *Trachurus trachurus* (Meynier, 2004; Kiszka *et al*., 2007).

More recently, concern has been expressed about the level of organochlorine and heavy metal contamination in small cetaceans in European waters, including harbour porpoise (*Phocoena phocoena*) and short-beaked common dolphins (e.g. Pierce *et al*., 2009). Understanding contaminant loading and expose requires information on the feeding ecology of these species. In addition, it has been suggested that one of the causes of the apparent decrease in abundance of common dolphins in the Mediterranean has been competition with fisheries and a decreasing prey resource (Bearzi *et al*., 2003). Thus, further investigation of the behaviour and ecology of common dolphins is required, and feeding ecology is addressed in this study.

METHODS

Collection of samples

The stomach contents analysed in this study were obtained from two sources. The offshore dolphins were collected as part of an observer programme looking at the ecological risks associated with the Irish tuna drift-net fishery in the northeast Atlantic (Rogan and Mackey, 1999; 2007) (Figure 1). All specimens were incidentally captured in the albacore tuna driftnet fishery between mid-June and October 1996-1999. This fishery operated over a wide area, from 46ºN to 54ºN and from 11ºW to 16ºW. The fishing gear used was multi-filament nylon twine gillnet with a mesh-size of 18cm, and the maximum length of net was 2.5 km. Fishing occurred at night, with the nets being shot in daylight and hauled the next morning. A total of 81 short-beaked common dolphins were observed incidentally captured during this study, and stomach analysis carried out on 58 dolphins. Of these, six were found to have empty stomachs, nine contained only milk, and prey items were found in the stomachs of the remaining 43 dolphins.

The inshore dolphins were collected mainly from stranding sites around the Irish coast, as well as a number incidentally captured in inshore fishing gear (Figure 1). These dolphins were collected in the period 1990 to 2004. A total of 76 common dolphins from these sources were analysed (48 stranded, 16 stranded and diagnosed as bycatch, and 5 obtained from inshore fisheries) with 69 found to have prey items in their stomachs.

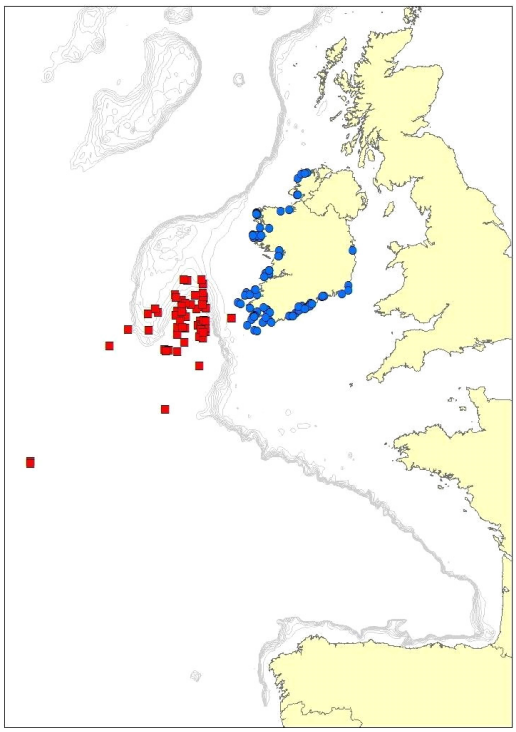

Figure 1. Short-beaked common dolphin sampling locations, squares = short-beaked common dolphins incidentally captured in the Irish tuna driftnet fishery, circles = short-beaked common dolphins stranded along the Irish coastline, or bycaught in inshore fisheries.

Post-mortem procedure

Full post-mortems were carried out on the carcasses that were returned to port as part of the bycatch programme and on all dolphins collected as part of the strandings programme. All post-mortems were performed in accordance with the protocol described by Kuiken and Garcia Hartman (1991). Stomachs were removed and ligatured at the oesophageal and duodenal ends. Once removed, stomachs were frozen for future analysis. Total body length was measured from the tip of the rostrum to the notch of the tail fluke. Individual dolphins were aged by counting Growth Layer Groups in the dentine of teeth samples, as outlined in Murphy and Rogan (2006). Sexual maturity was determined in males by assessing for evidence of spermatogenesis in

testicular tissue, and in females by the presence of either a *corpus luteum or albicans* in their ovaries (see Murphy *et al.*, 2005; Murphy *et al*., in press). Where reproductive tissue analysis was not carried out, maturity was based on age or total body length after Murphy *et al.* (2006); females were considered mature if 9 years or older, or ≥190cm, while males were considered mature if 10 years or older, or ≥200cm.

Stomachs were removed from the freezer and allowed to thaw prior to dissection and removal of contents. Each of the three stomachs was processed in turn. An incision was made along the mid-line of the stomach and the contents emptied into a basin. The stomach was then washed out to ensure no remains were left trapped in the folds. Parasites were removed and stored in 70% alcohol for future examination. Any abnormalities, such as ulcers or cysts, were also removed and stored in formalin for future examination.

The contents of the stomach were then washed through a set of nested sieves, to separate the hard parts from the liquefied remains. Teleost otoliths and bones were dried and stored in plastic ziploc bags, while cephalopod beaks and crustaceans were stored in tubes with 70% alcohol.

Dolphin age was determined from longitudinal sections of teeth as described in Murphy and Rogan (2006).

Analysis of stomach contents

Only hard part remains, such as teleost otoliths, cephalopod beaks and crustacean carapaces, were used to identify the prey species, as this allowed prey numbers to be calculated. The stomach contents of each dolphin were analysed using a binocular microscope with an eyepiece micrometer. Only sagittal otoliths were used to identify and enumerate the fish prey for a number of reasons. Otoliths were identified to species level where possible using a published material (Härkönen, 1986; Campana, 2004; Tuset *et al*., 2008), MSc theses (Browne, 1999; O'Callaghan, 2000) and a reference collection.

The minimum estimate method was used to enumerate prey items. Otoliths were separated into left and right, and the number of fish consumed was assumed to be equal to the number of left or right otoliths, whichever was greater (Silva, 1999). Those which could not be assigned to left or right due to damage or digestion were counted separately, divided by two and added to the number calculated from counting the left and right otoliths (after Silva, 1999).

Otoliths were measured using an eyepiece micrometer or digital callipers to allow fish length to be back-calculated from otolith length using regression equations. Only published equations were used, which limits the number of species for which lengths could be calculated (Gjøsæter, 1981; Härkönen, 1986; Granadeiro and Silva, 2000). For offshore samples, left or right otoliths were used from each sample, whichever had the most measurable otoliths present and only good condition otoliths were used. Left and right otoliths were combined for measurement in the neritic samples and otoliths used in the calculation of prey length ranged from good condition to extremely eroded, resulting in minimum estimates of prey length

Cephalopod beaks were identified to species level where possible using published references (Clarke, 1986) and type specimens identified by a cephalopod expert. Upper and lower cephalopod mandibles were separated and enumerated and the number of cephalopods present was calculated from the number of lower beaks present (Clarke, 1986).

Crustaceans were a very insignificant fraction of the diet, were in a poor state of preservation and are likely to be secondary prey or caught incidentally; hence they were not identified to lower taxa.

Statistical Analysis

The diet of the short-beaked common dolphin was described using a number of methods including number, percentage number, frequency of occurrence and percentage frequency of occurrence. Results from this analysis were used to calculate the Index of Importance for each prey item. The following equations were used to calculate these values:

Percentage Numbers (%N)

$$\%N = (N_i/N_t) * 100$$

Where N_i = Number of prey items in prey group i.
N_t = Total number of prey items.

Percentage Frequency of Occurrence (%O)

$$\%O = (O_i/O_t) * 100$$

Where O_i = Frequency of occurrence of prey type i (i.e. number of stomachs containing prey type i).
O_t = Total number of stomachs containing food.

Index of Importance

$$\% \text{ Importance} = (\%N_i * \%O_i)^{0.5}$$

Where $\%N_i$ = Percentage numbers represented by prey type i.
$\%O_i$ = Percentage occurrence represented by prey type i.

In order to further investigate aspects of the diet and feeding ecology of the short-beaked common dolphin, a number of variables were tested for statistical significance. Non-parametric statistical procedures were mainly used. Relationships between dolphin body length and total prey numbers in the stomach, number of fish species and the relative proportions of fish and cephalopods were investigated using Spearman's rank correlation. Further, age-sex variations in these three variables were investigated using the Kruskal-Wallis test. All statistical tests were carried out on SPSS PASW Statistics 17.0 and statistical references used were Zar (1996) and Dytham (2001).

RESULTS

Sample description

Temporal distribution
Due to the project-specific nature of the Irish albacore tuna driftnet fishery bycatch observer program, the sampling was limited to three years (1996, 1998 and 1999) and also within the period July-October, with 82% of dolphins bycaught in 1996 and 52% of dolphins bycaught in the month of August. Samples from stranded dolphins came from the years, 1990-2004 inclusive, with an average of 5.1±3.0 dolphins per year and a peak (16%) occurring in 2003. Most inshore dolphins were sampled in winter, with 25% obtained in February.

Table 1 Quarterly breakdown of age-maturity for short-beaked common dolphins stranded onshore and bycaught offshore.

	1st Quarter (Jan-Mar)	2nd Quarter (Apr-Jun)	3rd Quarter (Jul-Sep)	4th Quarter (Oct-Dec)
	Stranded			
Newborn/neonate (<1)	2	-	-	-
Yearlings (1-2)	1	2	1	1
Juveniles (2-9)	5	7	5	6
Mature Female	11	-	5	5
Mature Male	5	-	6	3
	Bycaught			
Newborn/neonate (<1)	-	-	26	4
Yearlings (1-2)	-	-	9	-
Juveniles (2-9)	-	-	6	1
Mature Female	-	-	6	2
Mature Male	-	-	9	3

Sex and age distribution
The offshore short-beaked common dolphin sample, incidentally captured in the Irish albacore tuna driftnet fishery, comprised both sexes, across a wide age range. The sample was dominated by younger dolphins <2

years (64%) (Figure 2), 12% of dolphins were in the range 2-9 years and the remaining 25% were all 10 years or older. The sex ratio of the bycaught dolphins where sex was determined was 1:1.76 (females to males). The female:male ratio of the stranded sample was 1:1.28, while the age distribution of the stranded sample was less skewed than that of the bycaught sample, with a more even age frequency distribution apparent (Figure 2). Table 1 presents the intra-annual distribution of stranded and bycaught dolphins broken down quarterly and by age/maturity status.

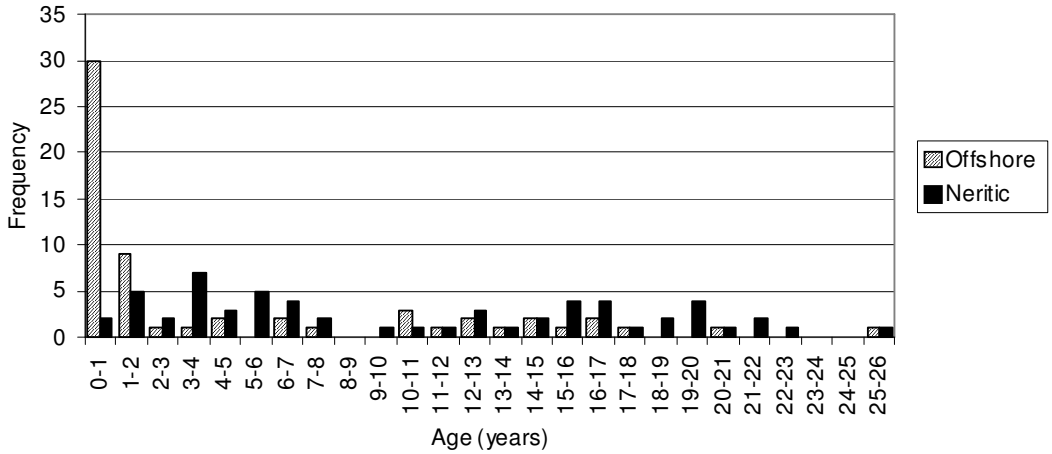

Figure 2. Age distribution of offshore and neritic short-beaked common dolphins

Offshore stomach content analysis

Stomach contents representing 15,283 prey items from 43 stomachs were analysed. The stomach of one dolphin, a mature male, contained the remains of 2,085 prey items. Number, percentage number, frequency of occurrence, percentage frequency of occurrence and the index of importance were calculated for each prey group, and are presented in Table 2.

Table 2 General diet composition of offshore short-beaked common dolphins (*n*=43).

Prey Group	Number	% Number	Frequency of Occurrence	% Frequency of Occurrence	Index of Importance
Fish	14529	95.1	40	93	94
Cephalopods	742	4.9	33	76.7	19.4
Crustaceans	12	0.08	6	7	0.8

From these data, it is clear that teleost fish are by far the most important prey group for offshore short-beaked common dolphins. Fish comprise 95% by number and 93% by frequency of occurrence, with an index of importance of 94. Cephalopods represent the second most important prey group at 5% by number, 77% by frequency of occurrence and an index of importance of 19.4. Crustaceans make up a negligible part of the diet of the short-beaked common dolphins sampled, comprising 0.08% by number, 7% by frequency of occurrence and an index of importance of 0.8. Owing to the negligible number of crustaceans recorded, and the possibility that they were ingested as secondary prey (Amir *et al*., 2005) or incidentally, they are excluded from further analysis.

Fish representing at least six families and 16 species were identified during the analysis of stomach contents, while four species of cephalopod were also identified. A full list of prey species with number, percentage number, frequency of occurrence, percentage frequency of occurrence and index of importance is presented in Table 3.

Table 3 List of fish and cephalopod species found in offshore short-beaked common dolphin stomach contents with relevant indices (*n*=43). (Classification follows Whitehead *et al*., 1986, 1989; Cephbase, 2005).

	Number	% Number	Frequency of Occurrence	% Frequency of Occurrence	Index of Importance
Fish					
Myctophidae					
Myctophum punctatum	4395	28.8	31	72.1	45.6
Notoscopelus kroyeri	3346	21.9	33	76.7	41.0
Benthosema glaciale	84	0.6	17	39.5	4.9
Lobianchia gemellari	63	0.4	5	11.6	2.2
Lampanyctus pusillus	14	0.1	3	7.0	0.8
Ceratoscopelus maderensis	5	<0.1	3	7.0	0.5
Carangidae					
Trachurus trachurus	5582	36.6	27	62.8	47.9
Paralepididae					
Arctozenus risso	486	3.2	20	46.5	12.2
Lestidiops affinis	21	0.1	3	7.0	0.8
Sternoptychidae					
Maurolicus muelleri	360	2.4	14	32.6	8.9
Gadidae					
Micromesistius poutassou	46	0.3	4	9.3	1.7
Belonidae					
Belone belone	1	<0.1	1	2.3	0.1
Unidentified Fish					
Type D	1	<0.1	1	2.3	0.1
Type E	1	<0.1	1	2.3	0.1
Type J	1	<0.1	1	2.3	0.1
Type P	4	<0.1	2	4.7	0.4
Unidentifiable Fish	119	0.8	18	41.9	5.8
Cephalopods					
Brachioteuthidae					
Brachioteuthis riisei	589	3.9	28	65.1	15.9
Gonatidae					
Gonatus steenstrupi	98	0.6	18	41.9	5.0
Taoniinae					
Teuthowenia megalops	38	0.3	10	23.2	2.6
Chiroteuthidae					
Chiroteuthis sp.	10	<0.1	5	11.6	0.9
Unidentified Cephalopod	7	<0.1	4	9.3	0.7

Myctophids are the best represented family of fish with six identified species represented by 7,907 fish (54% by number). The Carangidae *Trachurus trachurus* is the most numerically dominant species (38%) with a high index of importance (48), though only listed fourth in importance by % frequency of occurrence (63%). *Myctophum punctatum* (which represented 29% of all prey items, occurring with high frequency of occurrence 72%) and *Notoscopelus kroyeri* (22% number and 77% frequency of occurrence) were the next most important prey items. *Brachioteuthis riisei* was the only cephalopod species in the top six for all three indices, being fourth most important by % number and index of importance and third most important by % frequency of occurrence. *Arctozenus risso*, *Maurolicus muelleri*, *Benthosema glaciale* and *Gonatus steenstrupi* occupied the remaining places in the top six rankings. It can be seen that while the same species are found in the top six places in each index, their rank varies to a greater or lesser degree.

Fish prey length distribution
Prey lengths were calculated for *T. trachurus*, *N. kroyeri*, *M. muelleri* and *M. poutassou* from published equations. The resulting prey length ranged between 1-20cm, with a mode in the 4-5cm size range and a mean of 4.2cm (SD = 2.25). *T. trachurus* ranged from 1.0-7.9cm with a mean of 3.9cm (SD = 1.00). *N. kroyeri* ranged from 2.0-9.8cm with a mean length of 4.4 cm (SD = 0.85). *M. muelleri* had a range of 3.8 to 5.5cm, with a mean size of 4.2 cm (SD = 0.29). Whereas, *M. poutassou*, the largest of the fish prey species, had a range of 10.6 to 19.5cm with a mean length of 15.9cm (SD = 1.93).

Dietary variation according to sex, size and maturity
The existence of any dietary variation between dolphins of different size, sex or age-sex maturity groups was investigated. The variables considered were relative proportion of fish and cephalopods in the diet, number of prey species consumed and total prey numbers. A positive correlation was found between dolphin body length and total prey number ($r_s = 0.500$, n = 41, P<0.01) and dolphin body length and species number ($r_s = 0.413$, n=41, P<0.01), while no correlation was found between dolphin body length and the proportion of cephalopods in the diet. The relative proportion of cephalopods in the diet varied somewhat between the sexes and the sex-maturity groups (Table 4), with females consuming a higher proportion of cephalopods than males, though still in relatively low quantities compared to fish consumption, and immature females consuming the highest proportion of cephalopods. However, these differences were not found to be significant.

Table 4 Proportion of fish and cephalopod in diet by sex and maturity.

Sex	% Fish	% Cephalopod	Sex-Maturity	% Fish	% Cephalopod
Male	96.1	3.9	Immature Male	95.4	4.6
			Mature Male	96.6	3.4
Female	91.3	8.7	Immature Female	90.4	9.6
			Mature Female	92.9	7.1

Similarly, no significant difference was found between the total prey number or prey species number by sex or age-sex maturity group.

Milk
Nine of the dolphins analysed were found to contain only milk and all were aged less than 3 months. The stomachs of three dolphins contained milk and prey items and were aged 3-6 months.

Inshore stomach contents

Stomach contents representing 6,726 prey items from 69 stomachs were analysed. One stomach, from a 187cm female, contained the remains of 2,003 prey items, with 1,822 of these from the family Gobiidae. As with the offshore dolphins, number, percentage number, frequency of occurrence, percentage frequency of occurrence and the index of importance were calculated for each prey group, and are presented in Table 5.

Table 5 General diet composition of inshore short-beaked common dolphins (*n*=69).

Prey Group	Number	% Number	Frequency of Occurrence	% Frequency of Occurrence	Index of Importance
Fish	6533	97.1	61	88.4	92.7
Cephalopods	194	2.9	26	37.7	10.5

From these data, it is clear that teleost fish are by far the most important prey group for short-beaked common dolphins feeding in neritic waters. Fish comprise 97% by number and 88% by frequency of occurrence, with an index of importance of 93. Cephalopods comprise the remaining 2.9% of prey by number, with a frequency of occurrence of 38% and an index of importance of 11. No crustacean remains were found.

Analysis of fish and cephalopod species
Fish representing at least nine families and 14 species were identified during the analysis of stomach contents, while 11 species of cephalopod were also identified. A full list of prey species with number, percentage number, frequency of occurrence, percentage frequency of occurrence and index of importance is presented in Table 6.

Gadids are the best-represented family of fish with five identified species represented by 3,934 fish (59% by number). *Trisopterus* spp. (*Trisopterus esmarkii* and *Trisopeterus minutus*) are the most important species by all the indices, with 45% by number, 67% by frequency of occurrence and an index of importance of 54. *Trisopterus* spp. was the most common prey in the summer (Apr-Sept) overall (64%), and among mature male (39%) and mature female (33%) dolphins, but not in winter (Oct-Mar - 36% vs 40% for Gobiidae). The large number of Gobiidae found in just one dolphin is the main reason that they are placed as second most important by % number (28%) with an index of importance (17), and do not feature in the top six most important by % frequency of occurrence. *Micromesistius poutassou* was listed as third most important by % number (4%) and fourth most important by index of importance (6), though it does not feature in the rankings for % frequency of importance. *Merlangius merlangus* is ranked fourth most important by number (2%), fifth by % frequency of occurrence (16%) and third most important by index of importance (6). The only cephalopod to make it into ranking was an unidentified member of the Sepiolidae, as third most important by % frequency of occurrence (18.8%). *Argentina* sp., *Clupea harengus*, and *Sprattus sprattus* occupy the remaining places in the top six rankings.

Fish prey length distribution
Prey lengths were calculated for a number of the fish prey of the stranded short-beaked common dolphins, including *Trisopterus* spp., Gobiidae, Unidentified gadoids, *Micromesistius poutassou* and *Merlangius merlangus*. *Trisopterus* spp. had a mean length of 7.6cm (SD = 3.48) with a range of 1-24cm; however this figure masks the bimodal nature of the length curve, which suggests two size classes of *Trisopterus* spp., 5-6cm and 10-11cm, were being exploited. Gobiidae had a mean length of 5.7cm (SD = 0.84) and a range of 4-7cm. The mean length of unidentified gadoids was 8.5cm (SD = 4.63) with a range of 1-27cm. The mean lengths of *M. poutassou* and *M. merlangus* were 13.5cm (SD = 6.18, range 5-38cm) and 23.1cm (SD = 10.59, range 7-60cm), respectively. Both of these species showed a bimodal length distribution with modes at approximately 9-10cm and 23-24cm.

These prey sizes are considered minimum estimates owing the erosion of otoliths in the digestive process prior to, and in the period immediately after, dolphin death.

Dietary variation according to sex, size and maturity
The existence of any dietary variation between dolphins of different size, sex or maturity groups was investigated. The variables considered were relative proportion of fish and cephalopods in the diet, number of prey species consumed and total prey numbers. No correlation was found between dolphin body length and total prey number, dolphin body length and species number, or dolphin body length and the proportion of cephalopods in the diet for the whole onshore sample combined.

The relative proportion of cephalopods in the diet varied between the different sex and sex-maturity groups (Table 7), with males consuming a slightly higher proportion of cephalopods than females and mature males consuming the highest proportion of the four sex-maturity groups. However, these differences were not found to be significant.

Table 6 List of fish and cephalopod species found in inshore short-beaked common dolphin stomach contents with relevant indices (*n*=69). (Classification follows Whitehead *et al*., 1986; 1989; Cephbase, 2005).

Species	Number	% Number	Frequency of Occurrence	% Frequency of Occurrence	Index of Importance
Fish					
Clupeidae					
Clupea harengus	82	1.2	14	20.3	5.0
Sprattus sprattus	155	2.3	8	11.6	5.2
Argentinidae					
Argentina sp.	111	1.7	7	10.1	4.1
Myctophidae					
Benthosoma glaciale	93	1.4	1	1.4	1.4
Gadidae					
Melanogrammus aeglefinus /Pollachius pollachius/P. Virens	6	<0.1	1	1.4	0.4
Merlangius merlangus	162	2.4	11	15.9	6.2
Micromesistius poutassou	267	4.0	6	8.7	5.9
Trisopterus spp.	2990	44.5	46	66.7	54.4
Gadiculus argenteus thori	35	0.5	6	8.7	2.1
Unknown Gadidae	474	7.0	17	24.6	13.2
Merluccidae					
Merluccius merluccius	63	0.9	10	14.5	3.7
Carangidae					
Trachurus trachurus	62	0.9	12	17.4	4.0
Scombridae					
Scomber scombrus	4	<0.1	1	1.4	0.3
Gobiidae	1873	27.8	7	10.1	16.8
Atherinidae					
Atherina sp.	24	0.4	2	2.9	1.0
Unknown Fish	138	2.1	20	29.0	7.7
Cephalopods					
Sepiidae					
Sepia spp.	3	<0.1	3	4.3	0.4
Sepiolidae					
Sepietta oweniana	27	0.4	3	4.3	1.3
Unknown Sepiolidae	55	0.8	13	18.8	3.9
Loliginidae					
Loligo sp.	16	0.2	2	2.9	0.8
Alloteuthis sp.	29	0.4	7	10.1	2.1
Gonatidae					
Gonatus sp.	1	<0.1	1	1.4	0.1
Brachioteuthidae					
Brachioteuthis riisei	2	<0.1	1	1.4	0.2
Ommastrephidae					
Todaropsis eblanae	23	0.3	1	1.4	0.7
Unknown Ommastrephidae	26	0.4	10	14.5	2.4
Octopodidae					
Eledone cirrhosa	12	0.2	6	8.7	1.2

Table 7 Proportion of fish and cephalopod in diet by sex and maturity.

Sex	% Fish	% Cephalopod	Sex-Maturity	% Fish	% Cephalopod
Male	96.4	3.6	Immature Male	97.3	2.7
			Mature Male	90.5	9.5
Female	97.7	2.3	Immature Female	99.1	0.9
			Mature Female	95.0	5.0

A significant relationship was found between total prey number and sex (χ^2 =4.148, df = 1, P<0.05), with more prey items recorded from the stomach contents of stranded females.

No significant difference was found between total prey or prey species number by sex-maturity group or by sex.

DISCUSSION

This current study on the diet of the short-beaked common dolphin in the northeast Atlantic supports findings of previous work in this region (Silva, 1999; Lahaye, 2005; Pusineri *et al*., 2007), and globally (Young and Cockcroft, 1994; Chou *et al*., 1995), which show that the diet is dominated by fish, with cephalopods showing relatively high frequency of occurrence, but generally low numbers. While the dominance of fish in the diet of the short-beaked common dolphin is consistent between samples from dolphins bycaught in offshore waters and those stranded or bycaught in inshore waters, there are still considerable differences between the two sample groups, as has been suggested in other studies (e.g. Sekiguchi *et al*., 1992; Young and Cockcroft, 1994; Chou *et al*., 1995; Silva, 1999; Pusineri *et al*., 2007). The offshore sample in the current study shows the importance of species of the deep scattering layer (DSL), which migrate to the surface to feed during the night, to dolphins feeding in this region. In terms of numbers and occurrence, the myctophid species dominated the diet of the offshore short-beaked common dolphins, although the most common prey species recorded was Atlantic horse mackerel (*Trachurus trachurus*). In general, myctophids and the other species of the DSL stay at depths of greater than 800m during the day, while at night can be found from the surface to 250m (Hulley, 1984). This upward nocturnal movement brings the organisms of the DSL into the foraging range of the short-beaked common dolphin. Previous, limited, radio-telemetry work carried out with a female common dolphin off southern California showed that feeding started at dusk and continued throughout the night, with regular dives to depths of 50m and a maximum dive recorded of 280m (Evans, 1975; 1982; 1994). Experimental trawls made in the area where the radio-tracked dolphin was diving resulted in catches consisting of 90% bathylagiids and myctophids (Evans, 1994).

The exploitation of small, locally abundant, shoaling prey by common dolphins has been recorded elsewhere, in both offshore and neritic habitats (Young and Cockroft, 1994; Silva, 1999; Pusineri *et al*., 2007). The importance of Atlantic horse mackerel in the offshore diet was predominately influenced by the presence of remains of 2078 fish in the stomach of a single mature male dolphin bycaught in September 1996, which contributed considerably to the total by numbers (38%); however remains of *T. trachurus* were also recorded in a further 26 offshore stomachs. *T. trachurus* is one of the few species that was found in both the offshore and neritic samples, the others being *Micromesistius poutassou, Benthosema glaciale* and *Brachioteuthis riisei*. *T. trachurus* spawns in the waters off the south and southwest coast of Ireland in the period April-June before migrating northwards around the British Isles to the coast of Norway and the North Sea (Iversen *et al*., 2002). The fact that the average length for the *T. trachurus* (using otoliths in good condition) recorded in the offshore samples is 3.62cm (SD = 1.0) suggests that the prey exploited by the offshore group consisted of fish less than 1 year old (Waldron and Kerstan, 2001).

Prey size for offshore short-beaked common dolphins calculated for this study corresponds closely to data published in previous studies, such as Pusineri *et al*. (2007), with a modal size class of 4-5cm. This suggests a preference for selecting prey of this size in offshore waters of the northeast Atlantic; however without detailed data on the size distribution of the available prey in the area, this cannot be confirmed. Myctophids have been found to show size stratification with juveniles being nyctoepipelagic (Hulley, 1984), thereby making them more vulnerable to predation by surface-dependant predators like the short-beaked common dolphin. This size stratification may influence the prey captured by short-beaked common dolphins through affecting availability

to predation rather than active size-selection by predators. Limited information is available on the growth and maturity of myctophids. Hulley (1984) reported that *Myctophum punctatum* attained sexual maturity at 5cm, while length at sexual maturity for *Ceratoscopelus maderensis* is 6.2cm. Length at sexual maturity for *Notoscopelus kroyeri* is not known, though caudal glands develop at 6.2cm (Hulley, 1984). These data suggest that the juvenile myctophids recorded in the stomach contents, may be a result of differential surface migrations between juvenile and adult myctophids.

The average prey size for the inshore group is considerably larger than that of the offshore group at 9.7cm (SD = 6.45). The range of prey sizes consumed by the inshore group is considerable, ranging from 1-60cm. A number of fish species capable of attaining large sizes were recorded in the samples, such as *Trisopterus* spp., *M. poutassou* and *M. merlangus*. These three species all had large numbers of specimens ≥10cm in length: *Trisopterus* spp. 30%, *M. merlangus* 80% and *M. poutassou* 45%. In the case of *M. merlangus,* 40% of the fish present in the diet samples are above the commercial Minimum Landing Size (MLS). This issue is discussed further below.

In relation to the weaning of short-beaked common dolphin calves, data suggests that consumption of prey items initially occurs between 3 to 6 months of age, while up to that point they are entirely dependant upon maternal milk supply.

Migration in short-beaked common dolphins

Short-beaked common dolphins in the northeast Atlantic have been shown to exhibit changes in distribution and density, with increased abundance in inshore waters of the western English Channel and Celtic Sea during the wintertime (WGMME, 2005). These movements may be due to the dolphins following migrations of specific prey species, as been reported off South Africa (Cockcroft and Peddemors, 1990), or moving to exploit different prey for reasons of availability, or prey characteristics. In the current study, stranded short-beaked common dolphins were found to largely feed on *Trisopterus* spp. (35%) during the wintertime (Oct-Mar) (40% of prey in this period were Gobiidae, which was due to the very high occurrence of 1,822 Gobiidae in one stomach), while other prey of importance during this period were *Micromesistius poutassou* (4%) and *Merlangius merlangus* (3%). *Trisopterus* spp. were found in the stomach contents of stranded animals throughout the year, suggesting they are available to foraging dolphins in inshore waters year-round. Overall, there was little seasonal variation in the prey consumed by stranded short-beaked common dolphins.

The current study shows that offshore mature short-beaked common dolphins feed predominantly on myctophids during the summer period. Myctophidae are reported to have higher lipid content than other marine fish (Saito and Murata, 1998; Lea *et al*., 2002), such as *Trispoterus luscus* and *Trachurus trachurus*, which varies seasonally and in relation to spawning (Merayo, 1996; Van Damme *et al*., 2005). Merayo (1996) reported that the liver lipid content of *T. luscus* is lowest in the period March-April, coinciding with the spawning season; however this reduction in lipid content is likely to be delayed in the more northern waters off the southern coast of Ireland (Van Damme *et al*., 2005).

Many species of pelagic fish, such as *Trisopterus* spp., whiting, sprat, and Atlantic horse mackerel, spawn in the waters off the south and southwest coast of Ireland during the spring and summer months and then proceed to migrate to more northern latitudes post-spawning (Jákupsstovu, 2002; Dransfeld *et al*., 2004). As discussed, the lipid content of these spawning fish drops during the spawning period, reducing their calorific value as prey to predators. This reduction in the lipid content of neritic pelagic fish, combined with the lipid requirement of lactating short-beaked common dolphins and their dependant young, may contribute to the offshore movement of some individuals during the summer months. If this is the case, it requires a reassessment of the current perception of common dolphins as opportunistic feeders that concentrate on locally abundant, shoaling prey, as it would suggest that some individuals migrate offshore to take advantage of nutrient-rich prey at times when neritic prey are either nutrient-poor or have dispersed from the spawning grounds.

A previous study by Murphy and Rogan (2006) analysed data obtained from animals incidentally captured by the Irish tuna driftnet fishery. Within the age-sample (n=91), 43% of the individuals that were incidentally captured were >10 years in age, and only 9% of the aged individuals were between 3 and 8 years of age. Within the fishery, there was a high tendency for calves (≤1) to become entangled in fishing gear, as they comprised 37% of the aged by-catch sample. Further, short-beaked common dolphins less ≤ 2 years and/or ≤ 165cm comprised 51.2% of the whole bycatch sample obtained from interactions with the Irish tuna fishery between 1996-99, indicating a strong propensity for calves and yearlings to be captured in driftnets (Murphy and Rogan, 2006). The general absence of juvenile dolphins (3-8 years) in the sample may result from the fact that they were not present in the area where the driftnet fishery operated, thus suggesting age segregation in

this species the northeast Atlantic. The overlap with maternal groups (mature females and calves) and the driftnets used in the albacore tuna fishery may, in part, be due to mature females migrating to offshore areas to prey upon lipid-rich myctophids, as a result of possible dietary requirements for maintaining pregnancy and the production of milk. However, it cannot be ruled out there may be other reasons why maternal groups may forage in this location, e.g. the availability of small shoaling prey for calves learning how to capture prey.

Short-beaked common dolphins and fisheries

The diet of the short-beaked common dolphin in neritic waters of the northeast Atlantic has been shown to include, and indeed be dominated by, species of commercial value that are exploited by fisheries including mackerel, Atlantic horse mackerel, blue whiting, anchovy and sardine (Couperus, 1997; Silva, 1999; Santos *et al*., 2004; Meynier, 2004) and the current study also shows that this is also true for short-beaked common dolphins foraging in the coastal waters around Ireland. Where short-beaked common dolphins and fisheries are targeting the same fish resource, interactions are inevitable and these interactions may have negative effects on both the fishery, from the economic point of view, and also on the population of the short-beaked common dolphin through incidental mortality and resource competition. While data on prey size taken by short-beaked common dolphins suggest that dolphins concentrate on fish smaller than the MLS, discarding of undersized fish may result in a loss of prey to the dolphin, while predation on small fish by short-beaked common dolphins may negatively effect recruitment to the fishery (Meynier, 2004). The median length of *M. poutassou* discarded by the Dutch pelagic fleet in the period 2002-2005 was 24cm (Borges *et al.*, 2008), which is well within the size range of fish taken by the neritic group. The consumption of fish discarded by vessels, as has been reported in other areas (Svane, 2005), therefore cannot be ruled out. In the case of offshore short-beaked common dolphins, where Atlantic horse mackerel was the main prey item, discards would not appear to be a likely source of prey, as the median length of discards from the Dutch pelagic fleet was 19cm (Borges *et al*., 2008), considerably larger than the size recorded in the current study (3.9cm, SD = 1.0).

The interaction between short-beaked common dolphins and fisheries in offshore waters tends to be less direct, as each is targeting different fish species. The importance of the vertically migrating meso- and bathypelagic fish in the diet of the short-beaked common dolphin in oceanic waters had been clearly demonstrated (Pusineri *et al*., 2007; and this study), while offshore fisheries tend to target large pelagic species, such as tuna, with some exploitation of deep sea fish such as orange roughy (*Hoplostethus atlanticus*) (Shephard and Rogan, 2006, O'Donnell *et al*., 2007). In this situation, it is the overlap in the diet of the short-beaked common dolphin and the target species of the fishery (e.g. albacore tuna – O' Sullivan, 1999; Pusineri *et al*., 2004) that brings short-beaked common dolphins into contact with fishing gear, increasing their susceptibility to incidental mortality.

The high level of small cetacean (common and striped dolphins) and blue shark (*Prionace glauca*) mortality in European Waters attributable to interactions with driftnets was recognised by the introduction of Council Directive No. 1239/98 (Council of the European Union, 1998), banning the use of driftnets from 1 January 2002 for species listed in Annex VIII, which included albacore tuna, and later, the complete ban on driftnets from 1 January 2008 by Council Directive No. 812/2004 (Council of the European Union, 2004). This ban on the use of driftnets in European waters did result in a reduction in the bycatch rate from 2101 in 1999 to 128 in tuna pelagic trawl fisheries in 2003 (Northridge *et al.*, 2006; Rogan and Mackey, 2007). While the direct impact of fisheries on short-beaked common dolphin populations caused by incidental capture in fisheries has been recognised and action taken in the form of the above Council Directives, indirect effects of fisheries may yet impact upon these populations. In times where traditional fish stocks have been overexploited and stocks reduced to less commercially attractive levels, the phenomenon of 'fishing down the food chain' has emerged, where species of a lower trophic level are targeted following the overexploitation and removal of larger, predatory fish (Pauly *et al*., 1998a; Baum *et al*., 2003; Myers and Worm, 2003). The commercial targeting of fish species lower in the food web may have more pronounced effects on the offshore short-beaked common dolphins, which exploit species of the deep scattering layer (DSL), than on those of neritic waters. Fish species of the DSL such as *Notoscopelus kroyeri* and *Myctophum punctatum* feed largely on zooplankton (copepods, euphausiids, zoea and fish fry) and are preyed upon not only by larger piscivorous fish, but also by cetaceans and seabirds (Gjøsæter, 1981; Hulley, 1984; Filin, 1993; Pauly *et al*., 1998b, Thompson *et al*., 1998; Ringelstein *et al*., 2006). Currently, there is some interest in the commercial exploitation of myctophids, and experimental fishing has been conducted on this group (Filin, 1993; Shilat, 1998; FAO, 2005; Lamhauge *et al*., 2008) with indications of a commercial fishery for mesopelagics commencing in the northeast Atlantic by Iceland (Iceland Statistics, 2009). Some fisheries for myctophids have been conducted for human consumption, however, due to high levels of wax esters in some species, their use in fishmeal production may be more likely (Gjøsæter and Kawaguchi, 1980; Brodeur and Yamamura, 2005). Should fishing pressure increase on these

species, effects are likely on short-beaked common dolphins feeding on this resource in terms of reduced prey availability and also, depending on the fishing gear and bycatch reduction measures utilised, in terms of incidental mortality.

Current evidence suggests that some short-beaked common dolphins may migrate to take advantage of different prey species at different times of the year (winter-neritic, summer-offshore). This migration will have an effect on the temporal and spatial potential for interactions to occur between short-beaked common dolphins and fisheries. The targeting of offshore fish species during the summer and neritic species during the winter increases the risk of dolphin mortality occurring in the course of fishing operations.

Limitations of study

As with all investigations into the diet of dolphins using diagnostic hard parts remains, this study has a number of limitations that influenced the results. The offshore samples came from dolphins that were bycaught in the tuna driftnet fishery, which resulted in a bias towards younger animals. In addition, dolphins sampled were caught at night, during the period June – October in 1996, 1998 and 1999, which may well have an influence on prey available to predation and clearly limits the use of the data in investigating inter- and intra-annual variation in dolphin diet.

Biases are also possible in relation to the inshore samples, as stranded animals may not be representative of the population at large, while the diet of inshore bycaught dolphins may have been biased towards the prey species of that fishery. Of the inshore group, 21% showed signs of incidental capture in fishing gear, while 9% were retrieved directly from fishing gear.

Other limitations in this study are those that are applicable to all studies of the stomach contents of cetaceans. Occurrence methods give only a crude picture of the diet composition, while numerical methods may over-emphasise the importance of small prey taken in large numbers (Hyslop, 1980). The differential digestion of prey remains adds another source of error to any analysis of stomach contents. Marine mammals may accumulate cephalopod beaks, which are less digestible than otoliths, while otoliths and bones are digested or evacuated from the stomach (Bigg and Fawcett, 1985). While the accumulation of any hard parts in the digestive tract of a cetacean could bias the results of a dietary analysis, there is evidence that marine mammals engage in feeding bouts rather than feeding for long periods throughout the day, thereby lessening this impact of this factor on the results (Jobling and Breiby, 1986). The use of otoliths for the back-calculation of prey length or weight also has inherent biases, including partial digestion (Jobling and Brieby, 1986) and the accuracy of the equations used for any particular prey size category.

Finally, the lack of detailed information on the composition of the DSL within the sampling area limits attempts to identify prey selection by dolphins on the basis of prey species or size, which would shed light on the view that dolphins are opportunistic feeders, concentrating on locally abundant prey, rather than selecting specific prey (e.g. Young and Cockcroft, 1994).

CONCLUSION

The diet of the short-beaked common dolphin in the northeast Atlantic, both in offshore and neritic habitats, is dominated by teleost fish, with a small proportion of cephalopods consumed. The species present in the diet varied greatly with habitat, with myctophids dominant in the diet of the offshore dolphins, while gadoids were most abundant in the diet of the neritic sample. The suggested seasonal changes in distribution of short-beaked common dolphins in the northeast Atlantic and the lack of juveniles bycaught by the offshore tuna Irish driftnet fishery suggests that maternal groups (mature females with calves and yearlings), may migrate to offshore waters in order to prey upon lipid-rich myctophids. This high lipid diet may be important in the production of milk for calves still dependant upon their mothers for food, and/or maintaining pregnancy. Mature males were also incidentally captured in this fishery, a fact that may be explained by the coincidence of mating with the calving period (Murphy *et al*., 2005). However, other reasons for this movement to offshore waters may exist, for example availability of small shoaling prey for calves learning how to forage.

The data on the diet of the short-beaked common dolphin in the northeast Atlantic is important in relation to current and future interactions with fisheries. Dolphins foraging in neritic waters were found to feed upon species of commercial value, either for the food market or for processing to fishmeal. Offshore species of the deep scattering layer are not currently subject to commercial exploitation across most of the world, though

some fisheries do occur and experimental work continues. This competition for the same fish resource between short-beaked common dolphins and fisheries has the potential to have particularly negative effects on the short-beaked common dolphin population, primarily through direct loss in the case of incidentally captured dolphins, but also indirectly through a reduction in the food resource available to foraging dolphins.

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